Habitat partitioning in common dolphin (*Delphinus delphis*) and striped dolphin (*Stenella coeruleoalba*) in the western English Channel and Bay of Biscay.

By

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Thesis submitted in partial fulfilment of the requirements for the degree of MSc Marine Mammal Science, University of Wales, Bangor, U.K.
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This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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Abstract

This study describes the spatio-temporal distribution of two species of oceanic delphinids, short-beaked common dolphin (*Delphinus delphis*) and striped dolphin (*Stenella coeruleoalba*) in the western English Channel and Bay of Biscay. Over 62,000 km of survey effort was recorded during 72 monthly surveys between August 1995 and July 2002. Year-round data from a commercial passenger ferry enabled comparisons between species with respect to season and five regional areas. Environmental variables (EVs): depth, slope, distance to front, sea surface temperature (SST) and near-surface chlorophyll (CHL-a), were used to define habitat preferences for each species using a Geographical Information System.

Distribution and relative abundance for both species varied both spatially and temporally. A bimodal distribution pattern for common dolphin existed, with encounter rates (\(n/km\)) highest in shelf areas during the autumn and winter (\(n/km = 0.012\)), and in shelf-break and abyssal plain regions during spring and summer (\(n/km = 0.079\)). Striped dolphins were largely absent during the autumn and winter (\(n/km = 0.002\)) and most abundant during spring and summer (\(n/km = 0.006\)) in similar areas to common dolphin. Both species were non-randomly distributed in relation to depth, slope, SST and CHL-a, but with no relationship established to fronts. There was little variation found for striped dolphin distribution in relation to EVs, which was not the case for the more cosmopolitan common dolphin. The Bay of Biscay is near the northern limit of the typical range of striped dolphin in the northeast Atlantic and seasonal dispersal may be related to declines in SST.

Partitioning between the two species appears to occur spatially in relation to depth and slope when they are found in close proximity, with striped dolphin preferring areas of greater depth and steeper slopes. It is possible that habitat preferences, defined by EV values, are actually proxies for variables that primarily define partitioning, such as prey distribution. Resource partitioning could not be investigated fully but may occur given established dietary preferences. The two species are largely sympatric in spring and summer when there may be a high degree of niche and trophic overlap. This was reflected in the occurrence of mixed species groups, suggesting that tolerance between the two species is high.
CHAPTER 1

1.1 General Introduction

Species that occupy the same habitats and require the same resources tend to compete and effectively partition resources to reduce competition (Roughgarden, 1976). The species involved often do this in two key ways; by occupying different spatial or temporal locations or by feeding on different prey (Roughgarden, 1976).

The distribution of cetaceans is likely to be affected by a large number of factors. Although predator avoidance, inter-specific competition, reproductive strategies and anthropogenic impacts all may play a part, studies on energy budget requirements in small cetaceans indicate that they must probably feed every day. This is especially true of small cetaceans, which have been estimated to consume prey equivalent to up to 10% of their body weight daily (Smith & Gaskin, 1974; Kenney et al., 1985; Kenney & Winn, 1986). The primary influence of the physical environment on cetacean distribution is therefore likely to be the distribution and aggregation of prey species and habitat selection is largely determined by the availability of food (e.g. Kenney & Winn, 1986; Gowans & Whitehead, 1995; Woodley & Gaskin, 1996). Although several studies have investigated relationships between cetacean distribution and prey availability directly (Woodley & Gaskin, 1996; Baumgartner et al., 2001; Davis et al., 2002), studying the diet of cetacean species is difficult and beyond the scope of the research presented here.

In addition to the factors mentioned above, there are others that may influence the spatial and temporal distribution of cetaceans. For example, several studies have concentrated on physiographic and hydrographic characteristics of cetacean habitat and demonstrated correlations with animal distribution. Many of these have shown relationships between cetacean distribution and bathymetry, in particular ocean depth and seafloor slope (e.g. Hui, 1979, 1985; Selzer & Payne, 1988; Gowans & Whitehead, 1995; Hooker et al., 1998;
Baumgartner et al., 2001; Gregr & Trites, 2001; Macleod, 2001; Waring et al., 2001; Cañadas et al., 2002; Davis et al., 2002; Bannon, 2002; Hamazaki 2002; Griffin & Griffin, 2003; Schweder, 2003; Kiszka, 2003). Physiography can be important in a number of respects as undersea topography is often a major influence on productivity and the mechanisms which drive it. One of the keys to high biological productivity is the upwelling of ‘new’ nutrients from deep water into the euphotic zone and the subsequent entrainment of those nutrients by phytoplankton in stratified waters (Mann & Lazier, 1996). For example, typical steep shelf-break bathymetry encourages wind, current and tidally-driven mixing of surface and deep waters. This increases productivity at frontal systems where water masses of different density meet (Mann & Lazier, 1996; New, 1988; Pingree et al., 1988; Reid et al., 2003). Initial primary productivity can lead to enhanced secondary production and aggregations of zooplankton, cephalopods, pelagic fish and other fauna. Physiography can also limit the distribution of benthic or demersal prey species which are dependent on particular substrate characteristics (Macleod et al., 2004; Cañadas et al., 2002).

In addition other studies have demonstrated other ‘markers’, which can predict cetacean occurrence but may not be direct causal links. Several oceanographic characteristics, which may secondarily affect prey distribution and density, have been correlated with cetacean distribution. Water temperature can be important in two main respects. It has been shown that many species have preferred temperature ranges which can define distribution limits (Gaskin, 1968; Selzer & Payne, 1988; Gowans & Whitehead, 1995; Forney, 2000; Neumann, 2001; Ferrero et al., 2002). In addition, many oceanographic features have strong temperature signatures or gradients which are detectable from direct ‘in-situ’ surface and subsurface sampling or remotely-sensed data. Features such as eddies, oceanic fronts, river plumes, thermocline boundaries and up-welling systems may indicate areas of enhanced primary productivity and potential foraging areas for cetaceans (Reilly, 1990; Woodley & Gaskin, 1996; Goold, 1998; Baumgartner et al., 2001; Waring et al. 2001, Davis et al., 2002; Hamazaki, 2002; Moore et al., 2002). Other studies have shown relationships between cetacean distribution and chlorophyll (Smith et al., 1986; Jaquet et al., 1996; Griffin & Griffin, 2003), primary productivity (Littaye et al., 2004), thermocline depth (Reilly, 1990) and salinity (e.g. Forney, 2000; Gregr & Trites, 2001; Griffin & Griffin, 2003).
Habitat partitioning within dolphin populations has been investigated in several studies. Gowans and Whitehead (1995) suggested habitat partitioning amongst Atlantic white-sided dolphin (*Lagenorhynchus acutus*) and common dolphin in the Gully, Nova Scotia. Partitioning occurred temporally with the former species more abundant in the early summer period and with the latter species showing a peak in the late summer. Although the distributions of both species were similar in relation to topographic depth and slope, they observed significant differences in each species’ relationship with SST, with common dolphins preferring warmer waters during the survey period. Selzer & Payne (1988) observed a similar relationship between these two species off the northeast US in relation to SST but also concluded that common dolphin preferred more saline waters to those inhabited by Atlantic white-sided dolphin. However, both studies concluded that these factors were probably only secondarily influencing dolphin distribution and that physiographic and biotic factors were probably affecting prey distribution primarily. Griffin & Griffin (2003) found significant differences between habitat types for Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) over the eastern Gulf of Mexico continental shelf. Spotted dolphins were found to prefer slightly deeper waters, a point previously suggested in other studies (Davis *et al.*, 2002; Baumgartner *et al.*, 2001), greater surface transmittance levels (corresponding to lower chlorophyll levels) and lower or negative surface versus bottom salinity values. A study on four species of delphinid in the eastern tropical Pacific found both spatial and temporal differences in distribution between species (Reilly, 1990). Both spotted dolphins (*Stenella attenuata*) and spinner dolphins (*Stenella longirostris*) were associated with the seasonal development of a thermocline ridge and with the defined seasonal movements of water masses. Common dolphins were seasonally static in their preference of habitat type, preferring upwelling-modified water all year. Striped dolphins were intermediate between the two other *Stenella* species and common dolphin. Although habitat preferences were statistically meaningful for striped dolphins it was thought that other processes not directly related to the habitat characteristics defined in the study were probably more relevant to the partitioning observed in this species (Reilly, 1990).
1.2 Study rationale

1.2.1 Aims and Objectives

This research will investigate the specific role that oceanographic features play in the distribution of two oceanic delphinids; short-beaked common dolphin and striped dolphin. It will describe the relative abundance and distribution of these two species from single line transects conducted from a platform of opportunity in the western English Channel (France, U.K.) and Bay of Biscay (France, Spain) between August 1995 and July 2002. Through analysis of this dataset, the work will also examine the possibility of habitat partitioning between the two species both spatially and temporally.

To further these aims, four main objectives are to be met:

1. Compile observations of common dolphin and striped dolphin from fixed route, monthly surveys within the study area.

2. Describe the relative abundance and spatio-temporal distribution of these species, including the existence of population movements (migration) within the study area.

3. Define key habitats for these species in terms of a range of environmental variables.

4. Investigate the possibility of habitat partitioning at the mesoscale and suggest reasons for this.

1.2.2 Using ferries as platforms of opportunity

The work described here began as an initiative by the Biscay Dolphin Research Programme (BDRP) for utilising a commercial passenger ferry, the Pride of Bilbao, operated by P&O Ferries (U.K.), for the purposes of long-term surveying of cetaceans and other marine organisms, particularly seabirds. The route of the ferry, from Portsmouth (U.K.) to Bilbao
(Spain), enables sampling of a wide variety of marine habitats. It passes through a region which is home to a high diversity of cetacean species, probably due to the area’s status as a transition zone between boreal and northern sub-tropical bio-geographical regions (OSPAR, 2000a). The offshore areas covered by the ship’s track were previously largely inaccessible to biologists due to financial and logistic constraints. As a consequence, the study area has not been surveyed for cetaceans with any degree of regularity. The physical, chemical and biological oceanography of the area has been well studied and can contribute explanatory factors to aid understanding of cetacean distribution in this area.

The survey platform provides, in most cases, the opportunity to identify cetaceans and other fauna to the species level from a vessel moving at relatively constant speed over a route which is covered repeatedly. The limitations of such monitoring are that there is little control over diversions off the main route that would allow confirmation of data such as identification of species, numbers of individuals, etc. Crucially the scheduling of the ferry has allowed year-round monitoring through monthly surveys from a stable, protected platform. Although weather conditions and daytime hours are a major factor in limiting the quality and quantity of data collected, the opportunity to collect data during all months is of vital importance for understanding the seasonal movements and habitats of cetaceans and detecting changes in relative abundance and distribution of cetaceans. Sightings data can be subsequently related to distance travelled (a measure of survey ‘effort’) and corrected for factors, such as sea state, that affect the ability of observers to detect cetaceans.

Although systematic surveys can provide more accurate data to measure absolute abundance through representative sampling designs, there are problems with such methods. The July 1994 SCANS (Small Cetacean Abundance in the North Sea) survey notably recorded no common dolphins, minke whales (*Balaenoptera acutorostrata*) or harbour porpoises (*Phocoena phocoena*) in the English Channel during the one month survey period (Hammond *et al.*, 2002). All of these species are recorded regularly in the western English Channel on BDRP surveys (BDRP, unpublished data), which perhaps highlights one of the limitations of expensive ‘snapshot’ surveys and the benefits of more consistent and cost-effective effort.
Many groups now use a wide variety of vessels for cetacean research and the worth of long-term monitoring programmes from platforms of opportunity has been acknowledged by various authors (Marini et al., 1996; Leaper et al., 1997; Brereton et al., 2000; Bannon, 2002; Schweder, 2003; Kiszka, 2003; Evans & Hammond, 2004).

1.3 The Study area

The study area comprises the western English Channel and Bay of Biscay from roughly 0.5°E to 6.5°W and 43°N to 51°N (Figure 1.1).

1.3.1 Physiographic features

The study area is highly variable in terms of bathymetry and topography as the ferry route crosses areas of continental shelf, steep slopes, canyons, escarpments, ridges, troughs and abyssal plain, sampling depths of up to 4500 m (Figure 1.2).

The eastern English Channel is shallow with depths seldom exceeding 50m. Depth gradually increases from the mid-English Channel westwards. On the survey route, which travels through the central Channel, depths are generally between 50 and 100 m throughout the western English Channel, with the exception of the Hurd Deep, a narrow trough, where depths can reach 170m. There is little bathymetric variation in terms of slope, with measurements generally in the region of 0 - 0.1 degrees, except for the steeper sides of the Hurd Deep.

As the English Channel ends, the ferry route passes briefly over the Celtic Sea shelf and into the northern Bay of Biscay over the Armorican Shelf. The shelf deepens here to between 100-200 m, until the shelf-break is marked by the 200 m contour. The shelf-break which begins at c.46.5°N is characterised by highly variable topography, with depth increasing from 200 m to 4000 m over a perpendicular distance of c.50 km. The continental slope is relatively steep with a slope of the order of 10-20 degrees and is dissected by numerous valleys and canyons, which channel sediment transport off the shelf.
Fig. 1.1 Map of the northeast Atlantic and northwest Europe with the study area highlighted. Note that scales on all map figures are measured in kilometres.

The continental slope flattens at around 4000 m at c.45.5°N, where the abyssal plain of the Bay of Biscay begins. The ship’s track generally does not cross the true abyssal plain, which lies to the west. Slopes are still in the region of 0.5-1.5 degrees throughout this area which
comprises the ‘foothills’ of the shelf-break, until the continental slope is reached again at c.44.5°N. The main bathymetric feature of the southern Biscay slope is the Santander Canyon, a wide canyon which ends at the beginning of the narrow Cantabrian Shelf, which is only c.30km wide near Bilbao.

Fig 1.2: Map of study area with some areas of interest and depth in metres indicated.
1.3.2 Oceanographic features

The movements of water masses and their interactions with bathymetric features, tides, and freshwater run-off, govern the varied oceanographic conditions of the survey area. Most of the water masses in this region have a North Atlantic origin or result from interactions with northward flowing Mediterranean water. Generally layers within the ocean strata, which are composed of deep, intermediate or surface water masses, affect different areas. In the northeast Atlantic Ocean, deep water circulation is dominated by Northeast Atlantic Deep Water, which contains four local source water types; Iceland-Scotland Overflow Water, Lower Deep Water, Labrador Sea Water and Mediterranean Sea Water (van Aken, 2000a). At intermediate levels, essentially oligotrophic Mediterranean Sea Outflow Water travels north from the Straits of Gibraltar, where there is entrainment with Antarctic Intermediate Water, leading to increased levels of nutrients and a reduction in salinity (van Aken, 2000b). This water continues north along the western Iberian coastal margin and east into the Cantabrian Sea and collides with variable quantities of Labrador Sea Water of low salinity. This forms a sharp frontal zone running northeast to southwest in the Bay of Biscay. Intense diapycnal mixing at intermediate levels occurs over the continental slope and makes the Bay of Biscay a focal point for deep and intermediate mass water transformation (Pingree et al., 1986; van Aken, 2000b).

The upper water layers are occupied by Eastern North Atlantic Central Water, which is formed in two main areas: the first just to the south of the Atlantic Current which flows southeast into the western Bay of Biscay; this meets the second, which is formed along the northern margin of the Azores Current and flows northeast towards the Iberian coast, where the former sinks beneath the latter (Pollard et al., 1996).

The principal hydrodynamic processes in the region are seasonal in nature but are dominated by the following features (Figure 1.3): weak anticyclonic circulation in deep water areas of the Bay of Biscay; a poleward-flowing slope current which geostrophically adjusts from flowing east to north; coastal upwelling concentrated off the western Iberian coastline but also as far east as southwest France; northward-flowing Mediterranean Water; shelf circulation governed
by strong tidal forcing; river run-off (Loire, Gironde and Adour estuaries, France) and wind; and cross-shelf transport through submarine canyons (OSPAR, 2000a).

Tides are also very important and probably influence the greatest productivity in the survey area. The Celtic-Biscay shelf-break is often a region of cool surface water and high phytoplankton abundance during the summer (Pingree et al., 1986). Internal tides lead to physical mixing, resulting in upward transport of cool, nutrient rich water (Pingree, 1986), which can lead to bands of enhanced levels of near-surface chlorophyll in the central Bay of Biscay, caused by crests of internal tidal waves travelling away from the shelf break (da Silva et al., 2002). It has been suggested that the internal tides in the Bay of Biscay are the most energetic found anywhere in the world (Baines, 1982) and that mixing of the thermocline by internal tides is probable during the summer and at spring tides (New, 1988).

The shallow shelf seas around Brittany and the English Channel are responsible for dissipating a great deal of tidal energy (Mann & Lazier, 1996) and shallow sea fronts commonly form in the spring-autumn period. One of the most persistent and well defined is the Ushant front off the tip of Brittany. This front, which has been well studied, features high primary productivity in relation to the cycle of spring and neap tidal mixing (Pingree & Griffiths, 1978; Mann & Lazier, 1996). The tidal energy through the English Channel is notably high, with tidal stream amplitudes reaching 5 knots (c. 2.5 m/s) at average spring tides. Residual flow in the Channel is dependent on wind and tide but averages southwest to northeast and is responsible for the introduction of a narrow saline core of Atlantic water into the North Sea through the Straits of Dover (OSPAR, 2000b).

1.3.3 Biotic features

Although it is beyond the scale of the present study to give an exhaustive account of the marine fauna of this large and diverse area, the text which follows is an overview of the core species, from several taxa, which characterise the region.
1.3.3.1 Primary and secondary production

The varied and complex bathymetry and oceanography in the region as a whole and along the survey route in particular, provide diverse habitats for a large range of marine fauna to flourish. Primary productivity in the region is characterised by phytoplankton growth, which shows a typical cyclic pattern for a temperate sea. During the winter, low light levels and mixing of the water column prevent phytoplankton production despite high levels of nutrients. During the transitional periods of spring and autumn, surface stratification is accompanied by short-lived blooms of diatoms, which rapidly use up nutrients in the upper layers (OSPAR, 2000a). A greater proportion of the reduced phytoplankton biomass is stored below the euphotic zone and the vertical barrier of the pycnocline during the summer. The nutrient depleted surface layers have reduced levels of phytoplankton, now dominated by flagellates, and increased levels of zooplankton which consume the phytoplankton and excrete nutrients.

Figure 1.3: Schematic illustration of circulation in the Bay of Biscay. Source: OSPAR 2000a
During the autumn bloom, convection and wind increases mixing again and new nutrients are introduced into surface layers (Mann & Lazier, 1996). This basic model is applicable to most areas of the region; however different rules apply in areas where tidal mixing prevents summer stratification. In shelf areas in the western English Channel and Celtic Sea strong tidal mixing encourages the formation of frontal areas which can sustain high phytoplankton productivity throughout the spring, summer and autumn. Although mixing prevents the formation of stable stratified areas, this is compensated for by the increased nutrient flux from shallow sediments. Stratification occurs over the nutrient enriched waters close to the Ushant front with weakening currents during the neap tide, allowing intermittent phytoplankton production over a two-weekly cycle (Pingree & Griffiths, 1978; Mann & Lazier, 1996). Strong internal tides over the Armorican and Celtic shelf-breaks introduce another pattern of primary production into the overall dynamics. Interaction of weak oceanic barotropic tidal waves with the bathymetry of the shelf-break produces a strong internal tide, with maximum amplitude of around 60m. This twice daily tide, in combination with wind, encourages upwards forcing of the thermocline and upwelling of cold, nutrient rich water to surface layers (Pingree et al., 1986; Le Fèvre & Frontier, 1988; New, 1988).

In accordance with the two defined spring and autumn phytoplankton blooms in the region, there are two corresponding peaks in zooplankton abundance, which match those of the phytoplankton but lag behind temporally by 1-2 months (Valdés & Moral, 1998). In areas of near continuous water column mixing nutrient inputs are fairly constant and zooplankton is often abundant in phased pulses throughout the year (OSPAR, 2000a). However, this pattern is rather different between tidally mixed fronts and internal tide fronts as the pattern in phytoplankton production is phased differently. The two-weekly pattern of production at tidally-mixed shelf fronts, such as the Ushant front, is thought too infrequent to support strong populations of macro-zooplankton. Essentially, a brief two-week burst is followed by decline and increased abundance of bacteria and micro-zooplankton. In contrast, on shelf-break fronts where mixing occurs twice-daily, primary production is fairly constant and can support secondary production in the form of zooplankton grazers throughout the spring, summer and autumn months (Le Fèvre & Frontier, 1988; Mann & Lazier, 1996).
1.3.3.2 Fish

The biogeographical status of the region is governed by a sharp north to south temperature gradient between the boreal Atlantic province and the subtropical Lusitanian province which defines the population limits of many fish species found in the areas of the English Channel and Bay of Biscay. The boundary for cold, temperate species has been previously defined as around 47°N (Quéro et al., 1989).

Of the pelagic fish, fifteen species are common but only six are important commercially; sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicus*), mackerel (*Scomber scombrus*), horse mackerel (*Trachurus trachurus*), albacore (*Thunnus alalunga*) and blue-fin tuna (*Thunnus thynnus*). However, several other species are important in terms of biomass and include blue whiting (*Micromesistius poutassou*) and sprat (*Sprattus sprattus*) (OSPAR, 2000a; Quéro et al., 1989). Demersal fish comprise the highest proportion of fish diversity in the region and are strongly correlated with bottom topography. As with some of the pelagic fish the adults and recruits often occupy different areas of distribution with seasonal migrations important for species such as the mackerel, which spawn largely near the slope in the Southern Bay of Biscay before undertaking long migrations north for feeding (Uriarté & Lucio, 2001). In the eastern Bay of Biscay, groundfish surveys have described 191 species at depths between 15-600 m, with seven species making up over 80% of total catch; blue whiting, horse mackerel, dogfish (*Scyliorhinus canicula*), hake (*Merluccius merluccius*), monkfish (*Lophius piscatorius*), silvery pout (*Gadiculus argenteus*) and megrim (*Lepidorhombus whiffiagonis*) (Quéro et al., 1989).

1.3.3.3 Birds

The nesting seabird community is comparatively poor in terms of numbers and diversity in comparison to other areas in the European Atlantic. There are some locally important colonies of species like the kittiwake (*Rissa tridactyla*), European storm petrel (*hydrobates pelagicus*), guillemot (*Uria aalge*), and shag (*Phalacrocorax aristotelis*), mainly along the coastline and on offshore islands in the English Channel. The English Channel also supports good numbers of feeding birds from further north during the summer breeding season, including northern gannet (*Morus bassanus*), fulmar (*Fulmarus glacialis*), and manx shearwater (*Puffinus
During migration periods and winter months, the area is of greater importance for a range of seabird species. During the autumn migration in particular, the Bay of Biscay is important for a number of species, including several which are scarce in European terms. From Arctic Canada, Sabine’s gull (*Larus sabini*) and grey phalarope (*Phalaropus fulicarius*) are regular; from southern hemisphere breeding grounds sooty shearwaters (*Puffinus griseus*) and great shearwaters (*Puffinus gravis*) often spend the austral winter in this area. The latter is often found in large flocks around the Celtic-Biscay shelf-break, an area which appears to be important for migrant and non-breeding birds during the late summer and autumn. Two other species of shearwater, Cory’s shearwater (*Calonectris diomedea*) and Balearic shearwater (*Puffinus mauretanicus*) arrive on post-breeding dispersal from the Mediterranean during the late summer to moult in the Bay of Biscay, the latter rarely moves off the shelf while the former often feeds in deeper water in the late summer. Yet another species, the little shearwater (*Puffinus assimilis*) appears to move north to take advantage of late summer productivity from breeding grounds off North Africa (Hobbs *et al.* 2003). During the winter the western English Channel and northern Bay of Biscay are critical wintering grounds for several species of seabirds, many of which probably breed around the coastlines of northern Europe. In particular, this area seems to be important for the great skua (*Catharacta skua*), which breeds in relatively small numbers in northern Europe (Brereton *et al.* 2003).

### 1.3.3.5 Cetaceans

A large number of cetacean species have been recorded in the English Channel and Bay of Biscay. Table 1 summarises the distribution and status of all species which have been reliably recorded in the area.
Table 1.1: Status of cetacean species in the English Channel and Bay of Biscay. Sources: OSPAR, 2000a; Cresswell & Walker, 2001; Williams et al., 2002; Kiszka, 2003; Reid et al., 2003; BDRP unpublished data 1995-2004).

<table>
<thead>
<tr>
<th>English Name</th>
<th>Scientific Name</th>
<th>Habitat</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern right whale</td>
<td><em>Eubalaena glacialis</em></td>
<td>continental shelf</td>
<td>Possibly extinct. One recent record of single animal in 1993</td>
</tr>
<tr>
<td>Blue whale</td>
<td><em>Balaenoptera musculus</em></td>
<td>pelagic</td>
<td>Rare in European waters but now annually recorded in the Bay of Biscay during April-September</td>
</tr>
<tr>
<td>Humpback whale</td>
<td><em>Megaptera novaeangliae</em></td>
<td>pelagic and continental shelf</td>
<td>Rare and irregular, although annually recorded.</td>
</tr>
<tr>
<td>Minke whale</td>
<td><em>Balaenoptera acutorostrata</em></td>
<td>continental shelf</td>
<td>Fairly common in western English Channel and Armorican shelf. Irregular on Cantabrian shelf.</td>
</tr>
<tr>
<td>Fin whale</td>
<td><em>Balaenoptera physalus</em></td>
<td>pelagic</td>
<td>Common from July-October. Present all year.</td>
</tr>
<tr>
<td>Sei Whale</td>
<td><em>Balaenoptera borealis</em></td>
<td>pelagic</td>
<td>Rare but regular. Numbers vary between years.</td>
</tr>
<tr>
<td>Sperm whale</td>
<td><em>Physeter macrocephalus</em></td>
<td>pelagic</td>
<td>Regular in deeper waters of Bay of Biscay during May-October</td>
</tr>
<tr>
<td>Northern bottle-nosed whale</td>
<td><em>Hyperoodon ampullatus</em></td>
<td>pelagic</td>
<td>Rare but regular in Bay of Biscay, April-October.</td>
</tr>
<tr>
<td>Cuvier’s beaked whale</td>
<td><em>Ziphius cavirostris</em></td>
<td>pelagic</td>
<td>Frequently recorded year-round in Bay of Biscay, primarily over shelf-break/canyon areas.</td>
</tr>
<tr>
<td>Sowerby’s beaked whale</td>
<td><em>Mesoplodon bidens</em></td>
<td>pelagic</td>
<td>Infrequently recorded in southern Bay of Biscay.</td>
</tr>
<tr>
<td>Blainville’s beaked hale</td>
<td><em>Mesoplodon densirostris</em></td>
<td>pelagic</td>
<td>Single stranding in 1998</td>
</tr>
<tr>
<td>Bottlenose dolphin</td>
<td><em>Tursiops truncatus</em></td>
<td>continental shelf and shelf-break</td>
<td>Offshore ecotype. Common over both shelf and shallower shelf-break areas.</td>
</tr>
<tr>
<td>Short-beaked common dolphin</td>
<td><em>Delphinus delphis</em></td>
<td>all areas</td>
<td>Abundant and widespread.</td>
</tr>
<tr>
<td>Striped dolphin</td>
<td><em>Stenella coeruleolba</em></td>
<td>pelagic</td>
<td>Abundant over deeper waters of the Bay of Biscay.</td>
</tr>
<tr>
<td>Atlantic white-sided dolphin</td>
<td><em>Lagenorynchus acutus</em></td>
<td>pelagic</td>
<td>Infrequently recorded.</td>
</tr>
<tr>
<td>White-beaked dolphin</td>
<td><em>Lagenorynchus albirostris</em></td>
<td>continental shelf</td>
<td>Infrequently recorded.</td>
</tr>
<tr>
<td>Long-finned pilot whale</td>
<td>* Globicephala melas*</td>
<td>pelagic</td>
<td>Common, particularly over the shelf-break. Mainly April-October.</td>
</tr>
<tr>
<td>Short-finned pilot whale</td>
<td>* Globicephala macrorhynchus*</td>
<td>pelagic</td>
<td>Several strandings from north Spain.</td>
</tr>
<tr>
<td>False killer whale</td>
<td><em>Pseudorca crassidens</em></td>
<td>pelagic</td>
<td>Rare but regular in the Bay of Biscay.</td>
</tr>
<tr>
<td>Pygmy killer whale</td>
<td><em>Feresa attenuata</em></td>
<td>pelagic</td>
<td>Two confirmed records in Bay of Biscay. Several sightings records refer to this species or melon-headed whale.</td>
</tr>
<tr>
<td>Killer whale</td>
<td><em>Orcinus orca</em></td>
<td>All areas</td>
<td>Rare but regularly recorded</td>
</tr>
<tr>
<td>Risso’s dolphin</td>
<td><em>Grampus griseus</em></td>
<td>mainly shelf-break</td>
<td>Frequently recorded</td>
</tr>
<tr>
<td>Harbour porpoise</td>
<td><em>Phocoena phocoena</em></td>
<td>continental shelf</td>
<td>Common in northern shelf areas.</td>
</tr>
</tbody>
</table>
1.4 Study Species

1.4.1 Short-beaked common dolphin (*Delphinus delphis*)

1.4.1.1 Description

Common dolphins are small, slender dolphins with pronounced beaks, sharply demarcated from the melon. They range in length from 170-240 cm (Evans, 1987), with a mass of up to 200 kg (Perrin, 2002). The dorsal fin is high and falcate. They are dark grey on the dorsal surface and have a distinctive hourglass colour pattern, pale yellow/tan on the anterior thoracic patch and light to medium grey on the flanks, with a white belly. There are two black stripes on the body, one from the flipper to the lower jaw and another from the eye to the base of the beak. At sea, the most useful identification feature is the dark triangle of colouration from the dorsal fin to the centre of the hourglass pattern. (Evans, 1987; Perrin, 2002; Reid *et al.*, 2003)

![Illustration of common dolphin showing characteristic patterning and structure (courtesy of Martin Camm).](image1)

**Fig. 1.4:** Illustration of common dolphin showing characteristic patterning and structure (courtesy of Martin Camm).

![Breaching adult common dolphin in the Smalls, off Pembrokeshire, U. K. (courtesy of Janet Baxter).](image2)

**Fig. 1.5:** Breaching adult common dolphin in the Smalls, off Pembrokeshire, U. K. (courtesy of Janet Baxter).
1.4.1.2 Distribution and abundance

This species is widely, but discontinuously distributed throughout tropical, subtropical and warm-temperate seas from about 40-60°N (Evans, 1987; Perrin, 2002; Reid et al., 2003). The short-beaked common dolphin is possibly the most numerous cetacean species in the northeast Atlantic. They are found from northern Scotland south to the equator, although they have been recorded from Norwegian waters (Syvertsen et al., 1999, Reid et al., 2003). Common dolphins are widely distributed in western U.K. waters, but are largely absent from the eastern English Channel and the North Sea. They are seen regularly over the continental shelf off southwest England and Ireland throughout the year, with peak numbers in the winter months in the western English Channel and Celtic Sea (Brereton et al., 2000; Reid et al., 2003; Kiskza, 2003; Macleod & Walker, 2004). They are also abundant in the vicinity of the Celtic Sea Front off southwest Wales in May-September (Goold, 1998). There is also a notable inshore movement off west Scotland during June-September, although low numbers are involved (Reid et al., 2003). However, peaks in common dolphin numbers to the west of Scotland were recorded during September and November (Macleod, 2001). Animals are present year-round and throughout the Bay of Biscay and have a cosmopolitan distribution in both deep water and shallow areas (Collett, 1981; Brereton et al., 2000; Kiskza, 2003). There is also evidence of a northward, inshore movement during October - March into the waters of the western English Channel and Armorican Shelf/Celtic Sea (Brereton et al., 2000). Off northern Spain animals are most commonly recorded over the continental shelf or shelf-break, particularly off Galicia.
(Lopez et al., 2004) and northeast Spain (Brereton et al., 2000; Lopez et al., 2002). In the northeast Atlantic, common dolphins are usually found in fairly small school sizes of 5-20 animals. However, large concentrations from 1000-5000 animals have been observed (Brereton et al., 2000; Reid et al., 2003, Lopez et al., 2004; BDRP, unpublished data).

Several dedicated surveys have been conducted to estimate the population abundance of common dolphins in specific areas. The Mica survey of 1993, estimated an abundance of 62,000 (95% C.I.: 35,461 - 108,010) in the region of the French albacore drift net fishery in the Bay of Biscay (Goujon et al., 1993). The SCANS (Small Cetaceans in European Atlantic and North Sea) survey of 1994, estimated abundance for the Celtic shelf and produced an estimate of 75,540 (CV = 0.67; 95% C.I.: 23,000 – 149,000) common dolphins (Hammond et al., 2002). The two surveys overlapped on the shelf-break and Goujon (1996) suggested an overall abundance of 120,000 animals for both areas. A second survey in the Celtic Sea was based around the Irish tuna drift-net fishery and estimated abundance of 101,205 (95% C. I.: 55,125 – 185,802) common dolphins (Harwood et al., 1999). Off the Galician coast (NW Spain) a preliminary estimate of 8,137 (C.I.: 4,388 – 13,678) common dolphins were suggested for Galician coastal waters (Lopez et al., 2004).

1.4.1.3 Diet

Common dolphins have been recorded eating a wide range of prey species in the northeast Atlantic. The bulk of their prey is made up of small, pelagic schooling fish and cephalopods. In the Celtic Sea, 90.2% of fish prey was made up of myctophids, a deep scattering layer organism, usually epipelagic in origin (Murphy, 2004, and references therein). Analysis of stomach contents of stranded animals along the Irish coastline from 1990 – 2003 found common dolphin diet to be mainly piscivorous, involving species like hake, sprat, scad (Trachurus trachurus), herring (Clupea harengus), whiting (Merlangusis merlangus), blue whiting, mackerel and Trisopterus species (Murphy, 2004). Common dolphins recorded as bycatch in the French albacore drift-net fishery were found to consume significant quantities of meso to bathypelagic fish; although cephalopods constituted 60% of the diet (Hassani et al., 1997). Common dolphins off California were recorded to feed at dusk and throughout the night (Evans, 1994), which implies that common dolphins may feed at night on lethargic,
slow-moving prey from the deep-scattering layer. Goold (2000) also noted that common dolphin appeared to feed nocturnally in the deep scattering layer off west Wales.

Diet appears to change markedly with geographic areas and seasonal fluctuations in prey abundance and distribution. Off the U.K., common dolphins are thought to follow movements of Atlantic mackerel (*Scomber scombrus*) and herring (Evans 1980) and off France, dolphins were found to feed mainly on gadids, dominated by *Trisopterus* spp. and blue whiting (Collett, 1981). A study as part of the BIO-CET program in the Bay of Biscay examined stomach contents for 76 common dolphins stranded in western France. Only four taxa contributed the bulk of the stomach content: anchovy, *Engraulis*, sardine, *Sardina pilchardus*, horse-mackerel, *Trachurus* spp and *Trisopterus* spp. There were marked interannual and seasonal variations within the sample (Meynier, 2004).

From Galicia, stranded common dolphins were found to contain 20 fish taxa and 14 cephalopod taxa, with blue whiting, sardine and scad dominant in terms of biomass (Santos, 1998). Over 75% of the stomach contents of stranded and bycaught animals off the Portuguese coast were made up of four fish species, with sardine and blue whiting predominant (Silva, 1999). It seems likely that common dolphins are opportunistic feeders and capable of exploiting a range of habitat and prey types (Young & Cockroft, 1994; Silva, 1999).

**1.4.2 Striped dolphin (***Stenella coeruleoalba***)

**1.4.2.1 Description**

The striped dolphin is a small, slender dolphin between 2.0 and 2.4 m in length (Reid *et al.*, 2003). The trivial name ‘*coeruleoalba*’ refers to the distinctive pattern of blue and white stripes and flashes along the lateral and dorsal surfaces. The dorsal cape is dark-medium blue-grey, with a pale grey to white blaze extending from behind the eye to the dorsal cape below the dorsal fin. There is a darker grey stripe leading from the eye to the anus, which separates the lateral field from the generally paler ventral field, and another from the eye to the flipper with a faint secondary stripe in the ventral field (Archer, 2002). Morphologically, striped dolphins are similar to short-beaked common dolphins, with a long beak, well demarcated
from the melon and falcate dorsal fin. The two species can be difficult to separate at distance or with bad light but the lateral patterning is distinctive (Archer, 2002).

**Fig 1.7:** Illustration of striped dolphin showing characteristic patterning and structure (courtesy of Martin Camm).

**Fig. 1.8:** Striped dolphins breaching in the Straits of Gibraltar (courtesy of Pierre Gallego)

**Fig 1.9:** Juvenile striped dolphin in the Alboran Sea, off southern Spain (courtesy of Pierre Gallego)
1.4.2.2 Distribution and abundance

The striped dolphin is distributed worldwide in tropical, subtropical and warm-temperate waters. Its range is well documented in the western and eastern tropical Pacific, with most records below about 43˚N (Archer & Perrin, 1999). Its distribution in these areas has been related to seasonal changes in the depth of the thermocline (Reilly, 1990; Reilly & Fiedler, 1993). It is the most abundant species of cetacean in the western Mediterranean Sea (Forcada & Hammond, 1998; Cañadas et al., 2002) and favours areas of deep, oceanic water particularly between 2000 m and 2500 m in depth (Cañadas et al., 2002). The striped dolphin is largely oceanic in its distribution in the northeast Atlantic, with most records from beyond the 1000 m contour but with some records from waters < 60 m (Forcada et al., 1990). Typical distribution includes deep waters south of the U. K. and south to Spain and Portugal, but with extra-limital records from several areas, including Faeroe Islands, Iceland, Norway, the central North Atlantic and the Canary Islands (Reid et al., 2003). The only systematic survey to have estimated the abundance of striped dolphin in the northeast Atlantic was the MICA survey (see 1.4.1.2), which estimated abundance of 73,843 (C.I.: 95%, 113,000 – 150,990) striped dolphins for the outer Bay of Biscay and extending to 20˚W (Goujon et al., 1993). A study of the relationships between odontocete distribution and depth in the Bay of Biscay from ferry surveys, showed that striped dolphins were rarely found in depths of less than 2000 m and sightings were fairly evenly distributed over shelf-break and abyssal plain habitats (Kiskza, 2003).

1.4.2.3 Diet

Data on striped dolphin feeding habits are scarce. In the Mediterranean, an analysis of stomach contents from 28 striped dolphins during an epizootic in 1990 showed the importance of cephalopods in the diet, identifying four main species and three main families, *Enoploteuthidae, Ommastrephidae* and *Onychoteuthidae*, all of pelagic and bathypelagic habitat (Blanco et al., 1995). Data from stomach contents of 17 stranded animals along the French coast showed preference for pelagic fish, particularly Atherine (*Atherina presbyter*), blue whiting and *Trisopterus* spp. (CRMM, unpublished data). Similar results were found in the analysis of 20 striped dolphins bycaught in the French albacore drift-net fishery during
1992-3. Cephalopods made up 62% of reconstructed biomass, with cranchiid *Teuthowenia sp.*, the brachiotheuthid *Brachiotheuthis rissei* and the gonatid *Gonatus steenstrupi*, the most important species. Fish species were dominated by myctophids and paralepidids with significant numbers but low mass of crustaceans (Meynier *et al.*, 2002). Of interest is the fact that striped and common dolphins from the albacore fishery located in oceanic waters showed little difference in diet, especially in fish species taken, which is in contrast to the diets of animals stranded in France, where neritic common dolphins have diets consisting almost entirely of shallow-water species of fish and cephalopod and show little dietary overlap with striped dolphin (Meynier *et al.*, 2002; Meynier, 2004).

Spitz *et al.* (2003) examined the changing diet of striped dolphin from stomach contents of 23 animals stranded on the Biscay coast of France during 1999-2000 in comparison to a similar sample from the 1980’s. They found that observed trends linked to biomass indices from groundfish surveys, carried out by IFREMER (Institut Français de Recherche par l’Exploitation de la Mer) on the eastern continental shelf of the Bay of Biscay, showed that two species of fish had striking opposite trends temporally, *Gadiculus argenteus* and *Atherina presbyter*. The former species had declined in abundance and as a prey species for striped dolphin and the other species showed the opposite trend (Spitz *et al.*, 2003).

Many of the key species in the diet of the striped dolphin are organisms found in the deep-scattering layer and which may be more accessible as prey during the night. Studies in the Mediterranean using acoustic sampling have confirmed that striped dolphins do appear to be more active at night and that feeding bursts mainly take place at this time and close to the shelf-break (Gannier, 1999)

1.5 Threats

Probably the greatest known threat to common and striped dolphin populations in the northeast Atlantic is fisheries bycatch. Many studies have proven the relationship between fisheries operations and mortality through strandings records and observer programmes in a variety of fisheries.
During the 1990s, the albacore driftnet fishery was responsible for large bycatch rates of both common and striped dolphins. A study in 1992-3 on the French fleet in the Bay of Biscay, using 5km nets, found that approximately 1700 dolphins were being caught each year in these fisheries, comprising mainly striped dolphin and around 400 common dolphin (Goujon et al., 1993). A similar study on the smaller U.K. albacore driftnet fishery, which used 2.5km nets, found a lower total bycatch per year of around 61 common and 104 striped dolphin but a rate per 100km of net that was three times higher than French counterparts (SMRU, 1995). Studies among the Irish fleet showed increasing levels of dolphin bycatch during the 1990s as the driftnet fleet expanded in size. In 1998, the estimated total annual bycatch for the fleet was 964 striped dolphins and 2,522 common dolphins (Harwood et al., 1999). The driftnet fleet has now been banned in all areas.

During the last few years, the main threat has been from trawling, particularly pelagic pair-trawling. The BIO-ECO study into cetacean strandings along the French coast found that pelagic trawl bycatches of common dolphin are widespread with repeated heavy mortality likely in the Bay of Biscay, Western Approaches and Celtic Sea. In total, bycatch was thought likely to exceed 1% of the local summer population annually (Tregenza & Collet, 1998). Strandings for common dolphins have shown a pronounced winter peak, which reflects the apparent seasonal inshore movement of common dolphin at this time of year into the Celtic Sea, Western Approaches and English Channel (Brereton et al. 2000; Macleod & Walker, 2004). Also, a similar peak has been shown in France, Portugal and Spain (Tregenza & Collet, 1998; López et al., 2002, Silva & Sequeira, 2003). Varying rates of mortality among stranded animals have been ascribed to bycatch in different regions. In the U.K., recent strandings records show a clearly defined pattern, with the vast majority recorded during the first three months of the year and from the southwest of England, with a clear majority of animals examined being diagnosed as bycaught, for example 65% in 2002 (Sabin et al., 2003). In contrast, records from both Galicia and Portugal show that 23% of all stranded dolphins exhibited signs of bycatch (López et al., 2002, Silva & Sequeira, 2003).
Chapter 2

2. Methods

2.1. Data Sources

2.1.1 Cetacean surveys

Methodology used was that of a single line transect from a platform of opportunity. Data were collected by BDRP during shipboard surveys sponsored by P&O Portsmouth, onboard the P&O passenger ferry, the 37500 ton and 176.8m long Pride of Bilbao (Figure 2.1 and 2.2) between August 1995 and July 2002. The ferry follows a (more or less) fixed route between Portsmouth, England and Santurtzi (Bilbao), Spain. During this period 72 surveys were carried out at monthly intervals. Each three-day survey usually took place during the third week of the month to try and maintain temporal constancy of effort. In addition, three of the 72 surveys were undertaken during the first week of July (1) and October (2) as part of ‘whale and dolphin theme cruises’, sponsored by P&O Portsmouth. During these surveys, a larger team of 5-6 people would balance collecting sightings data with educational activities organised for the benefit of the ship’s passengers.

Fig 2.1: The survey vessel, the Pride of Bilbao.
A team of three observers was used for each survey, except for the period May-August (due to longer daylight hours) when four were used. Observers were located on the bridge of the ship, at a height of eye of 32m, and would scan with both binoculars and the naked eye in an arc 180 degree ahead of each beam. Throughout each survey the following data were recorded every 30 minutes and when conditions changed, using standardised BDRP vessel based effort proforma: date, time, ship’s position (latitude and longitude, using the ship’s GPS system), ship speed and bearing over ground, sea state (Beaufort scale), swell height (m), visibility (km), precipitation, wind speed and direction.

On sighting a cetacean(s), the effort proforma was recorded as well as the following additional fields: identification of species (to lowest possible taxonomic grouping and measure of certainty) and group size. Although distance and bearing to animals was recorded in most cases, data was not available for this analysis and was not used. The ship’s position was used as a proxy for the position of the animals, which is a limitation of the dataset available and one which should be corrected for future analyses. Other data collected simultaneously with a cetacean sighting included approximate age of animals, notes on behaviour and numbers and identification of any seabirds associated with the cetacean sighting, although these data were not applicable to this analysis.
2.1.2 Environmental variables

2.1.2.1 Bathymetry

Water depth was extracted from a digital bathymetric set compiled from the GEBCO digital atlas (GDA) Centenary Edition (2003) with a gridded resolution of 1-minute x 1-minute (*ca.* 1.2 x 1.8 km at Biscay latitude). The GDA software interface was used to extract an ASCII grid dataset for conversion to point data.

2.1.2.2 Sea Surface Temperature

Remotely-sensed SST data from the Advanced Very High Resolution Radiometer (AVHRR) carried onboard the National Oceanic and Atmospheric Administration (NOAA, U.S.A.) polar-orbiting environmental satellites were acquired from the Remote Sensing Group at Plymouth Marine Laboratory, U.K. (PML RSG). Due to problems in obtaining sufficient high numbers of cloud-free images at higher spatial and temporal resolution, weekly composite raster images were selected for analysis, with each image corresponding to the week in which the survey took place. The method created synoptic views of cloudy regions by calculating an average of the available values for each location during the weekly time period. Images were at a resolution of *ca.* 4.8 x 4.8 km and were supplied as geo-referenced GEOTIFF (Geo-referenced Tag Image File Format) files in equal-angle projection. A single band was used, with a scale of values suitable for conversion to SST. One problem which existed with the SST dataset was the presence of annotation on the map, in the form of two contour lines approximating the 500m and 3000m contours and composed of a line of single cells (Figure 2.3). These lines were assigned a value of 0 in original images (the same as cloud). Unfortunately, in the time period available, images could not be re-processed to remove annotation by PML RSG (Figure 2.3). Also, cloudy areas could not all be removed using the composite technique and were assigned a zero value. All analyses of SST were carried out without using cells assigned 0 values.

2.1.2.3 Chlorophyll-a

Remotely-sensed, near-surface CHL-a data was available from the Sea-viewing Wide Field of view Sensor (SeaWiFS), which was launched on the SeaStar spacecraft on the 1st August 1997
and received from PML RSG. The sensor measures Earth-leaving radiance in eight spectral bands. The addition of a 410 nm band in SeaWiFS allows photosynthetically-viable near-surface CHL-a to be separated from degradation products. This was not possible through the previous ocean colour satellite born sensor, the Coastal Zone Colour Scanner (CZCS), which was carried onboard the Nimbus 7 satellite between 1978 and 1986. As with the AVHRR images, the SeaWiFS sensor cannot penetrate cloud and composite GEOTIFF images were used at the same spatial and temporal resolution as the AVHRR images. A single band was used with a scale of values which could be converted to CHL-a. A major limitation of the CHL-a data was that no data was available until September 1997. In addition, cloudy areas were also assigned 0 values. All analyses of CHL-a were carried out without using cells assigned 0 values.

2.1.2.4 Composite Front maps

Detection and analysis of surface ocean features was previously based around manual analysis of long sequences of satellite images. In recent years, techniques have been developed for automating this process. Composite front maps have been developed by PML RSG as a method to enable the observation of dynamic ocean SST fronts, eddies and their spatio-temporal evolution and decline (Miller, 2004). The ‘composite front map approach’ (Miller, 2004) utilises single image edge detection (SIED), a robust automated method of locating temperature gradients. SIED was used to recognise a significant difference in mean water temperature between water masses by locating fronts exhibiting gradients of (originally) 0.4 Kelvin (K) or greater and thought to be genuine oceanic front features (Miller, 2004).

Miller’s technique represents an improvement from an original automated edge detection algorithm (Cayula & Cornillon, 1995), which had certain limitations. A major problem was movements of cloud over regions of interest, which had the effect of producing artificial front boundaries at cloud edges. The approach improves on previous techniques by requiring shorter time-scale image sequences to integrate data on strength and persistence of fronts into single images by combining segments of available data into composite images (Miller, 2001). Gradient magnitude at front pixels is weighted by the probability of detecting a front at a location during an image sequence, through calculation of the fraction of cloud-free images of
the pixel area in which the front was detected. In addition, the movement of fronts due to tides or advection, is accounted for by calculation of relative positions of fronts in the proximity of the original front in subsequent images, thereby giving a measure of front persistence through the attribution of higher front ‘values’ (Miller 2004).

Raster images with a cell resolution of \(ca.1.1 \times 1.1\) km were provided for the weekly period of each survey from PML RSG (Figure 2.3). For each weekly period two maps were provided, one of the Biscay (bi) area and one of the Celtic Sea and western English Channel area (pa). A limitation of the dataset was that pa maps available for analysis did not provide complete coverage of the survey area. The area between c.1-2° W (the latter representing Portsmouth) was unavailable and was not used in analysis of front data.

2.2 Data Processing

All data were exported into ArcView 3.3 (AV3, ESRI Systems 1992) and ArcGIS 8.0 (AG8, ESRI Systems 1999) software for processing. Bathymetric data from GEBCO 2003 was exported in ASCII format and then converted to a comma delimited text file for input into AV3. The data was converted into a grid file using the Spatial Analyst extension, with depth as the Z variable. This grid with a resolution of \(ca.1.2 \times 1.8\) km was then interpolated to a new grid using Spatial Analyst, with a final resolution of 4 x 4 km. The final grid cell size chosen was primarily to approximate the maximum distance between the ship and observed dolphins as exact positions of dolphins could not be determined. In addition, the cell size allowed partitioning between species at a relatively fine scale to be determined, without great loss of data resolution. However, track lines did not necessarily cross the middle of cells and did not necessarily leave a swathe (or expected maximum distance to sighting) of 2 km each side of the track line (mean length through cells = 2.72 km; Figure 2.6) Although it is likely that some dolphin sightings were assigned to cells incorrectly, the error involved should have been minimised using this method.

There are two sources of potential inaccuracy in depth, and therefore slope, data. The first concerns the limitations of the GEBCO 2003 dataset. Although data is thought to be largely accurate, GEBCO GDA is based around vector contouring of, mainly, deep-water areas.
Fig 2.3: Raster front map of Biscay (bi) area at c.1.2 km x 1.2 km (A); SST raster map, at c.4.8 km x 4.8 km resolution, showing reclassified front polylines of 1K for both Biscay (bi) and Celtic Sea (pa) areas with known major frontal areas indicated; and detail of map C (B) showing front polylines of Ushant Sea Front. All maps are composites from 17-23 May 1998. Map annotation, in the form of two white contour lines, is displayed.

Contouring of shallow shelf waters may have lead to some inaccuracy in these areas as well as the general problem of the terracing effect common with conversion of vector databases to a gridded one (GEBCO 2003). However, data was checked systematically in the survey area for
errors against existing bathymetric charts and very few apparently erroneous data points were detected. Secondly, depth and slope data are affected by re-sampling and interpolation. Using lower resolution data leads to increasing inaccuracy in data in terms of depth ranges as interpolation of varying depth data leads to smoothing of extremities. This is also true when slope is calculated from depth grids. Slope in degrees was calculated for each raster cell using the Slope command in Spatial Analyst (AV3). Slope values were calculated as the maximum rate of change in elevation over each cell and its eight neighbours. The output slope raster was calculated as degrees of slope with high slope values indicating steeper terrain (Figure 2.4).

Fig 2.4: Raster map of study area illustrating slope in degrees at 4 km x 4 km resolution.

From the raster grid of depth it was then possible to create a polygon grid using the Fishnet extension to AG8 and a point grid using the Grid to Point command in the Grid.
Transformation extension of AV3, with the centre points of each raster cell the basis of the grid.

Point files of effort were imported into AV3 and converted to polyline shapefiles representing effort segments using the X-Tools extension. Only segments containing effort recorded in Beaufort sea state 4 or visibility of five kilometres or more were used to minimise the effect of poor conditions on sightings rate. Although standard methodologies recommend using sightings recorded in sea-states of less than three (Palka 1996), a visual analysis of sightings rate of each species showed that there was little relative decline in common dolphin detectability with increasing sea state. The detectability of striped dolphin did, however, apparently decline in sea state > 2 (Figure 2.5). As most observations of sea states > 4 occurred during the autumn and winter, when striped dolphin was largely absent (see 3.3.2) analysis of striped dolphin detectability was carried out separately for the period April – October, and indicated that detectability declined less dramatically for this species without effort for November – March included. It was decided to define a cut-off at sea state < 5 to reflect the lack of influence of sea state on common dolphin detectability, although a slight negative effect on calculations of relative abundance in striped dolphin should be taken into account. The study does not deal with calculations of absolute abundance and the setting of this arbitrary limit is a minor limitation which is balanced by the effect of increased sighting sample size on statistical robustness.

**Fig. 2.5**: Effect of sea state on detectability of common dolphin and striped dolphin. Expected sightings show number of observations based on the assumption of a uniform distribution in proportion to effort in each sea state category.
Each segment was merged into a single effort line theme for each survey. From the polyline file an effort point grid was created for each survey by selecting cells which intersected the effort track. All grid cells which were intersected by the effort line were included in the effort grid file for each survey (Figure 2.6).

The effort point grid could then be used to extract values from point files of dolphin sightings after conversion of those files into separate grid files for both common and striped dolphin. For each cell on the survey track a value of 0 or 1, indicating absence or presence respectively, was assigned and a value of group size was assigned only to presence cells. This was repeated for both common dolphin and striped dolphin for every survey. The point grid was also used to extract values from each raster dataset for the dolphin grids and each environmental variable using a function in the Grid Analyst extension. For depth and slope, the resolution of the cells was the same (4 x 4 km) as the effort point grid for each of 72 surveys was created.
from the initial depth grid. For SST and CHL-a, the use of the point grid enabled extraction from raster datasets of the same projection but different resolution, (4.8 x 4.8 km) without interpolation.

Front maps were provided in raster format and re-classified in AG8 to show only the strongest and most persistent fronts (value of 1) (see Figure 2.3). This value was selected through analysis of the dataset, which indicated that most fronts detected were of this value. Selection of a single value, rather than a wide range of values, enabled direct comparison between the proximity of dolphins to fronts of uniform value. It also ensured that frontal features selected were likely to be persistent and therefore biologically significant (Mann & Lazier 1996). After re-classification, maps were converted from raster to polyline feature files in Spatial Analyst in AG8 and re-projected using the ArcView Projection Utility in the Geoprocessing extension in AV3. It was then possible to calculate the distance from individual sightings to front boundaries (DF) using the Spatial Join function in AV3’s Geoprocessing wizard. For the sightings data, distance was measured from the central point of each cell to which a sighting was assigned to the closest polyline indicating a front boundary.

In addition, it was possible to calculate the distance travelled (in km) through each grid cell by intersecting the polyline effort file for each survey with the polygon grid file. This enabled calculations of two measures of relative abundance for both species of dolphin. The first, referred to as encounter rate, is equivalent to the number of encounters \( (n) \) recorded per kilometre of survey effort. The second, referred to as relative density, is equivalent to the number of animals \( (N) \) recorded per kilometre of survey effort.

All values for each variable were added to an attribute table for each survey effort grid containing each cell sampled as a row and values for each variable associated with that cell as columns. Tables were then exported to Microsoft Excel 2002 (Microsoft Corporation 2002) for analysis.
2.3 Statistical analysis

2.3.1 Data characteristics

As a preliminary stage in data analysis, all data were tested for normality (Komolgorov-Smirnoff), equal variance (Bartlett’s test for normal data). Although all data groups had a normal distribution \( p < 0.05 \), all had unequal variance \( p < 0.05 \) (see appendix). Non-parametric statistics were used accordingly in all cases. All statistical analysis was carried out in MINITAB version 14 (Minitab Inc., 2001).

2.3.2 Spatio-temporal analysis

To aid analysis at finer scales and to highlight differences in patterns of habitat use and segregation between common dolphin and striped dolphin the data was split temporally and spatially. The former split was categorised into seasons, and the latter into regions.

After initial analysis of the temporal distribution and relative abundance of both species, seasonal patterns of distribution emerged for each species which roughly corresponded to the following arbitrary definitions of season:

**Season 1 – winter:** January, February, March

**Season 2 – spring:** April, May, June

**Season 3 – summer:** July, August, September

**Season 4 – autumn:** October, November, December

For regions, data were divided and classified according to two main criteria: the distribution and relative abundance of each species of dolphin; and the existence of natural, physical habitat zones based on physiographic, oceanographic and biotic features.
The following regions were classified (Figure 2.7, see sections 1.3.1-3):

- Region 1. Shelf North

From c.50.9°N to c.49°N. Comprising most of The English Channel (including the Hurd Deep), from Portsmouth (U.K.) west to the Celtic Sea and roughly delimited by the 100m contour. Characterised by low depth (10 – 100 m) and low slope (0 – 0.1 degrees).

**Fig. 2.7**: Map of the study area showing Regions 1 – 5.
• Region 2. Shelf South

From c.49°N to c.47°N: comprising mainly the Ushant sea area which borders the English Channel, Celtic Sea and Bay of Biscay. Characterised by low depth (100 – 200 m) and low slope (0 – 0.1 degrees).

• Region 3. Celtic Sea – Biscay shelf break.

From c.47°N to c.45.4°N: comprising the northern shelf-break and characterised by large depth differential (150 – 4000 m) and medium to high slope (0.1 – 20 degrees).

• Region 4. Abyssal plain of the Bay of Biscay

From c.45.4°N to c.44.4°N: comprising the deepest waters on the survey track and characterised by high depth (3500 – 4500 m) and medium slope (0.1-5 degrees).

• Region 5. Cantabrian Sea shelf-break and shelf.

From c.44.4°N to c.43.4°N: comprising the Santander Canyon, shelf-break and narrow shelf leading into Bilbao (Spain) and characterised by large depth differential (50 – 4000 m) and areas of both high (shelf-break) and low (shelf) slope (0 – 20 degrees).

2.3.3 Univariate analysis

The analysis of the sighting and effort datasets initially relied on the use of a series of simple chi-square ($\chi^2$) tests to determine if each species were distributed non-uniformly with respect to all variables (depth, slope, DF, SST, CHL-a) separately. The null hypothesis derived from this statistic is that both species are distributed uniformly in relation to each environmental variable. A univariate form of the $\chi^2$ test was employed to determine an expected distribution of each dolphin species using kilometres travelled as the measure of effort in each case. The observed distribution of dolphin encounters with respect to each variable was compared to the expected distribution using the $\chi^2$ statistic. The $\chi^2$ test has been applied successfully to a large number of cetacean studies (e.g. Hui, 1979, 1985; Selzer & Payne, 1988; Baumgartner, 1997; Cañadas et al. 2002).
The predicted distribution or frequency histogram was determined separately for each variable. However, the choice of categories was based upon a determination of the values of each variable such that each contained a fairly equal amount of effort, and therefore creating class sizes of equal probability and not equal intervals, whereby each class would predict an equal encounter rate for a uniform distribution (after Baumgartner 1997). The histogram of effort was then converted to an expected uniform distribution using the following equation: \( E_i = \frac{(n \times L_i)}{L_t} \), where \( E_i \) is the expected number of sightings in class \( i \), \( n \) is the total number of encounters and \( L_t \) is the total amount of effort (after Hui 1979). All statistics were considered significant at \( p = 0.05 \). For all variables, seven categories were defined. An accurate application of the \( \chi^2 \) statistic requires that each class has a frequency of five (equivalent to five dolphin encounters). Although more dolphin encounters for each species were recorded than 35 (minimum frequency multiplied by number of categories), data was then split into the sub-category of season with four further categories, which required that for each season a minimum of 35 dolphin encounters with each species was recorded, with 140 required in total across seasons. The application of seven categories across all tests of \( \chi^2 \) allows variation to be compared more easily.

The categories for each fixed variable (depth and slope) were calculated to allow for relatively even effort, however it was important to define categories also on the potential biological significance of different preferences for the two species. The categories selected for depth; 0 – 55 m, 56 – 80 m, 81 – 100 m, 101 – 120 m, 121 – 200, 201 – 3500 m, 3501 – 4514 m, reflected the majority of effort over shallow shelf waters but also included the shelf-break (200 – 3500 m) and abyssal plain (3501 – 4514 m) regions as defined classes of relatively equal effort.

For two non-fixed variables (SST, CHL-a), categories for each season were defined separately due to large variability in values across seasons, which would skew effort classes. For this reason regions were not included in this analysis as non-fixed variables would have to be categorised irrespective of season to maintain expected frequencies above five.

Mann-Whitney-U tests of medians were calculated to test the null hypothesis that no differences exist between the two dolphin species across the range of variables and between
seasons and regions. The same test was also used, in addition to chi-square tests, to test differences between distributions of each dolphin species in relation to the effort-related distribution of EVs. The Kruskal-Wallis one way analysis of variance by ranks was used to test whether seasons and regions could be differentiated across values of EVs assigned to each species of dolphin. The Kruskal-Wallis test statistic, $H$, is calculated as (Fowler & Cohen, 1995):

$$H = \left[ \frac{12}{N(N+1)} \sum_{j=1}^{k} n_j \bar{R}_j^2 \right] - 3(N + 1)$$

where

- $k$ = number of samples in the group;
- $n_j$ = number of observations in group $j$;
- $N$ = total number of observations in all groups;
- $\bar{R}_j$ = average of the ranks in the $j$th group.

Although it was possible to test differences between means, using parametric t-tests assuming unequal variances, the results of these tests would not be directly comparable to results from Kruskal-Wallis tests, which test differences between medians.

The analysis of sightings data for each species included sightings which were considered to involve mixed species groups (i.e. not monospecific). A separate analysis was carried out with mixed species groups, which were defined as sightings where both species were seen simultaneously and adjoining. In these cases, single sightings were ascribed to each species and behavioural notes were included, at the time of the observation, indicating that observers judged the groups to be mixed. Chi-squared analysis was not carried out for this class of sightings as sample sizes were too small (expected frequencies < 5) to enable comparisons with categories defined for the analysis of each species.
2.3.4 Multivariate analysis

Principle Component Analysis (PCA) was used to assess relationships within all variables. The technique enables the use of presence-only data to examine the relative importance of interdependent variables associated with sightings of both dolphin species. PCA is a multivariate technique producing a set of abstract variables (principal components), which condense information contained in the original variables into a smaller set of new composite dimensions. Each principal component is a linear combination of the original variables, and places similar entities in proximity in ordination space. The ‘ecological’ importance of each component is reflected in the value given to each variable defining the component. The relationships between sampling entities (e.g. different dolphin species) are evaluated by their relative positions on the ordination axes (McGarigal et al., 2002).
Chapter 3

3. Results

3.1 Survey effort

During the period August 1995 and July 2002, 72 three-day surveys were carried out with a total of 62784.6 km surveyed during the 8-year period. Survey data was collected with the ship travelling at a mean speed of 30 km/h.

Despite the attempt to create even effort segments for each month and season by conducting surveys at regular intervals and over a fixed route, there are several reasons why this is not possible. One of these was variation in daylight hours of observation through the seasons. The route and timing of the ship allowed for complete sampling of the representative habitats (see 1.3.1) along the route during daylight hours. During March - October, the entire length of the route was sampled at least once on most surveys, with some overlap during May - July. During November - February, approximately 75% of the route was sampled. Another factor was the generally worse weather during the winter months with higher average sea states, especially in February (Figs. 3.1-3). Also, surveys were not possible during some months in some years, particularly during January when the ship was often undergoing maintenance. There was a significant difference in effort between each season, as defined in this study. The lowest amount of effort was recorded in winter (8667.5 km) and autumn (13879.5 km) with the highest in spring (19454 km) and summer (20783.6 km). The survey effort also varied spatially between regions and is shown in Figures 3.4-7.
**Fig 3.1**: Cumulative monthly effort (km) in comparison with mean effort (km) per survey during each month.

**Fig 3.2**: Cumulative yearly effort in km in comparison to the number of surveys during each year.

**Fig 3.3**: Mean sea state by month during monthly surveys.
Fig 3.4: Seasonal distribution of effort (km) through survey cells during winter (January – March).

Fig 3.5: Seasonal distribution of effort (km) through survey cells during spring (April – June).
Fig 3.6: Seasonal distribution of effort (km) through survey cells during summer (July - September).

Fig 3.7: Seasonal distribution of effort (km) through survey cells during autumn (October - December).
3.2 Dolphin sightings and abundance

A total of 569 sightings of 22,200 individuals were recorded during the survey period. Of these, 499 sightings of 16,093 individuals, were identified as common dolphin, with total group size ranging from 1 to 1500 individuals, and 170 sightings of 6,107 individuals, were identified as striped dolphin, with total group size ranging from 1 to 400 individuals. Of these sightings, 22 from each species’ total were classed as mixed species groups (see 2.3.3). The number of sightings \( n \), individuals \( N \), encounter rate \( n/km \) and relative density \( N/km \) in each season and region, for both species, is summarised in Table 3.2.

3.3 Dolphin spatial and temporal distribution

The distribution of common dolphin, striped dolphin and mixed species groups (containing both species) in the study area is shown in Figures 3.9-11. Seasonal differences between species are illustrated on maps (Figures 3.12-15) showing the distribution of all species classes for each season.

3.3.1 Common dolphin distribution

Common dolphins were recorded in all seasons and in all regions in the study area. Differences between years were significant for both encounter rate \( H = 28.59, p < 0.001 \) and relative density \( H = 28.47, p < 0.001 \). Incomplete years (1995 & 2002), when surveys were only carried out for part of the year, were omitted from this test (see Figure 3.8). However, data were pooled across years for analysis. Differences in median group sizes were not significant across seasons \( H = 4.18, p = 0.243 \) and regions \( H = 7.54, p = 0.11 \) and results will refer to encounter rates \( n/km \) only.

Regional \( H = 346.13, p < 0.001 \) and seasonal \( H = 63.66, p < 0.001 \) differences in distribution were noted with this species. Overall, common dolphins relative abundance was highest in Region 2 \( n/km = 0.014 \), off the Brittany (France) coastline, and Region 3 \( n/km = 0.021 \), the Celtic Sea/Bay of Biscay shelf-break. This general trend, however, does not fully explain the complexity of the distribution of animals in relation to season and region and marked changes in
relative abundance were observed across both classes of data.

![Graph showing encounter rate and relative density for common dolphin and striped dolphin between 1996–2001.](image)

**Fig 3.8**: Encounter rate \( (n/km) \) and relative density \( (N/km) \) for both common dolphin and striped dolphin between 1996–2001 (incomplete years 1995 & 2002 were omitted).

Of the total number of sightings, the lowest proportion was during spring with 16.8\% \( (n = 84, \ n/km = 0.006) \). During this period animals may disperse to some extent, with animals largely absent from both Region 1 and Region 2. This apparent dispersal is not as evident for the deeper waters of Region 3 \( (n = 45, \ n/km = 0.012) \) and Region 4 \( (n = 19, \ n/km = 0.011) \). In the case of the latter area (the abyssal plain), the encounter rate for common dolphin peaks during this season.

During the summer, numbers of common dolphins increased from the spring. Animals were particularly common in the shelf-break waters of Region 3 \( (n = 96, \ n/km = 0.03) \) when relative density reached its peak overall \( (N = 4746, \ N/km = 1.487) \). However, this statistic was skewed by one very large group of 1500 animals recorded in July 1997. Although animals were still scarce in Region 1, intermediate encounter rates were recorded in Regions 2, 4 and 5.

A marked change in distribution occurred over all years during the autumn. The highest proportion of all sightings \( (32.4\% \ n = 162, \ n/km = 0.014) \) occurred during this period. An apparent influx of animals into the shelf-waters of Region 2 was indicated by higher encounter rates \( (n = 107, \ n/km = 0.027) \) than in summer.
Fig. 3.9: Distribution of striped dolphin in the study area.

Fig. 3.10: Distribution of common dolphin in the study area.
Fig 3.11: Winter distribution of common dolphin, striped dolphin and mixed species groups in the study area.

Fig 3.12: Distribution of mixed species groups (containing both common dolphin and striped dolphin in the study area.)
Fig 3.13: Summer distribution of common dolphin, striped dolphin and mixed species groups in the study area

Fig 3.14: Spring distribution of common dolphin, striped dolphin and mixed species groups in the study area
The possibility of shelf-break animals dispersing northwards seems likely in line with decreasing productivity in this region, although encounter rates in Region 3 \( (n = 26, n/km = 0.029) \) were similar to summer. One reason for this lack of contrast between summer and autumn in Region 3 may have been the relative lack of coverage in both November and December, with 75% of common dolphin sightings \( (n = 21) \) and 70% of effort (665.1 km) recorded during October, which is closer temporally to the summer period. Effort in Region 2 during autumn was nearly 450% higher than in Region 3 (4000.9 km), due to shortening daylight hours and worse weather later in the year.

During winter, a similar distribution pattern to autumn was observed, with numbers remaining high in Region 2 and a seasonal peak in Region 1 \( (n = 13, n/km = 0.004) \) reflecting movements of this species into the shallower waters of the English Channel.
Table 3.1: Summary of total effort (km), number of sightings (n), individuals (N), encounter rate (n/km), relative density (N/km) and mean group size by season and region during the survey period.

<table>
<thead>
<tr>
<th>Region</th>
<th>Effort (km)</th>
<th>N</th>
<th>n</th>
<th>N/km</th>
<th>n/km</th>
<th>mean group size</th>
<th>N</th>
<th>n</th>
<th>N/km</th>
<th>n/km</th>
<th>mean group size</th>
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<td>10.3</td>
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<td>4212</td>
<td>107</td>
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<td>0.132</td>
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<td>170</td>
<td>0.134</td>
<td>0.004</td>
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Encounter rate also increased during the autumn and winter in Region 5 (combined; \( n = 24, n/\text{km} = 0.0066 \)) which includes the narrow shelf waters of the Cantabrian Sea, close to Bilbao. This may reflect a general increase in shelf waters during the autumn and winter.

Overall, chi-square tests showed that differences in expected and observed encounter rates by season in Regions 1-3 were significant (\( p < 0.05 \)), but that Regions 4 - 5 showed little change over the seasons (\( p > 0.05 \)).

### 3.3.2 Striped dolphin distribution

Striped dolphins were recorded in all regions and seasons in the study area. Differences between years were non-significant for both \( n/\text{km} (H = 15.00, p = 0.1) \) and \( N/\text{km} (H = 15.08, p = 0.1) \) and data were pooled across years (see Figure 3.8). In addition, differences in median group sizes were not significant across seasons (\( H = 4.84, p = 0.184 \)) and regions (\( H = 9.62, p = 0.057 \)) and results will refer to encounter rates (\( n/\text{km} \)) only. However, there was a highly significant difference between group size of striped dolphin (median = 20) and common dolphin (median = 9.5) (Mann-Whitney, \( p < 0.001 \)), with striped dolphins usually found in larger monospecific groups.

Although striped dolphins were recorded in all region and all seasons, there was a marked difference in spatio-temporal distribution and encounter rate in comparison to common dolphin. Both regional (\( H = 262.56, p < 0.001 \)) and seasonal (\( H = 41.77, p < 0.001 \)) differences in distribution were noted. Overall, animals were scarce during autumn and winter (combined; \( n = 24, n/\text{km} = 0.002 \)) in comparison with spring and summer (combined; \( n = 146, n/\text{km} = 0.006 \)) when 85.9% of all animals were recorded. This provides strong evidence of dispersal from the survey area during the autumn and winter. During October, 12 sightings were recorded, which is 50% of the total for autumn and winter combined, indicating that dispersion may occur during November.
Numbers increased during spring reaching a peak in the summer (Figure 3.16). The regional distribution of striped dolphin remained relatively unchanged for spring and summer (sample sizes were too low to compare autumn and winter), with the centre of distribution in Regions 3-5. Animals were more frequently encountered in Regions 3 and 4 overall than Region 5. However, encounter rates in spring were higher in Region 3 \((n = 31, \text{n/km} = 0.009)\) than Region 4 \((n = 11, \text{n/km} = 0.007)\), whereas this trend was reversed in summer months (Region 3; \(n = 39, \text{n/km} = 0.012\): Region 4; \(n = 29, \text{n/km} = 0.014\)). Also, animals were recorded more frequently in Region 2 during summer than during any other period \((61.5\%, n = 8)\).

In comparison to common dolphin, encounter rate was lower in all seasons, but this was especially marked during autumn and winter, when encounter rates for common dolphin were higher than during spring and summer and striped dolphin were at their lowest. During spring and summer, there was a large increase in striped dolphin encounter rate, although encounter rate was still lower than common dolphin.
3.3.3 Distribution of mixed species groups

Fig. 3.17: Part of a mixed group of striped and common dolphins in the Bay of Biscay (courtesy of Clive Martin).

Although the sample size was too small for chi-square tests (expected frequencies < 5), it is relevant to note some patterns in the distribution of mixed species groups. In the autumn and winter 26.1% \((n = 11)\) of striped dolphin encounters involved mixed groups in comparison to spring and summer (11.5%). The highest proportion of mixed species groups were encountered in the spring, however, with 40.1% \((n = 9)\) of the total groups encountered. Predictably, considering the distribution of striped dolphin, 86.4% of sightings were in Regions 3 – 5, although 3 sightings in Region 2 constitute 27.2% sightings of striped dolphin within that area. Group sizes of mixed groups (median = 50.5) were significantly larger \((p < 0.05)\) than average values for either striped or common dolphin. However, when numbers of striped dolphins in mixed species groups (median = 8) were considered separately, they were lower than in monospecific groups of that species, with a borderline significant test result \((p = 0.059)\). The opposite was true of common dolphin numbers in mixed species groups (median = 30.5, \(p < 0.05\)). This reflects the overall ratio of common dolphin to striped dolphin (2.25:1) within mixed species groups. Of the 22 groups, 2 contained equal numbers of each species, with both groups totalling 80 individuals, 12 contained more common dolphins than striped dolphins and 9 contained more striped dolphins than common dolphins. In groups containing larger numbers of common dolphins, ratios ranged from 1.5:1 \((n = 25)\) to 150:1 \((n = 151)\) with a mean ratio of 25.8:1 \((n = 784)\). In groups containing more striped, ratios ranged from 3:1 \((n = 9)\) to 8:1 \((n = 90)\) with a lower mean ratio of 3.2:1 \((n = 425)\).
3.4 Dolphin distribution and environmental variables (EVs)

In order to highlight habitat preferences both within and between dolphin species, this section is broken down into five parts. The first deals with spatio-temporal variability within the ranges of EVs across seasons and regions. The second and third with EVs associated with each species of dolphin in turn. The third section, which concerns the distribution of striped dolphin, also compares the distributions of each species in relation to each other. The fourth section investigates differences in the relationship between EVs associated with mixed species groups and mono-specific groups of both common and striped dolphin. The fifth section examines the relationship of the two species with EVs using a multivariate PCA analysis, which assessed relationships between the values of all interdependent variables associated with dolphin sightings.

Sightings data was not consistent across variables as there were temporal limitations to the SST and CHL-a data. The former was limited by cloudy areas and map annotation (see 2.1.2.2) and the latter by cloudy areas and the temporal coverage of SeaWiFS data (see 2.1.2.3). Table 3.2 details the number of sightings for which values could be assigned for all data and for SST and CHL-a respectively.

3.4.1 Ranges within environmental variables

The distribution of dolphins within the study area could reasonably be expected to be defined by habitat preferences in terms of both physiographic and oceanographic variables. The variables available for analysis in this study were depth (m), slope (degrees), distance to front (DF) (km), SST (°C) and CHL-a (mg m\(^{-3}\)). The former two, which are fixed, physiographic variables, do not vary seasonally, although sampling of these variables is affected by seasonal differences in effort in different regions due to the fixed track of the ship and the effect of daylight hours on sampling frequency. Seasonal and regional variation in the values of dynamic variables is summarised in Figure 3.18.

Lower effort in deep-water areas (particularly the northern shelf-break, Region 3) during autumn
and winter led to a significant difference in the sampling of depth classes across seasons \((H = 42.82, \ p < 0.001)\).

Table 3.2: Number of sightings by season and region which could be assigned values for all variables. Depth, slope and DF values could be assigned to all sightings.

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<th></th>
<th>D. delphis</th>
<th></th>
<th>S. coeruleoalba</th>
<th></th>
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</thead>
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<td></td>
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<td>SST</td>
<td>CHL-a</td>
<td>All Data</td>
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<td>89</td>
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<td>146</td>
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<td>15</td>
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<td>46</td>
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This was also true of slope although the result was not highly significant \((H = 8.90, \ p = 0.031)\). As regional classes were defined partly due to physiographic characteristics, differences between the regions were highly significant for both these variables \((p < 0.001)\). As was expected, seasonal and regional differences in DF and SST values were both highly significant. In the case of frontal formation, greater stratification of the water column during the more settled spring and summer leads to the formation of stable fronts during this period. In the case of SST, temperatures are lower during the winter with a steady increase during spring and summer and a gradual decline in autumn. The definition of regions within the study area across latitudinal bands also means that these act as a proxy for SST, with Region 1 the coldest and Region 5 the warmest.
The relationship of CHL-a with season and region is more complex. Values were highest in spring with the onset of the spring bloom; they declined during summer and were lowest during autumn and winter. Values were also higher in shallow shelf areas in comparison to deeper, pelagic areas, throughout the year.
Fig 3.18: Box and whisker plots showing median and inter-quartile ranges of all EVs against season and region. Values for CHL-a and slope have been log-transformed (log_{10}) for ease of comparison. Asterisks denote outliers.

3.4.2 Common dolphin

The results of chi-square tests show that the distribution of this species with respect to depth, slope, SST and CHL-a is significantly different from the expected, uniform distribution (Table 3.3). The distribution with respect to DF, was not significantly different (p > 0.05) from a uniform distribution across all seasons.

A graphical illustration of data used for $\chi^2$ tests for both species for all seasons is provided in Figure 3.20, with additional inter-seasonal charts provided in the appendix.
The distribution of the common dolphin in respect to depth in all seasons was modal around the deeper parts of the shelf, particularly in the southern part of Region 2 and northern shelf section of Region 3, with 32.3% of all sightings seen at depths of 121 - 200 m ($n = 161$, $n$/km = 0.018). A large proportion of sightings were also seen in depths of 201 – 3500 m ($n = 136$, $n$/km = 0.015). Only five sightings were recorded in waters of < 80 m. However, there was significant seasonal variation as indicated in section 3.3.1. In the spring, the largest proportion of sightings was in the deepest water, 3501 – 4514 m ($n = 34$, $n$/km = 0.013), with a positive and linear relationship evident with increasing depth at this season (see appendix).
During the summer, the encounter rate was modal about the shelf-break at depths of 201-3500 m with 45.7% of sightings occurring in this depth class ($n = 77, n/km = 0.025$). The distribution in autumn closely matched the typical pattern for all seasons, with a modal distribution about the deeper waters of the shelf ($n = 76, n/km = 0.037$)

Table 3.3: Results for univariate $\chi^2$ tests. Degrees of freedom = 7 for all data. NA indicates that small sample sizes precluded meaningful analysis. A value of <0.05 indicates a distribution that is significantly different from a uniform distribution and a value of <0.001 indicates a highly significant difference.

<table>
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<td>89</td>
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</table>

In winter, the pattern was bimodal with 70.1% of sightings in three shelf depth categories between 81 – 200 m ($n = 63, n/km = 0.016$), and another small peak in the deepest water. The greater number of sightings in shallower water probably reflects the northward movement of animals across the shelf at this time.

The distribution of common dolphin with respect to slope in all seasons was bimodal with the
main peak in areas of highest slopes \( (n = 142, \tfrac{n}{km} = 0.016) \) and a second peak in areas of low-medium slope \( (0.031 - 0.05 \text{ degrees}) \). The areas of highest slope in the study area are the two shelf-breaks. The continental shelf is variable but with slopes generally between 0 – 0.05 degrees (see Figure 2.4). This bimodal pattern is evident to some degree in all seasons, but weakest in spring when animals show a positive linear relationship with increasing slope. In spring and summer, the peak in distribution is found at highest slope values with 48% of sightings in this category. In autumn and winter, when animals are found in greater abundance in shelf areas, peaks in distribution are found in the 0.11 - 0.5 category \( (n = 27, \tfrac{n}{km} = 0.021) \) in winter and in the 0.019 – 0.03 category in the autumn \( (n = 37, \tfrac{n}{km} = 0.016) \).

The bimodal distribution of common dolphins was again reflected in the distribution of sightings in relation to SST and CHL-a. In the case of the former across all seasons, two distinct peaks were noted, one at 11.6 - 13°C \( (n = 95, \tfrac{n}{km} = 0.011) \) and one at 18.6 – 24.1°C \( (n = 95, \tfrac{n}{km} = 0.012) \). These two peaks are likely to correspond, respectively, to autumn and winter distribution about the northern shelf and spring and summer distribution further south in the more southerly (warmer) shelf-breaks and abyssal plain in the southern Bay of Biscay.

To test this bimodality in relationship more coherently, a Kruskal-Wallis test of common dolphin distribution in relation to SST across regions was carried out. This showed a high degree of significance \( (H = 119.28, p < 0.001) \) and demonstrated that median values for Regions 1 (median
= 12.3°C) and Region 2 (median = 13°C), are much lower than those for Regions 3 (median = 17.7°C) and 4 (median = 17.4°C). The first two regions are shelf habitat and the low temperatures reflect the fact that common dolphins are more frequently found in this habitat during colder times of the year. However, it is pertinent to note that a Mann-Whitney test of common dolphin distribution against SST in comparison to that of the effort was non significant ($p > 0.05$), and reflects the cosmopolitan nature of common dolphin distribution.

With respect to CHL-a, the distribution of common dolphin was not bimodal but was certainly related to the prevalence of this species on or off-shelf at different seasons. CHL-a was generally higher in shelf-regions throughout the seasons (Fig. 3.18) and common dolphin displayed a more positive relationship with CHL-a during autumn and winter when species distribution was centred on the northern shelf. A Kruskal-Wallis test of common dolphin distribution against CHL-a across seasons revealed that common dolphins were found in areas of higher CHL-a concentration during autumn (median = 0.513 mg m$^{-3}$) and winter (median = 0.531 mg m$^{-3}$) than during spring (median = 0.3331 mg m$^{-3}$) and summer (median = 0.363 mg m$^{-3}$) ($H = 31.93$, $p < 0.001$). This trend is opposite to the overall trend for seasonal CHL-a concentration over all sightings effort (see Figure 3.19). During spring when the greatest proportion of sightings was in the deepest water class, the distribution of common dolphin showed a negative, linear relationship with CHL-a, with most sightings found in the 0.08 – 0.31 mg m$^{-3}$ class ($n = 23$, $n/km = 0.015$). During summer, when distribution was centred on the northern shelf-break (Region 3), the relationship with CHL-a was intermediate between spring, and autumn/winter. Although animals were found in deeper water (201 – 3500m), higher primary productivity over the shelf-break leads to higher CHL-a measurements than over the abyssal plain (see Figure 3.18).

3.4.3 Striped dolphin

The results of chi-square tests show that the distribution of this species with respect to depth, slope, SST and CHL-a were significantly different from the expected, uniform distribution during spring and summer (Table 3.2). This was not true of the distribution with respect to DF, which was not significantly different ($p > 0.05$) from a uniform distribution during spring and summer. Small sample sizes precluded meaningful analysis of striped dolphin distribution during autumn.
and winter using chi-square tests due to expected frequencies of $< 5$.

Unlike common dolphin, the distribution of striped dolphin, in relation to both physiographic and oceanographic variables, within the study area was relatively uniform across seasons. With respect to depth, this species showed a strong relationship with the deepest water areas, throughout the seasons. During spring, sightings were recorded almost exclusively in the two deepest water classes, with 98.2% of sightings attributed to these classes ($n = 56, \frac{n}{km} = 0.012$). A similar pattern was evident in the summer, with 87.6% of sightings in the two deepest water classes ($n = 78, \frac{n}{km} = 0.013$). During winter and autumn, this preference for deeper water appears to differ little for this species. There was a highly significant difference between the two species with respect to depth, with common dolphin found at lower average depth (median = 152 m) than striped dolphin (median = 3471 m) (Mann-Whitney, $p < 0.001$). This should be expected, considering the bimodal (shelf, off-shelf) relationship of common dolphin with depth at different seasons. However, if the study area is broken down into regions, a consistent pattern emerges of striped dolphin selecting areas of higher depth than common dolphin. Although this is not true of Region 1 and 2, sample sizes are too small for striped dolphin to elicit meaningful comparisons. However, in Region 3 (where there is great depth differential, 139 – 4310m) striped dolphin is found at higher average depths (median = 3080 m) than common dolphin (median = 1413 m) (Mann-Whitney, $p < 0.001$). Although this difference is not as significant for Region 4 (Mann-Whitney, $p < 0.05$), or Region 5 (Mann-Whitney, $p < 0.05$) the same pattern is found. This is also true across seasons, with one exception. During spring, when both species show preferences for high depths there is a non-significant difference between the two species (Mann-Whitney, $p = 0.053$). However, this result is bordering on significant (Mann-Whitney, $p = 0.059$), with striped dolphin again preferring deeper areas (median = 3371 m) to common dolphin (median = 3108.5 m), and probably reflects the fact that the highest encounter rate of both species is found in Region 4 at this time.

Striped dolphin distribution also shows a preference for areas of higher slope than common dolphin. Across the seasons, 48.2% of sightings are found in the highest slope category, ($n = 82, \frac{n}{km} = 0.01$), with 38.2% found in the next highest ($n = 65, \frac{n}{km} = 0.072$). This pattern is unchanged during spring and summer. As with depth, a significant difference should be expected with a comparison between the two species, due to the bimodal nature of common dolphin.
(median = 0.11 degrees) data in comparison to striped dolphin (median = 1.97 degrees) (Mann-Whitney, $p < 0.001$). When this comparison was divided into seasons and regions, a more complex pattern emerged. In all the following samples; summer, Region 4 and Region 5, there was a non-significant (Mann-Whitney, $p > 0.05$) distinction between the two species with respect to slope, perhaps suggesting that this factor is less important than depth when considering the possibility of habitat partitioning between the two species at this scale. Samples for Regions 1 and 2 and winter were probably too small for results to be meaningful.

The influence of SST on the distribution of striped dolphin is likely to be important in the study area as it probably nears the northern limit of the species’ range in the northeast Atlantic (see 1.4.2.2). Striped dolphin was found within a temperature range of 11.5 °C and 23°C (median = 18.7°C) but with 84.1% of sightings found within a range of 16°C - 23°C. Records of this species outside of the period April – October are scarce and may be related to seasonal declines in SST. In addition, most of the more northerly records of striped dolphin (in Region 2) occurred during the summer months. A comparison between the two species based on SST was highly significant (Mann-Whitney, $p < 0.001$), with striped dolphin preferring warmer waters (median = 18.5°C) than common dolphin (median = 15.5°C). The overall difference was reflected in most seasons and regions with highly significant results for summer and autumn (Mann-Whitney, $p < 0.001$), significant results for winter and Regions 2 – 5 (Mann-Whitney, $p < 0.05$) and non-significant results for spring, Region 4 and Region 1 (Mann-Whitney, $p > 0.05$), although the sample size for striped dolphin was very small for the latter ($n = 2$).

The relationship of striped dolphin to CHL-a was negative (median = 0.285 mg m$^{-3}$) and linear in nature with very low numbers found in areas of high CHL-a and, conversely, high numbers found in areas of low CHL-a. When compared to CHL-a concentrations in relation to effort, there was a highly significant relationship (Mann-Whitney, $p < 0.001$) as there was in comparison to common dolphin distribution (Mann-Whitney, $p = 0.001$), with common dolphins generally found in areas of higher CHL-a (median = 0.376 mg m$^{-3}$). This statistic reflects the distribution of striped dolphin in deep, offshore areas, where CHL-a concentrations are generally low. The overall difference was reflected in some seasons and regions but not in others, with highly significant results for summer and Region 3 (Mann-Whitney, $p < 0.001$). The latter result
possibly reflects the preference of striped dolphin for deeper waters in this area. There were significant results (Mann-Whitney, $p < 0.05$) for spring, autumn and Region 1 ($n = 2$) and non-significant results for winter, and Regions 2 - 5 (Mann-Whitney, $p > 0.05$).

### 3.4.4 Mixed species groups

Mann-Whitney tests were used to test if there was a significant difference between EVs assigned to mixed species groups and monospecific groups of both species. The distribution of mixed species groups was found to be significantly different to that of common dolphin with respect to depth, slope and CHL-a, but not in relation to DF and SST. In comparison to striped dolphin differences were only significant for SST (Mann-Whitney, $p > 0.05$). Mixed species groups were found at intermediate temperatures (median = 17.65°C), between those of monospecific groups of each species, which reflects the relatively high proportion of occurrences during autumn and winter.

### 3.4.5 PCA analysis

The univariate analysis using Chi-Square ($\chi^2$) test, Kruskal-Wallis and Mann-Whitney tests provides an adequate method of examining the importance of each variable individually to the distribution and habitat requirements of each species of dolphin. Differences have also been highlighted between the two species which indicate the possibility of segregation on the basis of defining habitat parameters. However, univariate analysis does not help to explain the nature of relationships between the variables as a whole. PCA analysis enables the linear ordination of multiple variables on multi-dimensional axes, without defining relationships between the set of interdependent variables in terms of the dependent sampling entities (common and striped dolphin). Although PCA will not confirm or refute relationships which are indicated through the univariate analysis, it provides a confirmatory tool to support the evidence provided in the first parts of this chapter.

Separate PCA analyses were carried out for all data and for each season and region in turn. Initial analyses involved all five variables (depth, slope, DF, SST, CHL-a). Only sightings to which all
values had been assigned could be used in the analysis, which excluded all sightings between August 1995 and August 1997, due to the temporal range of CHL-a data (SeaWiFS data was available from September 1997, see 2.1.2.3). A second analysis was then carried out using just four variables (depth, slope, DF and SST) (see appendix). Zero values for some SST data due to cloudy areas and areas with annotation on SST maps (see 2.1.2.2 and Table 3.2) limited the analysis.

Normal probability plots and Komolgorov-Smirnoff tests of normality (see appendix) indicated that all data was normally distributed and the assumption was made that univariate normality was a good step towards multivariate normality (i.e. hyperellipsoidal with normal varying density around the centroid), which suggests that linear axes (i.e. principal component scores) will adequately represent the data. Transformation of the data should then be unnecessary (McGarigal et al., 2002). For the analyses, including all variables, five principal component (PC) scores were attributed to the data, with four PC scores for those without CHL-a data. For each PC, an Eigenvalue is determined by the following equation: 

\[ R - \lambda I = 0, \]

where \( R \) is the correlation matrix, \( \lambda \) is the vector of Eigenvalue solutions, and \( I \) is the identity matrix. Eigenvalues represent variation of the corresponding PCs, with the extent of variation among sampling entities along the dimensional axes specified by the PC. Each Eigenvalue represents one PC. Each PC represents a single axis which defines the multi-variate space of the underlying data cloud. The first principal component (PC1) axis is drawn through the centroid of the cloud’s longest direction, and thus explains the largest proportion of the variation within the data.

The PC scores were then plotted onto X, Y scatterplots, with PC1 plotted against PC2, PC1 against PC3 and so on. Although all plots were investigated for significant patterns, most of the variance in variables is usually explained by the first two PCs. According to the latent root criterion, Eigenvalues of less than one should be dropped from the analysis and variables with low scores for these PCs are probably not significant in explaining the variance within the data. Although this criterion usually applies to larger sets of variables (20-50), it is still a useful indication of the significance of each PC axis for smaller sets (Cliff, 1988). These variables are usually the most significant in defining the ecological niche of each sampling entity (common dolphin, striped dolphin and mixed species groups).
When assessing the significance of scores, it is important to note the sign (+ or -) of each PC weight or eigenvector (EVT). Positive correlations indicate a direct relationship between a variable and a component, i.e. larger values of the variable are associated with positive values of the component. All variables were measured on a positive scale, except for depth, e.g. -393 m. The EVT score for each variable is indicative, rather than representative of significance. In general, the following rules can be applied: 1) the larger the sample size, the smaller the EVT to be considered significant; 2) The larger the number of variables being analysed, the smaller the EVT to be considered significant and 3) the larger the number of components, the larger the size of the EVT on later factors to be considered significant (McGarigal et al., 2002).

For all dolphin sightings which could be assigned values for all variables, the first two PCs explained 58.7% of the variance (PC1 = 0.379, PC2 = 0.208). The most important variable of PC1 was SST (EVT = -0.597), followed by depth (EVT = 0.524), slope (EVT = -0.508), CHL-a (EVT = 0.240) and DF (EVT = 0.230). The most important variables for PC2 were DF (EVT = -0.890), depth (EVT = 0.413), slope (EVT = -0.142), SST (EVT = 0.111) and CHL-a (EVT = -0.071) (Figure 3.21).
Figure 3.21: Scatterplot of PC1 against PC2 for all dolphin sightings to which values for all five variables have been assigned.

Figure 3.21 clearly displays spatial groupings which correspond to the results of the univariate analysis of dolphin distribution in relation to EVTs. Negative values on PC1 correspond to increasing depth, slope and SST as the most important PC1 EVTs, and decreasing CHL-a and DF. Negative values on PC2 correspond primarily to decreasing DF and increasing depth. There is a large cluster of both common and striped dolphin sightings associated with high depth, slope and SST which reflect areas where the two species overlap and a cluster of common dolphin sightings which are associated with low depth, low slope and low SST. The first cluster corresponds to the more southerly areas of the study area, in particular Regions 3-5, where common and striped dolphins are commonly found in close proximity, particularly in the spring and summer. All these regions are areas of high depth and high slope, with the exception of the very narrow Cantabrian shelf in Region 5, and high SST. The second cluster corresponds to the northerly shelf regions, where common dolphins are almost exclusively found, which are characterised by low depth, slope and SST, and slightly increased CHL-a and decreased DF (see
Fig. 3.18, DF in Region 2), although the latter two variables are not very important in explaining the variance of the data. This overall pattern and PC EVTs are largely unchanged when CHL-a is removed from the variable set, which underlines its lack of importance in determining the distribution of both species. The importance of DF in explaining variation on the Y-axis is not clear and differences between the two species are best explained using values on the X-axis.

This pattern is elucidated further when plots for seasonal and regional data are examined separately.

Spring

Autumn

<table>
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<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
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</thead>
<tbody>
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<td>-0.446</td>
</tr>
<tr>
<td>slope</td>
<td>0.253</td>
<td>-0.376</td>
</tr>
<tr>
<td>DF</td>
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<td>0.774</td>
</tr>
<tr>
<td>SST</td>
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<td>-0.185</td>
</tr>
<tr>
<td>CHL-a</td>
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<td>-0.161</td>
</tr>
</tbody>
</table>

Eigenvalue 2.048 1.1338
Proportion 0.41 0.227

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
</tr>
</thead>
<tbody>
<tr>
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<td>-0.21</td>
</tr>
<tr>
<td>slope</td>
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<td>-0.004</td>
</tr>
<tr>
<td>DF</td>
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<td>0.712</td>
</tr>
<tr>
<td>SST</td>
<td>-0.624</td>
<td>0.115</td>
</tr>
<tr>
<td>CHL-a</td>
<td>0.132</td>
<td>0.66</td>
</tr>
</tbody>
</table>

Eigenvalue 2.0601 1.0842
Proportion 0.412 0.217
Figure 3.22: Scatterplot of PC1 against PC2 for all dolphin sightings to which values for all five variables have been assigned, for the following seasons and regions: spring, autumn, Region 3, Region 5.

The plots contained in Figure 3.22 further explain the distribution of common dolphin and striped dolphin both spatially and temporally in relation to all EVs. The plot for spring shows that species use largely similar habitats at this time of year, with both species concentrated around the shelf-break and in the deeper water of the abyssal plain to the south. CHL-a is more important as an explanatory factor here with negative values on PC1 corresponding to higher CHL-a, lower SST and lower depth. The small cluster of common dolphin sightings and two striped dolphin sightings with high negative PC1 values correspond to northern shelf sightings (see Figure 3.13).
The tight cluster of both species corresponds to shelf-break and abyssal plain sightings, which are the core areas for both species at this time of year. Finally, the scatter of common dolphin sightings with positive values on PC1 and PC2 corresponds to a cluster of sightings on the southern shelf, in shallower and warmer water than striped dolphin sightings found in a similar area.

It is notable in the plot for autumn that four out of the five striped dolphin sightings in this season are all found at lower CHL-a values than common dolphins, indicating distribution in deeper waters, as is suggested by PC2 scores.

The plot for Region 3 shows that a large cluster of both species is strongly associated with high slope, which is the variable with the highest EVT score on PC1 and a defining characteristic of this predominantly shelf-break area. The cluster of common dolphin sightings with positive scores on PC1 are associated with high CHL-a, low depth, low slope and low SST. This indicates they are sightings from the narrow band of shelf waters in the north of Region 3.

Finally, the plot for Region 5 indicates that most striped dolphins are found in association with high depth, slope and high SST, probably representing a more northerly distribution over the Cantabrian shelf-break during warmer months, whereas the cluster of common dolphin sightings with positive PC1 scores are associated with high CHL-a and low SST, indicating that they are likely to be located over the shelf area during the autumn and winter, when common dolphin encounter rate peaks in Region 5.
Mean scores for all data within species classes and seasons

![Scatterplot of mean scores for PC1 and PC2 for each species class against season and region, for all dolphin sightings to which values for all five variables have been assigned (CD, common dolphin; SD, striped dolphin; MSG, mixed species group; S1, winter; S2, spring; S3, summer; S4, autumn; R1, Region 1; R2, Region 2; R3, Region 3; R4, Region 4; R5, Region 5; * denotes sample size less than 20)](image)

Mean scores for all data within species classes and regions

![Scatterplot of mean scores for PC1 and PC2 for each species class against season and region, for all dolphin sightings to which values for all five variables have been assigned (CD, common dolphin; SD, striped dolphin; MSG, mixed species group; S1, winter; S2, spring; S3, summer; S4, autumn; R1, Region 1; R2, Region 2; R3, Region 3; R4, Region 4; R5, Region 5; * denotes sample size less than 20)](image)

**Figure 3.23:** Scatterplot of mean scores for PC1 and PC2 for each species class against season and region, for all dolphin sightings to which values for all five variables have been assigned (CD, common dolphin; SD, striped dolphin; MSG, mixed species group; S1, winter; S2, spring; S3, summer; S4, autumn; R1, Region 1; R2, Region 2; R3, Region 3; R4, Region 4; R5, Region 5; * denotes sample size less than 20)
Mean scores for PC1 and PC2 were plotted for each species class against seasons and regions to show further differences. With respect to seasonal distributions, common dolphins are generally associated with low depth, low slope and low SST (- PC1 scores with ET’s < -0.5) during autumn and winter with intermediate scores for those variables during spring and summer. Striped dolphins are associated with high depth, high slope and high SST during spring, summer and autumn with a distribution similar to that of common dolphin during the winter. In autumn and winter, however the sample size for striped dolphin was probably too small to allow meaningful comparisons.

With regard to regions, common dolphin shows a similar distribution in regard to depth, slope and SST in Regions 2, 3 and 5. However, in Region 4, the distribution is closer to striped dolphin as was seen in the univariate analysis. Data for Region 1 seems anomalous but has a small sample size. Striped dolphin shows an almost identical cluster to the seasonal graph, with the two anomalous points (Region 1 and Region 2), probably attributable to small sample sizes. There is very little pattern discernable for the mixed species group class and this is probably attributable to small sample size.
Chapter 4

4. Discussion

4.2 Dolphin distribution

4.2.1 Common dolphin

This study shows that the common dolphin was more abundant than striped dolphin in all regions of the study area and in all seasons. The distribution of this species included almost all areas on the survey track, with the exception of the most easterly and shallow parts of the western English Channel. However, there is strong evidence of seasonal movements within the study area.

During spring, common dolphin relative abundance was lowest and distribution was largely confined to the deep waters of the abyssal plain and deeper continental shelf-break areas. At this time highest encounter rates were found at high depth (3501 – 4514 m), high slope (2.01 – 10 degrees), medium-high SST (16.6 – 20.4°C) and low CHL-a (0.08 – 0.31 mg m⁻³). In summer, peak encounter rates occurred in Region 3, but in shallower water than in spring with largest concentrations around the upper shelf-break (200 - 2000 m) and shelf adjacent to this area (120 – 200m). This region is characterised by high slopes on the shelf-break, with low slope on the shelf, medium-high SST and medium-low CHL-a values (see Figure 3.18 and appendix). In autumn, highest encounter rates were found in Regions 2 – 3 with reduced numbers in Region 3 and greatly increased numbers in depths of 80 – 200 m, with many sightings around the Brittany peninsular, where animals are relatively scarce in summer. The encounter rate in Region 5, which includes the Cantabrian shelf, was also highest during autumn and winter. The movement into shallower waters continued into winter, with highest encounter rates for Region 1 occurring at this time. Low encounter rates in Region 3 during November – February suggest that this species is largely absent from this area at this time, but this may be due to significantly lower survey effort. The arrival of animals into shelf areas during the autumn and winter marks a distinct habitat change for the species. The northern shelf area is characterised by low depth, low slope,
low SST and medium CHL-a, with median CHL-a values assigned to common dolphin sightings at their peak during this season, in contrast to the overall peaks in spring and summer.

The variation in relative abundance of common dolphin between seasons in the study area suggests that there is likely to be longitudinal, as well as latitudinal, movements off the survey track. This is impossible to verify without more extensive surveys of surrounding areas. This pattern of distribution has been noted in other studies in this area. Collett (1981) suggests from analysis of stranding data from the French coast, that common dolphin migrates to offshore areas of the Bay of Biscay in the spring. Desportes (1985) found that a higher proportion of pelagic prey species was eaten in the spring and summer. However, Meynier (2004) found mainly neritic species in stomachs of stranded animals from the Bay of Biscay, with lower concentrations of pelagic species during the summer, implying that the sample population was resident in shelf waters.

The possibility of an offshore movement of common dolphins during spring and summer is certainly supported by the results of this study. This assertion cannot be proven, however, as there is no evidence to support the assumption that animals observed in different seasons are the same animals or indeed originating from the same populations of common dolphins. There is dispersal from more northerly shelf areas after March, but there is not sufficient survey data from nearby areas available in the spring to ascertain where this population goes after dispersal. One possibility suggested by Evans (1980) is that common dolphins may migrate from the shelf to more oceanic areas for reproduction, although reasons for this are unclear. A study on the reproductive ecology of common dolphins in the northeast Atlantic found that mating and calving periods were estimated to take place during the months May to September, evidenced by marked seasonal changes in both testes mass and cellular activity in males, and the presence of ovulating and recently pregnant females during that time (Murphy 2004). This period coincides with the time period when common dolphins are found in deeper, offshore waters in the Bay of Biscay. Although data was not analysed in this study, the peak month for encounters with new-born calves in the study area is July - August (Williams pers. comm.).
In most areas of the northeast Atlantic common dolphins are more abundant in shelf regions during the winter period. However, off the west of Scotland and southwest Wales, there is a pronounced inshore movement at this time of year. The former may be associated with sandeel *Ammodytes* spp. distribution (Macleod, 2001) and the latter is associated with the development of the Celtic Sea Front during May – September (Goold, 1998).

Another possible explanation is that there are two populations of common dolphin in the northeast Atlantic, one offshore and the other on the shelf, which feed on different prey items and are spatially segregated. This suggestion is based on analysis of stomach contents of bycaught animals from the French albacore fishery in 1992 – 1993, where common dolphins fed on strictly pelagic prey items (Hassani, 1997; CRMM, unpublished data) and there was no overlap in diet with apparently neritic common dolphins. However, stomach contents analysis only reveals what the animal has been feeding on during the previous day, and common dolphins which occupy offshore habitats in one season could occupy shelf habitats at others. It has been suggested that analysis of persistent tissues (*e.g.* teeth) could help to test the hypothesis of two separate populations by testing differences in environmental features associated with different areas (Meynier 2004). Other studies of stomach contents in this area suggest that there may be some truth in the suggestion that common dolphins may be segregated in terms of a neritic/pelagic divide but that there is also evidence to suggest that at least a proportion of common dolphins move off shelf during the spring and summer into deeper water areas (Collett, 1981; Desportes, 1985). The movement of shelf animals may be confined to shelf-break areas with a separate population inhabiting the deepest waters > 4000 m. These hypotheses cannot be tested fully within the scope of this study.

Although certain EVs assigned to common dolphin sightings displayed a distribution that was significantly different from a uniform distribution (depth, slope, SST and CHL-a) the importance of these as predictive variables is open to debate. The distribution of common dolphin on a global scale in relation to EVs is difficult to define, but patterns emerge when the results of several studies are combined. In the northwest Atlantic, common dolphin is usually found in areas of medium depth, with distribution centered around the deeper, offshore parts of the shelf and the upper continental slope in areas of medium to high slope and medium SST (5 - 25°C), with more
northerly records during the summer attributed to higher SST (Selzer & Payne, 1988; Gowans & Whitehead, 1995; Hooker et al., 1999; Hamazaki, 2002). This distribution closely matches the observed distribution in this study, especially when considering that most of these studies were carried out during June – September, with one, during March – November accounting for much of the variability in SST. Off California, common dolphins have been shown to show strong relationships with medium-high (increasing) SST (Forney, 2000), high slope (Hui, 1985) and medium to high CHL-a and SST variability (Smith et al., 1986). In the eastern tropical Pacific, a strong affinity with areas of cooler, upwelling modified waters has been proven in several studies (e.g. Reilly, 1990; Palacios, 2003). In the Mediterranean, common dolphins are generally found over the shelf and upper continental slope and in areas of medium – low slope (Bourreau & Gannier, 2003). In the Alboran Sea, in the western Mediterranean, where common dolphin is more abundant than in the rest of the area, a similar pattern was found (Cañadas et al., 2002).

In this study, a bimodal relationship with most EVs was established. This pattern makes it difficult to explain the distribution of common dolphin with respect to variability within assigned EV values across the range of spatio-temporal distribution. It is highly likely that common dolphin distribution is closely related to that of its prey and in-depth knowledge of this parameter may aid explanation of the secondary importance of EVs to common dolphin distribution. The cycle of productivity in temperate waters can be correlated effectively to its primary component (CHL-a), but relationships between CHL-a and potential prey species of dolphins is more difficult to establish. A time-lag of between 75 and 150 days between peak CHL-a concentration and the development of 3 trophic levels was estimated by Sette (1955). This would indicate that relationships between dolphin distribution and CHL-a are not likely to be directly related at the time of the observations or even within temporal scales of months or seasons. Analysis of dolphin distribution at larger spatial scales may prove a more reliable indicator that, in general, they are more likely to be distributed in areas of general high productivity (Jaquet et al., 1996). This factor may also explain why the location of fronts was not related to dolphin distribution in this study, as general productivity, in terms of different trophic levels associated with thermal fronts, may also be subject to a time lag.

The areas of peak common dolphin encounter rates are known to be areas of high general productivity. Pronounced frontal systems develop in Regions 1 and 2 in summer and combine
with continuously mixed waters and tidal regimes to stimulate high primary productivity (Mann & Lazier, 1996). This region is also very important for commercial fisheries during the autumn and winter, with exploited species such as Atlantic mackerel and horse mackerel known to be potential prey items for common dolphins (see Figure 4.1) (Morizur et al., 1999). The shelf-break in Region 3 is characterised by strong internal waves and tidal forcing (New, 1988), which are likely to increase turbulent transportation of nutrients above the pycnocline and cause phytoplankton to oscillate vertically throughout the twice daily tidal cycle (Mann & Lazier, 1996, and references therein). Much of the peak CHL-a concentration in these areas is probably locked near the pycnocline and would not appear in satellite images, which are measured from the reflectivity of the first few millimeters of the water column. This point may explain why CHL-a concentrations in this area were often low, even during times of presumed high productivity, and that common dolphins were not associated with high CHL-a in this area. The low resolution of CHL-a data both spatially and temporally would also contribute to this problem. Averaging values will lead to smoothing of variability, which may disguise local CHL-a maxima.

The shelf-break region is important for various commercial fisheries and also for spawning fish, including hake, Atlantic mackerel and blue whiting. Although fish larvae are perhaps unlikely to make up large proportions of common dolphin diet due to their small size and low nutritional content, Meynier (2004) found that neritic common dolphins in the Bay of Biscay fed mainly on immature classes of fish of ages 0+ and that all of the principal prey species of common dolphins in this area (sardine, anchovy, Atlantic mackerel and horse mackerel) are target species of commercial fisheries in this area.

Common dolphins in other shelf-break areas have been found to feed at night on deep-scattering layer organisms (Evans, 1994) and this may also be the case on the two shelf-breaks in the study area. The preponderance of myctophids and deep-sea smelt (*Leuroglossos stilbius*) in stomach contents of animals from Californian waters (Evans, 1994) reflects findings from stomach contents of common dolphins bycaught in the French tuna driftnet fishery in 1992 – 3, when myctophids and oceanic cephalopods, including *Teuthowenia megalops* and *Gonatus steenstrupi* were mainly found (CRMM, unpublished data).
4.2.2 Striped dolphin

The distribution of striped dolphin differed markedly from common dolphin in the study area. Sightings of striped dolphin occurred almost exclusively over the deeper waters of Regions 3 – 5, with very few sightings from shelf areas. Seasonally, animals appear to disperse from the area during November – March, with dramatically reduced encounter rates during this time. However, it is possible that low effort in Region 3 (in particular) during this period may not reflect true striped dolphin abundance. The arrival of striped dolphin into the area during spring continues into the summer, with peak numbers recorded during the latter period.
The pattern of distribution matches the known range of striped dolphin in the northeast Atlantic. The northern limit of normal distribution is thought to be 50˚N, and in deep water areas, although occasional incursions onto the shelf and into more northerly waters have been recorded (Forcada et al., 1990; Goujon et al. 1993; Macleod, 2001; Reid et al., 2003).

This pattern is also similar to other areas. In the northwest Atlantic, the distribution of striped dolphin is related to high (deep) depth, slope (steep) and medium SST (Hooker et al., 1999; Hamazaki, 2002). Studies in the eastern tropical Pacific have found a marked lack of correlation between striped dolphin and particular oceanographic conditions, with striped dolphins generally found where spotted, spinner and common dolphins are not (Reilly, 1990; Palacios, 2003). In the Mediterranean, including the Alboran Sea, striped dolphins are found in offshore areas of high depth and slope (e.g. Cañadas et al., 2002; Bourreau & Gannier, 2003).

Striped dolphins in the study area were found in association with consistently high depths and high slope. This relationship may be related to prey availability. Like common dolphin, striped dolphins are opportunistic feeders with a wide variety of prey species recorded. Fish form an important part of the diet of striped dolphins in the northeast Atlantic, with various species of benthic and mesopelagic fish recorded from stomach contents of stranded animals (Desportes, 1985; Reid et al., 2003; Meynier, 2004). However, in most areas where striped dolphins occur and dietary analysis has been carried out, cephalopods form the largest proportion of the diet (Miyazaki et al., 1973; Clarke, 1986; Blanco et al., 1995). In several studies, a high proportion of luminescent cephalopods were found. This may indicate that striped dolphins use vision as well as echo-location for finding food, and that they may feed at night (Blanco et al., 1995). The latter point was confirmed by nighttime acoustic detections in the Mediterranean, which indicated movements onshore during the evening and offshore during the morning co-incident with apparent night feeding (Gannier, 1999).

It is difficult to explain the distribution of striped dolphin in relation that of its food, as so little is known about the life histories and movements of potential pelagic prey species in the northeast Atlantic. There was a negative relationship between the distribution of this species with CHL-a in the study area, which indicates that surface primary productivity is not important in the
distribution of striped dolphin. The occurrence of this species in areas of high depth and high slope may imply that foraging occurs at night on the deep-scattering layer and with animals feeding at depth on pelagic and bathypelagic species.

The distribution of striped dolphin with respect to season and SST was typical of a species at the edge of its preferred temperature range, as dispersal during the autumn and winter coincided with inevitable declines in SST. Also, there was evidence of more sightings occurring in more northerly areas during the warmest, summer months. Encounter rates in Regions 2 and 3 reached a peak at this time. The normal SST range of striped dolphin appears to be in temperatures of 16°C and above, with only 15.9% of sightings falling outside this range. Average SSTs within the southeast Bay of Biscay are higher than other areas of the bay, which suggests that fairly long-distance migration must occur in this species if SST does place a limit on the normal distribution of this species off the Iberian Peninsula. Water temperatures are generally colder further west along the north coast of Spain and animals would presumably have to move round the ‘corner’ of Spain and into Portuguese waters during colder times of the year if this assumption is true.

4.4 Habitat partitioning between common and striped dolphin

A principal aim of this study was to investigate the possibility of habitat partitioning between the two study species at the mesoscale. The spatio-temporal distribution of the two species shows a wide degree of overlap in certain seasons. Common dolphin inhabits all of the areas in which striped dolphins occur and have a relatively cosmopolitan distribution within the study area. Although it is possible that partitioning is occurring temporally, the marked differences found in autumn and winter are not likely to be pertinent as the absence of one species does not necessarily imply partitioning. Common dolphins are found in highest abundance at this time in areas where striped dolphins are uncommon at all times, which makes it unlikely that one species is excluding the other from its normal habitats. During the spring, both species are found in similar areas over the deepest waters of the northern shelf-break and abyssal plain, and during summer both species are found in highest abundance in the area of the northern shelf-break.
The existence of habitat partitioning does not, however, necessarily require segregation over large spatial scales. A basic assumption of habitat partitioning is that two species have either evolved to exclude competition, or to minimise it (Roughgarden, 1976). This may be achieved through spatial or temporal segregation or it may be achieved through exploitation of different resources (ecological segregation?). Spatial segregation at small scales can occur if species are occupying different habitat niches within a small area. Differences between the two species’ diets in the northeast Atlantic indicate that partitioning may occur in relation to targeting different prey species. This is certainly true of the diet of neritic common dolphins and may also be true of the diet of some common dolphins feeding over the shelf-break. However, data on bycaught animals from the French tuna driftnet fishery suggests that there is a high degree of overlap in trophic niche between the two species in these areas (Meynier, 2004). It is possible that common dolphins indirectly exclude striped dolphin from deep-water areas during the autumn and winter through inter-specific competition due to depleted prey abundance at these times of year, with common dolphins taking a dominant role in defining species distribution. However, too little is known about seasonal distribution and abundance of pelagic prey species to draw conclusions and low sampling effort may not reflect true abundance during these seasons.

If both species can be found to be relying on similar resources in the same areas at the same time then habitat partitioning may not occur. When environmental conditions are taken into account, there are significant differences between both species in both seasons and regions. In relation to SST, striped dolphins are found at significantly higher temperatures in most regions and seasons. However, comparisons are not applicable as common dolphins are found throughout most of the range of temperatures at all seasons and striped dolphins are largely absent during the colder periods of the year. Indeed, where the ranges of both coincide both spatially and temporally, there is little difference in the relationship of each species with SST. The same point is true of CHL-a. Although common dolphin is found in areas of higher CHL-a in general, the differences are not significant in areas and times where both species are found in close proximity.

When distribution in relation to physiographic variables is considered, there are more consistent indicators of differences in habitat preferences between the species. In areas where both species are found together at similar times of year, significant differences between the two species occur
in relation to depth and slope. In general, striped dolphin occupies higher depth and slope classes to common dolphin. If there is a basis for habitat partitioning between the two species, then bathymetry would appear to be the strongest candidate. The three regions in which both species are commonly found in close proximity in the spring and summer are all areas of great bathymetric variability. This is especially true of the two shelf-break regions where differences between the two species are greatest. In these areas fine-scale features can be exploited by different species during the same period, and prey composition and distribution may be markedly different from one feature to the next. Topographic features are known to influence oceanographic processes that may act to concentrate and also segregate prey (Hui, 1985; Stefanescu et al., 1994, Baumgartner, 1997). These areas are known to be areas of high prey concentration which may also lead to a reduction of interspecific competition for limited resources. Animals may also feed at different times of the day and night, perhaps even on the same prey species, as has been documented for butterflyfish feeding on coral in the Red Sea (Zekeria et al., 2002). Also, the presence of animals in close proximity during daylight hours may not reflect the distribution of animals at other times of the day or when feeding. Partitioning may occur in relation to location in the water column and not simply latitude and longitude at the surface.

The choice of 4 km x 4 km cells in this study was a compromise designed to match the spatial resolution of the EV raster datasets. The attempt to ensure that equating the position of the ship with that of dolphin sightings (in the absence of accurate sighting positions) did not lead to inaccurate assignments of values of EVs to sightings, and also lead to the use of a cell size which would include the likely position of sightings. It is possible, however, that animals are partitioning habitat at much smaller spatial scales than this study will indicate, and that larger cells will smooth differences in habitat through spatial interpolation (depth, slope) and averaging of values over both spatial and temporal periods (SST, CHL-a). Figure 4.2 shows sightings positions of both species over the northern shelf-break (Region 3) during spring and summer. The scale of the raster slope grid is 1 x 1 km and demonstrates the complexity of the habitat that dolphins may be partitioning at fine spatial scales.
existence of mixed species groups involving both species apparently complicates the issue of habitat partitioning between the two species. Mixed groups of common and striped dolphins, sometimes involving other species, have been documented in several parts of the world, including the Mediterranean (Garcia, 2000; Cañadas et al. 2002; Frantzis & Herzing, 2002) and the eastern tropical Pacific (Palacios, 2003). Observations of both species co-mingling, and apparently co-operating, indicates that tolerance of each species by the other is high, at least in these particular circumstances. Interpretation of the biological ‘meaning’ of this is problematic as many different scenarios are possible. It is possible that species are tolerating each other due to abundance of food, or alternately, co-operating to maximise foraging efficiency. The former may be an explanatory factor in the close proximity of the two species in spring and summer in areas of high
productivity and the latter may explain the comparatively high average size of mixed species groups.

It is also possible that animals outside the normal range of distribution or excluded from association with the same species may join a group of another species for protection or to forage more efficiently (Frantzis & Herzing, 2002). These factors may explain the high proportion of mixed species groups encountered during the autumn and winter in relation to the normal distribution of striped dolphin.

**Conclusions**

The aims of this study, which are detailed in section 1.2.1, were to describe the relative abundance and spatio-temporal distribution of common and striped dolphin and define key habitats for these species. In addition, the possibility of habitat partitioning was to be investigated for these two species within the study area.

Both species of dolphin have markedly different spatio-temporal distributions, and habitat preferences have been established for both species within the ranges of the environmental data available. Common dolphin primarily occupies shelf areas during autumn and winter and shelf-break and abyssal plain areas in the spring and summer. Two separate populations may exist but seasonal movements probably account for some of the variability. Striped dolphin is found in shelf-break and deep water areas throughout spring and summer and largely disperses during the autumn and winter. However, there are significant overlaps at certain seasons in particular areas, with the two species largely sympatric in spring and summer in Regions 3 – 5.

Habitat partitioning may exist in relation to each species’ preference for different depths and slopes in areas where they are found together. However, these habitat preferences are likely to be proxies for other variables of primary importance in defining partitioning, such as prey distribution. Partitioning may exist at finer spatial scales than can be revealed in this study and may also be related to foraging distribution rather than simple spatial or temporal proximity at the surface of the water column when animals are recorded as present.
Observations of mixed groups in the study area reinforce the fact that tolerance between the two species is high and that there is a high degree of niche and trophic overlap.

**Recommendations for future research**

There are several ways in which this study could be expanded and improved upon in future work.

Sightings data has been collected from other commercial ships using similar methodologies in other areas of the northeast Atlantic. This data was not available for this study but could be utilised in future to enlarge the spatial coverage of the current study and allow for more comprehensive comparisons across species. This data would also allow for predictive modelling of the spatial and temporal distribution of cetacean species. Modelling could be attempted at different spatial scales and using different statistical techniques to assess the predictive power of each. The predictive power of models could be tested in relation to other ferry data by using the latter as a testing dataset. Further multivariate analysis would also allow for greater accuracy in the determination of habitat preferences. Linear relationships within data could be explained using logistic regression analysis within the framework of generalised linear modelling (GLMs). GLMs have been used widely in cetacean studies to link the incidence of species to habitat variables. This study has shown that non-linear relationships exist between dolphin distribution and EVs in many cases and new modelling techniques like generalised additive modelling (GAMs) may provide the ideal framework for modelling species’ distributions for a study of this type (Forney, 2000). Both of these techniques use both presence and absence data to predict species’ occurrence. It is also possible to model predictively using only presence data within the framework of PCA (Schweder, 2003).

The variables used in this study are secondary indicators of cetacean habitat preferences. More comprehensive oceanographic data and a greater range of variables should ideally be used to increase the chance of variables being accurate predictors of cetacean presence or absence. The spatial and temporal resolution of SST, CHL-a and DF data was also a limitation in this study. Since 2003, contemporaneous and continuously sampled oceanographic data (SST, CHL-a and
salinity) has been available from the ‘Pride of Bilbao’ from a project conducted by the Southampton Oceanographic Institute (SOC). In future studies, the data from this project could be used to improve data resolution and accuracy. An ideal scenario would involve a collaborative approach between cetacean biologists and other scientists from related fields. Biologists specialising in other taxa, such as zooplankton or fish could aid understanding of prey distribution and oceanographers could elucidate physical and chemical processes to aid explanation of species’ distributions.

More extensive surveying using dedicated research vessels would enable several improvements to be made to this study. Greater spatial coverage could enable calculation of absolute abundance estimates using distance sampling methods, as was the case with the SCANS and MICA surveys (Goujon et al., 1993; Hammond et al., 2002). Additional variables which could be examined could include biotic community structure and diversity by sampling for organisms, such as plankton, zooplankton and fish. Sampling could be carried out at different depths concurrent with use of CTD recorders to enable accurate sampling of temperature through the water column and therefore thermocline positions at depth. Acoustic monitoring would aid cetacean detection and elucidate diel variations in activity, in addition to offering possibilities of identifying prey concentrations with acoustic backscatter techniques.

Use of dedicated survey vessels would also improve gathering of behavioural data, which was not available for this study. Associations between the two species could be recorded with a consideration of species interactions at fine scale. Animals could be aged within realistic degrees of accuracy to better determine reproductive strategies and community structure and group behaviour could be assigned to behavioural classes with greater accuracy.
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References


