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RESUMO

Os mares europeus possuem uma grande diversidade de habitats e espécies que, lamentavelmente, continua a perder-se a um ritmo dramático, quase sempre em resultado das actividades humanas. No que diz respeito às populações de cetáceos, o espectro de potenciais impactos é alargado, sendo as capturas acessórias das pescas (‘*bycatch*’) e as alterações climáticas, aparentemente, as maiores ameaças.

O Golfo da Gasconha é reconhecido como uma das áreas mais produtivas e como o centro de maior diversidade de cetáceos no Nordeste Atlântico. Das 86 espécies de cetáceos, actualmente reconhecidas pela UICN (União Internacional para a Conservação da Natureza), cerca de 20 têm a sua área de distribuição no Golfo da Gasconha, incluindo tanto misticetes como odontocetes.

No Golfo da Gasconha e nas águas ao largo da Península Ibérica, as pescas constituem uma actividade primordial e, como tal, o ICES (Conselho Internacional para a Exploração dos Mares) considerou o *bycatch* de cetáceos, nesta região, um problema fundamental. Existe o Regulamento 812/2004 da UE que estabelece medidas respeitantes às capturas acidentais de cetáceos nas pescas, no entanto, estas medidas ainda não estão a ser implementadas por todos os países envolvidos, entre os quais, Espanha e Portugal. Na área de estudo, o golfinho-comum é, de longe, o mais capturado acidentalmente, e estes incidentes ocorrem particularmente nas pescarias com arrasto pelágico e arrasto de fundo com parelha usando redes de grande abertura vertical.

As alterações na distribuição, abundância e composição das comunidades de presas de cetáceos estão fortemente relacionadas com factores climáticos, particularmente a temperatura da água, e parecem constituir a maior ameaça resultante das alterações climáticas para as populações de mamíferos marinhos. Com excepção das espécies dependentes do gelo e daquelas que efectuam migrações sazonais de larga distância, as outras espécies devem mostrar alguma adaptabilidade de resposta a alterações graduais do meio, a menos que os efectivos populacionais já registem níveis baixos.

Está a tornar-se cada vez mais óbvio que, em resposta a estes problemas sobre o estado do meio marinho, urge direccionar esforços de conservação para os oceanos. Uma análise efectuada na Europa detectou uma estrutura institucional inadequada para a gestão dos mares. Assim, muito recentemente, em Junho de 2008, a UE estabeleceu um quadro para a protecção, preservação e restauração do meio marinho – Directiva-Quadro 'Estratégia Marinha' (DQEM) – cujo principal objectivo é atingir ou manter um 'bom estado ambiental' até ao ano de 2020, através da implementação de Estratégias Marinhas Regionais que devem contemplar uma abordagem ecossistémica.

Surge, então, a necessidade de haver indicadores ecológicos que possam ser aplicados em série para caracterizar o estado actual do meio e detectar, seguir e /ou prever alterações significativas na estrutura e função do ecossistema, em resposta a perturbações ambientais. Estes indicadores são necessários para avaliar o progresso dos objectivos das políticas ambientais, permitindo indicar a necessidade de acção e orientar as políticas e gestão sobre a complexidade do ecossistema marinho de forma simples e quantificável.

Há uma grande variedade de estudos que indicam que a distribuição e abundância relativa de predadores marinhos podem estar relacionadas com algumas características ambientais, podendo portanto, ser utilizadas como indicadores das distribuições das presas e processos do ecossistema subjacentes.

Neste contexto, este estudo propõe-se investigar a distribuição espacial de Verão dos cetáceos em águas oceânicas da região do Golfo da Gasconha, através do uso de variáveis fisiográficas (profundidade - DEP) e oceanográficas (temperatura superficial da água - SST, clorofila-a - CLA e altura do nível do mar - SSH), bem como gerar modelos (GAM) de ocorrência e densidade relativa e os respectivos mapas preditivos para as espécies mais avistadas (baleia-comum, golfinho-comum e golfinho-riscado).

Este estudo baseou-se nos dados do projecto CODA (*Cetacean Offshore Distribution and Abundance*) que decorreu em Julho de 2007. Durante a campanha foram identificadas 13 espécies de cetáceos, das quais 3 de misticetes e 10 de odontocetes. Apesar da menor riqueza específica, as baleias representaram mais de metade do número total de avistamentos (~56%). As espécies mais frequentes foram a baleia-comum, seguida pelo golfinho-comum, golfinho-riscado e cachalote. De entre os zífios, o mais comum foi a baleia-de-bico-de-Cuvier.

As baleias foram mais observadas na região Oeste da área de estudo sobre a planície abissal, enquanto os delfinídeos e os zífios foram predominantemente avistados na parte interior do Golfo. Os cachalotes estavam distribuídos de forma uniforme. Foi evidente uma maior diversidade de espécies sobre os canhões submarinos e áreas adjacentes. Esta afinidade já foi anteriormente relatada e pode dever-se ao facto de estruturas topográficas abruptas poderem concentrar zooplâncton.

Modelos Aditivos Generalizados foram utilizados para determinar se as três espécies mais avistadas, a baleia-comum, o golfinho-comum e o golfinho-riscado, estavam distribuídas de forma não uniforme em relação às variáveis ambientais. A análise decorreu em duas etapas. Na primeira, a probabilidade de presença foi modelada em função das variáveis ambientais. Na segunda, foi modelado o número de indivíduos condicional à presença.

Para os dados de baleia-comum, o modelo de presença explicou 24,10% do desvio dos dados e reteve três covariáveis, SST, CLA e SSH, e ainda, um termo de interacção entre a profundidade e o nível do mar. A variável mais significativa foi a clorofila ($p = 0.00642$). A densidade relativa da baleia-comum foi ajustada por um modelo minimal contendo apenas a temperatura e um termo de interacção entre esta e a profundidade. Ambos os termos eram altamente significativos e o modelo explicou 37,90% do desvio.

Aquando da modelação da ocorrência e densidade dos golfinhos comum e riscado, ambos os modelos retiveram um único predictor, a altura da superfície do mar, aceite como um termo linear e muito significativo; os golfinhos mostraram uma clara preferência por zonas com menores anomalias à superfície. Contudo, estes modelos explicaram desvios baixos, ~5% no modelo de presença e ~11% no de densidade relativa.

As probabilidades previstas de ocorrência e densidade relativa foram calculadas a partir dos modelos aditivos finais de modo a poderem ser criados mapas de distribuição para a área de estudo. Estes mapas mostraram uma clara segregação espacial entre as duas espécies de golfinhos e a baleia-comum. Os golfinhos, distribuindo-se principalmente no interior do Golfo e as baleias, na zona Oeste, com especial incidência em torno do Banco da Galiza.

Os resultados obtidos neste estudo fornecem informação sobre a distribuição espacial de cetáceos, no Verão, em águas oceânicas da região do Golfo da Gasconha, e permitem uma melhor compreensão do modo como as espécies mais avistadas interagem com os factores ambientais analisados para modelar as suas distribuições.

De acordo com a DQEM, é necessária a avaliação da dinâmica populacional, distribuição e estado dos mamíferos marinhos (tabela 1 do anexo III da Directiva). Esta Directiva apela a uma abordagem ecossistémica, e as áreas marinhas protegidas (AMPs) têm potencial para propiciar esta abordagem holística. Tanto quanto sabemos, na área de estudo, existem algumas reservas marinhas ao longo das costas Espanhola e Francesa, mas apenas uma em águas profundas (ao largo das províncias espanholas das Astúrias e da Cantábria). Alguns sítios já foram propostos como ZEP's – Zona Especial de Conservação sob a Directiva Habitats da EU – uma no Banco da Galiza, duas em águas asturianas e outras duas em águas bascas.

Os resultados deste estudo permitem a identificação de áreas correspondentes a picos de ocorrência, abundância e /ou diversidade de cetáceos, o que possibilita o estabelecimento de reservas pelágicas.

A grande parte das iniciativas conservacionistas são conduzidas por razões económicas e, consequentemente, a maior parte das AMPs são avaliadas tendo em vista a recuperação das pescas. No entanto, os cetáceos têm grande potencial para actuar como espécies indicadoras e podem ser de grande valor para o planeamento, promoção e implementação de AMPs.

Sendo grandes, e muitas vezes numerosos, predadores, os cetáceos são ecologicamente significativos como acumuladores e movimentadores de nutrientes e energia, intra e entre ecossistemas. Eles apresentam uma grande diversidade trófica, desde as baleias aos golfinhos e, consequentemente, desempenham funções variadas e importantes na estrutura da rede trófica e na função do ecossistema, o que lhes confere valor como indicadores do estado de conservação do meio marinho. Adicionalmente, são também particularmente susceptíveis à bioacumulação de contaminantes.

Pelas razões acima mencionadas, entre outras, os cetáceos parecem ser adequados para actuar como espécies potencialmente indicadoras de ecossistemas oceânicos, a largo prazo e em larga escala.

Para além destas razões 'intrínsecas', os cetáceos, sendo espécies carismáticas, podem ser usados para encabeçar acções públicas de educação ambiental e campanhas para a protecção do habitat marinho bem sucedidas, que se traduzem no reforço das medidas de gestão e no aumento de fundos disponíveis para AMPs conduzindo, por sua vez, a maiores áreas de oceano sob gestão ecossistémica.

Assim, os cetáceos, pelo seu valor educacional, científico e económico, bem como, em geral, pela sua necessidade de grandes áreas de conservação, podem proporcionar uma solução para a protecção dos habitats marinhos.

O conhecimento adquirido com este trabalho é, portanto, de enorme importância para estabelecer locais potencialmente críticos para os cetáceos e, como tal, identificar as zonas mais importantes para proteger, o que constitui uma valiosa informação para atingir objectivos de conservação e cumprir os planos de gestão para o Golfo da Gasconha. Adicionalmente, esta investigação melhora o nível de conhecimento das relações cetáceo-habitat o que é essencial para desenvolver medidas de gestão mitigadoras mais incisivas e efectivas.

Os resultados deste estudo têm de ser complementados com outras investigações uma vez que representam somente a distribuição de Verão, avaliada num único ano. Para definir com firmeza áreas de especial importância para a conservação, é necessária a obtenção de dados adicionais de forma a abranger uma escala temporal mais alargada.

Finalmente, é preciso salientar que o uso de cetáceos como indicadores ecológicos deve integrar outros estudos elaborados com diferentes métricas, baseadas também noutros grupos taxonómicos, e que combinadas permitem a obtenção de um quadro completo sobre o estado ambiental do ecossistema marinho de acordo com a DQEM.

Apesar de todos os comentários acima descritos, os resultados obtidos têm certamente valor para ajudar a atingir o objectivo final da DQEM, e de outros assuntos relacionados com a conservação e gestão sustentável do meio marinho.

Palavras-chave: Directiva-Quadro ‘Estratégia Marinha’, cetáceos, indicadores ecológicos, estado ambiental, áreas marinhas protegidas em águas oceânicas, Golfo da Gasconha.

ABSTRACT

European seas are subjected to continuous degradation and cetaceans, in particular, are vulnerable to several threats, being the fisheries bycatch and the climate change the greatest ones. The Bay of Biscay has been found to be the centre of highest cetacean diversity in the Northeast Atlantic.

In response to these problems concerning the state of the marine environment, in June 2008, the UE established the Marine Strategy Framework Directive (MSFD), which aims to achieve a 'good environmental status' by 2020. Hence, a requirement arises for ecological indicators based on an ecosystem approach.

In this context, this study, relying on data from CODA project, proposes to investigate the summer spatial distribution of cetaceans in the offshore waters of the Bay of Biscay, using physiographic and remotely-sensed oceanographic variables.

During the survey, 13 cetacean species were identified, being the most frequent, the fin whale and the common dolphin. A higher species richness was evident over the submarine canyons. Distribution of the three most sighted species (fin whale, common and striped dolphins) was modelled spatially, using generalised additive models, in relation to environmental features. Spatial segregation was clear, with dolphins distributed in the inner part of the Bay, and the whales towards West with special incidence around the Galician Bank.

These results permit the identification of potential cetacean 'hotspots' in the Bay of Biscay region, enabling the establishment of marine protected areas. Cetaceans do have a great potential to act as indicator species and may be valuable assets for planning, promoting, and implementing MPAs. Their use as ecological indicators should be accomplished with other studies where different metrics are applied, also based on other taxonomic groups, which combined will provide a comprehensive panorama of the environmental status of the marine ecosystem to achieve the conservation objectives of the MSFD and comply with management plans for the Bay of Biscay.

Keywords: Marine Strategy Framework Directive, cetaceans, ecological indicators, environmental status, offshore marine protected areas, Bay of Biscay.

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1. INTRODUCTION

Europe encompasses a great diversity of habitats and species, and despite many efforts to protect it, recent reports show that the diversity of flora and fauna continues to be lost at a dramatic rate, in almost all cases as a result of human activities (Walder, 2006).

The seas around Europe are of vital importance to the people living there, and are used for fishing, transport, recreation and many other activities of economic importance. European coasts are also popular for many human activities that impact the habitats not only on the coast but also in the sea. The risk of potential threat by unsustainable development is either high or moderate for 86% of the European coasts (Frid *et al.*, 2003). Even parts of the ocean previously relatively untapped, such as the deep sea, are now facing potential increased exploitation (Hooker, 2004).

Early this year, Halpern *et al.* synthesised spatial data on the distribution and intensity of human activities and the overlap of their impacts on marine ecosystems. From the resulting map, it was selected the region regarding to the study area (Fig. 1), which is subjected to impacts mainly ranging from low to medium predicted cumulative scores.

Particularly, in what concerns cetacean populations, the array of potential threats range from climate change, fisheries bycatch and overfishing to noise pollution, oil, gas and chemical pollution, eutrophication and harmful algae blooms. Although, impacts on cetacean populations remain poorly known, fisheries bycatch and climate change appear to be the greatest threats (Walker, 2005).

The Bay of Biscay has been found to be one of the most productive areas and the centre of highest cetacean diversity in the Northeast Atlantic (Hoyt, 2005). Amongst the currently recognised 86 cetacean species by IUCN (International Union for the Conservation of Nature), around 20 have its distribution range in the Bay of Biscay, including both mysticetes and odontocetes (Aguilar *et al.*, 1997; OSPAR, 2000; Reid *et al.*, 2003; Castro *et al.*, 2004; Walker, 2005). This represents a diversity of form and function that demands effective conservation. The most common species appears to be the short-beaked common

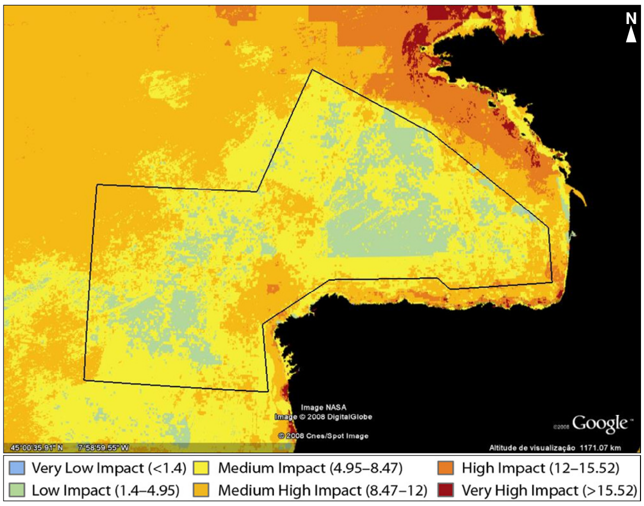

Figure 1. Map of cumulative human impact in the study region. Black solid line delimitates research area. Source: Halpern *et al.* (2008).

dolphin (*Delphinus delphis*). And the most threatened ones are the blue whale (*Balaenoptera musculus*) and the humpback whale (*Megaptera novaeangliae*) (Aguilar *et al.*, 1997; OSPAR, 2000; Frid *et al.*, 2003; Reid *et al.*, 2003; Castro *et al.*, 2004; Walker, 2005; Kiszka *et al.*, 2007; Certain *et al.*, 2008). However, in 2003, the International Council for the Exploration of the Sea (ICES) stated that it seemed likely that humpback whales were recovering from the whaling activity early in the 20th century (Frid *et al.*, 2003). As listed in appendices I and II of Bonn and Bern Conventions, respectively, both the blue and humpback whales are under strict protection. The blue whale is even mentioned in the OSPAR's list of threatened and/or declining species (OSPAR, 2004).

In the northeastern Atlantic, fisheries are a major activity and an economic basis for many coastal communities. It has many impacts on marine ecosystems, primarily from the catch of large amounts of fish and shellfish, and the resulting changes associated with their removal from food webs (Reeves *et al.*, 2003; CIESM, 2004; Walker, 2005), as well as from the catch of other non-target marine animals, such as fish, invertebrates, seabirds and marine mammals that are incidentally caught in the fishing gear – 'bycatch'. The bycatch can affect biodiversity through impacts on top predators, the removal of individuals from many species, or by elimination of prey (Hall et al., 2000). The UN Food and Agriculture Organisation (FAO) stated, in 2004, that the global summed discard rate has been decreasing in the last decade and estimated that about 8 percent of the total catch was thrown over side (FAO, 2004). With rapidly advancing technologies and the evolution of large-scale industrial fisheries, in the last decades, the effects of unsustainable levels of by-catch were increasingly detrimental to populations, communities and entire ecosystems (Read, 2000), and some authors believe that they are set to continue aggravating (Walker, 2005).

In the Bay of Biscay and the waters off the Iberian Peninsula, fisheries are characterised by a large number of species of commercial interest (Pusineri *et al.*, 2004; Walder, 2006) and, in fact, in 2003, the ICES Report on the Environmental Status of the European Seas considered the bycatch of common dolphins in the Bay, a major problem (Frid *et al*, 2003). However, according to data of the European Commission on European fishing fleets[1], since the last few years, there has been a tendency for a decrease in the number of vessels, tonnage and engine power of the main fleets fishing in the study region.

With most fisheries data collected in ports (Hall *et al.*, 2000), bycatch remains a largely unstudied phenomenon (Morizur *et al.*, 1999; Read, 2000; Lewison *et al.*, 2004). The ICES Study Group for Bycatch of Protected Species noted that despite all the observations made under EU Council Regulation 812/2004, very few extrapolated estimates of small cetacean bycatch have yet been made, and nowhere has a comprehensive estimate been obtained for all nations' fleets fishing in any single region (ICES, 2008a). This Regulation lays down measures concerning incidental catches of cetaceans in fisheries, which requires reporting on bycatch observer programmes by member states in certain prescribed fisheries (EU, 2004). Nevertheless, these measures are not yet being implemented by all the countries involved (ICES, 2008a). Concerning the countries surrounding the Bay of Biscay, UK and France have a national monitoring scheme since 2005 and 2006, respectively; Spain has no plan in place yet, but the Spanish fishing administration recently contacted national institutes in order to do so; and no information was received from Portugal (ICES, 2007). Morizur et al. (1999) suggested that the monitoring programmes should be incorporated into fisheries management programmes so that this information would be collected in a systematic and consistent manner.

This study group also reviewed the implementation of pinger deployment requirements under the same regulation, and recognised that its implementation has been problematic;

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[1] http://ec.europa.eu/fisheries/fleetstatistics/index.cfm?lng=en

on the one hand, the fishing industry has been reluctant to adopt a technology widely seen as expensive and unreliable, and on the other hand, it is apparent that there is still only a limited knowledge on the behaviour of marine mammals around fishing gear and this has hindered the development of more acceptable solutions (ICES, 2008b).

Cetaceans have been recorded entangled in a wide range of fishing gear (Ross, 2003; Walker, 2005; ICES, 2005, 2006; Certain *et al.*, 2008). The annual reports of the ICES Working Group on Marine Mammals Ecology have been consistent, since the last 4 years, when stating that the short-beaked common dolphin is, by far, the most bycaught species in the ICES' area VIII (Bay of Biscay), mainly from December to March. Moreover, it reports that in this region, bycatches occur particularly in fisheries using pelagic trawls (British, French and Irish fleets) and bottom pair trawls using very high vertical opening nets (Spanish fleets) (ICES, 2005, 2006, 2007, 2008a).

There are also some European projects focused on this bycatch issue, such as PETRACET and NECESSITY, and others, at a national level, as PROCET in France. From 2004 to 2007, NECESSITY aimed at developing ways of modifying trawls to enable bycatch species to escape unharmed from the trawl, while in 2004 and 2005, PETRACET monitored about 5% of annual fishing effort among the main French, Irish, UK, Danish and Dutch pelagic trawl fisheries operating in the Celtic Seas and Bay of Biscay region. Based on these observations, it reported that it was unlikely that pelagic trawl fisheries in this area represented a significant or immediate conservation threat to common dolphins (Northridge *et al.*, 2006). It shall be noted however that bycatches are known from other fisheries in the same area, and that annual bycatch rates can fluctuate considerably (ICES, 2005).

Possibly the greatest threat to biodiversity comes from climate change. There is evidence of changes in ocean circulation and water mass characteristics that could be due to climate change (Frid *et al.*, 2003). These climatic changes affect entire ecosystems and its effects are likely to have the most detrimental impacts on habitats that are already under considerable stress from human activities (Roessig *et al.*, 2004; MacLeod *et al.*, 2005; Walker, 2005).

Changes in the distribution, abundance, and community composition of cetaceans' preys are strongly related to climatic factors, particularly sea temperature (UNEP, 2006), and are likely to be the greatest threat resulting from changing climate to marine mammal populations and are already affecting cetacean communities (*e.g.* increase in the representation of southern-water species in the North Sea) (Frid *et al.*, 2003; MacLeod *et al.*, 2005; Leaper *et al.*, 2006; UNEP, 2006; ICES, 2007). Marine mammals that will be most affected by climate change are those influenced by arctic ice, and those that undertake large-scale seasonal migrations. Changes of migratory routes in response to changing climatic conditions have been documented. Apart from these, most other species should show fairly plastic responses to slowly developing change. However, as relative population sizes are at low levels, they may not be as adaptable to climate change and variation (UNEP, 2006; ICES, 2007).

It has long been known that collisions with vessels occasionally kill or injure cetaceans (Laist *et al.* 2001). The significance of these events becomes, evidently, greater in areas of intense maritime traffic; Frid *et al.* (2003) considered the Iberian Coast one of these busy areas. Although there is a lack of clear available information on the maritime traffic in the Bay of Biscay, it is assumed that in the eastern part of the study area the traffic is less intense, while in the western part, the navigation may be more intense since it is one of the ways to access the Strait of Dover (English Channel) – the world's busiest international seaway (Suárez de Vivero & Mateos, 2007). Nevertheless, no report is available on cetaceans' ship strikes in the study area.

There is increasing concern that intense anthropogenic sounds in the marine environment may potentially have a substantial impact on marine organisms, including marine mammals. Depending upon the magnitude of the signal, there may be no impact on animals or the impact may involve disruption of behaviour (*e.g.* social interactions) or even physical (*e.g.* temporary or permanent loss of hearing) or physiological (*e.g.* stress responses) damage to the animals. These sounds may have different sources such as ships, sonars, seismic prospecting, military exercises, background sounds in hatcheries and oceanariums, among others (Richardson *et al.*, 1995; McCauley *et al.*, 2003; Popper, 2003; Hildebrand, 2004; Hardman-Mountford & Huthnance, 2006; Tyack, 2008). Shipping is probably the most extensive source of noise in the oceans (Popper, 2003; Tyack, 2008) and, in particular, in the Bay of Biscay, although other sources of human-generated underwater noise are present in the study area (Guerra *et al.*¸2004). In spite of the absence of knowledge about the maximum range at which they may need to communicate, it is known that marine mammals have a variety of mechanisms to compensate for increased noise. They have been shown to avoid some human sound sources at ranges of kilometres, raising concern about displacement from their important habitats (Tyack, 2008).

Concerning pollution, in both France and Spain there are offshore oil and gas industries, however their effects on the environment can be considered of small extent when compared with others, such as the ones in the North Sea (Frid *et al.*, 2003). Moreover, in the EU, the discharges of oil with drill cuttings have effectively ceased, and most oil is now discharged with produced water. Understandably, areas with a heavier maritime traffic run a higher risk from spills and, in the last decade, in the vicinity of the study area some accidents occurred, such as the oil spills 'Erika' in 1999 (Brittany) and 'Prestige' in 2002 (Galicia); and the chemical spills 'Balu' in 2001 (Bay of Biscay) and 'Lykes Liberator' in 2002 (Brittany). Surprisingly, Varela *et al.* (2006) analysed the plankton community structure after the Prestige shipwreck and reported that no changes were evident in the community, probably due to the high dynamics of the water masses and the large and meso-scale hydrographic processes in the region.

The persistent organic pollutants (POP) constitute another concerning source of pollution. Although many of them are no longer produced or its use is severely restricted, they can still be present at concentrations that can affect marine life (Frid *et al.*, 2003). The bioaccumulation of these contaminants is particularly high in animals at the top of the food webs and with large blubber deposits, such as the major part of marine mammals, and their high concentration has been linked to reproductive and immunological abnormalities (Frid *et al.*, 2003; Walker, 2005).

In the study area, some authors have analysed the concentration of organochlorines in cetaceans. In 1983, Aguilar measured residues of POP's in sperm whales from the waters off Spanish northwestern coast and the levels found were intermediate to other cetaceans, probably due to their feeding habits mainly based on squid and bottom fish. More recently, Borrell *et al.* (2001), in the same region, compared the concentration of DDT between the 80's and the 90's, in common dolphins, and following the widespread trend in cetacean populations, DDT concentrations were lower in the individuals sampled in the 90's, while the proportion of metabolised forms was greater, reflecting the aging of the environmental load and suggesting that the environment has not been exposed to significant releases of these contaminants in recent years. Taking into consideration that a number of Delphinidae populations were apparently doing well with blubber organochlorine concentrations much higher than those found in the study, and assuming that the sensitivity to the effects of these pollutants is similar in closely related species, the authors considered unlikely that these compounds had significantly affected the species studied. Holsbeek *et al.* (1998) determined heavy metal concentrations in dolphins stranded along the French Atlantic coast between 1977 and 1990, and detected no difference in contamination between former and latter years, for any heavy metal, which seemed to imply that heavy metal concentrations were not significantly decreasing in the North-East Atlantic, during this period. Some years later, in 2001-2002, Caurant and colleagues (2006) measured lead concentrations, in mainly the same species from the same location, as in the last study mentioned. The concentrations found were far lower than the threshold value inducing toxic effects in humans and reflected the decrease in the production of alkyl lead in Europe, *i.e.*, the increasing use of unleaded gasoline.

In what refers to eutrophication and harmful algae blooms, the study area is not particularly affected, even if there are reports of these events along the Bay of Biscay and Iberian coasts. These events are more frequent in coastal waters since in the Western Europe seas, the highest concentrations of nutrients enter the sea via rivers. Fortunately, these discharges of contaminants and nutrients have been reducing significantly since the mid-80’s improved sewage treatment, reduced industrial discharges and changed to phosphate-free detergents, in result of the adoption of the EU Urban Waste Water Treatment Directive in 1991, as well as regulations by OSPAR countries (Frid *et al.*, 2003).

The threats to marine diversity only received attention quite recently, compared with terrestrial mammals (Frid *et al.*, 2003; Reid *et al.*, 2003; Hoyt, 2005; Schipper *et al.*, 2008) but, fortunately, these menaces to cetacean populations have seen a concomitant rise in the number of studies devoted to them. Nevertheless, focused research into pelagic species diversity, including cetaceans, is still surprisingly sparse, and little is known of cetacean natural history (Reid *et al.*, 2003; Hardman-Mountford, 2005; Walker, 2005; ICES, 2007; Schipper *et al.*, 2008). This is largely due to their inaccessibility (*e.g.* they can occur in low densities, are highly mobile, and spend most of their time underwater) (ICES, 2007).

It is becoming increasingly apparent that, in response to these problems concerning the state of the marine environment, conservation efforts are urgently required for the oceans, and policy-makers worldwide tend to develop strategies to balance socioeconomic growth and marine environmental protection.

There are presently numerous international and regional agreements and conventions, which establish quantitative objectives for the conservation status assessments, which are crucial to the development of a monitoring strategy for cetaceans (Hardman-Mountford & Huthnance, 2006; ICES, 2007). However, little articulation or coordination occurs among them and there is poor implementation and a lack of enforcement (Borja, 2006). It is worth emphasising that gaps in international law pertaining to high seas leave the cetacean species that move through vast expanses of ocean especially vulnerable in these areas where over-exploitation and unregulated activities may occur (CIESM, 2004; Davies *et al.*, 2007). A list synthesising the most relevant legal instruments concerning the protection of the marine environment in European waters is available in appendix I.

In Europe, an analysis undertaken has detected an inadequate institutional framework for the management of the sea (Borja, 2006). Hence, very recently, in June 2008, the European Commission established a framework for Community action in the field of marine environment policy, known as “Marine Strategy Framework Directive” (MSFD) (2008/56/EC), showing that there is a clear commitment to develop management actions to restore and preserve biological diversity in European seas. The MSFD establishes a framework for the protection, preservation and restoration of the marine environment and its main aim is to achieve or maintain a ‘good environmental status’ by the year 2020 at the latest (EU, 2008).

Nowadays, it is generally accepted that responsible stewardship of the ocean implies ecosystem-based management, *i.e.*, managing human interactions with ecosystems in order to protect and maintain ecosystem integrity and to minimise adverse impacts (Hoyt, 2005). The MSFD follows this worldwide trend that ought to consider an ecological context in some holistic way.

A requirement then arises for ecosystem-based indicators that can be applied in serial fashion to characterise current status of the environment and to detect, track and/or predict significant change in ecosystem structure and function in response to environmental disturbances (Jackson *et al.*, 2000; Maury & Lehodey, 2005), *i.e.*, there is a need to identify characteristics of the ecosystem that capture the imperative to quantify its somewhat elusive properties such as health, vigour or resilience – ecological indicators (Platt & Sathyendranath, 2008).

These ecological indicators are required to assess the progress attained towards environmental policy objectives, showing the need for action and giving simple and quantifiable information for policies and management, regarding the complexity of marine ecosystems. When scientific information has been available, the indicators have proven to be valuable tools for assessing environmental quality, in a great variety of estuarine and coastal habitats (Muniz *et al.*, 2005). For oceanic habitats no information was found. However, if indicators are too expensive to provide adequate spatial representativeness and to implement sufficiently often to document change, they have little merit as operational metrics (Platt & Sathyendranath, 2008).

Although satellites do not observe cetaceans directly, due to their continuity, global coverage, and high temporal and spatial resolution, remotely-sensed data can be very useful to characterise and monitor oceanographic information in near real-time (Jones *et al.*, 1997) and thus, can be considered a consistent, simple and cost-effective tool in the development and application of ecological indicators for the pelagic marine ecosystem. Platt & Sathyendranath (2008) suggested combining satellite observations with well-designed *in situ* observations because of the complementarity of the two types of data. Notwithstanding the many advantages remote sensing provides in the development of ecological indicators, the applications to date have been very few.

There is a wide range of studies indicating that the distribution and relative abundance of marine predators can be related to some environmental features, and thence, be used as indicators of underlying prey distributions and ecosystem processes (Tershy *et al.*, 1991; Croll *et al.* 1998; Baillie *et al.*, 2004; Dubroca *et al.*, 2004; Hooker & Gerber, 2004). So far, diversity indices have rarely been applied to cetaceans due to a lack of survey effort in offshore areas where the majority of species occur (Walker *et al., 2005;* ICES, 2007).

In this context, this study proposes to investigate the summer spatial distribution of cetaceans in the offshore waters of the Bay of Biscay region, using physiographic (depth) and remotely-sensed oceanographic variables (sea surface temperature, chlorophyll-a and sea level height), as well as to generate occurrence and relative density models (GAM) and respective predicted maps for the most sighted species (*i.e.*, fin whale common and striped dolphins). The results of this study will provide information on cetacean ‘hotspots’ in the research area and allow a better understanding of the relationships with the environmental features used. With basis on the results, the implications of the MSFD for the conservation of cetaceans in the Bay of Biscay will be discussed.

2. METHODOLOGY

1.1.Study Area

The study area is situated in the Northeast Atlantic and it comprises the offshore waters of the Bay of Biscay and the Galicia seamount region (Fig. 2). By offshore waters is meant beyond the continental shelf edge, *i.e.*, it includes the continental shelf slope, abyssal plane and topographic features such as canyons and seamounts.

The survey took place during 23 days of July 2007, between the 4th and the 30th.

These offshore waters have only been partially surveyed, so this offshore data are of particular importance to complement on-shelf surveys and acquire information on a fairly unknown area.

The majority of these waters are under Spanish jurisdiction although one small fraction belongs to the exclusive economic zone of France and still a minor portion is classified as international waters.

The area encompasses almost the entirety of the ICES' region VIII and part of region IX[2].

In what refers to the MSFD, the research area comprehends the marine region (b) – North East Atlantic Ocean – and sub-region (iii) - Bay of Biscay and Iberian Coast (EU, 2008).

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[2] http://www.ices.dk/aboutus/icesareas.asp

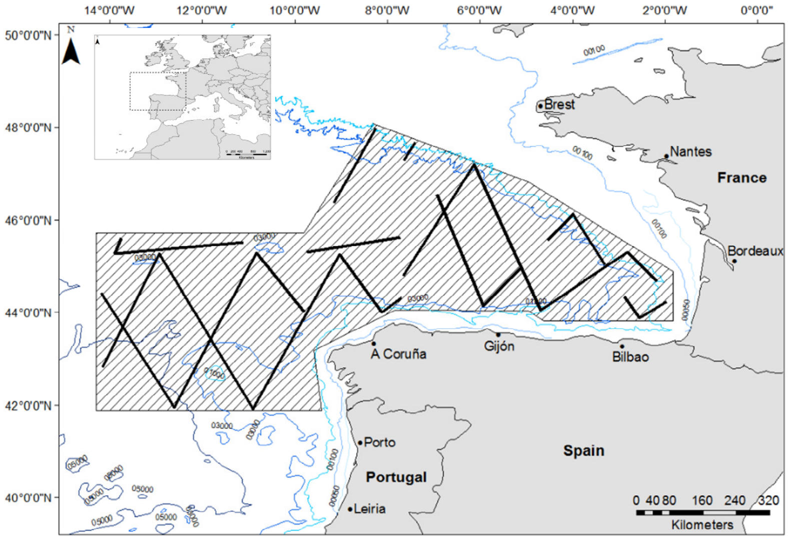

Figure 2. Study area (shaded) and shipboard transects (black solid lines)

1.2. Survey methods

This study relies on data from the Cetacean Offshore Distribution and Abundance in the European Atlantic project (CODA).

This shipboard survey was carried out in July 2007 and both visual and passive acoustic techniques were employed. For the purpose of this study, only the visual data will be used.

The survey method was a combination of line transect distance sampling and mark-recapture methods.

Line transect surveys are widely used to estimate the distribution and density of wildlife populations (Marques *et al.*, 2001; Thomas *et al.*, 2002; Castège *et al.*, 2004; Rovero & Marshall, 2004; Yen *et al.*, 2004; Hounsome *et al.*, 2005; Rovero *et al.*, 2006; Teelen, 2007), including cetaceans (Walker, 2005; Barlow, 2006; Thomas *et al.* 2007, Williams & Thomas, 2007), such as harbour porpoise (Carretta *et al.*, 2001), sperm whale (Barlow & Taylor, 2005), minke whale (Hedley & Buckland, 2004), killer whale (Zerbini *et al.*, 2007), Cuvier's beaked whale (Ferguson, 2005), common dolphin (Cañadas & Hammond, 2008) and bottlenose dolphin (Cañadas & Hammond, 2006).

In the line transect distance sampling, for each object detected the distance from the trackline is recorded. A fundamental assumption of this method is that animals on the trackline (*i.e.* the perpendicular distance is zero) are certain to be detected.

The survey followed the so called ‘trial configuration’ (Laake & Borchers, 2004 *in* MacLeod et al, 2008), which implies the use of two mutually independent observation platforms – a primary platform (PP) and a tracking platform (TP) (Thomas *et* al., 2002). The observers on the PP search close to the ship (within 500 metres) by naked eye, and the observers on the TP search with Bigeye or 7x50 binoculars far ahead of the ship. A third observer is informed of all detections as they are made and is responsible for classifying duplicates. A duplicate sighting occurred when a sighting made on TP was subsequently recorded on PP (Macleod *et al*., 2008).

A ‘sighting’ was defined as a group of animals of the same species seen at the same time and place exhibiting similar behaviour although not necessarily with a synchronised surfacing pattern (Uriarte *et al*., 2007). The number of individuals of each pod was estimated.

Upon detection of a duplicate sighting, this was classified according to the probability of being so, *i.e.* D-definite duplicate (at least 90% likely); P-possible (more than 50% likely); R-remote chance (less than 50% likely). In the data analysis of this study all the three types (D, P and R) were considered to be duplicates.

The sighting data were only considered suitable for analysis if collected in Beaufort sea states 4 or lower because cetacean detection capability tends to be biased downwards in weather conditions worse than that (4% of the total).

These methods followed by CODA survey are described in detail in Macleod *et al.* (2008) and Uriarte *et al*. (2007).

1.3. Environmental features

Physiographic (depth) and oceanographic (sea surface temperature, chlorophyll-a and sea surface height) features were collated for the study area and adjacent region.

Bathymetric data were extracted from the ETOPO2v2 dataset (Smith & Sandwell 8.2. database) available at the NOOA/NGDC (National Geophysical Data Center) website[3].

Data on chlorophyll-a was used as a proxy for primary production. Being the only biological component of the marine ecosystem accessible to remote sensing[4], the chlorophyll-a provides a key metric for assessing the health and productivity of the marine ecosystem.

Data on sea level height anomalies was used as a proxy for ocean surface currents direction and intensity as well as for the degree of surface dynamics.

The altimetry has the advantage of providing sea level measurements under any meteorological condition, while sensors working in the infrared or in the visible have the handicap of not being capable to measure optimally sea surface radiance in the presence of clouds. This is particularly important in the study area which is inserted in a cloudy region (Caballero *et al.*, 2005).

Both sea surface temperature (SST) and chlorophyll-a concentration (CLA) data were taken from NASA/Goddard Space Flight Center DAAC website[5]. MODIS (Moderate Resolution Imaging Spectroradiometer) sensor is aboard Aqua EOS (Earth Observing System) satellite which has a daily temporal resolution and a source spatial resolution of 1.8 km.

The altimeter-derived sea surface height anomalies (SSH) data were obtained from NASA/JPL-PO DAAC (Jet Propulsion Lab - Physical Oceanography) satellite mission

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[3] http://www.ngdc.noaa.gov/mgg/global/etopo2.html

[4] http://www.pfeg.noaa.gov/~cwilson/fishsat/index.htm

[5] http://aqua.nasa.gov/index.php

named Jason-1 (near-real-time product)[6]. It has a temporal and spatial resolution of 7 days and 1.8 km, respectively.

The satellite imagery of SST, CLA and SSH was binned and averaged on a 0.016667 degree grid for different time periods, *i.e.*, for the whole month of July 2007 and for each 5-days period of the same month.

1.4. Data analysis

1.4.1 Exploratory Analysis

The sampling unit is the effort leg – distance covered in sighting effort - the length of each effort leg is not constant.

Each effort leg was characterised by the presence or absence of each cetacean species and by the mean of the environmental parameters (depth (DEP), SST; CLA and SSH).

The 'sighting per unit effort' rate (SPUE) was calculated per species for each effort leg and for the whole study area as the number of sightings per kilometre searched. In this case only the occurrence was analysed, the number of individuals in each sighting was not considered.

In order to obtain a more detailed descriptive analysis the variables were divided into classes.

For depth seven ranges at 1000 m intervals (except for the deepest one) were established: 0-999, 1000-1999, 2000-2999, 3000-3999, 4000-4999 and ≥ 5000 m. For temperature and chlorophyll seven and six classes, respectively, were defined: SST < 16.5, [16.5-17[, [17-17.5[, [17.5-18[, [18-18.5[, [18.5-19[and ≥ 19 ºC ; CLA [0.1-0.2[, [0.2-0.3[, [0.3-0.4[, [0.4-0.5[, [0.5-0.6[and > 0.6 mg.m^{-3}.

And finally, for surface height six ranges were determined: SSH < 0, [0-2[, [2-4[, [4-6[, [6-8[and > 8 cm.

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[6] http://nereids.jpl.nasa.gov/cgi-bin/ssh.cgi?show=overview

All the classes for the four covariates were arbitrarily chosen. The extreme intervals are often broader because of the smaller number of sightings falling in these classes.

Habitat associations were explored, using ArcGIS 9 Geographic Information System software (ESRI Inc., 1999-2005), by overlaying the cetaceans' sightings over each explanatory variable images.

1.4.2 Statistical Analysis

For statistical analysis purpose, two species of dolphins – short-beaked common and striped – were coupled into a single group to increase sample size.

The Kruskal-Wallis test was used to compare the distribution among the different species/groups and to test whether they could be differentiated with basis on the studied covariates. Mann-Whitney U test was used for further pairwise testing.

This test was performed in two different data sets, one including three monospecific groups and one group containing two species, and another dataset including four cetacean families, which together contain all the observed species during the survey. Due to sample size not all the species could be considered *per se*, therefore the first dataset analysis was applied to five species: the fin whale (*Balaenoptera physalus*), the short-beaked common dolphin (*Delphinus delphis*) and the striped dolphin (*Stenella coeruleoalba*) together in the same group, the sperm whale (*Physeter macrocephalus*) and the long-finned pilot whale (*Globicephala melas*). In the second dataset the four families analysed were the Balaenopteridae (including *Balaenoptera physalus* (fin whale), *B. borealis* (sei whale) and *B. acutorostrata* (minke whale)); the Delphinidae (including *Delphinus delphis* (short-beaked common dolphin), *Stenella coeruleoalba* (striped dolphin), *Globicephala melas* (long-finned pilot whale), *Tursiops truncatus* (bottlenose dolphin), *Grampus griseus* (Risso's dolphin) and *Lagenorhynchus acutus* (white-sided dolphin)); the Physeteridae (including *Physeter macrocephalus* (sperm whale)); and Ziphiidae (including *Ziphius cavirostris* (Cuvier's beaked whale), *Hyperoodon ampullatus* (Northern bottlenose whale) and *Mesoplodon bidens* (Sowerby's beaked whale)).

The Kruskal-Wallis nonparametric test was preferred over a parametric ANOVA because of the large interspecific differences in sample size and variance (Zar, 1999). Moreover, in the presence of outliers this test is more adequate as it compares medians instead of means.

This analysis was performed using StatGraphics Plus 5.0 software (Statistical Graphics Corp., 1994-2000) and a significance level of 0.05.

Generalised Additive Models (GAM) (Hastie & Tibshirani, 1990) were used to determine if the different species of cetaceans were distributed non-uniformly with respect to the environmental variables. This nonparametric regression was considered to be a good approach because unlikely conventional regressive methods it is not dependent on specific functional relationships (*e.g.*, linearity) and it is less restrictive in its assumptions about the underlying statistical distribution of the data (Maravelias, 1999). In a GAM, the covariates are assumed to affect the dependent variable, in this case, cetacean presence and relative density, through additive and unrestrictive smooth functions (Hastie & Tibshirani 1990).

Furthermore, GAMs can be used to quantitatively explore species-habitat relationships when little is known about the underlying mechanisms responsible for generating the observations (Guisan et al., 2002; Olivier and Wotherspoon, 2005), which might prove to be useful.

The GAM analysis was implemented using the package *mgcv* v. 1.4-1 (Wood, 2001) for R 2.7.2 software (The R Foundation for Statistical Computing, 2008). Williams *et al.* (2006) encouraged the use of this package for such methods because it incorporates cross validation, and requires user-driven input in model selection.

Given the different physiographic and oceanographic characteristics within the study area it had been hoped to be able to fit separate models for two sub-areas: the inner Bay of Biscay and the Galicia bank region. However, due to sample size issues, the results were more robust when the whole research area was modelled rather than each sub-area separately.

Once again, owing to insufficient sample size, the GAMs could only be performed for the three most sighted species: the fin whale, the short-beaked common dolphin and the striped dolphin (the two last ones pooled into a single group). One of the risks of applying GAMs with few data is ‘overfitting’ the model by using many parameters; in general, bias decreases and variance (uncertainty) increases as the number of parameters in a model increases (Burnham & Anderson 2002).

As a consequence of being a multispecies sampling, which frequently leads to designs not optimal for one or more surveyed species (Borchers *et al.*, 1997) and due to cetaceans being k-selected species, there is a widespread occurrence of zeros in the dataset. Data with such a high proportion of zeros are usually difficult to model in one step (Maravelias, 1999). Besides this, both species of dolphins analysed showed a wide range in size group which might result in over-dispersed data.

Therefore, the analysis was undertaken in two stages. A first one where the probability of presence was modelled as function of the environmental variables, despite the number of groups or individuals sighted. And a second stage where the number of individuals conditional on presence was modelled (Borchers *et al.*, 1997). It is important to note that relative density was modelled, and not abundance. To estimate abundance, the probability of detection should have been estimated. Appropriate link function and error distribution were chosen on the basis of residual plots.

For the first modelling stage, a binomial family with a logit link function was used, since the response was a binary (0-1) variable (0-effort leg with no animals recorded; 1-effort leg with at least one animal recorded).

In the second stage, regarding the number of individuals given presence, a GAM with log function and a gamma error distribution was found to be adequate for the data. The response variable was the individuals per unit effort (IPUE), *i.e.*, the number of individuals sighted per kilometre searched. A gamma error model was preferred to a Poisson given the nature of the response variable. It assumes only positive or null values, has a high number of zeros and the standard errors are approximately proportional to the mean (rather than proportional to the variance) (Borchers *et al.*, 1997; Fletcher *et al.*, 2005).

All the four variables (DEP, SST, CLA and SSH) were initially included in the model. Rows with missing values were omitted before the model selection, so that all models were based in the same observations.

Backward stepwise procedure was adopted and variables were removed when p-value > 0.05 thus yielding a reduced model which contained only significant predictor variables.

First-order interactions between the previously selected significant variables were then included in the model chosen before. At last, the percentage of explained deviance along with UBRE (Un-Biased Risk Estimator) / GCV (Generalised Cross Validation) score (in which smoothing parameters, *i.e.*, number of knots and degrees are freedom, are chosen by the software to minimise the score of the model) were used to select the smoothing predictors to include in the final model that best fitted the data. The models with a very small difference in GCV/UBRE were considered to have equivalent support from the data and in such cases, the most parsimonious model was selected. These selection criteria were adapted from Wood & Augustin (2002) and are similar to the ones adopted recently by several authors (Cañadas & Hammond, 2006; Planque *et al.*, 2007; Gómez de Segura *et al.*, 2007; Zarauz *et al.*, 2007; Cañadas & Hammond, 2008). By default, the goodness of fit of the binomial distribution models is investigated using the UBRE score (given that the scale parameter $\phi = 1$), whereas for the gamma distribution GCV is applied (ϕ is estimated). Similarly, to test the null hypothesis a chi-square statistic is used in binomial error structure models, and *F*-statistic is applied to gamma error distributions (Venables & Dichmont, 2004). For all the models, the residuals were inspected visually.

Predicted probabilities of presence and relative density, for the two groups (fin whales; common and striped dolphins), were calculated from the final GAMs in order to create surface maps throughout the study area because they allow the delimitation of ‘hotspots’ which is very useful for a variety of conservation purposes. Spatial Analyst extension of ArcGIS 3.2 (ESRI Inc., 1992-2000) was used to generate these interpolated surfaces.

3. RESULTS

2.1. Exploratory Data Analysis

A sampling effort of 4 573 km (~2468 nmi), during 23 days, covered an area of 362 392 km^2.

During the whole survey 13 species of cetaceans were identified of which 3 were mysticetes - fin whale, sei whale and minke whale - and 10 odontocetes (Table 1). In total, 777 sightings were registered, amounting to 3726 animals. In spite of the lower species richness, the baleen whales represented more than half of the total number of sightings (~56%), the odontocetes accounted for 43% and only 1% of the cetacean sightings were not identified.

The most common species were the fin whale, followed by the common dolphin, the striped dolphin and the sperm whale. Among the ziphids, the most common was the Cuvier's beaked whale. For five of the species present only a single animal was sighted: minke whale, Risso's dolphin, northern bottlenose whale, white-sided dolphin, and Sowerby's beaked whale.

Mixed aggregations were only observed for two species, the common and the striped dolphins.

The cluster size was highly variable, ranging from solitary animals up to 100 animals. Mean cluster size was higher for small delphinids (common and striped dolphins) and the lower for the three species of baleen whales (Table 1).

The baleen whales were mostly observed in the western region of the study area, while the delphinids and ziphids were predominantly seen the inner part of the Bay of Biscay. The sperm whales were distributed rather uniformly in the research area. It is relevant to stress that several delphinids sightings occurred over regions of steep and heterogeneous bathymetry such as submarine canyons and the continental slope (Fig. 3).

Table 1. Number and percentage of sightings, estimated individuals and mean cluster size, and sightings per unit effort (SPUE) per species/family

	Sightings		Individuals		Cluster size	SPUE
	No.	%	No.	%		
Species						
Balaenoptera physalus	297	38.22	353	9.47	1.19	0.0666
Delphinus delphis	112	14.41	1293	34.70	11.54	0.0251
Stenella coeruleoalba	43	5.53	732	19.65	17.02	0.0096
D. delphis & S. coeruleoalba	68	8.75	805	21.60	11.84	0.0153
Physeter macrocephalus	42	5.41	71	1.91	1.69	0.0094
Globicephala melas	18	2.32	75	2.01	4.17	0.0040
Balaenoptera borealis	18	2.32	21	0.56	1.17	0.0040
Ziphius cavirostris	13	1.67	25	0.67	1.92	0.0029
Tursiops truncatus	8	1.03	41	1.10	5.13	0.0018
Balaenoptera acutorostrata	1	0.13	1	0.03	1.00	0.0002
Grampus griseus	1	0.13	4	0.11	4.00	0.0002
Hyperoodon ampullatus	1	0.13	2	0.05	2.00	0.0002
Lagenorhynchus acutus	1	0.13	25	0.67	25.00	0.0002
Mesoplodon bidens	1	0.13	2	0.05	2.00	0.0002
Groups						
Balaenopteridae	434	55.86	504	13.53	1.16	0.0974
Delphinidae	270	34.75	3099	83.17	11.48	0.0606
Physeteridae	42	5.41	71	1.91	1.69	0.0094
Ziphiidae	24	3.09	43	1.15	1.79	0.0054
Unidentified cetacean	7	0.90	9	0.24	1.29	0.0016
TOTAL	777	100.00	3726	100.00	4.80	0.1744

Legend: '*D. delphis & S. coeruleoalba'* refers to mixed groups of both species. Balaenopteridae: *Balaenoptera physalus* (fin whale), *B. borealis* (sei whale), *B. acutorostrata* (minke whale); Delphinidae: *Delphinus delphis* (short-beaked common dolphin), *Stenella coeruleoalba* (striped dolphin), *Globicephala melas* (long-finned pilot whale), *Tursiops truncatus* (bottlenose dolphin), *Grampus griseus* (Risso's dolphin), *Lagenorhynchus acutus* (white-sided dolphin); Physeteridae: *Physeter macrocephalus* (sperm whale); Ziphiidae: *Ziphius cavirostris* (Cuvier's beaked whale), *Hyperoodon ampullatus* (Northern bottlenose whale), *Mesoplodon bidens* (Sowerby's beaked whale).

The mean depth of the study area was 3817 m (sd=1358) (Table 2), with fin whales, striped dolphins, sperm whales and ziphids occurring in the deepest waters (approximately 70% of the sightings of these species took place on the 4000 m isobath or deeper), and common dolphins and long-finned pilot whales in more shallow zones with 70 and 80% of the individuals occurring below the 4000 m and 3000 m isobaths, respectively (Table 3).

It appears that species occurring in deeper waters area associated with zones with lower chlorophyll values (Table 3 and Fig. 4).

Although the variation in SST within the study area was over 6ºC (Table 2), cetaceans did not revealed clear associations with this variable, and the mean SST at which all the species were located was about 18ºC (Table 3).

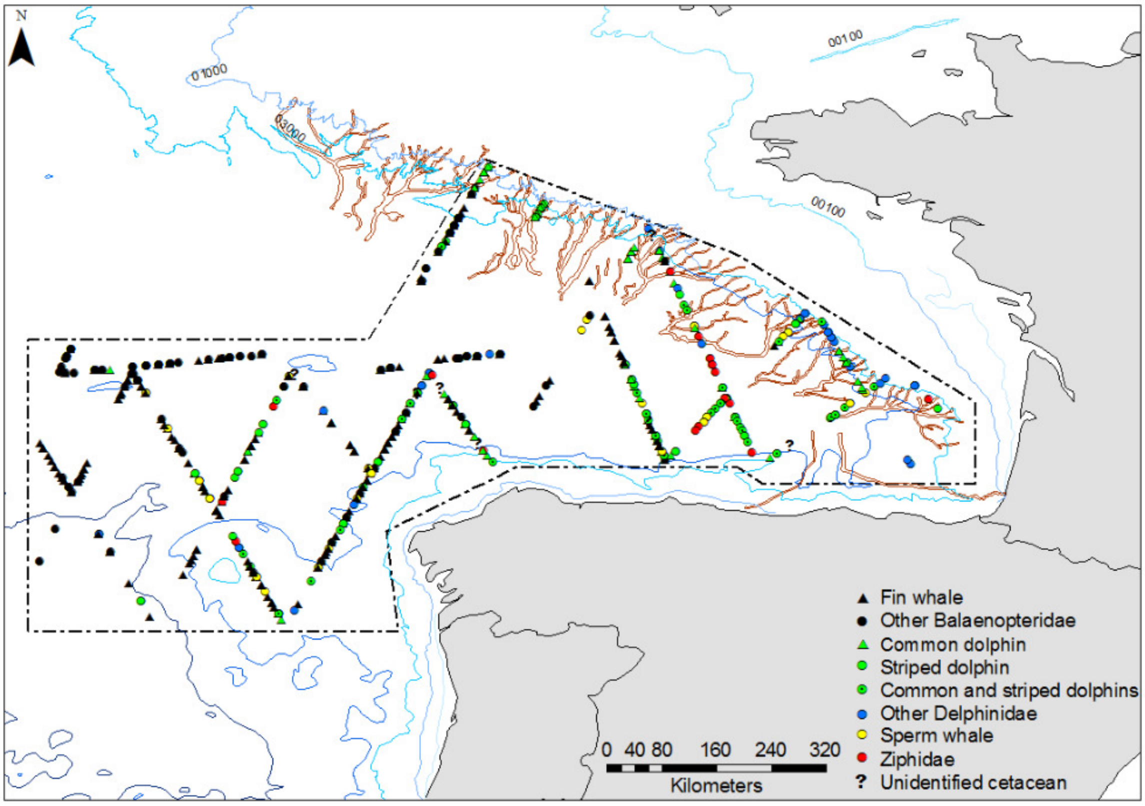

Figure 3. Spatial distribution of sightings of cetaceans made during the ship-based survey. The dashed black line delimits the study area and the brown lines demarcate the submarine canyons (note: the canyons are not mapped for the whole study area, so unidentified canyons may exist)

Table 2. Brief descriptive statistics of each explanatory variable for the whole study area

	DEP (m)	SST (°C)	CLA (mg.m^{-3})	SSH (cm)
Mean	-3817	18.17	0.2962	2.527
St. Dev.	1358	1.10	0.1170	3.408
Range	[-5311 ; -131]	[13.89 ; 20.40]	[0.1211 ; 0.9831]	[-3.243 ; 13.16]

Concerning the sea level, the baleen whales were mainly sighted in areas with clearly higher altimetric values (mean = 4.05 cm), while members of the families Delphinidae and Ziphiidae occurred in regions where sea surface height suffered a minor variation (*i.e.*, SSH close to zero), and sperm whales occupying an intermediate position (Table 3 and Fig. 4). The interval with the higher number of sightings was the [4; 6] cm for the Balaenopteridae even if more than 50% of the survey effort was made in waters with a sea level below 4 cm. In contrast, the majority of the sightings and individuals of delphinids (1711 animals out of 3099) and ziphids (31 of 43 animals) were recorded in the class with negative values of sea height. Detailed tables with the number of sightings and individuals distributed in classes, for each variable, are available in appendix II (Tables 1-4).

Table 3. Brief descriptive statistics of each explanatory variable for each species/family

	DEP			SST			CLA			SSH		
	Sz	Mean	Sd	Sz	Mean	Sd	Sz	Mean	Sd	Sz	Mean	Sd
<u>Species</u>												
B. physalus	154	-4191	937	151	18.20	0.98	152	0.265	0.087	154	3.84	3.00
D. delphis	48	-3466	1301	44	17.82	1.20	41	0.392	0.170	48	0.53	2.61
S. coeruleoalba	31	-4223	929	32	18.47	0.77	26	0.272	0.097	32	1.97	3.01
D.d. & *S.c.*	51	-3717	1287	47	18.24	0.78	51	0.371	0.158	51	0.52	2.51
D.d. and/or *S.c.*	108	-3738	1242	102	18.17	0.99	90	0.342	0.140	108	0.93	2.82
P. macrocephalus	28	-3908	1038	26	18.37	0.94	26	0.278	0.077	28	2.54	3.06
G. melas	11	-2598	1869	9	18.29	0.92	11	0.365	0.106	11	1.33	3.86
<u>Groups</u>												
Balaenopteridae	185	-4251	914	182	18.09	1.02	182	0.275	0.096	185	4.05	3.12
Delphinidae	133	-3555	1407	124	18.17	0.99	114	0.343	0.132	133	1.06	3.00
Physeteridae	28	-3908	1038	26	18.37	0.94	26	0.278	0.077	28	2.54	3.06
Ziphiidae	21	-3881	1239	20	18.13	0.82	18	0.337	0.116	21	0.32	2.45

Legend: Sz – sample size; Sd – standard deviation. *D.d.* – *Delphinus delphis; S.c.* - *Stenella coeruleoalba*. '*D.d.* & *S.c.*' refers to mixed groups and '*D.d.* and/or *S.c.*' to all the common and striped dolphins observed.

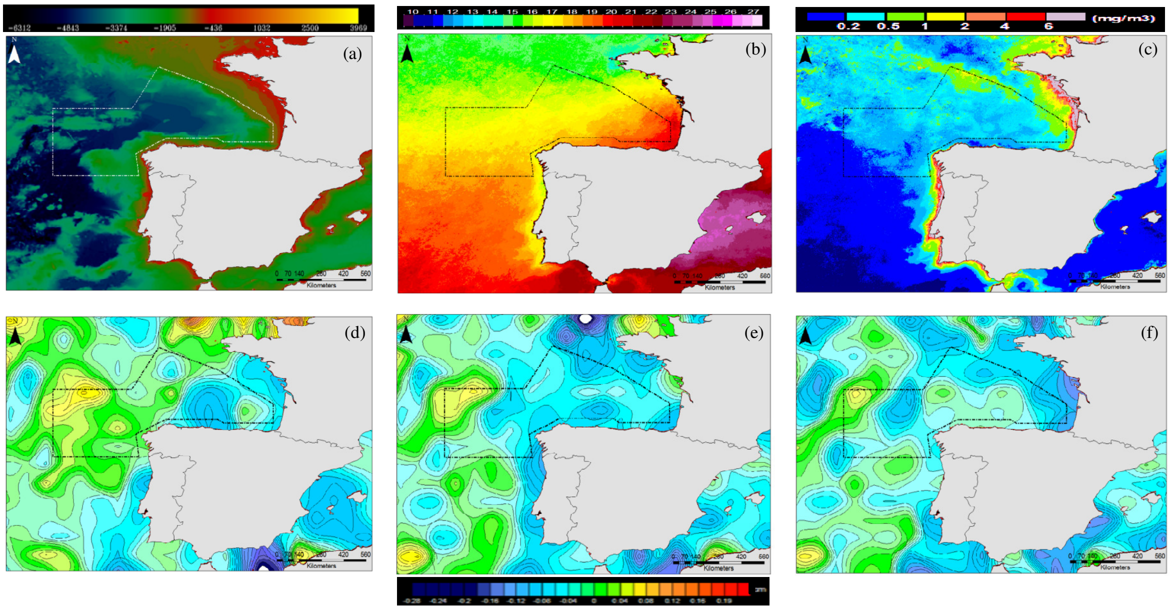

Figure 4. (a) bathymetric model (m), (b) remote-sensed sea surface temperature (ºC), (c) remote-sensed chlorophyll-a concentration (mg.m-3), (d, e, f) remote-sensed sea surface height (m). The dashed line delimits the study area. (b) and (c) are composite images of July 2007, while (d), (e) and (f) are images from the 4th, 15th and 25th of July 2007, respectively. As sea surface height has a higher temporal variability is was not considered appropriate to create a monthly composite image, as it was done for CLA and SST.

2.2. Comparison of distributions among species

The descriptive analysis in section 2.1 is underpinned by the results of the Kruskal-Wallis test.

Inter-species (Kruskal-Wallis: H = 1.09, df = 3, $p = 0.7790$) and inter-families differences (H = 0.54, df = 2, $p = 0.7617$) were not found for sea surface temperature. Nevertheless, for the other three environmental variables significant variations were found.

Variation in the water depths over which different single/two- and multi-species groups were found was significant (H = 15.85, $p = 0.0012$ and H = 26.03, $p < 0.0001$, respectively).

At a 95.0% confidence level, the results showed a highly significant variation in sea surface height anomalies at which species and families occur (H = 54.17, $p < 0.0001$ and H = 73.81, $p < 0.0001$, respectively).

Finally, the chlorophyll-a also exhibited an important significant variation although the statistic was lower than for SSH. For the mono/bispecific analysis, H = 29.66 ($p = < 0.0001$), and for the multi-species groups, H = 25.80 ($p = < 0.0001$).

For the three variables that showed variation, post-hoc comparisons were made by using the Mann-Whitney U-test and the results are displayed in Table 4.

Despite the variable (DEP or CLA or SSH), the results suggested that at least two groups could be differentiated. The common and striped dolphins and long-finned pilot whales in one group, and the fin whales in a second group. The first group was characterised by shallower waters, higher CLA levels and low sea level height, and the second one by the opposite conditions.

The sperm whale showed a less clear pattern, occupying different possible positions according to the analysed feature. When examining depth, the sperm whale could be included in the dolphins group because although the test between this species and the fin whale had a non-significant *p*-value, its value was 0.0713, not much higher than 0.05. A similar situation occurred with SSH where the *p*-value for U, when these two species are tested, was 0.0540. But in this case, in contrast with depth, the sperm whale could not integrate the dolphins groups, but a third group instead. In what referrers to chlorophyll-a, the sperm whale followed the fin whale trend for regions with lower CLA levels, when compared with common and striped dolphins and pilot whales, thus formed a group with the fin whale.

Table 4. Results of the Mann-Whitney U test

	DEP		CLA		SSH	
	U	*p*	U	*p*	U	*p*
Species						
FW / CS	6354	**0.0012**	4306	**<0.0001**	3983	**<0.0001**
FW / SP	1693	0.0713	1713	ns	1662	0.0540
FW / LF	479.5	**0.0165**	374.5	**0.0023**	451	**0.0098**
CS / SP	1432	ns	839	**0.0287**	1025	**0.0088**
CS / LF	409	0.0905	376.5	ns	573	ns
SP / LF	98	0.0832	71	**0.0175**	105.5	ns
Groups						
Bal / Del	8422	**<0.0001**	6951	**<0.0001**	5915	**<0.0001**
Bal / Phy	1918	**0.0270**	2219	ns	1921	**0.0278**
Bal / Zip	1362	**0.0251**	1116	**0.0259**	698	**<0.0001**
Del / Phy	1653	ns	1022	**0.0137**	1295	**0.0114**
Del / Zip	1317	ns	1006	ns	1263	ns
Phy / Zip	281.5	ns	168	ns	166	**0.0099**

Legend: FW – fin whale; CS – common and striped dolphins; SP – sperm whale; LF – long-finned pilot whale; Bal – Balaenopteridae; Del – Delphinidae; Phy – Physeteridae; Zip – Ziphiidae. In bold the significant *p*-values (<0.05); *p*-values > 0.1 are indicated as 'ns' (nonsignificant).

As for the family groups, a clear distinction was noticed between Balaenopteridae on one side, and Delphinidae and Ziphiidae on the other. It is relevant to remind that the Ziphiidae family had no representatives in the comparative analysis by species. In this study, the Physeteridae is a monospecific group and hence it follows the same patterns described previously for the sperm whales. Nevertheless, when CLA was analysed for the pair Physeteridae/Ziphiidae, the *p*-value was non-significant (0.1179) and the U statistic equal to 168. This could be due to small sample size of the ziphids group, and in such conditions U does not follow a normal distribution and the results of the test should be used with caution.

In short, the use of all the four variables at the same time, DEP, SST, CLA and SSH, in order to classify the associations between species, suggested a strong spatial segregation between the baleen whales and small toothed cetaceans (including delphinids and ziphids), with the sperm whales occupying an unclear position.

2.3. Modelling spatial distribution

There was no significant correlation amongst the four environmental variables. The highest correlation coefficient was between sea surface temperature and chlorophyll-a ($r = 0.48$) and still low enough not to interfere with the modelling techniques (Zuur *et al*., 2007).

The relationships between the presence/relative density of the two analysed groups and the descriptors of the environment are summarised in Figure 5. The corresponding significance of smooth terms is given in Table 5.

For the fin whale data, the generalised additive model for presence retained three covariates, SST, CLA and SSH, plus an interaction term between depth and sea level, and explained 24,10% of the data deviance. Temperature and chlorophyll were incorporated as smoothing splines whereas surface height as a nearly linear term (edf = 1.517). The most valuable variable was the CLA ($p = 0.00642$), followed by the SSH and the interaction term, with the surface temperature being the least informative of the variables kept by the model. The GAM estimated a higher probability of sighting fin whales over areas of chlorophyll-a concentrations roughly between 0.15-0.30 and 0.50-0.60 $mg.m^{-3}$ (Fig. 5b). It was also apparent that this probability would increase linearly towards higher sea surface height values (Fig. 5c). This SSH trend was also supported by the interaction term, with the probability of occurrence being maximum in deeper waters with high surface anomalies (Fig. 5d).

The fin whale density was fitted by a minimal model containing surface temperature as a smoothing spline with 8 d.f. and an interaction term between depth and temperature. Both terms were very significant influences on the relative density of fin whales during July 2007 and the model explained 37.90% of the deviance. A tendency for bimodality with surface temperature was defined, with a peak between 17-18 ºC and another, less prominent, in slightly warmer waters (18.5-19.5 ºC) (Fig. 5f). Likewise the presence model, the density was expected to be higher at these temperature peaks over deeper waters (Fig. 5g).

When modelling occurrence and density for common and striped dolphins, both models retained a single predictor, the sea surface height, accepted as a linear and very significant term ($p = 0.00002$) for the first model and showing a little departure from linearity in the density model (edf = 1.643). Figures 5e and 5h highlight the probability of occurrence as well as the density of the dolphins following an inverse and linear (almost linear, in the case of density) function of SSH, with a clear preference for zones with smaller sea surface anomalies. Nonetheless, these GAMs explained low deviances, ~5% in the presence model and ~11% in the relative density one, even if the examination of residuals revealed no unacceptable patterns and the data were adequately represented by the binomial and gamma models, with estimates of dispersion parameters very close to one (0.83 and 1.28, respectively).

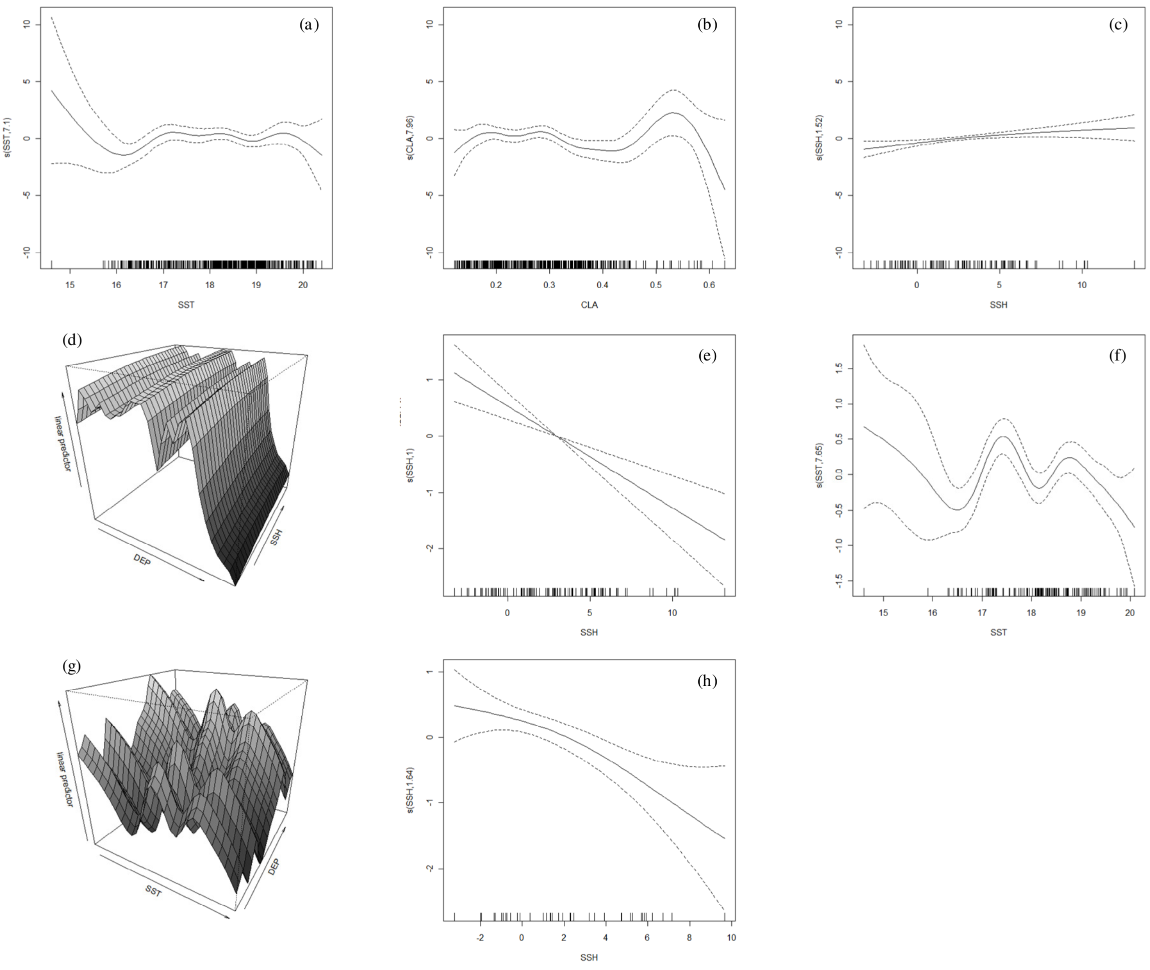

Figure 5. Smoothing splines of the fitted GAMs depicting the partial effect of the environmental covariates selected for (a, b, c, d) fin whale – presence – SST, CLA, SSH, and DEP:SSH, respectively; (e) common and striped dolphins – presence – SSH; (f, g) fin whale – density – SST and DEP:SST; (h) common and striped dolphins – density - SSH. The y-axis represents the value of the smoother indicating the strength and direction of the effect (degrees of freedom are in parentheses). The solid line is the estimate of the smooth function. The dashed lines represent the 95% confidence limits. The Tick marks on x-axis indicate the distribution of the observations (rugplot). The two 2-dimensional curves (d, g) represent interaction terms.

Table 5. Results for the GAM best models selected for fin whale and common and striped dolphins

		Approximate significance of smooth terms				
		Predictor	edf	Chi-sq / F	*p*-value	% Exp. dev.
Presence vs. Absence	FW	*Main Effects*				
		SST	7,103	16,32	0,03108	3,78
		CLA	7,957	22,03	0,00642	7,52
		SSH	1,517	8,95	0,01161	5,40
		Interactions				
		DEP:SSH	21,595	37,13	0,02362	7,40
		Total				24,10
	CD + SD	*Main Effects*				
		SSH	1,000	19,89	0,00002	4,77
		Total				4,77
Density	FW	*Main Effects*				
		SST	7,651	4,17	0,00017	17,50
		Interactions				
		DEP:SST	11,905	2,31	0,00989	20,40
		Total				37,90
	CD + SD	*Main Effects*				
		SSH	1,643	5,94	0,00320	11,30
		Total				11,30

Legend: FW – fin whale; CD+SD – common and striped dolphins; edf – effective degrees of freedom (1=linear; >1 nonlinear); Exp. dev. – explained deviance

Figures 6 and 7 present the distributions maps resulting from GAMs predictions and clearly show spatial segregation between the species of dolphins and the fin whale. The dolphins are mainly distributed in the inner part of the Bay of Biscay, with a peak of abundant off the Spanish provinces of Asturias and Cantabria (where it is situated the offshore bank 'El Cachucho'), and the whales towards West with special incidence around the Galicia bank.

The predictions made by the GAMs of fin whale are well supported by the observed data, which indicates that both models, the presence and the density one, provide a reliable description of the spatial distribution of this species although explaining less than 40% of the deviance of the data.

When the observed data were superimposed to the predicted distribution maps of the dolphins, and although it is evident a higher density in an expanded area in the most inner part of the Bay, as expected, it is also noticeable that the performance of these models is poorer, specially the one that models the probability of occurrence.

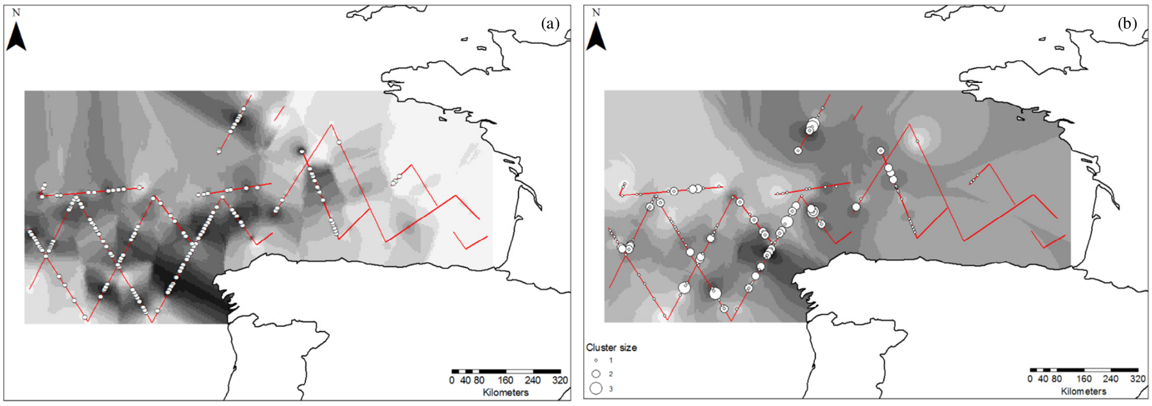

Figure 6. Distribution maps of fin whale resulting from the GAM models representing: (a) predicted probability of occurrence and (b) predicted density. Increasing probability/density from light to dark grey tones. Red solid lines represent the survey transects. White circles symbolise observed occurrence of animals.

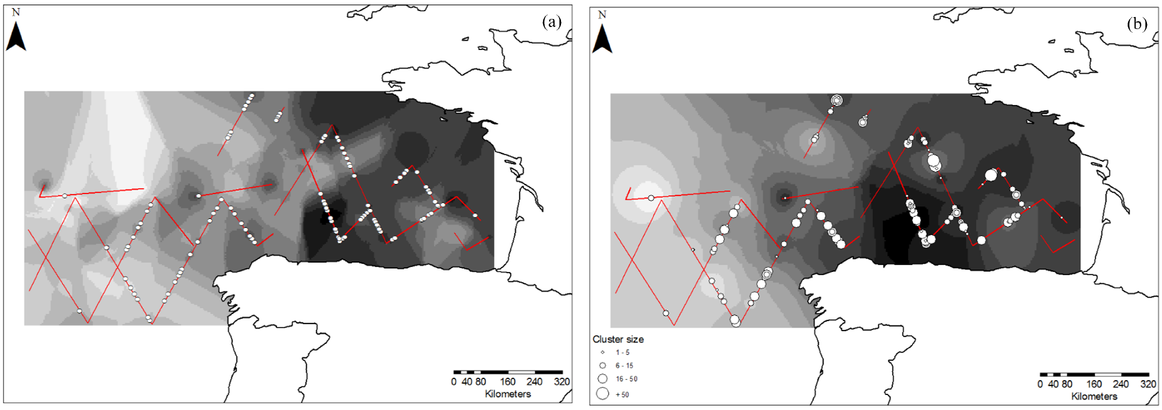

Figure 7. Distribution maps of common and striped dolphins resulting from the GAM models representing: (a) predicted probability of occurrence and (b) predicted density. Increasing probability/density from white to black colours. Red solid lines represent the survey transects. White circles symbolise observed occurrence of animals; different sizes symbolise different group sizes as indicated in the legend of the map.

4. DISCUSSION

3.1. Summer Spatial Distribution

To our knowledge, three studies on the distribution of cetaceans in the Bay of Biscay were carried out. None of them included the region surrounding the Galician Bank. Both Kiszka *et al.* (2007) and Walker (2005) focused in the inner Bay of Biscay and English Channel, but Kiszka and colleagues considered only the toothed cetaceans, whereas Walker took into account both odontocetes and mysticetes. Certain *et al.* (2008) restricted the study to delphinids occurring on the continental shelf and shelf break of the French coast of the Bay.

As observed in this study, Kiszka *et al.* and Walker referred to the Cuvier's beaked whale as the commonest of all the beaked whales sighted.

Among the delphinids sighted by Certain *et al.*, common and bottlenose dolphins were by far the most frequent, followed by the striped dolphins and the pilot whales. It was not surprising that the present study registered a low number of bottlenose dolphin sightings because in the Northeast Atlantic this species is more common near-shore (Reid *et al.*, 2003). In fact, the author mentioned that no bottlenose dolphin was observed in oceanic waters. Kiszka and colleagues obtained similar results, except that striped dolphins were more sighted than bottlenose dolphins; this was expected since the striped dolphins are most common in deep oceanic waters of the Bay. In Walker's research, the fin whale and common dolphins were the most sighted species, followed in decreasing occurrence by striped dolphins, pilot whales and bottlenose dolphins. These results are in agreement with the ones obtained in this study; exception made for the sperm whale.

In this research, as presented in the Results chapter (Table 1) the sperm whale was the fourth most sighted species, after the fin whale and common and striped dolphins. Both in Kiszka *et al.* and Walker studies this species was less frequent than the pilot whales and Cuvier's beaked whales. This issue remains unclear.

The group size was also analysed by Kiszka *et al.* and although it was highly variable, delphinids were characterized by larger group size, and the larger species by smaller, as it was ascertained in this study.

It was evident a higher diversity of species over the submarine canyons and contiguous areas (Fig. 3), especially delphinids but also some ziphids. This affinity of delphinids for canyons and shelf-breaks had been already reported by Certain *et al.* (2008), Guerra *et al.* (2004), Uriarte *et al.* (2004) and Uriarte & Castro (2003). Abrupt topographical features such as shelf breaks and canyons can concentrate zooplankton, which tend to aggregate by adopting counter-current swimming behaviour against up- or downwelling events (Genin, 2004; Guerra *et al.*, 2004; Shanks and Brink, 2005; Vivanco, 2007) and, if sufficiently persistent, can attract organisms belonging to high trophic levels. Furthermore, canyons function also as refuge and nursery zones for different fish species, as well as mating and breeding zones for some cetaceans (Uriarte & Castro, 2003).

It was also previously verified that ziphids had a preference for steep slope areas (Waring *et al.*, 2001; Cañadas *et al.*, 2002; Hooker *et al.*, 2002; D'Amico *et al.*, 2003; MacLeod *et al.*, 2004; Wimmer & Whitehead, 2004), that is likely to match the habitat of their preys (Davis *et al.*, 1998; Hooker *et al.*, 2002; Reid *et al.*, 2003; Ferguson *et al.*, 2006b).

The sperm whale occurred mainly along the continental slope and its vicinity (Fig. 3), as expected by Evans *et al.* (2002).

Conversely, baleen whales were not frequent close to these topographic features, which agree with Uriarte *et al.* (2004) who stated that in the Bay of Biscay, the fin whales were mainly spotted in oceanic waters over the abyssal plain.

The clustering of species according to depth was also in agreement with the literature, although for the long-finned pilot whale, in a less clear way.

Fin whales (Uriarte *et al.*, 2004), striped dolphins (Cañadas *et al.*, 2002; Kiszka *et al.*, 2007), sperm whales (Panigada *et al.*, 1999; Cañadas *et al.*, 2002; Reid *et al.*, 2003; Kiszka *et al.*, 2007) and ziphids (Davis *et al.*, 1998; Reeves *et al.*, 2002; Reid *et al.*, 2003; Balance *et al.*, 2006; Ferguson *et al.*, 2006b; Kiszka *et al.*, 2007; Robinson & MacLeod, 2008) have all been widely reported as species encountered most often in deep offshore waters.

The short-beaked common dolphin has also been extensively accepted as a species sighted mainly in shallower waters (Cañadas *et al.*, 2002; Kiszka *et al.*, 2007; Stevick *et al.*, 2008)

According with some literature, the long-finned pilot whale was expected to occur in more deep waters (Cañadas *et al.*, 2002; Reid *et al.*, 2003). Nonetheless, some authors mentioned that the species often appear along the edges of the continental shelf and over canyons (Reid *et al.*, 2003; Uriarte *et al.*, 2004, 2005), and Uriarte & Castro (2003) and Uriarte *et al.* (2004, 2005) reported several sightings of long-finned pilot whales, in the Bay of Biscay, in less deep waters. Moreover, Ballance *et al.* (2006) mentioned that, in the Eastern Pacific, pilot whales often shared habitat preferences with common and striped dolphins probably due to the nature of the prey.

The results of the tests undertaken to compare the distributions among species/families suggested there is a spatial segregation and it is hypothesised that it reflects the distribution of different prey preferences. There are studies reporting the influence of prey availability both on baleen whales (Panigada *et al.*, 1999; Murase *et al.*, 2002; Dubroca *et al.*, 2004; Panigada *et al.*, 2005; Friedlaender *et al.*, 2006; Bluhm *et al.*, 2007; Tetley *et al.*, 2008) and odontocetes (Cockcroft & Peddemors, 1990; Neumann, 2001; Cañadas *et al.*, 2008; Certain *et al.*, 2008; Doksæter *et al.*, 2008) distributions.

In an abridged way, the fin whales feed mainly on zooplakton (namely, euphausiids) (Orsi Relini et al., 1994; Benson et al., 2002; Uriarte *et al.*, 2005; Panigada *et al.*, 2008); the common and striped dolphins and long-finned pilot whales feed primarily on a mixture of fish and squid, although in different proportions (Berrow & Rogam, 1995; Vázquez, 1998; Benson *et al.*, 2002; Meynier, 2004; Pusineri, 2006; Doksæter *et al.*, 2008); and sperm whales prey consists mainly on demersal squids (Vázquez, 1998; Reeves *et al.*, 2002; Reid *et al.*, 2003). These preferences are in agreement with the groups of species established upon comparison (see Results in section 2.2).

When families were compared, the delphinids and ziphids were put together in the same assemblage, and this relationship remains unclear. Although some sources said ziphids feed on a great diversity of demersal preys, from fish to squids and crustaceans (Walker, 2005), there is still little accurate information on ziphids diet as said by Ferguson *et al.* (2006b).

Therefore, for benthic or demersal prey species, physiography may play a very important role in limiting distribution directly by depth, slope and type of substrate, while for other species of cetacean prey, such as pelagic fish or cephalopods, physiography could play a more indirect role through mechanisms such as topographically induced upwelling of nutrients, increased primary production, and aggregation of zooplankton due to the enhanced secondary production or convergence of surface waters (Cañadas *et al.*, 2002).

The classification of cetaceans based on depth, sea surface temperature and sea surface height, in the study area, is roughly matching their feeding habitats. Once this accepted, it is possible to state that physiography of the study area play an important role in concentrating the prey of these cetaceans.

Yet, it is of importance to note that seasonal residents or migrants may be using the habitat in different ways than those that are resident throughout the year. Migrants may not be feeding, and so may cue into current strength and direction or atmospheric dynamics rather than prey abundance and availability. In such cases, oceanography as it pertains to the foraging ecology of these species may reveal little (Ballance *et al.*, 2006). Is is known that, at least, the fin whales (Reid *et al.*, 2003), Cuvier's beaked whale (Coles *et al.*, 2001; Cresswell & Walker, 2002) and bottlenose dolphins (Reid *et al.*, 2003) are present throughout the year in the Bay, suggesting that the populations may be residents. Concerning the other species, populations living offshore have not been studied (Castro *et al.*, 2004, Kiszka *et al.,* 2007).

Several authors have been using generalised additive models to predict distributions based upon modelled relationships between habitat predictors and the occurrence of aquatic species (Granadeiro *et al.*, 2004; Hedger *et al.*, 2005; Jensen *et al.*, 2005; Planque *et al.*, 2007; Jowett *et al.*, 2008; Reid *et al.*, 2008; Schismenou *et al.*, 2008; Zainuddin *et al.*, 2008), including cetaceans (Ferguson *et al.*, 2006a, 2006b; Gómez de Segura *et al.*, 2007; Cañadas & Hammond, 2008; Panigada *et al.*, 2008; Stockin *et al.*, 2008). In the Bay of Biscay cetacean habitat associations has been previously explored by Walker (2005) and Certain *et al.* (2008).

As mentioned in the Results chapter, the modelling analysis in this study evidenced that the fin whales would concentrate more in the Western part of the study area, whilst common and striped dolphins would occur more often inside the Bay itself. Even though this qualitative evidence was possible through the predictive surface maps, the models did not explained a high variability in the observed data, especially in the dolphins' case. The proportion of total variation explained would have been further increased had longitude and latitude been introduced in the models. However, it was decided not to do so because they are not environmental variables.

The GAMs accommodate continuous functional forms of almost any shape, and to a large degree, they allow data to determine the most suitable shape to adopt (Augustin *et al.*, 1998). This is surely the strength of this regression technique, making of it a powerful tool for modelling the variation of ecological data, but this flexibility also forces one to use its results with caution because the model selection in GAMs is still an area of active research (Hedley & Buckland, 2004). In particular, overfitting and 'edge effects' could yield unrealistic results and surface maps (Gómez de Segura *et al.*, 2007). The obtained models are not complex and do not include many explanatory variables, except for the model of fin whale presence, therefore it is believed that the overfit issue may be discarded.

A further potential source of bias in the models is related with the GAMs' assumption that model errors are independent. Spatial autocorrelation is likely to be present in this dataset because observations were made along continuous transects and, thus, close observations may be due to 'intrinsic' reasons unrelated to environmental characteristics, such as reproductive status (Bernard & Hohn, 1989; Bräger & Schneider, 1998; Certain *et al., 2008;* Stockin *et al*., 2008), feeding strategies (Neumann, 2001; Burgess, 2006; Stockin *et al*., 2008; Wiseman, 2008) or social behaviour (Cañadas *et al*., 2008; Stockin *et al*., 2008). Distribution and habitat use of species with complex ecology, social structure and behaviour, such as cetaceans are very likely influenced not only by environmental factors (biotic and abiotic) but also intrinsic ones (Cañadas *et al*., 2008). This autocorrelation was not taken into account in this study, and it may have affected model conclusions since estimates of uncertainty and significance tests can be invalid, leading to excessive small *p*-values (Panigada *et al*., 2008).

The fact that common and striped dolphin were analysed together may have also generated some bias because in what refers to depth, this two species appear to have different preferences. In this study, the mean depth over which striped dolphins occurred was 4223 m, against 3466 m for the common dolphins (Table 3). In previous studies, it was generally accepted that the striped dolphin tends to occur in greater depths than the common dolphin (Cañadas *et al.*, 2002; Evans, 2002; Reid *et al.*, 2003; Kiszka *et al.*, 2007).

Yet this decision was considered reasonable in order to increase sample size and able the modelling. Even so, as previewed, the dolphins' models had a lower percentage of deviance explained than the fin whale's ones. This decision was made not only because there were, in this study, 68 sightings of mixed groups, *i.e.*, individuals of both species occurring in the same group, but also interspecific interactions between these two species have been reported in several previous studies (García *et al*., 2000; Cañadas *et* al., 2002; Frantzis & Herzing, 2002; Mesnick, 2005; Cañadas & Hammond, 2008). Doksæter (2008) suggested that both species had overlapping habitats even if they had somewhat different diets and fed at different depths; when the author compared differences between species with respect to physical and biological variables, the sea surface temperature and salinity were the most powerful variables determining dolphin distribution and these parameters divided the species into two groups, being one of these comprised by common and striped dolphins together.

In 2006, Ballance *et al.*, stated that at a macro-scale, cetacean habitat associations seem to be based on preferences for specific water masses, and Au & Perryman by analysing these relationships, in Eastern Pacific, recognised two major cetacean communities, being one of these composed by striped and common dolphins. This preferred habitat corresponded with regions of highly variable oceanographic features and the authors hypothesized that the mechanisms for these preferences were based on differences in the nature of epipelagic prey.

In addition, LeDuc *et al*. (1999) analysed the phylogenetic relationships among the delphinids based on full cytochrome b sequences and concluded that the monophyly of Stenella could not be taken for granted, the genus was indeed an artificial assemblage of species; through a taxonomic analysis of the subfamily Delphininae, obtained a well-supported clade that included both the common (*Delphinus delphis*) and striped (*Stenella coeruleoalba)* dolphins.

Very recently, in 2007, Amara *et al*. made a similar study and analysed the genera *Stenella, Tursiops* and *Delphinus* in the Northeast Atlantic. The results showed that within the species of these three genera, *S. coeruleoalba* and *D. delphis* were the most similar species.

Finally, it is also possible that the variables used were not the most appropriate in order to identify the existing patterns of the modelled species. Clearly, there may be other unmeasured variables with the potential to explain variability in the data, however, one can only use the available data. Some of the studied environmental variables were incorporated with the assumption that they act as proxies and therefore cetaceans may not be responding directly to these variables, but, for instance, to prey that respond to oceanographic features and processes. Nonetheless, as said by Cañadas *et al.* (2005), even an incomplete description is valuable both to improve understanding of how at least some factors affect distribution and to inform the selection of the best areas for marine protected areas. As more information becomes available, the models can be rerun and adjustments made to recommendations, as appropriate.

Ballance (2006) stated that because many cetaceans are apex predators, statistical correlations between cetaceans and any given set of oceanographic parameters may be weak relative to values for organisms feeding lower on the food chain; there is general consensus that large scale distribution patterns may be constrained by large water masses or surface currents, while local oceanographic features, often due to their effects on prey distribution, may play a stronger role in determining small scale distribution patterns.

In truth, several studies mentioned the prey availability as the primary influence of the physical environment over cetacean distribution (Angel *et al.*, 1994; Baumgartner, 1997; Tynan, 1997; Davis *et al.*, 1998; Forney, 2000; Cañadas *et al.*, 2002; Davis *et al.*, 2002; Ballance *et al.*, 2006; Redfern *et al.*, 2006; Stockin *et al.*, 2008), although predictive models of cetacean distribution rarely include direct data on prey distribution (Allen *et al.*, 2001; Heithaus, 2001; Benoit-Bird & Au, 2003) because prey sampling is more difficult than sampling of abiotic variables (Benson *et al.*, 2002; Gómez de Segura *et al.*, 2007; Torres *et al.*, 2008). Notwithstanding, a very recent research done by Torres *et al.* (2008) on whether including prey distribution data in predictive models of bottlenose dolphin habitat selection would improve predictive capacity, concluded that due to high habitat heterogeneity and the spatial variability of prey patches, models would be more successful if environmental variables were used as predictor variables of predator distributions rather than relying on prey data as explanatory variables. However, predictive modelling of prey distribution as the response variable based on environmental variability did produce high predictive performance of dolphin habitat selection, particularly foraging habitat.

Even if the variability explained by the models was not high, the interpretation of the selected covariates have some biological significance.

In order to verify the predominant winds, in the study area, during the survey period, surface wind fields were obtained from Quick Scatterometer satellite (QuikSCAT)[7]. The dataset consists of global grid values of meridional and zonal components of wind, twice daily measured on an approximately 0.25 x 0.25 degree grid. It was observed that during July 2007, northerly winds were predominant along the Iberian west coast, and along the Cantabrian coast, westerly winds were consistent.

The survey took place during the Galician upwelling season, which takes place from April to October, under the influence of predominantly northerly winds, which caused positive upwelling in the west coast. The surface water was displaced offshore, due to the surface winds and their direction relative to that of the coastline, a lower sea level sets in (Figs. 4d, 4e, 4f) forcing colder (Fig. 4b) and nutrient-rich (Fig. 4c) water from below to move upwards. (Alvarez *et al.*, 2004, 2005). A phytoplankton bloom developed over the shelf, being initially restricted to coastal waters but later extending to outer shelf and oceanic regions (Bode *et al.*, 2003).

A feature of the upwelling Galician region is the alternation of strong upwelling events on north and west coasts. Upwelling is, indeed, also present in the northern coast, remaining distant from the coast (near the edge of the continental shelf) (Fig. 4a), although is not as common (Prego & Bao, 1997; Torres *et al.*, 2003; Alvarez *et al.*, 2005). As it can be clearly seen in Figure 4c, the concentration of chlorophyll is much lower in the Cantabrian coast, in part also because the fluvial discharge is weak and dispersed (Prego & Vergara, 1998), in contrast with the Galician Coast where there are four significant estuaries locally named as *Rías Baixas* (Alvarez *et al.*, 2005).

Although several weeks may separate peaks in chlorophyll and zooplankton, as well as peaks in zooplankton and high concentrations of fin whales (Littaye *et al.*, 2004 & Notarbartolo di Sciara *et al.*, 2008 *in* Panigada *et al.*, 2008), the resulting enhancement of primary productivity, due to the supply of nutrients to surface waters, can be seen in the chlorophyll concentration image (Fig. 4c). The phytoplankton, in turn, was used as proxy

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[7] http://www.ifremer.fr/cersat/en/data/tools/browse.htm

for zooplankton concentration, as it has been previously done by several authors, namely in the multi-disciplinary study SEAMAR[8]. This may explain the preference of the fin whales for the west region of the study area (Fig. 8).

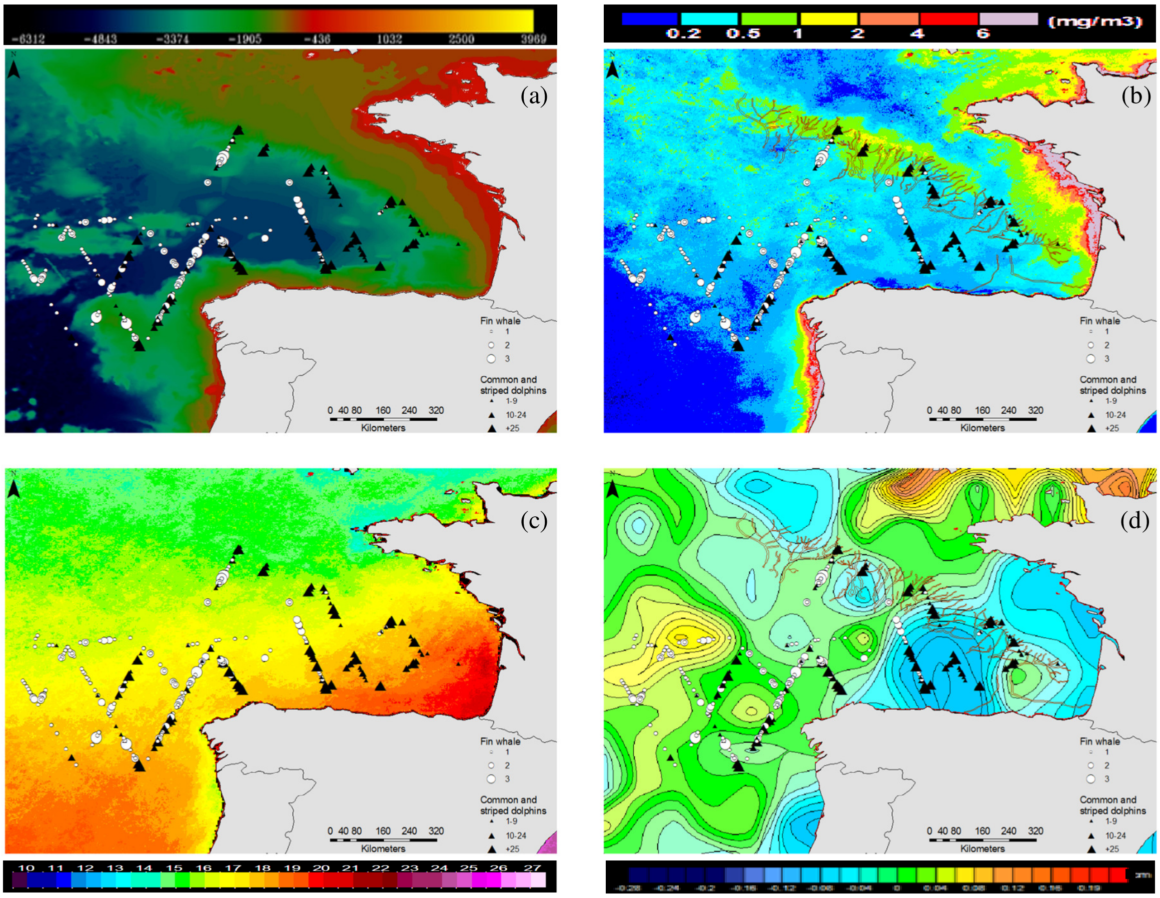

Figure 8. (a) bathymetric model (m), (b) remote-sensed chlorophyll-a concentration (mg.m-3), (c) remote-sensed sea surface temperature (ºC), (d) remote-sensed sea surface height (m). (b) and (c) are composite images of July 2007, while (d) is an image from the 4th July 2007. The black triangles represent the common and striped dolphins and the white circles represent the fin whales; different sizes symbolise different group sizes as indicated in the legend of the map The brown lines demarcate the submarine canyons (note: the canyons are not mapped for the whole study area, so unidentified canyons may exist).

In the *rías* of Galicia, phytoplankton blooms and high total plankton biomass are found at all seasons, except in winter, while zooplankton peak in spring and summer (Bode *et al.*, 2005). As mentioned earlier, the fin whales feed mainly on euphausiids, and Olaso *et al.*

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[8] http://cordis.europa.eu/data/PROJ_BIOTECH/ACTIONeqDndSESSIONeq25382200595ndDOCeq28ndTBLeqEN_PROJ.htm

(2004, 2005), Abollo *et al.* (2001) and Lindley (1982) reported the presence of these crustaceans in Galician waters. Although the euphausiid bloom occurs in April, they are only large enough to become attractive prey in July (Benson *et al.,* 2002). The distribution of fin whales evidenced by the results of this work may be explained by the prevalence of these suprabenthic invertebrates.

Furthermore, it is relevant to stress the existence of the Galicia Bank, a large seamount located at 42° 67' N and 11° 74'W, about 200 km west of the Galician coast of Spain (Fig. 4a). The large three-dimensional structure of seamounts, such as the Galicia Bank, force nutrient-rich water, from the surrounding abyss, up to the ocean surface and provides a higher number of microhabitats than the barren surroundings. Consequently, the primary productivity is often higher and seamounts host a more biodiversed community around them than in the open ocean (WWF Marine Protected Areas North-East Atlantic Programme[9]). Many invertebrates, fishes, turtles and cetaceans tend to aggregate in their vicinity and use them as feeding and spawning grounds (Stevick *et al.*, 2008). The results obtained are in compliance with other studies that have mentioned that fin whales favour areas with high topographic variation such as underwater sills or ledges, and upwelling and frontal zones with high zooplankton concentrations (Relini *et al.*, 1994; Woodley & Gaskin, 1996; Reid *et al.*, 2003).

The retention of the covariate depth by the models for presence and density of the fin whales was not surprising, since depth is considered to be one of the primary habitat features explaining cetacean distribution (Cañadas et al., 2002; Kiszka et al., 2007; Gómez de Segura et al., 2008). The distribution of fin whales, in particular, has also been related to depth by various authors (Gregr & Trites, 2001; Hamazaki, 2002; Laran & Gannier, 2008; Panigada et al. (2008)).

Both dolphins' models selected a single and the same covariate, the sea surface heigh. Unlike fin whales, the dolphins showed preference for the most eastern part of the study area, where in spring and summer, typically, northerly and easterly winds are prevalent (Borja *et al.*, 1996; Valencia *et al.*, 2004; Walker, 2005; Gil, 2008). Nonetheless, in July 2007, this wind pattern did not occur and, instead, westerly winds, non-upwelling

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[9] http://www.ngo.grida.no/wwfneap/Projects/MPA.htm

promoting, were dominant. However, in early spring, the thermal balance between the atmosphere and ocean becomes almost neutral; it reverses throughout this season, producing an increase in the temperature of the surface waters (Valencia *et al.*, 2004). The evaporation increases, resulting in a convergence of winds induced by the low pressures of thermal origin, which can be identified by the bluish rings (low SSH values) in Figure 8d. The divergence of surface water at these points can lead to weak upwelling events (González et al., 2004). Due to the low intensity of the summer winds, allowing some degree of stability and stratification, the upwelling effect can be restricted to pushing up the thermocline close to the surface, but rarely rising up and breaking into the surface layer (Borja et al., 1996; Valencia et al., 2004), avoiding the detection of low SST patches in Figure 8c. Yet, light becomes more accessible to the plankton at this fringe and the subsurface chlorophyll maximum increases, which may explain the preference of the dolphins for these low SSH areas (Fig. 8d), as well as its greater relative density predicted by the model. The importance of the thermocline depth and strength as predictors of abundance and distribution for many species of cetaceans was analysed in detail by Ballance *et al.* (2006).

In fact, Gil *et al.* (2002) said that water motion associated with eddies and upwelling filaments could lead to significant variations in the distribution and abundance of planktonic populations. This idea was corroborated by Logerwell (2002) who stated that cyclonic eddies, even though intermittent, constitute highly productive habitat features, where larvae production is an order of magnitude higher than in inshore, slope, offshore and anti-cyclonic eddy habitats.

Still, the western region of the study area is subjected to upwelling events of a much higher strength, so it is comprehensible that the whales concentrate more in this area, while the dolphins, with more mobile preys, may also opt for the eastern part of the Bay.

As noted before, the effect of bathymetry, such as in submarine canyons and shelf-slope breaks, also provides local characteristics that lead to different upwelling situations with mesoscale dimensions (Gil, 2008). In Figure 8b it is clear a higher chlorophyll-a concentration and a high number of common and striped dolphins’ sightings over these features.

3.2. Implications of the Marine Strategy Directive for the conservation of cetaceans

The results obtained in this study provide information on the summer spatial distribution of cetaceans in offshore waters of the Bay of Biscay region, and allow a better understanding of the way in which the most sighted species interact with the environmental features analysed to model their distributions.

The fact that the predicted distribution for the three most frequent species was modelled in relation to relevant environmental variables instead of being restricted to simple sightings maps, is a crucial improvement indeed because it means that the predicted distribution is actually based on habitat preference, representing, thus, a better description of it. Additionally, when new or updated data is available, the models can be rerun and refitted to clarify preferences and/or detect any changes. This possibility is extremely useful when considering monitoring programmes or if the aim is to address future research on the underlying mechanisms regulating these species-habitat relationships (Cañadas *et al.*, 2005).

The newly Marine Strategy Framework Directive, of June 2008, sets up a framework for the protection and preservation of the marine environment, the prevention of its deterioration and where practicable the restoration of that environment in areas where it has been adversely affected. Aiming at that purpose, Regional Marine Strategies shall be developed and implemented with the target of achieving or maintaining ‘good environmental status’ in the marine environment by the year 2020 at the latest (EU, 2008).

For the purpose of this work, by ‘environmental status’ is meant the overall state of the environment in marine waters, taking into account the structure, function and processes of the constituent marine ecosystems together with natural physiographic, geographic and climatic factors, as well as physical and chemical conditions including those resulting from human activities in the area concerned, as defined by the MSFD. And by ‘good environmental status’ is considered the environmental status of marine waters where these provide ecologically diverse and dynamic oceans and seas which are clean, healthy and productive within their intrinsic conditions, and the use of the marine environment is at a level that is sustainable, thus safeguarding the potential for uses and activities by current and future generations (EU, 2008).

The abovementioned Marine Strategies implicate (1) the initial assessment of the current environmental status of the waters concerned and the environmental impact of human activities thereon; (2) the determination of ‘good environmental status’ for those waters; (3) the establishment of environmental targets and associated indicators; and (4) the establishment and implementation of a monitoring programme for ongoing assessment and regular updating of targets (EU, 2008).

One of the biological features requiring assessment (pursuant to table 1 of annex III, MSFD) applies to the population dynamics, range and status of the marine mammals occurring, in this case, in the sub-region (b-iii) – Bay of Biscay and Iberian Coast. Some of the environmental impacts on these waters, briefly discussed in the introductory chapter of this report, are mentioned in the indicative list of impacting elements (table 2 of annex III, MSFD).

Following the current trend, this directive calls for an ecosystem-based approach which consists in a strategy for a comprehensive integrated management of ecosystem resources based on the best available scientific knowledge, in order to identify, plan and take action on influences which are critical to the health of marine ecosystems, thereby achieving conservation and sustainable use of ecosystem goods and services and maintenance of ecosystem integrity in an equitable way (OSPAR Commission, 2003; HELCOM, 2006).

Marine protected areas (MPA) have the potential to take this type of holistic approach providing protection both to the species of concern and to the entire ecosystem.

In recent years, MPAs have become a highly advocated tool of marine conservation in a sustainable perspective (Allison *et al.*, 1998; Mangal, 2000; Hooker & Gerber, 2004; Gubbay, 2006a; De Santo, 2007; Doyen, 2007). The MPAs promote conservation of biodiversity, ecosystem protection, reestablishment of ecosystem integrity, enhancement of the size and productivity of harvested populations to help support fisheries outside the reserve, and insurance against environmental and management uncertainty (Allison *et al.*, 1998; Hooker & Gerber, 2004, Gubbay, 2006b).

To our knowledge, in the study area, there are a few marine reserves along the Spanish and French coasts, and only one in offshore waters. This one is located in an offshore bank ‘El Cachucho’ (*a.k.a.* Le Danois Bank) close to the Spanish provinces of Asturias and Cantabria. Some sites were already proposed as SAC’s – Special Areas of Conservation under the EU Habitats Directive – one in the Galician Bank, two in Asturian waters and other two in Basque waters (Hoyt, 2005). Despite the lack of details about their sizes and exact locations, it is more likely that the last four proposed SAC's in the Cantabrian Sea comprise a minimal percentage, if any, of offshore waters. However, a EU Life Project scheduled for the next few years aims at identifying possible areas, in oceanic waters under Spanish jurisdiction, susceptible to be proposed as MPAs (Uriarte, pers. comm.).

In fact, the Plan of Implementation of the World Summit on Sustainable Development (2002) called for a comprehensive, representative and effectively managed network of MPAs to be established by 2012, consistent with international law and based on scientific information (reinforced at the 7th Conference of Parties to the Convention on Biological Diversity); in 2003, a joint Ministerial meeting of the Helsinki and OSPAR Commissions resulted in a work programme aimed at designating a network of inshore and offshore MPAs by 2010. In this context, it is expected that in the next few years more MPAs will be created, inclusively in oceanic waters of the Bay of Biscay.

The results of this study allow the identification of areas representing peaks of occurrence, abundance and/or diversity of cetaceans. Once this knowledge is acquired, the establishment of pelagic reserves based on distributional 'hotspots' and complementary species protection should be enabled (Gaston & Rodrigues, 2003; Hooker & Gerber, 2004; Gómez de Segura *et al.*, 2008). The existence of offshore cetacean MPAs in the Bay of Biscay, underpinned by existing solid scientific understanding, may produce great benefits not only for cetaceans but also for many more, if not most of the species involved, including humans. Nonetheless, it is important to stress that conservation efforts outside MPAs must complement this one because MPAs are not isolated from all critical impacts, such as contamination by chemicals and, therefore, their effectiveness will be compromised (Allison *et al.*, 1998).

Most conservation initiatives are driven by economic reasons and, thence, most evaluation of MPAs has been concerned with fishery recovery (Hooker & Gerber, 2004). However, sustainable harvesting of natural resources not only requires management of marketed species, but also the mitigation of indirect effects on non-target species (Jennings *et al.*, 2001). Cetaceans do have a great potential to act as indicator species and may be valuable assets for planning, promoting and implementing MPAs.

The ICES interprets ‘ecologically indicative species’ as any species that shows responses to hydrodynamics and sea temperature (ICES, 2007). As discussed earlier in this report, many cetacean species, and not only the ice-dependent ones, are likely to be affected by climate changes and therefore are encompassed by this definition and can be regarded as potential ecological indicators therefrom.

As large and sometimes numerous predators, cetaceans are ecologically significant as accumulators and movers of nutrients and energy, within and among ecosystems. They show a great trophic diversity, from baleen whales carrying biological production directly from the bottom of the animal food web (zooplankton) to smaller cetaceans having a diet based on much larger species and, consequently, play very different roles in ecosystem dynamics (CIESM, 2004). Therefore, they can potentially indicate any problem in the food web brought on by overfishing or other problems (Hoyt, 2005). This important role in food-web structure and ecosystem function, confers them a general value as indicators of marine ecosystem conservation state and exposes them to several types of anthropogenic pressures (Lewison *et al.*, 2004).

Cetaceans are particularly susceptible to bioaccumulation of contaminants in tissues due to several reasons. They have a high metabolic rate, a long life cycle, their body contains large amounts of blubber capable of retaining lipophilic compounds such as organochlorines, and some of them (odontocetes) being situated high in the marine trophic webs, usually base their diet on moderately or highly polluted prey species. This high concentration of contaminants has been linked to reproductive and immunological abnormalities. (Aguilar, 1983; Holsbeek *et al.*, 1998; Frid *et al.*, 2003; CIESM, 2004; Aguilar & Borrell, 2005; Walker, 2005; Caurant *et al.*, 2006).

In contrast with benthic indicators, commonly used, cetaceans are highly mobile and therefore integrate the contaminant profile of the offshore water mass at large; the information is not limited to a restricted area they inhabit. Additionally, cetaceans have the capacity to metabolise organochlorine compounds, which likely allows characterising the contaminant mixtures resulting from the highly complex processes common to marine ecosystems and, therefore, yielding a more comprehensive image of the long-term contaminant trends in oceanic ecosystems (Aguilar & Borrell, 2005).

For the reasons pointed above, cetaceans are predicted to have a great effect in structuring their ecosystems and, hence, are suited to act as potentially indicator species of long-term and wide-scale change in oceanic ecosystems therefrom (Bowen, 1997; Bouquegneau *et al*., 1997; Hooker & Gerber, 2004; Aguilar & Borrell, 2005; Torres & Urban, 2005; Torres *et al.*, 2008).

Apart from these 'intrinsic' reasons, cetaceans, as charismatic species, can be used to spearhead successful public marine education and campaigns for marine habitat protection. This is translated into reinforced management measures and increased funding for MPAs, leading in turn to larger areas of ocean under ecosystem-based management (Hooker & Gerber, 2004; Hoyt, 2005).

Thereby, cetaceans due to their educational, scientific, and economic value, as well as, in general, to their need for large conservation areas, may provide a key to protecting ocean habitats (Hoyt, 2005).

It is relevant to underline that indicator species, may reveal something about the environment, but cannot be expected to convey information on the entire ecosystem because they are not properties of the ecosystem-at-large, they have only restricted value as ecological indicators (Platt & Sathyendranath, 2008). However, more recently, the tendency has been to consider simple indicators as part of a suite of indicators that reflect the present status of the marine environment. These series should provide a comprehensive picture of the state of the marine environment as a whole (Hardman-Mountford & Huthnance, 2006).

5. FINAL REMARKS

This work allowed the acquisition of information on the summer distribution of cetaceans in offshore waters of the Bay of Biscay region, namely through the study of the relationships they establish with certain environmental features. This contribute is of high importance since cetacean surveys, in most part of the research area, had never been conducted before.

This knowledge is of utter importance to establish potential critical sites for cetaceans and, thus, identify the most important zones to protect, which in turn, constitute valuable information to achieve conservation objectives and comply with management plans for the Bay of Biscay. In addition, this research improves our understanding of the cetacean-habitat relationships that is essential to develop targeted and more effective mitigation strategies.

Yet, as presented in the Results chapter, the fin whales models had a reasonable amount of variability explained, but the same did not happened with the dolphins' models. So the challenge will be to identify the most appropriate environmental parameters for predictive modelling of their habitat.

The results of this study must be complemented with other researches since it represents solely the summer distribution surveyed during a single year. The firm definition of areas of special concern requires the gathering of additional data in order to cover a broader temporal scale, to subsequently map and define the regions of typically high and predictable probability of occurrence, within the study area. This is essential because seasonal and/or interannual variability may exist (Murase et al., 2002; Keiper *et al.*, 2005) and if it is understood and modelled, the likelihood of false correlations can be minimised and the adoption of effective management measures maximised. Moreover, the predictive power of the obtained models should be tested; due to the limited number of sightings, cross-validation could not be attempted.

Although the "intrinsic" factors have to be taken into account when studying cetaceans, the prey availability, as suggested in this report, seems to play a major role in the distribution and abundance of cetaceans and, therefore, more studies should be undertaken on their feeding ecology.

Finally, it must be emphasised that the use of cetaceans as ecological indicators should be accomplished with other studies where different metrics are applied, also based on other taxonomic groups, which combined will provide a comprehensive panorama of the environmental status of the marine ecosystem in compliance with the MSFD.

Despite all the remarks made above, the results obtained are certainly valuable to help achieving the ultimate goal of the MSFD, and surely helpful to other issues related with conservation and sustainable management of the marine environment.

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Appendix I. Some relevant legal instruments concerning the protection of the marine environment in European waters.

Year	*Legal Instrument*	*Appendices covering cetaceans*
1979	***Bern Convention** on the conservation of European wildlife and natural habitats*	*Appendix II: strict protection - common dolphin, bottlenose dolphin, harbour porpoise, blue whale, humpback whale, northern right whale and bowhead whale* *Appendix III: all other cetaceans may be exploited as long as regulation keeps the populations out of danger*
1979	***Bonn Convention** on the conservation of migratory species of wild animals*	*Appendix I: strict protection – blue whale, humpback whale, bowhead whale and northern right whale* *Appendix II: all other cetaceans are considered to have unfavourable conservation status*
1992	***EU Habitats Directive** (92/43/CEE) on the conservation of natural habitats and of wild fauna and flora*	*Annex 2: requiring the designation of Special Areas of Conservation (SAC) - harbour porpoise and bottlenose dolphin* *Annex 4: strict protection for all other cetaceans*
1992	***Convention on Biological Diversity***	
1992	***OSPAR Convention** on the protection of the marine environment of the North-East Atlantic*	
2002	*Plan of Implementation of the **World Summit on Sustainable Development** calling for a comprehensive, representative and effectively managed network of MPAs to be established by 2012*	
2004	***EU Council Regulation 812/2004** laying down measures concerning incidental catches of cetaceans in fisheries*	
2008	***EU Marine Strategy Framework Directive** 2008/56/EC establishing a framework for community action in the field of marine environmental policy*	

Appendix II. Number of sightings and estimated individuals of each species/family according to each variable (per classes).

Legend: *D. delphis* & *S. coeruleoalba'* refers to mixed groups of both species. Balaenopteridae: *Balaenoptera physalus* (fin whale), *B. borealis* (sei whale), *B. acutorostrata* (minke whale); Delphinidae: *Delphinus delphis* (short-beaked common dolphin), *Stenella coeruleoalba* (striped dolphin), *Globicephala melas* (long-finned pilot whale), *Tursiops truncatus* (bottlenose dolphin), *Grampus griseus* (Risso's dolphin), *Lagenorhynchus acutus* (white-sided dolphin); Physeteridae: *Physeter macrocephalus* (sperm whale); Ziphiidae: *Ziphius cavirostris* (Cuvier's beaked whale), *Hyperoodon ampullatus* (Northern bottlenose whale), *Mesoplodon bidens* (Sowerby's beaked whale).

Table 1. Depth (m)

Class	< 500		[500; 1000[		[1000; 2000[		[2000; 3000[		[3000; 4000[		[4000; 4500[		[4500; 5000[		≥ 5000	
Distance searched (km)	88,85		168,40		288,43		424,42		653,40		574,91		1776,61		481,21	
-	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind
<u>Species</u>																
Balaenoptera physalus	0	0	0	0	17	19	34	41	38	47	42	53	140	163	26	30
Delphinus delphis	0	0	2	70	24	420	12	102	37	284	15	111	22	306	0	0
D. delphis & S. coeruleoalba	2	35	0	0	5	28	6	58	19	208	3	115	33	361	0	0
Stenella coeruleoalba	0	0	0	0	0	0	10	259	3	45	5	99	18	280	7	49
Physeter macrocephalus	0	0	0	0	4	10	2	5	6	7	6	8	16	25	8	16
Globicephala melas	0	0	10	40	3	14	1	8	0	0	0	0	3	9	1	4
<u>Groups</u>																
Balaenopteridae	0	0	0	0	20	22	38	47	59	74	60	73	224	250	33	38
Delphinidae	4	38	17	135	35	468	34	436	61	543	24	329	86	1092	9	58
Physeteridae	0	0	0	0	4	10	2	5	6	7	6	8	16	25	8	16
Ziphidae	0	0	2	2	0	0	2	4	4	7	8	12	8	18	0	0

Table 2. Sea surface temperature (ºC)

Class	< 16		[16; 16,5[		[16,5; 17[		[17; 17,5[		[17,5; 18[		[18; 18,5[		[18,5; 19[		[19; 19,5[		≥ 19,5	
Distance searched (km)	61,57		368,64		314,86		367,71		427,99		939,79		754,37		679,56		395,02	
-	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind
Species																		
Balaenoptera physalus	3	4	8	10	15	16	46	62	30	33	60	71	61	68	58	70	13	16
Delphinus delphis	8	71	28	200	14	297	5	21	2	4	10	185	18	258	8	68	2	32
D. delphis & S. coeruleoalba	0	0	5	24	2	100	3	18	11	114	23	234	14	201	4	66	2	35
Stenella coeruleoalba	0	0	0	0	1	60	3	35	9	218	6	110	11	148	11	147	2	14
Physeter macrocephalus	0	0	2	3	0	0	4	7	3	5	4	10	16	26	10	17	1	1
Globicephala melas	0	0	1	8	0	0	0	0	1	2	4	19	3	7	2	6	0	0
Groups																		
Balaenopteridae	4	5	28	30	48	50	75	99	43	47	81	93	69	77	68	82	15	18
Delphinidae	8	71	36	238	20	542	12	79	25	367	51	580	49	630	30	297	7	82
Physeteridae	0	0	2	3	0	0	4	7	3	5	4	10	16	26	10	17	1	1
Ziphidae	0	0	1	2	2	8	1	1	4	5	9	15	3	7	3	4	0	0

Table 3. Chlorophyll-a (mg.m^{-3})

Class	[0,1; 0,2[		[0,2; 0,3[		[0,3; 0,4[		[0,4; 0,5[		[0,5; 0,6[		[0,6; 0,7[		[0,7; 0,8[		≥ 0,8	
Distance searched (km)	874,40		1504,26		1122,60		324,02		159,56		22,16		38,52		21,60	
	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind
Species																
Balaenoptera physalus	70	80	150	179	52	63	12	17	9	9	0	0	0	0	0	0
Delphinus delphis	3	42	19	342	15	146	10	47	20	403	0	0	27	197	0	0
D. delphis & S. coeruleoalba	1	10	17	287	22	298	6	56	1	6	0	0	8	32	0	0
Stenella coeruleoalba	9	180	13	186	7	74	4	182	0	0	1	3	0	0	0	0
Physeter macrocephalus	5	10	22	33	10	18	2	2	1	4	0	0	0	0	0	0
Globicephala melas	1	4	2	3	1	8	14	60	0	0	0	0	0	0	0	0
Groups																
Balaenopteridae	**78**	90	202	233	87	100	30	42	26	27	2	2	0	0	0	0
Delphinidae	19	246	54	824	54	651	45	392	21	409	1	3	35	229	0	0
Physeteridae	5	10	22	33	10	18	2	2	1	4	0	0	0	0	0	0
Ziphidae	2	3	9	13	4	9	4	6	2	2	0	0	0	0	0	0

Table 4. Sea surface height (cm)

Class	< 0		[0; 2[		[2; 4[		[4; 6[		[6; 8[		[8; 10[		≥ 10	
Distance searched (km)	1293,39		627,62		949,54		1074,69		255,15		103,42		152,41	
_	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind	Sig	Ind
Species														
Balaenoptera physalus	25	26	70	83	79	100	84	98	21	25	6	8	12	13
Delphinus delphis	75	880	28	313	2	19	6	75	0	0	1	6	0	0
D. delphis & S. coeruleoalba	40	387	14	122	10	251	2	35	2	10	0	0	0	0
Stenella coeruleoalba	19	337	6	144	8	142	8	93	2	16	0	0	0	0
Physeter macrocephalus	10	17	9	17	7	8	14	27	1	1	0	0	1	1
Globicephala melas	13	60	1	1	1	2	2	10	0	0	0	0	1	2
Groups														
Balaenopteridae	38	39	87	101	116	148	124	140	25	29	17	19	27	28
Delphinidae	159	1711	52	610	27	425	22	235	6	29	3	87	1	2
Physeteridae	10	17	9	17	7	8	14	27	1	1	0	0	1	1
Ziphidae	17	31	3	4	2	5	1	1	1	2	0	0	0	0