

Habitat preference of bottlenose dolphin

Habitat Preference of Bottlenose Dolphin (*Tursiops truncatus*) in Cardigan Bay

Katia Freire C F Lopes

Dissertation presented in partial fulfilment of the requirements for the degree of Master of
Marine Environmental Protection

Under the guidance of
Dr. Peter Evans and James Waggitt

School of Oceans Sciences
Bangor University
Menai Bridge
LL59 5EY
www.osp85c@bangor.ac.uk



In association with:



Submitted in September, 2017

DECLARATION



PRIFYSGOL
BANGOR
UNIVERSITY

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

This dissertation is being submitted in partial fulfilment of the requirements for the degree of Master of Science.

This dissertation is the result of my own independent work/investigation except where otherwise stated.

I hereby give consent for my dissertation, if accepted, to be available for photocopying and for interlibrary loan, and for the title and summary to be made available to outside organizations.

A handwritten signature in blue ink that reads "Katarina Lopez". The signature is written in a cursive style with a large initial 'K'.

Candidate:

Date: 15th September, 2017

ACKNOWLEDGMENTS

I would like to thank Chevening Scholarship, the UK government's global scholarship programme, funded by the Foreign and Commonwealth Office (FCO) and partnership organization for giving me the opportunity to complete my Master's degree in Bangor University. It has allowed me to gain new skills that are valuable to my work and has given me an opportunity to improve and grow as a professional and as a person.

I am very grateful for the friends I made here through my Chevening Scholarship and my flatmates who have encouraged me to excel. Together we have made the most memorable memories that I will forever cherish as I return home at the end of this journey. I could not have done it without their support.

It is with esteem and appreciation that I thank both my supervisors, Dr. Evans and Dr. Waggitt for taking me onboard on this project, who have shown great support throughout these months of arduous work. Because of their patience and commitment to this project I was able to enjoy my work and learn a great deal from them. I hope to further improve the skills I have learned under their guidance and apply the knowledge I have acquired to my work back home in the Cape Verde Islands.

There are three important women in my life that have always been there for me and without their support I would have not been here. My mother and my grandmother who have shaped my life and made me who I am today, and my dear twin sister who has always been there for me and has always believed in me even when I doubted myself. I would like to dedicate this thesis to them as a thank you for their support after all these years.

Last but not least, I would like to thank God for this opportunity and for giving me the strength to complete this journey. May He be by my side when I return home to continue the work I set out to do, protect our environment and educate others of its importance.

ABSTRACT

Understanding the dynamic functions of a species habitat use requires knowledge of its distribution and habitat characteristics which provides valuable baseline information that can be implemented in their habitat management planning. Bottlenose dolphins (*Tursiops truncatus*) are commonly found across different regions in temperate and tropical waters in both inshore and offshore habitats. Recent studies conducted in Cardigan Bay have shown a shift in the habitats used within and outside the Cardigan Bay SAC, which could be an indication of decrease in habitat quality. This study was carried out to investigate how environmental features have influenced bottlenose dolphin spatio-temporal distribution in Cardigan Bay. Data were collected from boat surveys carried out mainly by Sea Watch Foundation between 2003 and 2016 in Cardigan Bay. Generalised Additive Models were used to fit four environmental variables: bathymetry, sediment, sea surface temperature, and chlorophyll *a*. All the variables significantly influenced bottlenose dolphin group size. All variables show to significantly predict the probability of dolphin presence with exception of chlorophyll *a*. The probability of encountering a dolphin was higher in shallow waters, peaking when the sea surface temperature was $>15^{\circ}$, and in areas with small sediment size ($<200\text{mm}$). Their group size increased with increasing distance from shore, with an increase in sea surface temperature and productivity, and in areas composed of coarse sediments (sediment size ranging between 100-200mm). Their predicted distribution showed no annual changes, remaining mostly constant throughout the years with slight changes in density observed in certain areas potentially due to variation in chlorophyll *a* and SST. Furthermore, bottlenose dolphins were predominantly found in areas characterized by high productivity including reefs and estuaries suggesting that their habitat use pattern is correlated with prey availability which is driving their distribution.

Table of Contents

Declaration.....I
Acknowledgements.....II
Abstract.....III
List of Figures.....V
List of Tables.....VI
Abbreviations.....VII
Section 1- Introduction.....1
 1.1 Bottlenose dolphin conservation status and threats.....1
 1.2 Habitat preference and distribution.....2
 1.3 Cardigan Bay, West Wales.....5
 1.4 Bottlenose dolphin, in Cardigan Bay.....7
 1.5 Aims and objectives.....9
Section 2- Methodology.....10
 2.1 Study site.....10
 2.2 Data collection.....11
 2.2.1 Distance-sampling survey.....11
 2.2.2 Dedicated non-linear survey.....11
 2.3 Data analysis13
Section 3- Results.....15
 3.1 Bottlenose dolphin habitat preference.....15
Section 4- Discussion.....24
 4.1 Bottlenose dolphin habitat preference24
 4.2 Limitations and Recommendations.....28
Section 5- Conclusions.....31
Section 6- References.....32
Appendices.....43

LIST OF FIGURES

Figure 1 – Map of Cardigan Bay and Pen Llŷn a’r Sarnau Special Area of Conservation.....7

Figure 2 – Map of the UK and Cardigan Bay..... 10

Figure 3 – Distance-sampling line transect survey and bottlenose dolphin sighting survey in Cardigan Bay from 2014 to 2016.....12

Figure 4 – Non-line transect survey and bottlenose dolphin sighting survey in Cardigan Bay from 2014 to 2016.....13

Figure 5- GAM predicted smoothing splines for bottlenose dolphin as a function of their presence/absence. The dashed lines represent the 95% CI. Variable codes: Chlorophyll a (CHL), sediment (Sedi2).....16

Figure 6- GAM predicted smoothing splines for bottlenose dolphin as a function of their group size. The dashed lines represent the 95% CI. Variable codes: chlorophyll a (CHL), sediment (Sedi2).....16

Figure 7- Fitted relationship of environmental variables and probability of bottlenose dolphin presence/absence. The red dotted lines represent CI.....19

Figure 8- Fitted relationship of environmental variables and bottlenose dolphin density distribution. The red dotted lines represent CI.....20

Figure 9.1- Figure 9.1 Bottlenose dolphin predictive group density map based on GAM models result in Cardigan Bay, West Wales from 2003 to 2006, with 1km² per grid cell.....21

Figure 9.2 Bottlenose dolphin predictive group density map based on GAM models result in Cardigan Bay, West Wales from 2007 to 2010 with 1km² per grid cell.....22

Figure 9.3 Bottlenose dolphin predictive group density map based on GAM models result in Cardigan Bay, West Wales from 2011 to 2014 with 1km² per grid cell.....23

Figure 9.4 Bottlenose dolphin predictive group density map based on GAM models result in Cardigan Bay, West Wales from 2015 to 2016, with 1km² per grid cell.....24

LIST OF TABLES

Table 1 – GAM numerical results for the parametric and smooth terms from the presence/absence model for the following environmental variables: sediment (Sedi2), bathymetry (Bat), sea surface temperature (TMP), and chlorophyll a (CHL). * represents the significant terms.....17

Table 2 – GAM numerical results for the parametric and smooth terms from the presence/absence model for the following environmental variables: sediment (Sedi2), bathymetry (Bat), sea surface temperature (TMP), and chlorophyll a (CHL). * represents the significant terms.....18

ABBREVIATIONS

%	Percentage
‰	Parts per thousands
ANOVA	Analysis of variance
CV	Coefficient of variation
Defra	Department for Environment Food & Rural Affairs
EU	European Union
FAO	Food and Agriculture Organisation of the United Nations
GAM	General additive model
GLM	General linear model
GPS	Global Positioning System
hp	Horse power
HABMAP	Habitat mapping for conservation and management of the Southern Irish Sea
SAC	Special Area of Conservation
SST	Sea Surface Temperature
UK	United Kingdom

1. INTRODUCTION

1.1 Bottlenose dolphin conservation status and threats

Bottlenose dolphins are one of the most commonly known and well-studied cetacean species due to their wide distribution and accessibility (Smith *et al.*, 2013). Coastal populations are more exposed to anthropogenic threats resulting from increased development (industrial, commercial, and residential) occurring in coastal areas (Zanardo *et al.*, 2016). Dolphin species have been directly impacted by activities such as hunting, bycatch in fishing gear, and ship-strikes, in addition to indirect impacts resulting from chemical and noise pollution, overexploitation of prey resources and the effects of climate change (, 2001; Evans, 2009; Hammond *et al.*, 2013). In addition, development in marine renewable energy construction such as wind farms, wave and tidal devices, have increased the pressure on their populations, especially those inhabiting coastal areas (Carstensen *et al.*, 2006; Evans, 2009; Brandt *et al.*, 2011; Dähne *et al.*, 2013; Nuuttila *et al.*, 2017). These disturbances have proven to affect dolphin behaviour and distribution (Heithaus & Dill, 2002; Lusseau, 2005; Bejder *et al.*, 2006; Zanardo *et al.*, 2016).

Bottlenose dolphins are a wide-ranging species with a heterogeneous distribution, making it extremely challenging to gather data on their populations (Antonella *et al.*, 2017). Some areas have inshore and offshore populations that differ morphologically and genetically (Tezanos-Pinto *et al.*, 2008). Their mobility becomes challenging when it comes to delineating marine protected areas that fit their needs and can actually provide them the protection they need. Furthermore, with worldwide climate change, organisms are forced to adapt and/or migrate to cope with the alterations in their environments across space and time (Pacifci *et al.*, 2015; La Manna *et al.*, 2016). Highlighting the need to improve projections of future status of marine biodiversity that are subjected to rapid changes in conditions (Pacifci *et al.*, 2015; La Manna *et al.*, 2016). The designation of critical habitat can be established by assessing the spatial distribution of habitat features that are important to their feeding, breeding or calving (Hoyt, 2011; Keller *et al.*, 2012; Hartman & Fernandez, 2014), socializing, and resting (Lusseau & Higham 2004; Tyne *et al.*, 2015). Nonetheless, without sufficient spatial data, habitats can be under or over protected (Hartel *et al.*, 2015). An example of such cases is the protected area established in the Bay of Islands in New Zealand where studies showed that the areas previously used between 1996-2000 were barely

used in 2007-2010, consequently not providing them the protection from tourism they needed. This study showed that the dolphin habitat use patterns are very flexible and can change over time, hence the importance of re-accessing the effectiveness of static boundaries to protected areas, especially for highly dynamic species (Hartel *et al.*, 2015).

In the UK, bottlenose dolphins are protected under the 1992 EU Habitats and Species Directive (92/43/EEC) (Evans & Anderwald, 2016). Moreover, all cetaceans in European waters are listed under the Annex IV requiring strict protection (Evans & Anderwald, 2016). In 2008 the EU adopted the Marine Strategy Framework Directive (MSFD) aiming to achieve or maintain the Good Environmental Status (GES) by 2020 (Evans & Anderwald, 2016). The Member States under the same region or sub region are then required to coordinate and establish marine strategies for their waters (Evans & Anderwald, 2016). Therefore, the UK is required under the Habitats Directive to monitor bottlenose dolphin populations and report their health, life history parameters (Evans & Anderwald, 2016), abundance, movement/migration patterns, (Lohrengel *et al.*, 2017). However, in-depth knowledge of their distribution leading to the identification of critical habitats is key for implementing adequate management and mitigation plans.

1.2 Habitat preference and distribution

Marine ecosystems are characterised by physical and biological processes that are in general strongly heterogeneous in space and time (Barry & Dayton, 1991; Lambert *et al.*, 2016). Ecosystems with high environmental variability conditions are characterised by patchiness and variability in the distribution of predator resources (Hunt & Schneider, 1987; Stewart *et al.*, 2000; Lambert *et al.*, 2016), and the extent of predictability and patchiness of these resources are dependent on temporal and seasonal scales. These vary from large-scale features which are more frequent and highly predictable to fine-scale features which are ephemeral and less predictable (Lambert *et al.*, 2016). Consequently, predators over time have developed traits to adapt to such variability in order to survive (Wiens, 1989; Lambert *et al.*, 2016).

Studying habitat preferences is key to understanding the biological and ecological requirements of animals and the strategies they adopt to survive (Freitas *et al.*, 2008; Cribb *et al.*, 2015). Moreover, data on their habitat use are an essential requirement for the implementation of both management

and conservation strategies (Redfern *et al.*, 2006; Cribb *et al.*, 2015). Several studies have demonstrated that cetacean distributions can be correlated with environmental factors such as bathymetry, seabed gradients (Selzer & Payne, 1988; Baumgartner, 1997; Bailey & Thompson, 2006; Ferguson *et al.*, 2006; Azzellino *et al.*, 2008; Blasi & Boitani, 2012; Marini *et al.*, 2015), sea surface temperature (e.g. Selzer & Payne, 1988; Forney, 2000; Baumgartner *et al.*, 2001; Hamazaki, 2002; Hastie *et al.*, 2005), and salinity (e.g. Selzer & Payne, 1988; Forney, 2000; Hastie *et al.*, 2005). For instance, distance from shore and bathymetry have been shown to be strongly correlated with bottlenose habitat use (Blasi & Boitani, 2012). An example is the study conducted by Marini *et al.*, (2015) which examined how different physiographic features such as depth, distance from coast, distance from 100m contour, and slope influenced bottlenose dolphin distribution in the north-western Mediterranean Sea. Of all variables analysed, depth, distance from coast, and the 100m contour were shown to significantly influence their distribution. The study determined that in this area the dolphins preferred shallower waters and their presence decreased as the distance from shore increased beyond 5km. In addition, the study suggested such patterns could be closely related to prey distribution as one of the mostly frequently used habitats were a known nursery area for prey species that were part of the bottlenose dolphin diet (Marini *et al.*, 2015).

Spatial structuring of predator abundance and diversity in the oceans is dictated by oceanographic features where marine biodiversity is driven by sea surface temperature (Scales *et al.*, 2014). Globally, sea surface temperature drives marine biodiversity with the highest diversity taking place in mid-latitudes (Worm *et al.*, 2005; Tittensor *et al.*, 2010; Scales *et al.*, 2014). At an ocean-basin scale, the highest diversity occurs in productive zones connected to major water transitions, currents, upwellings, and bathymetric features (Chavez & Messié, 2009; Scales *et al.*, 2014). Oceanographic dynamics occurring within these productive regions form important ecological features such as fronts and eddies (see Godø *et al.*, 2012; Scales *et al.*, 2014). For example, estuaries are highly used by bottlenose dolphins because of their unique characteristics that are suitable for prey aggregation. Tidal currents are an important aspect of coastal ecosystems including estuaries as they induce environmental variability by mixing and stratifying fresh and saltwater (Largier, 1993; McLusky & Elliott, 2004; Lin *et al.*, 2013). Such processes trigger fish migration (Krumme, 2004, 2009) as they adapt to these changes and dolphin migration as they follow their prey (Karczmarski *et al.*, 2000; Carlstrom, 2005; Akamatsu *et al.*, 2010; Soldevilla *et*

al., 2010; Lin *et al.*, 2013). For instance, foraging hotspots are formed at fronts as a result of biophysical coupling where primary productivity is boosted by mixing and nutrient retention (Traganza *et al.*, 1987; Franks, 1992; Scales *et al.*, 2014). However, the degree of productivity at the fronts depends on the physical characteristics of the region, the front type and properties of the surrounding water mass (Le Fevre, 1986; Scales *et al.*, 2014). Several studies have linked dolphin's habitat use to tidal cycles. The study by Mendes *et al.*, (2002) examined the bottlenose dolphin spatial and temporal distribution relation to the tidal cycle and fronts that occurring over the flood tide in the Kessock Channel, Moray Firth. The study findings detected higher dolphin abundance during the flood tide linking their distribution with areas near the surface features of the fronts. Hence, the tidal fronts played an important role in determining the bottlenose dolphin habitat use in the area (Mendes *et al.*, 2002).

Another determining factor in species habitat use and of increased concern is the impact of anthropogenic activities. With an increase in coastal development, many regions are facing an increase in coastal activities. For instance, commercial shipping (Hildebrand, 2009; Pirotta *et al.*, 2015), boat traffic, industry development, recreational activities and cetacean tour vessels (McCarthy, 2004; O'Connor *et al.*, 2009; Pirotta *et al.*, 2015) have raised concerns about noise pollution on coastal populations, particularly those that use echolocation to navigate and forage (Nowacek *et al.*, 2007; Pirotta *et al.*, 2015). Increasingly, studies are being dedicated to understanding human impacts on marine mammal populations (Harwood & Wilson, 2001; Evans, 2009; Alter *et al.*, 2010; Becker *et al.*, 2011; New *et al.*, 2013). These studies have investigated the links between human disturbance and behavioural change, and their effects on population dynamics, as they can have detrimental effects on population health, socialisation or resting, consequently impacting key life functions such as reproduction and survival (New *et al.*, 2013). Studies investigating the effects of boat traffic on dolphin populations have shown different patterns. For instance, Mattson *et al.*, 2005 study found that motor boats and jet skis tend to cause more disturbance than larger slower moving vessels. In addition, high speed and erratic movements caused animals to change direction and behaviour. Although this study detected behavioural changes on the dolphin population as a result of cetacean watching tours (Mattson *et al.*, 2005), the study conducted by Bejder *et al.*, (2006) did not detected any behavioural changes suggesting the dolphins were accustomed to these boats. Nevertheless, boat disturbance has been shown to

cause both short-term and long-term impacts on dolphin behaviour (Papale *et al.*, 2012), leading to temporary or permanent site avoidance (Bejder *et al.*, 2006).

Several studies conducted in Cardigan Bay showed that boat presence has had a negative impact on the bottlenose dolphin population (Feingold & Evans, 2014). For instance, New Quay has experienced an increase in boat traffic coinciding with a decrease in the bottlenose dolphin population since 2006 (Feingold & Evans, 2014). Moreover, Pierpoint *et al.* (2009) found that bottlenose dolphin presence was inversely correlated with an increase in boat traffic between the years of 2004-07, raising the concern of the potential negative impacts of boat traffic in Cardigan Bay dolphin population.

Successful conservation of wild populations depends upon understanding the relationship between a population and its habitat which can be achieved primarily by identifying which habitats are used with higher frequency (Cañadas *et al.*, 2005; Dinis *et al.*, 2016). To do so, it is important to understand how environmental factors, and human pressures influence their distribution patterns.

1.3 Cardigan Bay, West Wales

Cardigan Bay is relatively shallow with depths reaching up to 60m, which contribute in part to its turbidity. The temperature in the bay fluctuates depending on the distance from the coast and the season, ranging from 5⁰ C to 16⁰ C offshore and 20⁰ inshore (SAC, 2008). Furthermore, the Bay experiences seasonal variation in salinity, and is influenced by water stratification ranging from 34.2‰ in the summer to 33‰ in the winter. The tidal current is mainly semi-diurnal with a mean spring tide roughly between 4-5m and currents not exceeding 3.3 km/h running northwards during the flood tide and southwards during the ebb tide (SAC, 2008). The substrate composition varies across the Bay and is driven by tidal currents. Areas with strong currents are predominantly composed of gravel, boulders and rocks whereas lower energy areas are composed of muds. In addition, areas closer to coast are predominantly composed of sand (SAC, 2008).

The unique habitat features of Cardigan Bay support a diversity of shellfish and fish species including sea lamprey (*Lampetra fluviatilis*), river lamprey (*Petromyzon marinus*), sand eel (Ammodytidae), and flat fish (Pleuronectidae) (Pierpoint *et al.* 2009). The Atlantic grey seals (*Halichoerus grypus*) use reefs, sandbanks and shingle/rocky beaches as resting areas, and have pups in sea caves and on remote sandy beaches. Other cetaceans include the harbour porpoise

(*Phocoena phocoena*) whilst the river otter (*Lutra lutra*) can be seen along the coast that fringes the bay. The Bay is an important breeding habitat providing shelter for bottlenose dolphin calves and food resources for adults. Other species known to use this area occasionally include the basking shark (*Cetorhinus maximus*) and leatherback turtle (*Dermochelys coriacea*) whilst a variety of seabirds' breed on the cliffs (SAC, 2008). The Bay is also an important nursery ground for a diversity of demersal fish some of which are commercially valuable (SAC, 2008).

The European Community adopted the Habitats Directive in 1992, following the Biodiversity Convention signed at the Rio Earth Summit (SAC, 2008). The goal of this EU legislation was to alert Europe to the need for all Member States to preserve biodiversity: "The aim of the Habitats Directive is the maintenance or restoration of habitats and species of European importance to a Favourable Conservation Status (FCS)" (SAC, 2008). Moreover, habitats and species listed under the Habitats Directive are protected through the designation of Special Areas of Conservation (SACs) (SAC, 2008). Due to its important breeding and foraging area for cetacean species and the unique habitat features, two SACs were established within Cardigan Bay in 2004. The Pen Llŷn a'r Sarnau SAC which is located in the north of Cardigan Bay covering an area of 1460.35 km², and comprising sea, coast and estuary habitats (Figure 2). Cardigan Bay SAC, on the other hand, is located in the southern part of Cardigan Bay encompassing an area of 960 km², with boundaries extending from Aberarth to Pembrokeshire, reaching 12 miles offshore (Figure 2). The bottlenose dolphin is the primary feature in Cardigan Bay SAC and a qualifying feature in Pen Llŷn a'r Sarnau SAC under Annex II of the Habitats Directive.

The establishment of the SAC has raised the awareness of Cardigan Bay as a critical habitat for the bottlenose dolphin (Evans, 2008). The dolphins have drawn touristic industries which have developed Cardigan Bay. Local communities have been able to benefit from the tourist development which has brought thousands of people to the area. In addition, it has encouraged research and educational programmes promoting awareness campaigns on bottlenose dolphin, other marine life, and other conservation issues faced by the local marine environment (Evans, 2008).

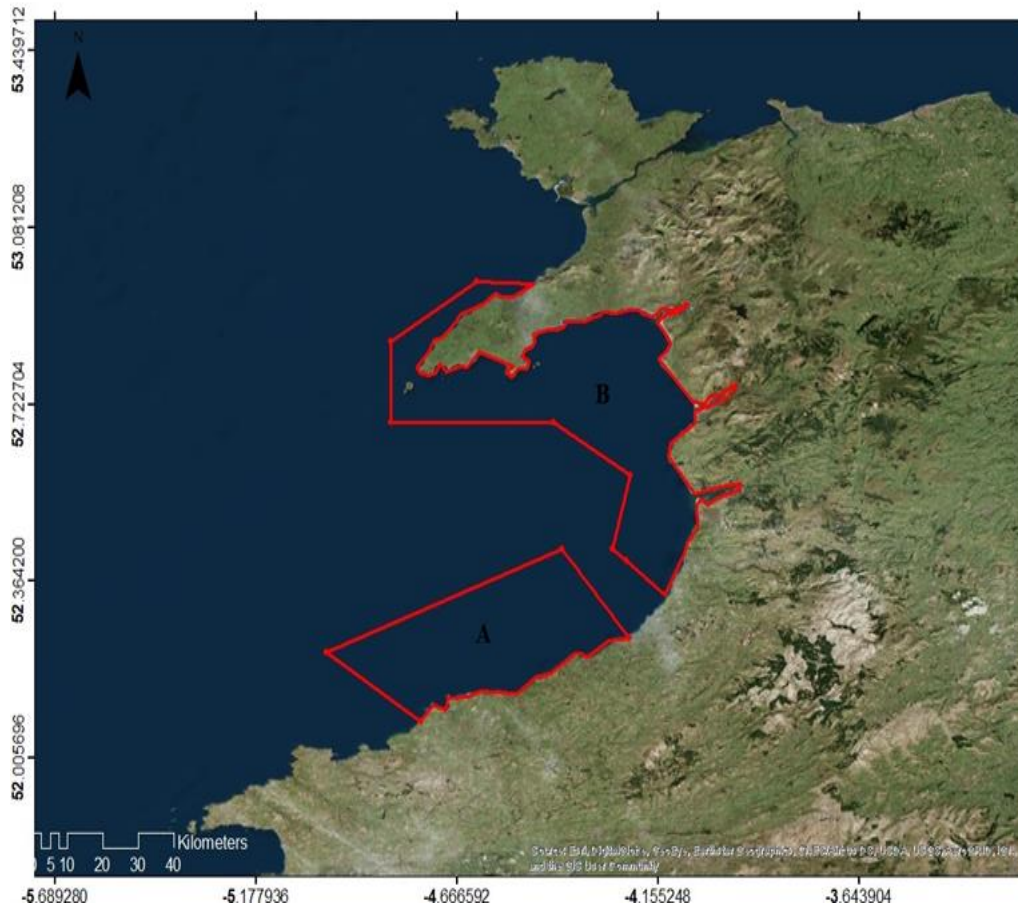


Figure 1. Map showing the location of Cardigan Bay SAC (A) and Pen Llŷn a'r Sarnau SAC (B) in Cardigan Bay, West Wales.

1.4 Bottlenose dolphins in Cardigan Bay, West Wales

The largest semi-resident coastal UK population of bottlenose dolphins occurs in Cardigan Bay in West Wales, followed by Moray Firth in Scotland (Pesante *et al.*, 2008). Cardigan Bay has been variably used by bottlenose dolphins over the years, the population being characterised as a mixture of residents, occasional visitors and transients (Lohrengel *et al.*, 2017), with 7% of individuals showing site fidelity to the Cardigan Bay SAC area (Feingold & Evans, 2014). The bottlenose dolphin population has fluctuated, rising from 129 in 2001 to a peak of 239 in 2008 but declining since then, with the latest abundance estimate being 147 individuals in the Cardigan Bay SAC (Lohrengel *et al.*, 2017). The wider Cardigan Bay was first surveyed in 2005, yielding a population estimate of 195, rising to a peak of 319 in 2009, and then declining, with the latest

estimate being 174 (Lohrengel *et al.*, 2017). Their full range is still unknown, although individuals photographed in Cardigan Bay SAC have been re-sighted off North Wales and around the Isle of Man (Feingold & Evans, 2014a, b; Norrman *et al.*, 2015; Lohrengel *et al.*, 2017). Whereas bottlenose dolphins summering in Cardigan Bay tend to disperse and migrate northwards to North Wales and beyond in winter (Feingold & Evans, 2014a, b; Lohrengel *et al.*, 2017; Nuuttila *et al.*, 2017), recognisable individuals increasingly have been emigrating from the bay and are now recorded only from North Wales or the northern Irish Sea (Feingold & Evans, 2014a, b; Lohrengel *et al.*, 2017). These changes could be an indicative of some degradation in habitat quality. These findings have highlighted the importance of careful monitoring of this population in order to understand what is causing these shifts in their distribution and implications for their conservation. Cardigan Bay is as an important breeding ground for bottlenose dolphins, where females are known to breed throughout the year although the calving season peaks during summer, with 65% of births occurring between the months of July and September (Lohrengel *et al.*, 2017). Calf mortality rates are higher during the first two years, reaching 15% in the first year, and 17% in the second year, then decreasing to 7% by the third year (Lohrengel *et al.*, 2017).

In Cardigan Bay, bottlenose dolphins are mostly sighted in small groups averaging around 5 individuals, although group sizes range from 1-20 animals (Lohrengel *et al.*, 2017). This area is mostly used by this species for feeding, socialising and nurturing calves (SAC, 2008). However, studies have also reported bottlenose dolphins displaying aggressive behaviour towards porpoises, another common species in the UK (Ross & Wilson 1996; Pesante *et al.*, 2008; Norrman *et al.*, 2015; Nuuttila *et al.*, 2017). Both species are distributed over a wide range with seasonal and diel fluctuations, their patterns showing opposite trends between the two species, suggesting potential avoidance behaviour (Simon *et al.*, 2010; Nuuttila *et al.*, 2017). Although the reasons behind this aggressive behaviour are still unknown, it is not uncommon as it has also been observed between bottlenose dolphin and other species including short-beaked common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleoalba*), and Risso's dolphin (*Grampus griseus*) (Cotter *et al.*, 2012).

Foraging cetaceans are known to prefer high productivity areas resulting from upwellings as they are rich in nutrients (Genin, 2004; Dinis *et al.*, 2016) and are typically formed by abrupt topography such as shelf breaks, steep slopes, canyons, shallow banks and seamounts (Baumgartner *et al.*, 2001; Yen *et al.*, 2004; Cañadas *et al.*, 2005; Dinis *et al.*, 2016). The habitat

features of Cardigan Bay have greatly contributed to its suitability for bottlenose dolphin as it supports various species that constitute their prey diet. For instance, the bottlenose dolphin population in Cardigan Bay has shown a preference for habitats that are characterised by steep sloping bottom topography (Ballance, 1992; Wilson *et al.*, 1997; Ingram & Rogan, 2002). Moreover, monitoring surveys have recorded dolphins displaying foraging behaviour showing preferences for certain areas within the Bay, most particularly New Quay Head, Ynys Lochtyrn, Aberporth Head, and Mwnt (Lewis & Evans, 1993; Baines *et al.*, 2000; Pesante *et al.*, 2008; Feingold & Evans 2014a). An example of some fish species known to be part of bottlenose dolphin diet include flatfish such as dab, flounder and bib (Pleuronectidae), sand-eel (Ammodytidae), pollock (*Pollachius pollachius*), wrasse (Labridae), salmon and sea trout (Salmonidae), blennies (Blenniidae), mullet (Mullidae), mackerel (*Scomber scombrus*), and sea bass (*Dicentrarchus labrax*) (Arnold, 1993; Evans *et al.*, 2002; Pierpoint *et al.*, 2009; Evans & Hintner, 2009). The prey availability is suggested to peak between the months of April and August, and to decline later in the season towards October (Feingold & Evans, 2014a). Prey distribution is likely to dictate bottlenose dolphin distribution. Hence, understanding the interaction between bottlenose dolphin and their prey and how those may affect their distribution over the years is important for their conservation. However, including prey availability data as a direct predictor of bottlenose dolphin distribution can be challenging due to the difficulties faced in sampling prey (Torres *et al.*, 2008). The alternative adopted by many, is to relate their distribution to environmental factors. Such environmental variables typically describe the habitat use either as a measure of space (e.g. water depth, bottom topography, distance to shore, or thermocline depth) or is based on the water's physical and/or chemical properties (e.g. temperature, current velocity, water clarity, salinity). These abiotic features may directly influence cetacean distribution or act upon their prey distribution (Jaquet & Whitehead, 1996; Fiedler *et al.*, 1998; Bräger *et al.*, 2003).

1.5 Aims and objectives

As previously mentioned, a shift in habitat use by bottlenose dolphins in Cardigan Bay SAC and the wider Cardigan Bay has been observed with evidence decrease in habitat use (a decrease in population size, individuals that once used the Bay sighted in other areas outside the Bay, low birth rates) (Norman *et al.*, 2015). As an area of conservation importance that supports bottlenose dolphin, a key species, it is critical to gather information and determine the reasons behind this

new pattern. Thus, modeling their distribution will help determine their habitat preference and identify the environmental features driving their distribution. To further understand the reasons behind any bottlenose dolphin population shifts within Cardigan Bay SAC and the northern Cardigan Bay area, the aim here is to study the seasonal and annual changes in habitat use by the species in Cardigan Bay by examining the relationship between observed spatio-temporal patterns and physical and oceanographic features. Through this approach, I propose to determine (1) whether the dolphins have any preferences for particular locations over others; and (2) which habitat features, if any, are associated with the preferred locations.

2. METHODOLOGY

2.1 Study Site

With a total area of 4,986.86 km², Cardigan Bay is the largest embayment in the UK, extending over 100km from the western tip of the northernmost part in the Llyn Peninsula (52° 47' 45'' N, 004° 46' 00'' W) to the southernmost area in Saint David's Head (51° 54' 10'' N, 005° 18' 54'' W) (Lohrengel *et al.*, 2017) (Figure.1).

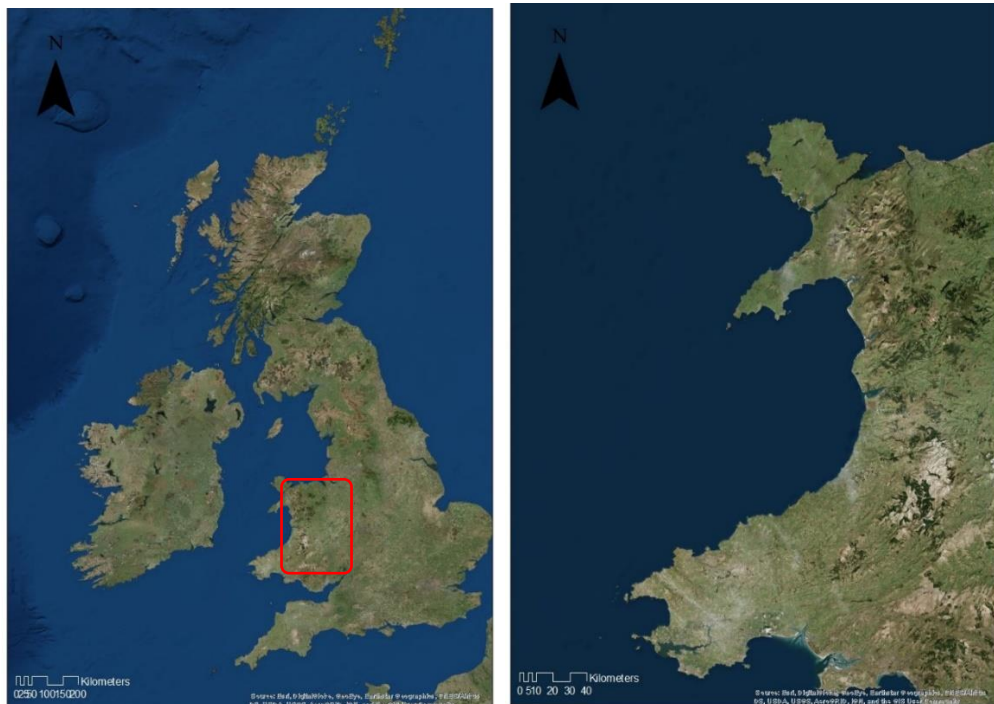


Figure 2. Map of the UK (left) and Cardigan Bay (right).

2.2 Data collection

The data used in this study were collected over a period of 14 years (2003-2016). For the purpose of this study, the surveyed area was divided into Cardigan Bay SAC and northern Cardigan Bay (the wider Cardigan Bay and Pen Llŷn a'r Sarnau SAC). To retain consistency, the data followed the same design as previous years (Pesante *et al.*, 2008). Bottlenose dolphin sightings were collected using distance-sampling line-transect and non-line transect surveys (Lohrengel *et al.*, 2017). Detailed information on the vessels used to conduct the surveys over the years is summarised in Appendix I.

2.2.1 Distance-sampling transect surveys

The surveys were conducted by a trained team including staff members from the Sea Watch Foundation (SWF). The survey vessels travelled at a constant speed, although this varied between vessels. The surveys were conducted under good weather conditions with Beaufort Sea state ≤ 3 , good visibility >1 km, and generally no precipitation. If the weather conditions were less than optimal, an alternative pre-determined transect line was chosen. However, if the bad weather persisted, the survey was abandoned.

Distance-sampling line transects (see Figure 3 for examples) were used to survey the Cardigan Bay SAC and northern Cardigan Bay. To obtain reliable estimates from distance-sampling surveys, a grid of systematically spaced lines was superimposed over the two SAC areas. In addition, Cardigan Bay SAC was split into an inshore and offshore stratum. The boundary between the strata was defined by a line between the coordinates 52.15°N, 4.89°W and 52.33°N, 4.31°W, with the outer boundary of the inshore and offshore strata at roughly 11 and 23 km from the coast. The transect numbers were randomly chosen and followed for the survey period. During the surveys, four types of effort were recorded: (1) pre-determined distance-sampling line transects with observers searching for sightings, (2) dedicated non-line transects with a single platform where observers scanned for dolphins without following a set line, (3) casual watching which took place in poor weather conditions without dedicated searching of the sea for cetaceans, and (4)

photo-identification where boats temporarily abandoned the transect line to approach and follow a group of dolphins in order to obtain photo-ID shots.

Distance sampling techniques were used to conduct the surveys, with 2-4 onboard observers. The pairing was done such that at least one observer had a minimum of 20 hours of survey experience (Feingold and Evans, 2014a). The data recorded by the observers included sightings, distance to the animal(s), angle of the animal to the boat, and their GPS position. In addition, environmental variables (sea state, visibility, swell, boat course, and transect leg) were also recorded.

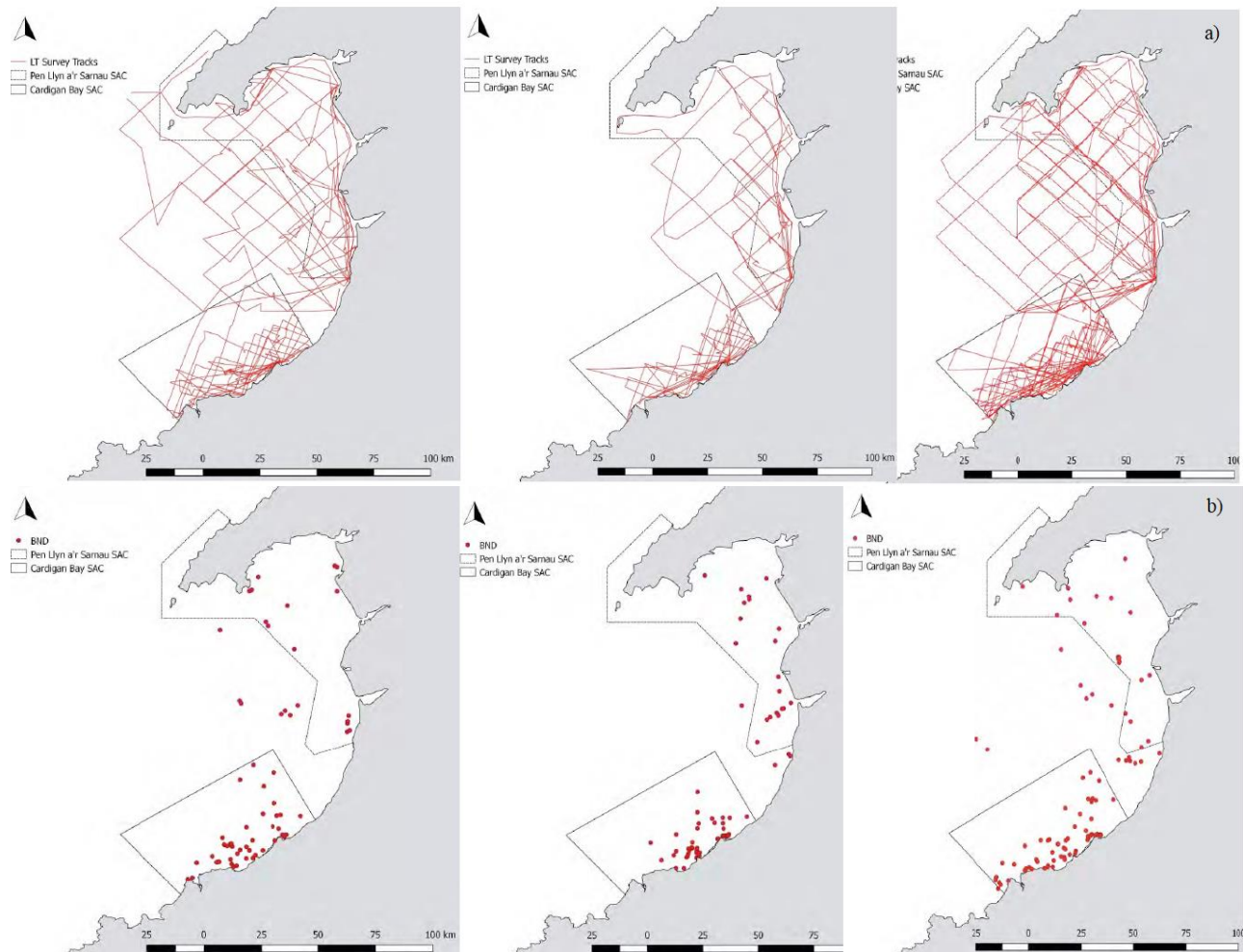


Figure 3. Survey for (a) distance-sampling line transects, (b) Bottlenose dolphins sighted using dedicated non-line transect survey in Cardigan Bay in 2014 (left), 2015 (middle), and 2016 (right) (from Lohregel *et al.*, 2017).

2.2.2 Dedicated non-line transect surveys

Dedicated non-line transect surveys were conducted only when conditions were less than ideal or the survey time was limited to a certain period. They used the same general protocols as line transects but did not follow a set transect line (Figure 4).

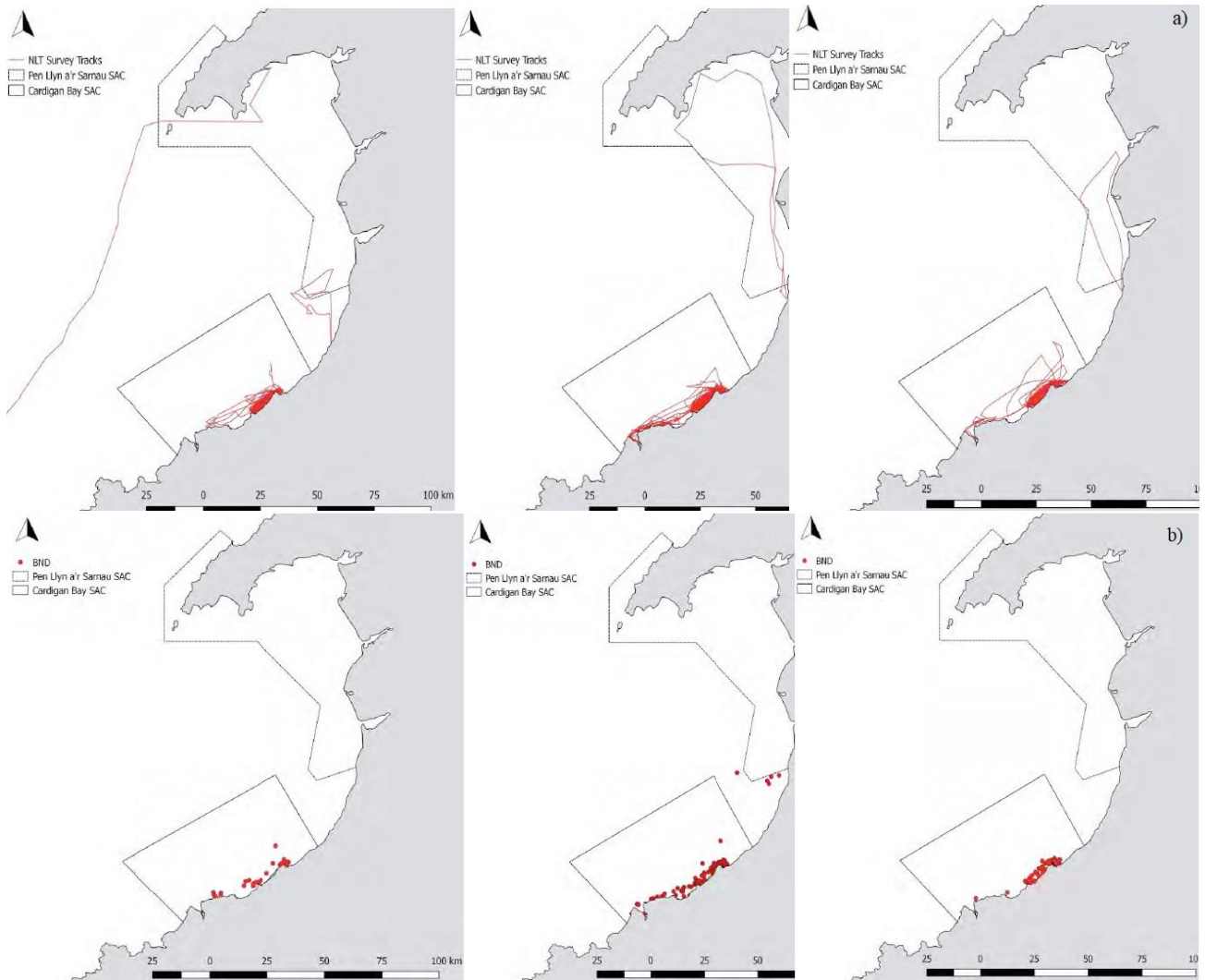


Figure 4. Survey for (a) dedicated non-linear transect, (b) Bottlenose dolphin sighted using dedicated non-linear transect survey in Cardigan Bay in 2014 (left), 2015(middle), and 2016 (right) (from Lohrengel *et al.*, 2017)

2.3 Data analysis

Bottlenose dolphin abundance estimates for the years 2003-2016 in Cardigan Bay SAC were calculated using Multiple Covariate Distance Sampling test from Mark-recapture distance sampling (MRDS) using R (Lohrengel *et al.*, 2017). The environmental data were chosen based on data availability or because they were applied in previous studies showing their potential ecological significance. The environmental features (chlorophyll *a*, bathymetry, current speed, sea surface temperature and bathymetry anomaly) were provided by the NOAA MODIS Satellite system. The sediment data was provided from HABMAP and categorised by following the Krumbein phi scale. The sediment size was categorised based on their grain size from fine to large sediments prior to being fitted into the model (Appendix II). The different categories consisted of sand, mud, gravel, rock, pebble, cobble, mixture, and a mosaic with rock. A monthly average of data between April-August for the years 2003 to 2016 was used for the environmental features, where the mean value for each feature was estimated for each grid cell. The data sets were processed to generate corresponding grid for the environmental data at the selected resolution of 1km² which covered an area of 8991 km².

The grid cells described were used as data units where the sea state and the vessel height were covariates. The dolphin density per 1km² grid cell was calculated by dividing the number of dolphins by the area covered in that grid cell. The maximum degrees of freedom, measured as number of knots, allowing for the smoothing function were restricted to the main effects at $k=3$ (Giannoulaki *et al.*, 2017).

All the data analyses were performed in R Studio v. 1.0.143 using the mgcv package (Zuur *et al.*, 2009). The statistical approach chosen to determine dolphin-habitat relationships on a fine spatial scale was Generalised Additive Models (GAM), a semi-parametric extension of GLM, were used as well. In this study, GAM with negative-binominal structure was used to related bottlenose dolphin density with environmental variables. To address possible heterogeneity, the dataset was also converted into presence/absence data to increase the number of replicates for non-zero data. For presence/absence data, GAM model with binomial structure was fitted. Prior to the model fitting process, the Pearson correlation analysis was carried out to test correlation among environmental variables (Appendix III). The Pearson coefficient (*r* value) from two variables that were either lower than -0.5 or higher than 0.5 were considered correlated, and removed from the

model. Current speed and bathymetry anomaly were correlated to bathymetry and *SST* and thus were removed from modelling processes. Model selection was performed using AIC values. The best fitted model, which had the lowest AIC, were used to create density prediction maps (Appendix IV) (Zuur *et al.*, 2009). The best fitted model included the following variables (bathymetry, sediment size, chlorophyll *a*, and temperature). The environmental factors were fitted through the model as parametric and as smoothing terms to determine the bottlenose dolphin presence and group size in each cell. The sea surface temperature (*SST*) and bathymetry were fitted as parametric terms while chlorophyll *a* and sediment were fitted as smoothing terms. The result from both models were combined into single predicted grid. The predicted values in each cell was calculated by multiplying the probability of bottlenose dolphin presence by their group size. Additionally, to predict the probability of bottlenose dolphin presence and group size, the fitted lines were constricted by changing the environmental a particular environmental factor and maintaining the remaining variables constant.

3. RESULTS

3.1 3.1 Bottlenose dolphin habitat preference

The optimal GAM models for presence/absence and for group size included bathymetry, sea surface temperature, chlorophyll *a*, and sediment type (Figure 5).

Habitat preference of bottlenose dolphin

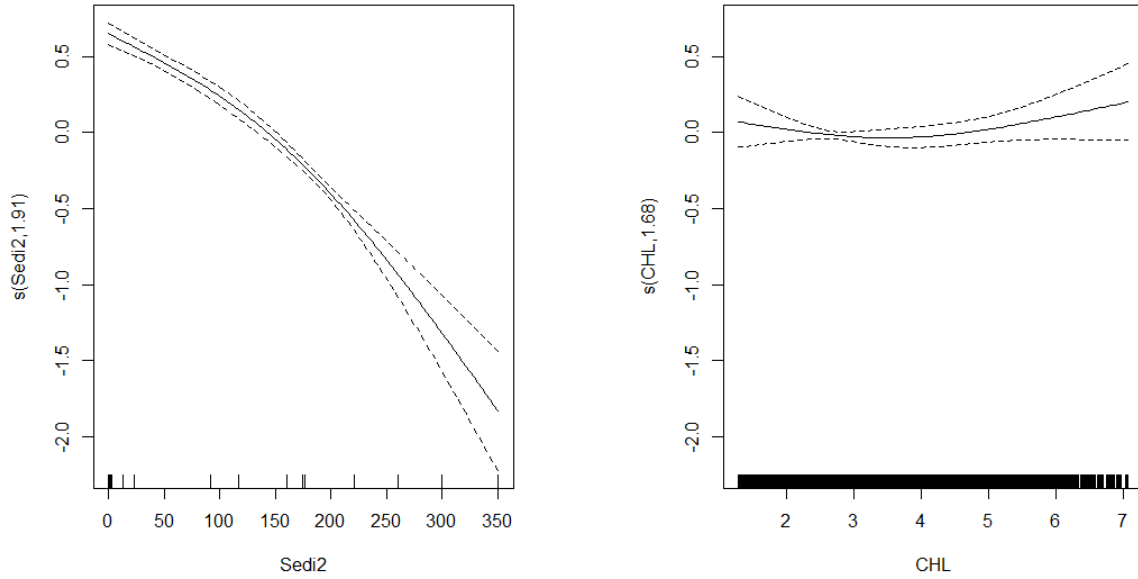


Figure 5. GAM predicted smoothing splines for bottlenose dolphin as a function of their presence/absence. The dashed lines represent the 95% CI. Variable codes: Chlorophyll *a* (CHL), sediment (Sedi2).

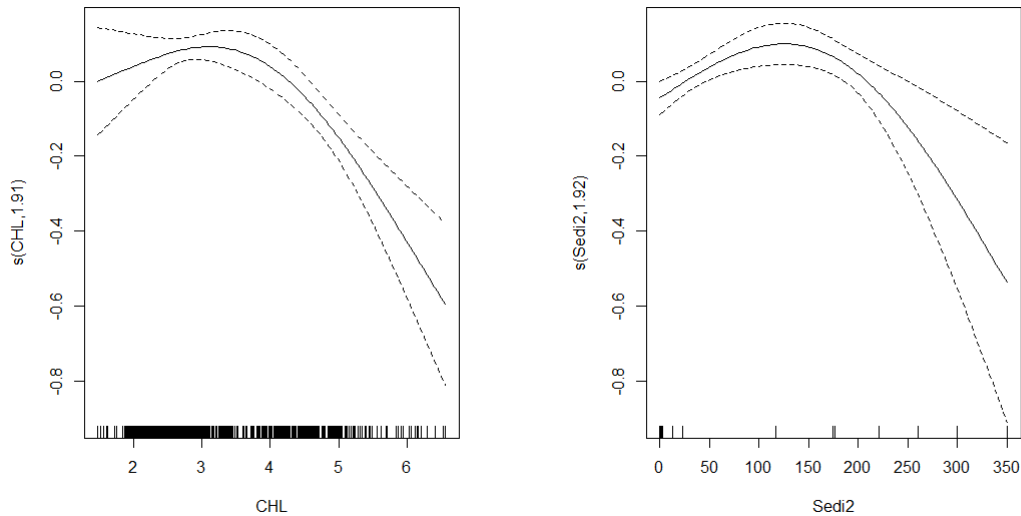


Figure 6. GAM predicted smoothing splines for bottlenose dolphin as a function of their group size. The dashed lines represent the 95% CI. Variable codes: chlorophyll *a* (CHL), sediment (Sedi2).

The GAM model used to verify smoothing terms showed that both parametric and smoothing terms yielded a significant effect between these two environmental features and bottlenose distribution (Tables 1 and 2). Moreover, the binomial (presence/absence) and the negative binomial (density) models performed with 9.38% and 6.96% deviance explained respectively.

Table 1. GAM numerical results for the parametric and smooth terms from the presence/absence model for the following environmental variables: sediment (Sedi2), bathymetry (Bat), sea surface temperature (TMP), and chlorophyll *a* (CHL). * represents the significant terms.

Approximate significance of smooth terms:

Predictors	Ref.df	Chi.sq	p-value
s(Sedi2)	1.992	374.728	<0.001*
s(CHL)	1.899	2.906	0.269

Parametric Terms:

Predictors	Chi.sq	p-value
Bat	779.65	<0.001*
TMP	87.42	<0.001*

Deviance explained = 9.38%

Table 2. GAM numerical results for the parametric and smooth terms from the density model for the following environmental variables: sediment (Sedi2), bathymetry (Bat), sea surface temperature (TMP), and chlorophyll *a* (CHL). * represents the significant terms.

Approximate significance of smooth terms:

Predictors	Ref.df	Chi.sq	p-vale
s(CHL)	1.992	32.91	<0.001*
s(Sedi2)	1.993	13.73	0.001*

Parametric Term:

Predictors	Chi.sq	p-value
Bat	74.238	< 0.001*
TMP	8.044	0.0046*

Deviance explained = 6.96

The prediction function model found a higher probability of dolphin presence in areas of smaller sediment size. However, larger groups of dolphins were encountered in areas with coarse substrate. The probability of sighting dolphins increased closer to the coast, whereas their group size increased with an increase in distance to the coast. In addition, dolphin presence and group size increased with increase in sea surface temperature. Chlorophyll *a* was shown to influence bottlenose dolphin group density, which increased to an optimal level of 4 ppm and then decreased with increase in chlorophyll *a*, however the probability of dolphin occurrence was not significantly correlated to chlorophyll *a* (Figure 6).

Habitat preference of bottlenose dolphin

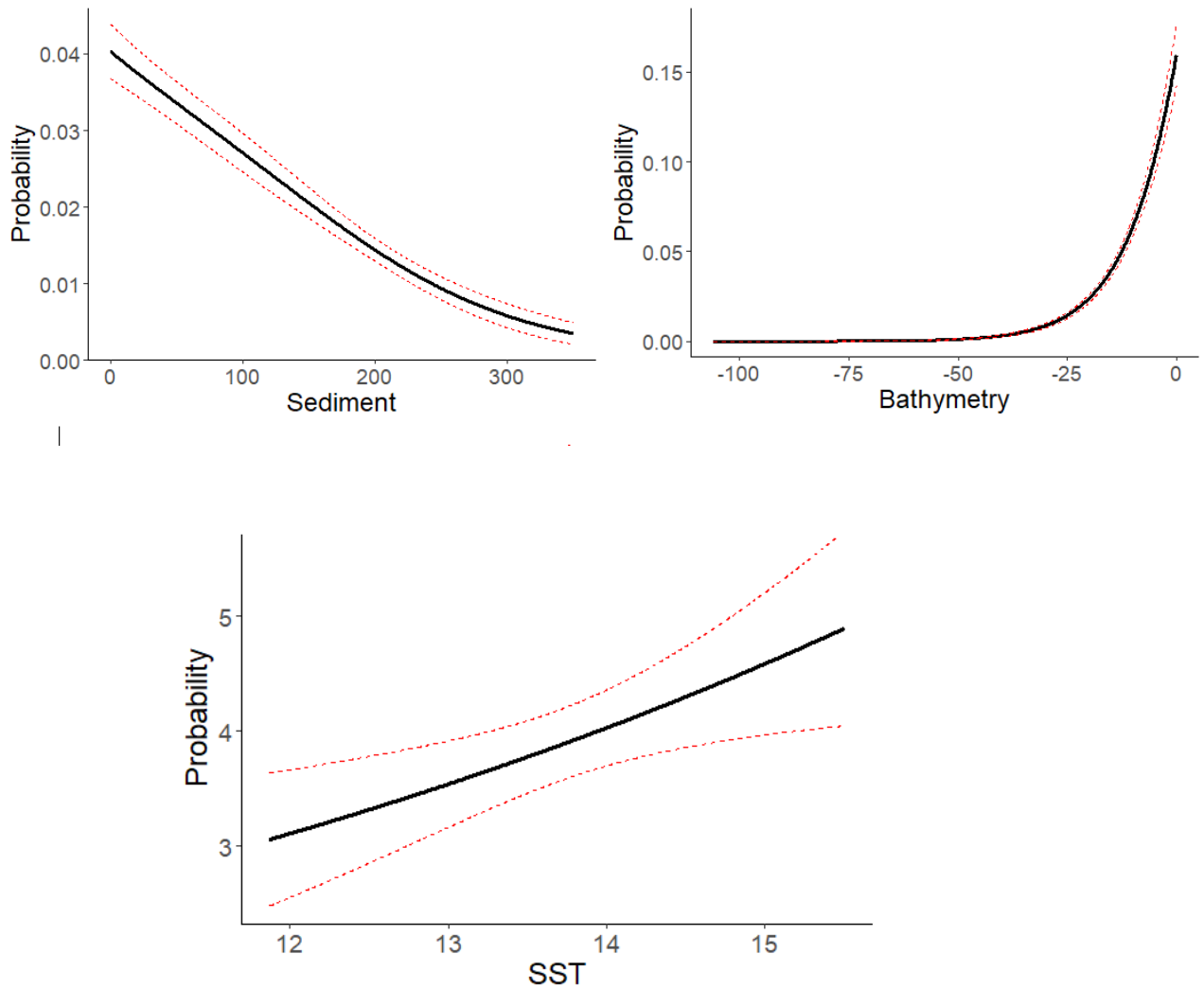


Figure 7. Fitted relationship of environmental variables and probability of bottlenose dolphin presence/absence. The red dotted lines represent CI.

Habitat preference of bottlenose dolphin

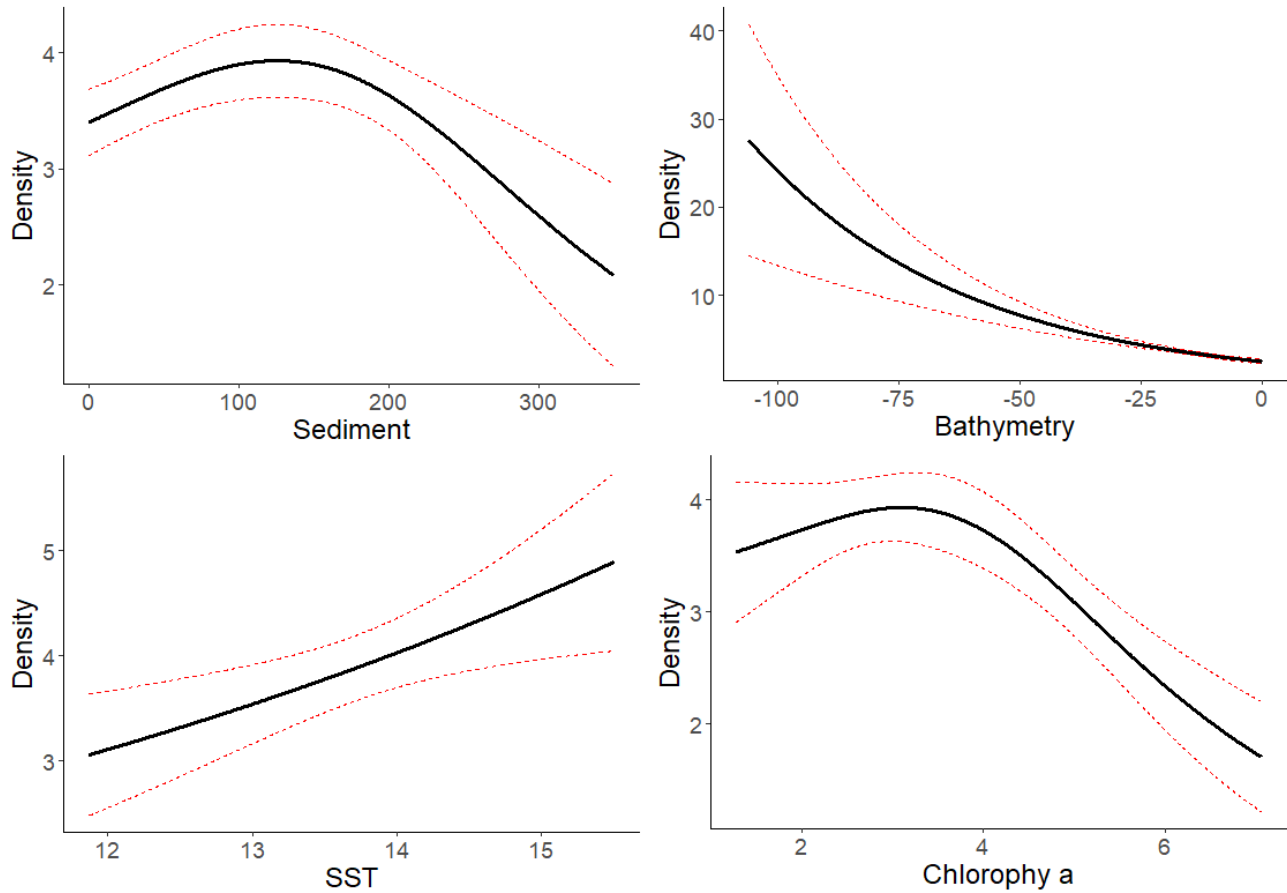


Figure 8. Fitted relationship of environmental variables and bottlenose dolphin density distribution. The red dotted lines represent CI.

The density prediction output maps displayed in Fig. 7 show bottlenose dolphin distribution patterns with highest frequencies predominantly in the northwards including Pen Llŷn a'r Sarnau SAC, and to a lesser extent in the south in Cardigan Bay SAC. These finds differ from the sighting patterns observed during the survey conducted in the Bay (see Appendix V). In addition, they were present predominantly in the shallow areas of Cardigan Bay. Moreover, group size varied between 2 to 7 dolphins, although mostly in small groups (up to 2 individuals). The largest groups were concentrated in the northern areas in Pen Llŷn a'r Sarnau SAC. The analysis found no obvious annual change between April and August on bottlenose dolphin distribution patterns remained relatively constant through the years. The dolphins seem to be present in areas of higher productivity such as reefs and estuaries.

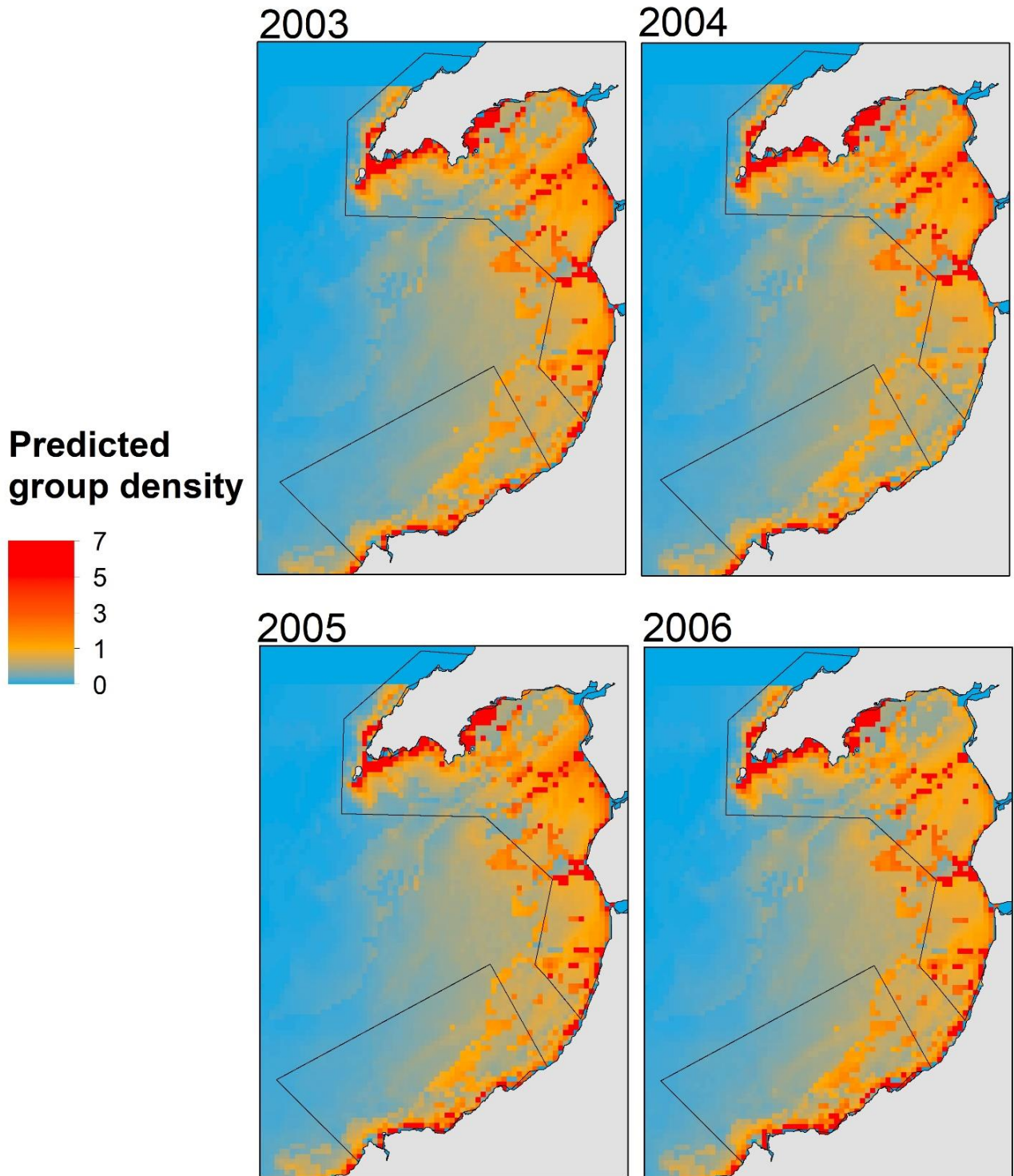


Figure 9.1 Bottlenose dolphin predictive group density map based on GAM models result in Cardigan Bay, West Wales from 2003 to 2006, with 1km² per grid cell.

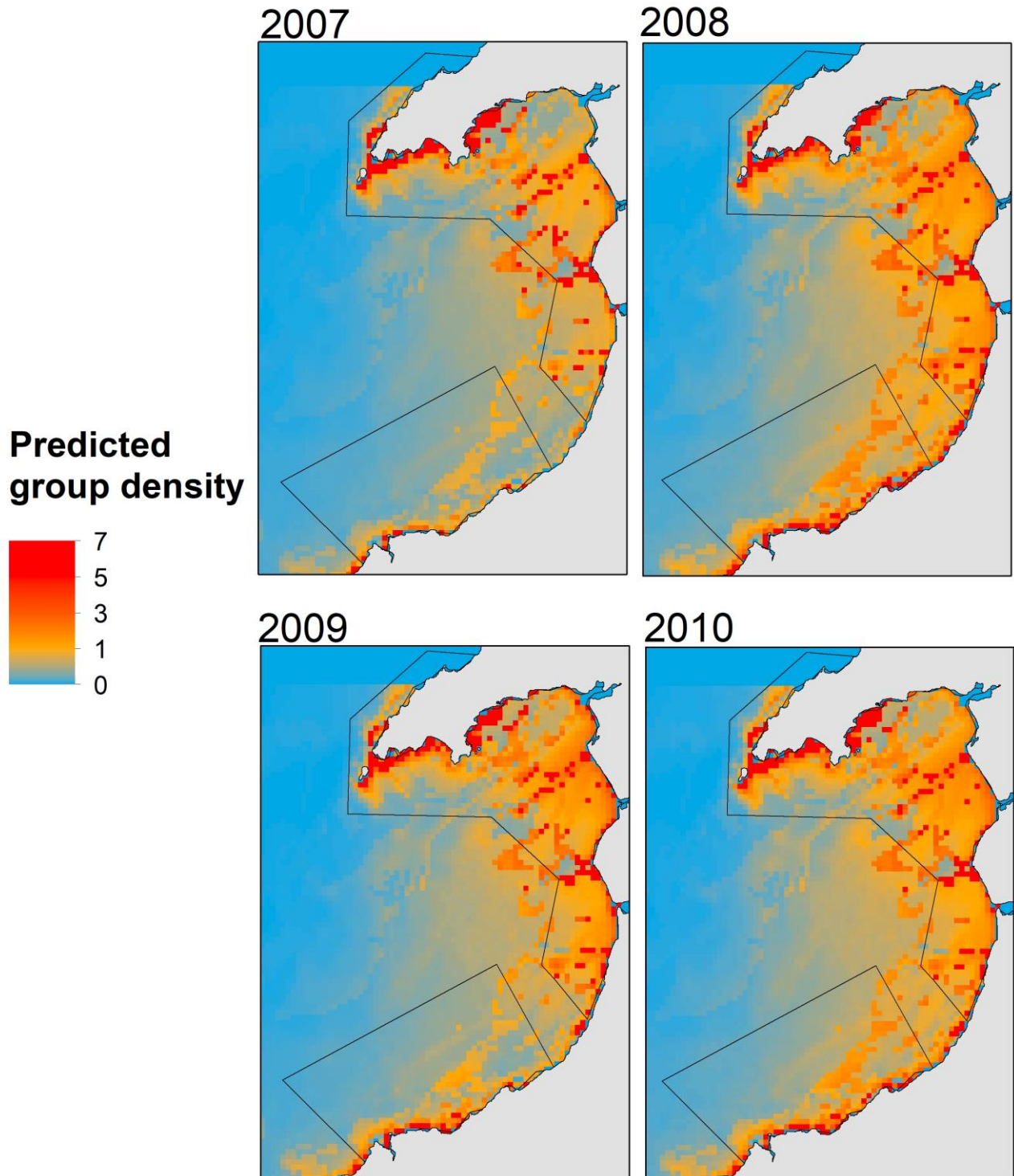


Figure 9.2 Bottlenose dolphin predictive group density map based on GAM models result in Cardigan Bay, West Wales from 2007 to 2010, with 1km² per grid cell.

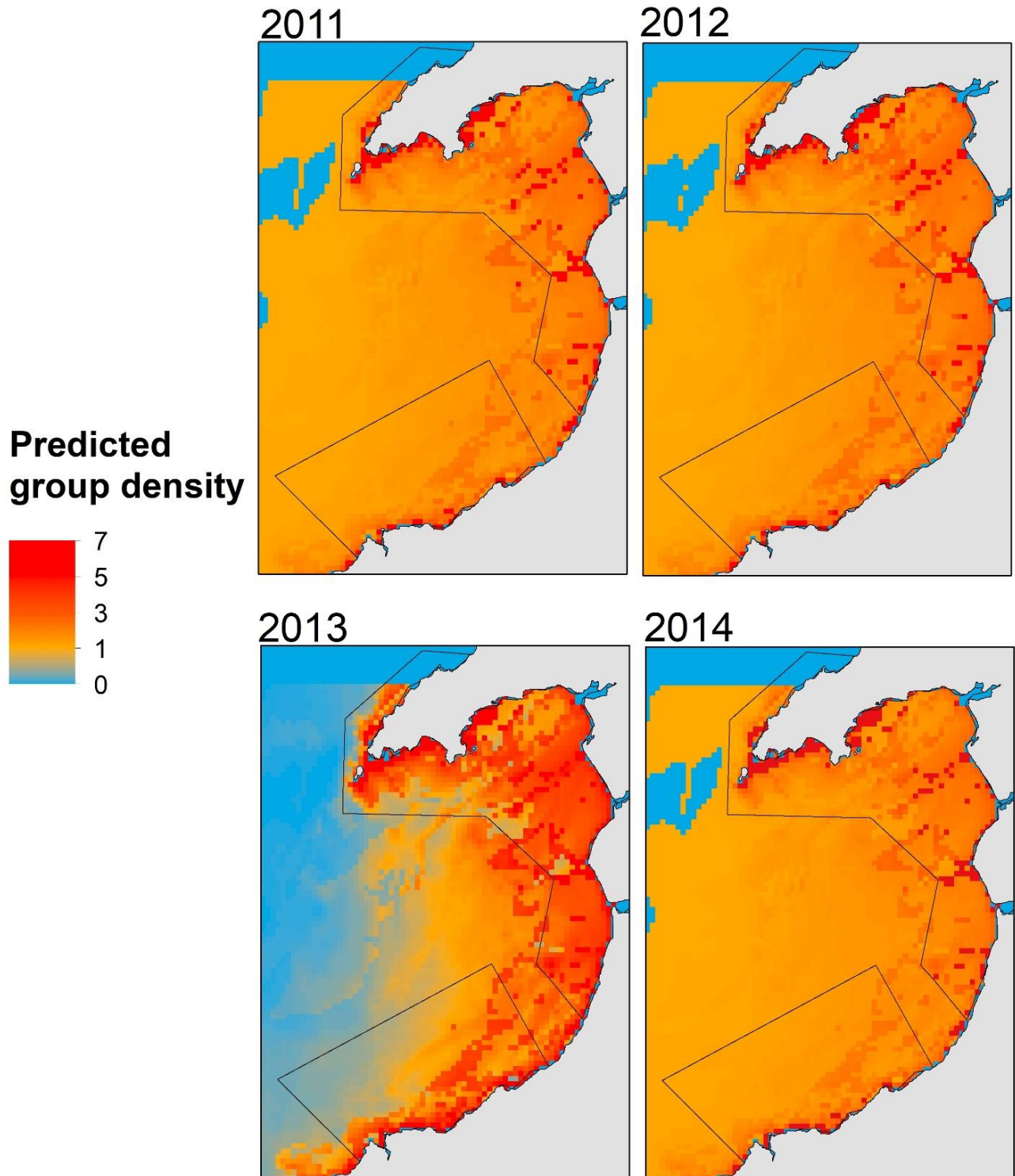


Figure 9.3 Bottlenose dolphin predictive group density map based on GAM models result in Cardigan Bay, West Wales from 2011 to 2014, with 1km² per grid cell.

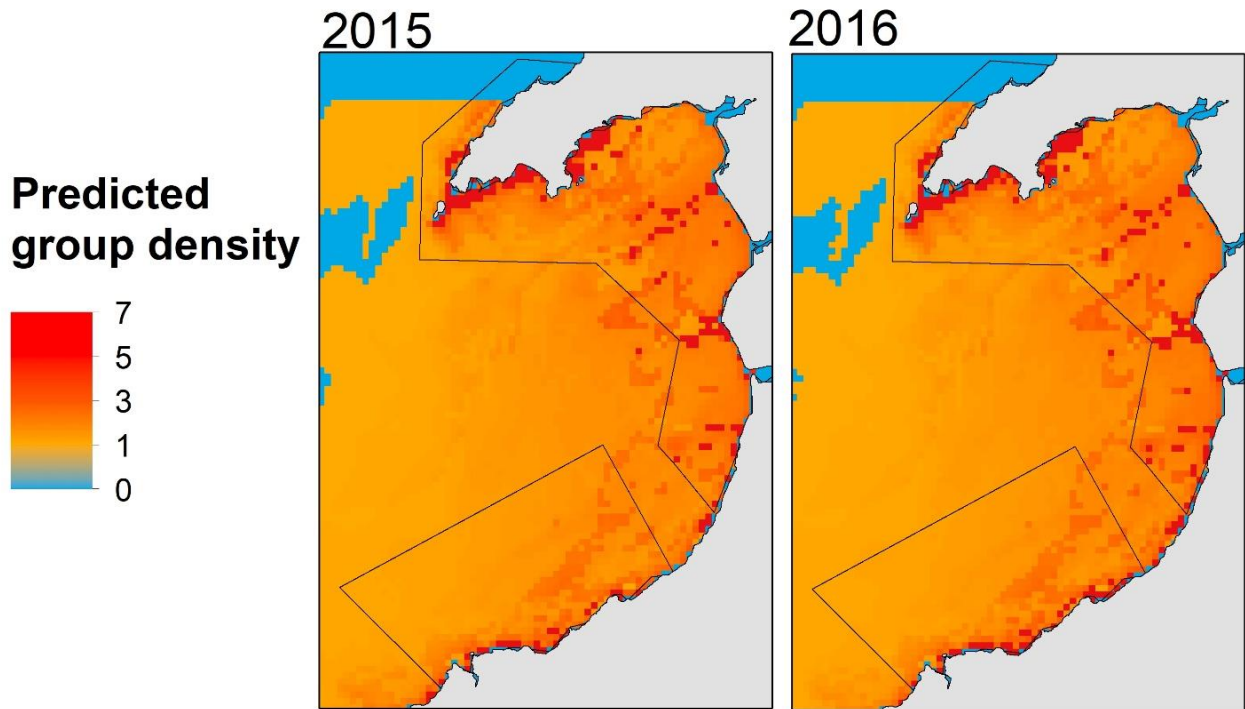


Figure 9.4 Bottlenose dolphin predictive group density map based on GAM models result in Cardigan Bay, West Wales from 2015 to 2016, with 1km² per grid cell.

4. DISCUSSION

4.1 Bottlenose dolphin habitat preference

Determining which environmental features are driving marine mammal distributions and habitat preferences is vital to understanding ecological processes and for planning of effective conservation measures. In fact, various environmental factors have been linked to bottlenose dolphin distributions. However, their role varies across regions and species, impeding any generalisation of their relationship (Blasi & Biotani, 2012). Hence, clear understanding of which environmental variables influence bottlenose dolphins will facilitate the implementation of management plans that will effectively protect this species and their habitat.

This study was set out to determine bottlenose dolphin habitat use patterns and the environmental features influencing its distribution in Cardigan Bay. The findings have identified important habitats and the environmental drivers associated with them that influence bottlenose dolphin distribution in this region. For instance, bathymetry is shown to predict bottlenose distribution in Cardigan Bay where the probability of sighting a dolphin increased in shallow waters and decreased with increasing distance to shore, while group size increased with increasing depth. For instance, shallow waters are known for concentrating cetaceans due to their abrupt topography which are characterized by shelf breaks, steep slopes, canyons, shallow banks and seamounts (Baumgartner *et al.*, 2001; Yen *et al.*, 2004; Cañadas *et al.*, 2005; Dinis *et al.*, 2016). In addition, features such as islands, headlands and channels can cause currents to change pattern creating small eddies and fronts (Johnston & Read 2007; Bailey & Thompson, 2010). These features are highly productive resulting from upwelling-driven nutrients available (Genin 2004; Dinis *et al.*, 2016) which in turn aggregate different prey species attracting top predators. Other research investigating bottlenose distribution has also found bottlenose dolphin showing preference to shallow waters. An example is the research by La Manna *et al.*, 2016 conducted in Lampedusa which investigated the relationship between environmental variables to spatial and temporal distribution of bottlenose dolphin using a Species Distribution Model, most particularly the Maximum Entropy method. In their study, the dolphins were predominantly found close to the island's coast occurring with most frequency in areas with depths not exceeding 60 m (La Manna *et al.*, 2016). Furthermore, these represented critical areas for this species because they supported complex feature such as reef and sea grass bed (Lloret *et al.*, 2002; La Manna *et al.*, 2016) which provided optimal feeding grounds. The group size differences between shallow and deep waters could be a foraging strategy used by dolphins to adapt to the prey distribution. For example, large groups are believed to occur in deeper waters and this can be used as an effective foraging strategy when feeding on large patches of prey where there is enough prey benefiting each group member, or when shoals of prey are in midwater and require herding to the surface. Shallow water supports smaller prey patches thus being more efficient to hunt solitarily or in smaller groups (Neumann, 2001; Cañadas & Vazquez, 2017). Therefore, bathymetry can be indirectly linked to bottlenose dolphin distribution and used as proxy for prey availability (Marini *et al.*, 2015). Additionally, shallow waters could be potentially used as shelter by mother and calves from adult male harassment (Hartman & Fernandez, 2014). Calves lack basic survival skills and become more

vulnerable in deeper waters as mothers would need to leave them unattended while descending to forage (Hartman & Fernandez, 2014). This behaviour is widely adopted by a range of mammal species and some studies have been able to document their occurrence. For instance, humpback whales (*Megaptera novaeangliae*) (Craig *et al.*, 2014), dusky dolphin (*Lagenorhynchus obscurus*) (Weir *et al.*, 2008), and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) (Fury *et al.*, 2013) maternal female have been observed to choose habitats that males would less likely be present (Craig *et al.*, 2014).

According to this study's result, sediment size was an important feature determining bottlenose dolphin distribution, where the probability of sighting a dolphin increased in areas with smaller sediment sizes. In addition, dolphin group size changed as sediment size changed with larger group sizes aggregating over coarse sediments. A possible explanation for the observed pattern is the patchiness in the distribution of prey resources across Cardigan Bay. Mixed sediments are typically found in reef features of the SAC areas, which support rich and diverse benthic communities (SAC, 2008). Consequently, these areas would also support a diversity of prey species which in turn attract aggregations of dolphins towards these locations (SAC, 2008). For instance, Gregory & Rowden (2001) suggested the variation of dolphin group size can be associated with foraging strategy. Where larger groups of dolphins forage in shallower waters in search of inconspicuous prey species which require more dolphins to search for prey (Gregory & Rowden, 2001). On the other hand, deeper waters pelagic species are less conspicuous and can be detected more easily requiring less search time and fewer dolphins (Gregory & Rowden, 2001). Doing so could be beneficial to the dolphins as it would reduce their energy cost and increase their foraging success rate.

A positive relationship was observed between bottlenose dolphin distribution and sea surface temperature (*SST*) as the probability of encountering a dolphin and their group size increased with an increase in temperature. *SST* can be associated with nutrient-rich upwelling (Croll *et al.*, 1998; Bräger *et al.*, 2003), supporting a diversity of prey species which is ideal for bottlenose dolphin as they feed on a wide range of species (Giannoulaki *et al.*, 2017). Similar findings were observed in research conducted by Bräger *et al.* (2003) who investigated the importance of water depth, water clarity and *SST* on habitat selection of Hector's dolphin (*Cephalorhynchus hectori*) in New Zealand. In their study, all three parameters significantly influenced Hector's dolphin habitat selection. A positive correlation had been previously established between *SST* and some prey

species suggesting that their habitat preferences were indirectly associated with resource availability. In addition, to food availability, *SST* was an important factor for habitat selection because of its benefits to thermoregulation and reduced energy demands for mothers and calves (Bräger *et al.*, 2003). For instance, calving has been linked to warmer water temperatures in bottlenose dolphins (Mann *et al.*, 2000; Smith *et al.*, 2016). During the calving season, both food and warmer water are important as they provide the mothers with enough resources during the lactation period which could improve the mother's milk production and promote rapid calf growth while minimising thermoregulation-related stress, increasing infant survival (e.g., Rutberg, 1987; Gaillard *et al.*, 1993; Rechsteiner *et al.*, 2013; Fruet *et al.*, 2015), in addition to providing shelter from predators (Hartman & Fernandez, 2014). Cardigan Bay is known as an important breeding ground for this species (Lohrengel *et al.* 2017), and *SST* could be playing an important role for the site selection by mother and calves.

Chlorophyll *a* did not significantly predict the probability of detecting a dolphin, however they significantly predicted their group size. Being responsible for primary production, chlorophyll *a* could be used as a proxy for other biotic features (Moure *et al.*, 2012; La Manna *et al.*, 2016) such as the distribution of zooplankton, or zooplankton eating fish (La Manna *et al.*, 2016), and may be used to determine dolphin habitat preferences based on their prey distribution. Hence, areas with high productivity levels would be expected to aggregate prey and attract dolphins. As previously explained dolphins tend to associate with other dolphin as a foraging strategy to maximize their successful rate of capturing their prey (Cañadas & Vazquez, 2017). Therefore, areas with high concentration of chlorophyll *a* are more likely to attract larger groups of dolphins. In this study, bottlenose dolphin group size increased with increased productivity being a good indicator of key foraging areas. Moreover, from these results it can be inferred that resources are patchily distributed which could drive their distribution patterns and influence their foraging behavior. La Manna *et al.*, (2016) aimed at investigating the spatial distribution patterns of bottlenose dolphins at different temporal scales in the southern Mediterranean Sea found chlorophyll *a* to be the second strongest predictor and was a good proxy for prey availability. Their study showed chlorophyll *a* to be a useful parameter in identifying important hotspots where they aggregate (La Manna *et al.*, 2016). The locations in Cardigan Bay associated with higher dolphin frequency and larger group sizes were in close proximity to reefs and estuaries which are known to support high diversity of species.

Aside from a slight variation in group density, the annual distribution of bottlenose dolphin remained relatively constant between 2003 and 2016. Dolphins were predominantly found in shallow areas with some transient occurrences in deeper areas. The locations with the highest group densities were close to estuaries and reef areas. Estuaries have been shown to represent important habitats for dolphin species as they are characteristically rich in nutrients and support high concentrations of many prey species (Crib *et al.*, 2013), in addition to being used as nursery areas (Lusseau, 2005). Reef systems are another important feature of Cardigan Bay and Pen Llŷn a'r Sarnau SAC areas, supporting a diversity of benthic communities which leads to species rich communities (SAC, 2008). Consequently, the reef systems are directly or indirectly contributing to the food source of many species in the bay including the bottlenose dolphin (SAC, 2008). The surveys conducted in this area were able to determine certain locations in the norther Cardigan Bay, including and Tremadog Bay, to be key to bottlenose dolphin. Whereas areas that have been shown to be important and have been used either for shelter, nursing or feeding (New Quay, Ynys Lochtyn, Aberporth, Teifi Estuary) were being used to a lesser extent when compared to the northern parts (Pesante et al., 2008). According to previous surveys conducted in Cardigan Bay (see Appendix V), dolphins were mostly sighted in Cardigan Bay than in Pen Llŷn a'r Sarnau SAC, however that could be explained by the increased survey effort in Cardigan Bay compared to Pen Llŷn a'r Sarnau SAC. Even though the Pen Llŷn a'r Sarnau SAC was less surveyed the encounter rate in this area suggested the probability of seeing a dolphin in this area were high considering the amount of survey conducted in this area. Additionally, anthropogenic factors could also be affecting their movement as increasing boat traffic in the Cardigan Bay SAC or scallop fisheries could be potentially driving their distribution to areas of less disturbance. Nevertheless, Cardigan Bay SAC still remain an important area for dolphin population in this area.

4.2 Limitations and Recommendations

A limitation to this study was the correlation between some environmental factors which did not allow one to model some interesting variables such as current speed and bathymetry anomaly. Moreover, other factors that were not included in the study that could also have an impact include anthropogenic factors with their potential negative impacts on bottlenose dolphin populations. This aspect is really important when it comes to Cardigan Bay because besides its conservation value,

Cardigan Bay SAC is of significant economic importance in Wales, creating some conflicts of interest between the two (Lambert *et al.*, 2015). Recently the Welsh government approved the expansion of scallop fishery into the marine protected area raising concerns of its potential negative impacts on critical habitat features that bottlenose dolphins depend upon. This type of fishery is one of the most damaging to the seabed communities and may indirectly affect bottlenose dolphin populations as it can deplete prey availability making the habitat unsuitable (Craven *et al.*, 2013). However, the degree to which an area is affected by fishing disturbance is dependent on the degree of fishing activity relative to natural disturbance, the habitat type, and the prey species in the area (Collie *et al.*, 2000, Kaiser *et al.*, 2002, Henry *et al.*, 2006, Kaiser *et al.*, 2006, Lambert *et al.*, 2011; Sciberra *et al.*, 2013). Nevertheless, benthic habitats such as reefs are more susceptible to the negative impacts of scallop dredging, and their removal can have adverse effects on the local biodiversity and recruitment processes (Howarth & Steward, 2014). Such changes to the habitat could lead to a cascade event affecting top predator species. Consequently, in order to cope, predators may be forced to seek prey elsewhere, causing a shift in habitat use. Previous studies conducted in Cardigan Bay SAC did not detect any negative impact of dredging upon the benthic community. However, these studies were focused on areas used with less frequency by bottlenose dolphin. Therefore, to accurately understand the potential effects of scallop fishery on bottlenose dolphin distribution patterns, studies should be conducted on the habitats that both dolphins and dredging activities occur and across different habitat types within the SAC area.

This study used static (bathymetry and sediment type) and dynamic (SST and chlorophyll *a*) variables to describe bottlenose dolphin habitat use patterns in Cardigan Bay. From the results, it can be inferred that static variables were important predictors of dolphin distribution as their presence in an area and group size were strongly correlated to depth and sediment size. Since their distribution remained relatively constant over the years, static MPAs here may be adequate for protection of this species in this area. In addition, this population seems to use small areas within the Bay for foraging, nursing and shelter, suggesting the best management plan for it is already in place, i.e. the protection of a number of small areas within the Bay. However, caution is needed, as they are mostly found in proximity to the coast and more vulnerable to anthropogenic impacts. Anthropogenic activities in the area are also experiencing an increase as boat traffic has increased and scallop dredging has been expanded into other areas within Cardigan Bay SAC. Therefore, further research examining the implications of the increase in such activities are required as they

can potentially affect bottlenose dolphin distribution. Another important aspect to consider is bottlenose dolphin interaction with their prey distribution as all the environmental variables in this study were either directly or indirectly interacting with prey availability and distribution which in turn influenced bottlenose dolphin distribution. Thus, future studies on bottlenose dolphin prey distribution is key in understanding the patterns of their habitat use.

5. CONCLUSIONS

Marine organisms are characteristically found in heterogeneous three-dimensional water masses. Defining the habitat for an organism, a species or a community is then limited by the inaccessibility of the world's oceans, and the logistics involved to effectively study marine organisms underwater (Cribb *et al.*, 2015). Hence, marine animals that are wide-ranging and migratory by nature, including cetaceans, increase the difficulty in defining their habitat boundaries (Hoyt 2005; Cribb *et al.*, 2015). Nonetheless, as a mobile species, their heterogeneous distribution over a wide range of habitats (Arcangeli *et al.*, 2016) characterises them as indicator species, providing an opportunity to evaluate the impacts of anthropogenic activities on ecosystem functions (Carlucci *et al.*, 2016). Hence, reliable and spatially explicit analyses of the environmental factors affecting the habitat selection are valuable tools in identifying possible threats to key species as top predators, and their outputs should be implemented in the management and conservation planning (Marini *et al.*, 2015).

Cardigan Bay supports important habitat features, providing optimal foraging and breeding sites for various species including the bottlenose dolphin. A thorough understanding of how these species use this habitat is critical to effectively protect them and their habitat. It also highlights the need to investigate habitat preferences at a population level by incorporating both biotic and abiotic features as their interaction can directly or indirectly affect bottlenose dolphin distributions (Wells *et al.*, 1980; Scott *et al.*, 1990; Wells & Scott, 2002; Blasi & Biotani, 2012). For instance, depth and sediment composition on their own may not directly affect bottlenose habitat preference. However, they may be important factors acting upon other biotic variables such as prey abundance. Aggregation of prey is known to attract more dolphins to certain areas, and in such cases the abiotic factors are indirectly driving their distribution. Hence, oceanographic and physiographic features

can be used as proxies for prey availability when investigating bottlenose dolphin distribution in Cardigan Bay.

This study was unable to investigate another important factor that can potentially affect bottlenose dolphin distribution - scallop fisheries within the SAC area. As an activity damaging the seabed, this type of fishery can be detrimental to bottlenose dolphin habitat and consequently drive them away. Therefore, future studies should focus upon examining the potential effects of scallop dredging on bottlenose dolphin habitat preference to determine if and how they are affecting their habitat use.

Although mobile, this population distribution is being driven by static environmental features, depth and sediment type, suggesting that static protected areas can be effective tools of conservation for this species within Cardigan Bay. Furthermore, because their use of this area is patchy, providing extra protection to small sections within the Bay through zoning of activities would be most effective. This study highlighted the importance of the two SAC areas already in place, as the most important habitats used were located in Pen Llŷn a'r Sarnau SAC and Cardigan Bay. Nevertheless, this population has shown to use a wider area outside the bay where they could be exposed to other threats. Therefore, close monitoring is crucial to gather information which would help determine the importance of the current SAC, if new boundaries are needed or new SAC are required. Further studies into other environmental factors such as: distance to shore, current speed, and salinity, should be investigated as they could potentially affect bottlenose dolphin habitat use patterns. In addition, due to their predominant presence in shallow waters, close monitoring of their population and the anthropogenic activities there is essential as they are vulnerable to any impacts, and an increase in such activities could be potentially detrimental to their population.

REFERENCES

- Akamatsu, T., Nakamura, K., Kawabe, R., Furukawa, S., Murata, H., Kawakubo, A., and Komaba, M. (2010). Seasonal and diurnal presence of finless porpoises at a corridor to the ocean from their habitat. *Marine Biology*, 157(8), 1879-1887.
- Alter, E.S., Simmonds, M.P., and Brandon, J.R. (2010). Forecasting the consequences of climate-driven shifts in human behavior on cetaceans. *Marine Policy*, 34, 943–954.
- Antonella, A., Ilaria, C., and Bologna, M. A. (2017). Influence of seasonality on cetacean diversity, abundance, distribution and habitat use in the western Mediterranean Sea: Implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 1-6.
- Arcangeli, A., Campana, I., and Bologna, M.A. (2017). Influence of seasonality on cetacean diversity, abundance, distribution and habitat use in the western Mediterranean Sea: Implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems*. DOI: 10.1002/aqc.2758
- Arnold, H. (1993). Distribution, abundance, and habitat use of bottlenose dolphins in Cardigan Bay, Wales, 1992. *European Research on Cetaceans*, 7, 63–66.
- Azzellino, A., Gaspari, S., Airoidi, S., and Nani, B. (2008). Habitat use and preferences of cetaceans along the continental slope and the adjacent pelagic waters in the western Ligurian Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, 55(3), 296-323.
- Bailey, H., and Thompson, P. (2006). Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. *Journal of Animal Ecology*, 75(2), 456-465.
- Bailey, H., and Thompson, P. (2010). Effect of oceanographic features on fine-scale foraging movements of bottlenose dolphins. *Marine Ecology Progress Series*, 418, 223-233.
- Baines, M.E., Evans, P.G.H., and Shepherd, B. (2000). Bottlenose dolphins in Cardigan Bay, West Wales. *Report to EU INTERREG and Countryside Council for Wales*. Sea Watch Foundation, Oxford. 35pp.
- Ballance, L. T. (1992). Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. *Marine Mammal Science*, 8(3), 262-274.
- Barry, J.P., and Dayton, P.K. (1991). Physical heterogeneity and the organization of marine communities. In Kolasa, J. Pickett, S.T.A (eds), *Ecological Heterogeneity*, Springer-Verlag, New York, pp. 270-320.
- Baumgartner, M.F. (1997). The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. *Marine Mammal Science*, 13, 614-638.

- Baumgartner, M.F., Mullin, K.D., May, L.N., and Leming, T.D. (2001). Cetacean habitats in the northern Gulf of Mexico. *Fishery Bulletin-National Oceanic and Atmospheric Administration*, 99(2), 219-239.
- Becker, B.H., Press, D.T., and Allen, S.G. (2011). Evidence for long-term spatial displacement of breeding and pupping harbour seals by shellfish aquaculture over three decades. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 21, 247–260.
- Bedjer, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., Flaherty, C., and Krützen, M. (2006). Decline in relative abundance of bottlenose dolphins exposed to long term disturbance. *Conservation Biology*, 20, 1791–1798.
- Blasi, M., and Boitani, L. (2012). Modelling fine-scale distribution of the bottlenose dolphin *Tursiops truncatus* using physiographic features on Filicudi (southern Tyrrhenian Sea, Italy). *Endangered Species Research*. 17, 269-288.
- Bräger, S., Harraway, J.A., and Manly, B.F.J. (2003). Habitat selection in a coastal dolphin species (*Cephalorhynchus hectori*). *Marine Biology*, 143(2), 233-244.
- Brandt, M.J., Diederichs, A., Betke, K., and Nehls, G. (2011). Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. *Marine Ecology Progress Series*, 421, 205-216.
- Carlström, J. (2005). Diel variation in echolocation behavior of wild harbor porpoises. *Marine Mammal Science*, 21(1), 1-12.
- Cañadas, A., Sagarminaga, R., De Stephanis, R., Urquiola, E., and Hammond, P. S. (2005). Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 15(5), 495-521.
- Cañadas, A., and Vázquez, J.A. (2017). Common dolphins in the Alboran Sea: Facing a reduction in their suitable habitat due to an increase in Sea surface temperature. *Deep Sea Research Part II: Topical Studies in Oceanography*, 141, 306–318.
- Cardigan Bay Special Area of Conservation (SAC) (2008). Call for answer on Draft Management Scheme. [online] Available at: http://www.cardiganbaysac.org.uk/pdf%20files/Cardigan_Bay_SAC_Management_Scheme_2008.pdf [Accessed June 2017]
- Carlucci, R., Fanizza, C., Cipriano, G., Paoli, C., Russo, T., and Vassallo, P. (2016). Modeling the spatial distribution of the striped dolphin (*Stenella coeruleoalba*) and common bottlenose dolphin (*Tursiops truncatus*) in the Gulf of Taranto (Northern Ionian Sea, Central-eastern Mediterranean Sea). *Ecological Indicators*, 69, 707–721.

- Carstensen, J., Henriksen, O.D., and Teilmann, J. (2006). Impacts on harbor porpoises from offshore wind farm construction: acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). *Marine Ecology Progress Series*, 321, 295–308.
- Chavez, F.P., and Messié, M. (2009). A comparison of eastern boundary upwelling ecosystems. *Progress in Oceanography*, 83, 80–96.
- Collie, J.S., Hall, S.J., Kaiser, M.J., and Poiner, I.R. (2000). A quantitative analysis of fishing impacts on shelf-sea benthos. *Journal of Animal Ecology*, 69, 785–798.
- Cotter, M.P, Maldini, D., and Jefferson, T.A. (2012). “Porpicide” in California: Killing of harbor porpoises (*Phocoena phocoena*) by coastal bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, 28(1), E1–E15.
- Craig, A. S., Herman, L. M., Pack, A. A., and Waterman, J. O. (2014). Habitat segregation by female humpback whales in Hawaiian waters: avoidance of males? *Behaviour*, 151(5), 613-631.
- Craven, H.R., Brand, A.R., and Stewart, B.D. (2013). Patterns and impacts of fish bycatch in a scallop dredge fishery. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 23(1), 152–170. <https://doi.org/10.1002/aqc.2289>.
- Cribb, N., Miller, C. and Seuront, L. (2013). Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) habitat preference in a heterogeneous, urban, coastal environment. *Aquatic Biosystems*, 9(1), 3.
- Cribb, N., Miller, C., and Seuront, L. (2015) Towards a standardized approach of cetacean habitat: past achievements and future directions. *Open Journal of Marine Science*, 5, 335-357.
- Croll, D.A., Tershy, B.R., Hewitt, R.P., Demer, D.A., Fiedler, P.C., Smith, S.E., Armstrong, W., Popp, J.M., Kiekhefer, T., Lopez, V.R., Urban, J., and Gendron D (1998). An integrated approach to the foraging ecology of marine birds and mammals. *Deep-Sea Research II*, 45, 1353–1371.
- Dähne, M., Gilles, A., Lucke, K., Peschko, V., Adler, S., Krügel, K., Sundermeyer, J., and Siebert, U. (2013). Effects of pile-driving on harbor porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. *Environmental Research Letters*, 8(2). [doi:10.1088/1748-9326/8/2/025002](https://doi.org/10.1088/1748-9326/8/2/025002)
- Dinis, A., Carvalho, A., Alves, F., Nicolau, C., Ribeiro, C., Kaufmann, M., Cañadas, A. and Freitas, L. (2016). Spatial and temporal distribution of bottlenose dolphins, *Tursiops truncatus*, in the Madeira archipelago, NE Atlantic. *Arquipélago-Life and Marine Sciences*, 33, 45-54.
- Evans, P.G.H., Baines, M.E., Shepherd, B., and Reichelt M. (2002). Studying bottlenose dolphin (*Tursiops truncatus*) abundance, distribution, habitat use and home range size in Cardigan Bay: implications for SAC management. In Abstracts, 16th Annual Conference of the European Cetacean Society Liege, Belgium, 7–11, p. 12.

- Evans, P.G.H (2008). Selection criteria for marine protected areas for cetaceans. *In Proceedings of the ECS/ASCOBANS/ACCOBAMS workshop*. ECS (European Cetacean Society). Special Publication Series (No. 48, p. 13).
- Evans, P.G.H. (2009). Habitat pressures. In W.F. Perrin, B. Würsig and J.G.M. Thewissen (eds), *Encyclopedia of Marine Mammals*. 2nd Edition. Academic Press, San Diego, pp. 513-516.
- Evans, P.G.H. and Anderwald, P. (2016). Addressing human pressures upon marine mammals: a European and global perspective. *Journal of the Marine Biological Association of the United Kingdom*, 96(4), 779-781.
- Feingold, D., and Evans, P.G.H. (2014a). Bottlenose Dolphin and Harbour Porpoise Monitoring in Cardigan Bay and Pen Llyn a'r Sarnau Special Areas of Conservation 2011-2013. *Natural Resources Wales Evidence Report Series No. 4*. 124pp.
- Feingold, D., and Evans, P.G.H. (2014b). Connectivity of Bottlenose Dolphins in Welsh Waters: North Wales Photo-Monitoring Report. *Natural Resources Wales Research Report*. 15pp.
- Ferguson, M.C., Barlow, J., Fiedler, P., Reilly, S.B., and Gerrodette, T. (2006). Spatial models of delphinid (family Delphinidae) encounter rate and group size in the eastern tropical Pacific Ocean. *Ecological Modelling*, 193(3), 645-662.
- Fiedler, P.C., Barlow, J., and Gerrodette, T. (1998). Dolphin prey abundance determined from acoustic backscatter data in eastern Pacific surveys. *Fishery Bulletin*, 96(2), 237-247.
- Franks, P.J.S. (1992). Phytoplankton blooms at fronts: patterns, scales, and physical forcing mechanisms. *Reviews in Aquatic Sciences*, 6, 121– 137.
- Freitas, C., Kovac, K.M., Lydersen, C., and Ims, R.A. (2008). A Novel Method for Quantifying Habitat Selection and Predicting Habitat Use. *Journal of Applied Ecology*, 45, 1213-1220.
- Forney, K.A. (2000). Environmental models of cetacean abundance: reducing uncertainty in population trends. *Conservation Biology*, 14, 1271-1286.
- Fruet, P.F., Genoves, R.C., Möller, L.M., Botta, S., and Secchi, E.R. (2015). Using mark-recapture and stranding data to estimate reproductive traits in female bottlenose dolphins (*Tursiops truncatus*) of the Southwestern Atlantic Ocean. *Marine Biology*, 162(3), 661-673.
- Gaillard, J.M., Delorme, D., Jullien, J.M., and Tatin, D. (1993). Timing and synchrony of births in roe deer. *Journal of Mammalogy*, 74(3), 738-744.
- Genin, A. (2004). Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems*, 50, 3–20.
- Giannoulaki, M., Markoglou, E., Valavanis, V.D., Alexiadou, P., Cucknell, A., and Frantzis, A. (2017). Linking small pelagic fish and cetacean distribution to model suitable habitat for coastal dolphin

- species, *Delphinus delphis* and *Tursiops truncatus*, in the Greek Seas (Eastern Mediterranean). *Aquatic Conservation: Marine and Freshwater Ecosystems*, 27(2), 436-451.
- Godø, O.R., Samuelsen, A., Macaulay, G.J., Patel, R., Hjøllø, S.S., Horne, J., Kaartvedt, S., and Johannessen, J.A. (2012). Mesoscale eddies are oases for higher trophic marine life. *PLoS ONE*, 7, 30161.
- Gregory, P. R., and Rowden, A. A. (2001). Behaviour patterns of bottlenose dolphins (*Tursiops truncatus*) relative to tidal state, time-of-day, and boat traffic in Cardigan Bay, West Wales. *Aquatic Mammals*, 27(2), 105-113.
- Hammond, P.S., Macleod, K., Berggren, P., Borchers, D.L., Burt, M.L., Cañadas, A., Desportes, G., Donovan, G.P., Gilles, A., Gillespie, D.M., Gordon, J.C.D., Hiby, L., Kuklik, I., Leaper, R., Lehnert K., Leopold, M., Lovell, P., Øien, N., Paxton, C.G.M., Ridoux, V., Rogan, E., Samarra, F.I.P., Scheidat, M., Sequeira, M., Siebert, U., Skov, H., Swift, R.J., Tasker, M., Teilmann, J., Van baneyt, O., and Vázquez, J.A. (2013). Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. *Biological Conservation*, 164, 107–122.
- Hamazaki, T. (2002). Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, U.S.A. to Nova Scotia, Canada). *Marine Mammal Science*, 18, 920-939.
- Hartman, K.L., Fernandez, M., and Azevedo, J.M. (2014). Spatial segregation of calving and nursing Risso's dolphins (*Grampus griseus*) in the Azores, and its conservation implications. *Marine Biology*, 161(6), 1419-1428.
- Harwood, J., and Wilson, B. (2001). The implications of development of the Atlantic Frontier for marine mammals. *Continental Shelf Research*, 21, 1073–1093.
- Harwood, J. (2001). Marine mammals and their environment in the twenty-first century. *Journal of Mammalogy*, 82(3), 630-640.
- Hartel, E.F., Constantine, R., and Torres, L.G. (2015). Changes in habitat use patterns by bottlenose dolphins over a 10-year period render static management boundaries ineffective. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 25(5), 701-711.
- Hastie, G.D., Swift, R.J., Slessor, G., Thompson, P.M., and Turrell, W.R. (2005). Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. *ICES journal of Marine Science*, 62(4), 760-770.
- Heithaus, M.R., and Dill, L.M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, 83, 480–491.
- Henry, L.A., Kenchington, E.L.R., Kenchington, T.J., MacIsaac, K.G., Bourbonnais-Boyce, C. and Gordon, D.C. Jr. (2006). Impacts of otter trawling on colonial epifaunal assemblages on a cobble

- bottom ecosystem on Western Bank (northwest Atlantic). *Marine Ecology Progress Series*, 306, 63–78.
- Howarth, L.M., and Stewart, B.D. (2014). The dredge fishery for scallops in the United Kingdom (UK): effects on marine ecosystems and proposals for future management. Report to the Sustainable Inshore Fisheries Trust. *Marine Ecosystem. Management Report no. 5*, University of York, 54 pp.
- Hildebrand, J.A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*, 395, 5–20.
- Hoyt, E. (2005). Marine protected areas for whales, dolphins and porpoises: A worldwide handbook for cetacean habitat conservation. Earthscan, London.
- Hoyt E (2011). Marine protected areas for whales, dolphins and porpoises: a world handbook for cetacean habitat conservation and planning. *Earthscan/Taylor & Francis*, London and New York.
- Hunt, G.I.J., and Schneider, D. (1987). Scale-dependent processes in physical and biological environment of marine birds. In Croxall, J.P. (ed), *Seabirds, Feeding Ecology and Role in Marine Ecosystems*. Cambridge University Press, Cambridge, pp. 7-41.
- Ingram, S.N., and Rogan, E. (2002). Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. *Marine Ecology Progress Series*, 244, 247–255.
- Jaquet, N., and Whitehead, H. (1996). Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. *Marine Ecology Progress Series*, 135, 1–9.
- Johnston, D.W., and Read, A.J. (2007). Flow-field observations of a tidally driven island wake used by marine mammals in the Bay of Fundy, Canada. *Fisheries Oceanography*, 16, 422–435.
- Kaiser, M.J., Collie, J.S., Hall, S.J., Jennings, S., and Poiner I.R. (2002). Modification of marine habitats by trawling activities: prognosis and solutions. *Fish and Fisheries*, 3, 114–136.
- Kaiser, M.J., Clarke, K.R., Hinz, H., Austen, M.C.V., Somerfield, P.J., and Karakassis, I. (2006). Global analysis of response and recovery of benthic biota to fishing. *Marine Ecology Progress Series*, 311, 1-14.
- Karczmarski, L., Cockcroft, V.G., and McLachlan, A. (2000). Habitat use and preferences of Indo-Pacific humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. *Marine Mammal Science* 16, 65-79.
- Krumme, U. (2004). Patterns in tidal migration of fish in a Brazilian mangrove channel as revealed by a split-beam echo sounder. *Fisheries Research*, 70, 1–15.

- Krumme, U. (2009). Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. In Nagelkerken I (ed), *Ecological connectivity among tropical coastal ecosystems*, Springer Netherlands. Dordrecht, pp. 271–324.
- Lambert, G.I., Jennings, S., Kaiser, M.J., Hinz, H., and Hiddink, J.G. (2011). Quantification and prediction of the impact of fishing on epifaunal communities. *Marine Ecology Progress Series* 430, 71–86.
- Lambert, G.I., Murray, L.G., Hiddink, J.G., Hinz, H., Salomonsen, H., and Kaiser, M. J. (2015). Impact of scallop dredging on benthic communities and habitat features in the Cardigan Bay special area of conservation Part I – Impact on infaunal invertebrates. *Fisheries and Conservation Report No. 59*, 97.
- Lambert, C., Laran, S., David, L., Dorémus, G., Pettex, E., Van Canneyt, O., and Ridoux, V. (2016). How does ocean seasonality drive habitat preferences of highly mobile top predators? Part I: The north-western Mediterranean Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*.
- Largier, J.L. (1993). Estuarine fronts: how important are they? *Estuaries*, 16:1–11.
- La Manna, G., Ronchetti, F., and Sara, G. (2016). Predicting common bottlenose dolphin habitat preference to dynamically adapt management measures from a Marine Spatial Planning perspective. *Ocean & Coastal Management*, 130, 317-327.
- Le Fevre, J. (1986). Aspects of the biology of frontal systems. *Advances in Marine Biology*, 23, 164–299.
- Lewis, E.J., and Evans P.G.H. (1993). Comparative ecology of bottlenose dolphins (*Tursiops truncatus*) in Cardigan Bay and the Moray Firth. *European Research on Cetaceans*, 7, 57–62.
- Lin, T. H., Akamatsu, T., and Chou, L. S. (2013). Tidal influences on the habitat use of Indo-Pacific humpback dolphins in an estuary. *Marine Biology*, 160(6), 1353-1363.
- Lohrengel, K., Evans, P.G.H., Lindenbaum, C.P., Morris, C.W., and Stringell, T.B. (2017). Bottlenose dolphin monitoring in Cardigan Bay 2014-2016, NRW Evidence Report No: 191, 163pp, Natural Resources Wales, Bangor.
- Lloret, J., Gil de Sola, L., Souplet, A., and Galzin, R. (2002). Effects of large-scale habitat variability on condition of demersal exploited fish in the north-western Mediterranean. *ICES Journal of Marine Science*, 59(6), 1215-1227.
- Lusseau, D., and Higham, J.E.S. (2004). Managing the impacts of dolphin based tourism through the definition of critical habitats: the case of bottlenose dolphins (*Tursiops* spp.) in doubtful sound, New Zealand. *Tourism Management*, 25, 657–667.
- Lusseau, D. (2005). Residency pattern of bottlenose dolphins *Tursiops* spp. in Milford Sound, New Zealand, is related to boat traffic. *Marine Ecology Progress Series*, 295, 265–272.

- Mann, J., Connor, R.C., Barre, L.M., and Heithaus, M.R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group size effects. *Behavioral Ecology* 11, 210–219.
- Marini, C., Fossa, F., Paoli, C., Bellingeri, M., Gnone, G., and Vassallo, P. (2015). Predicting bottlenose dolphin distribution along Liguria coast (northwestern Mediterranean Sea) through different modeling techniques and indirect predictors. *Journal of Environmental Management*, 150, 9-20.
- Mattson, M.C., Thomas, J., and Aubin, D. St. (2005). Effects of boat activity on the behavior of bottlenose dolphins (*Tursiops truncatus*) in waters surrounding Hilton Head Island, South Carolina. *Aquatic Mammals*, 31(1), 133–140. <https://doi.org/10.1578/AM.31.1.2005.133>
- McCarthy, E. (2004). *International Regulation of Underwater Sound: Establishing Rules and Standards to Address Ocean Noise Pollution*. Kluwer Academic Publishers, Boston, MA.
- McLusky, D.S., and Elliott M (2004). The estuarine ecosystem: ecology, threats, and management. *Oxford University Press*, New York.
- Mendes, S., Turrell, W., Lütkebohle, T., and Thompson, P. (2002). Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. *Marine Ecology Progress Series*, 239, 221-229.
- Moure, A. E., Sillero, N., and Rodrigues, A. (2012). Common dolphin (*Delphinus delphis*) habitat preferences using data from two platforms of opportunity. *Acta Oecologica*, 38, 24-32.
- Neumann, D.R. (2001). Activity budget of free-ranging common dolphins (*Delphinus delphis*) in the northwestern Bay of Plenty, New Zealand. *Aquatic Mammals*, 27(2), 121–136.
- New, L. F., Harwood, J., Thomas, L., Donovan, C., Clark, J. S., Hastie, G., Thompson, P.M., Cheney, B., Scott-Hayward, L., and Lusseau, D. (2013). Modelling the biological significance of behavioural change in coastal bottlenose dolphins in response to disturbance. *Functional Ecology*, 27(2), 314-322.
- Norrman, E.B., Duque, S.D., and Evans, P.G.H. (2015). Bottlenose dolphins in Wales: Systematic mark-recapture surveys in Welsh waters. *Natural Resources Wales Evidence Report Series No. 85*. Natural Resources Wales, Bangor. 83pp.
- Nowacek, D.P., Thorne, L.H., Johnston, D.W., and Tyack, P.L. (2007). Responses of cetaceans to anthropogenic noise. *Mammal Review*, 37, 81–115.
- Nuuttilla, H.K., Courtene-Jones, W., Baulch, S., and Simon, M. (2017). Don't forget the porpoise: acoustic monitoring reveals fine scale temporal variation between bottlenose dolphin and harbor porpoise in Cardigan Bay SAC. *Marine Biology*, 164:50.
- O'Connor, S., Campbell, R., Cortez, H., and Knowles, T. (2009). *Whale Watching Worldwide: Tourism Numbers, Expenditures and Expanding Economic Benefits*. Yarmouth, MA.

- Pacifici, M., Foden, W.B., Visconti, P., Watson, J.E.M., Butchart, S.H.M., Kovacs, K.M., Scheffers, B.R., Hole, D.G., Martin, T.G., Akçakaya, H.R., Corlett, R.T., Huntley, B., Bickford, D., Carr, J.A., Hoffmann, A.A., Midgley, G.F., Pearce-Kelly, P., Pearson, R.G., Williams, S.E., Willis, S.G., Young, B., and Rondinini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change*, 5(3), 215.
- Papale, E., Azzolin, M., and Giacoma, C. (2012). Vessel traffic affects bottlenose dolphin (*Tursiops truncatus*) behaviour in waters surrounding Lampedusa Island, south Italy. *Journal of the Marine Biological Association of the United Kingdom*, 92(08), 1877-1885.
- Pesante, G., Evans, P.G.H., Baines, M.E., and McMath, M. (2008). Abundance and Life History Parameters of Bottlenose Dolphin in Cardigan Bay: Monitoring 2005-2007. *CCW Marine Monitoring Report No. 61*: 1-75.
- Pierpoint, C., Allan, L., Arnold, H., Evans, P., Perry, S., Wilberforce, L., and Baxter, J. (2009). Monitoring important coastal sites for bottlenose dolphin in Cardigan Bay, UK. *Journal of the Marine Biological Association of the UK*, 89(5), 1033–1043.
- Pirotta, E., Merchant, N.D., Thompson, P.M., Barton, T.R., and Lusseau, D. (2015). Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. *Biological Conservation*, 181, 82-89.
- Rechsteiner, E.U., Rosen, D.A.S., and Trites, A.W. (2013). Energy requirements of Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) as predicted by a bioenergetic model. *Journal Mammalogy*, 94, 820–832.
- Redfern, J.V., Ferguson, M.C., Becker, E.A., Hyrenbach, K.D., Good, C., Barlow, J., Kaschner, K., Baumgartner, M.F., Forney, K.A., Balance, L.T., Fauchald, P., Halpin, P., Hamazaki, T., Pershing, A.J., Qian, S.S., Read, A., Reilly, S.B., Torres, L., and Werner, L. (2006) Techniques for Cetacean-Habitat Modelling. *Marine Ecology Progress Series*, 310, 271-295.
- Ross, H. M., and Wilson, B. (1996). Violent interactions between bottlenose dolphins and harbour porpoises. *Proceedings of the Royal Society of London B: Biological Sciences*, 263(1368), 283-286.
- Rutberg, A. T. (1987). Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *The American Naturalist*, 130(5), 692-710.
- Scales, K.L., Miller, P.I., Hawkes, L.A., Ingram, S.N., Sims, D.W., and Votier, S.C. (2014). On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, 51(6), 1575-1583.
- Sciberras, M., Hinz, H., Bennell, J.D., Jenkins, S.R., Hawkins, S.J., and Kaiser, M.J. (2013). Benthic community response to a scallop dredging closure within a dynamic seabed habitat. *Marine Ecology Progress Series*, 480, 83-98.

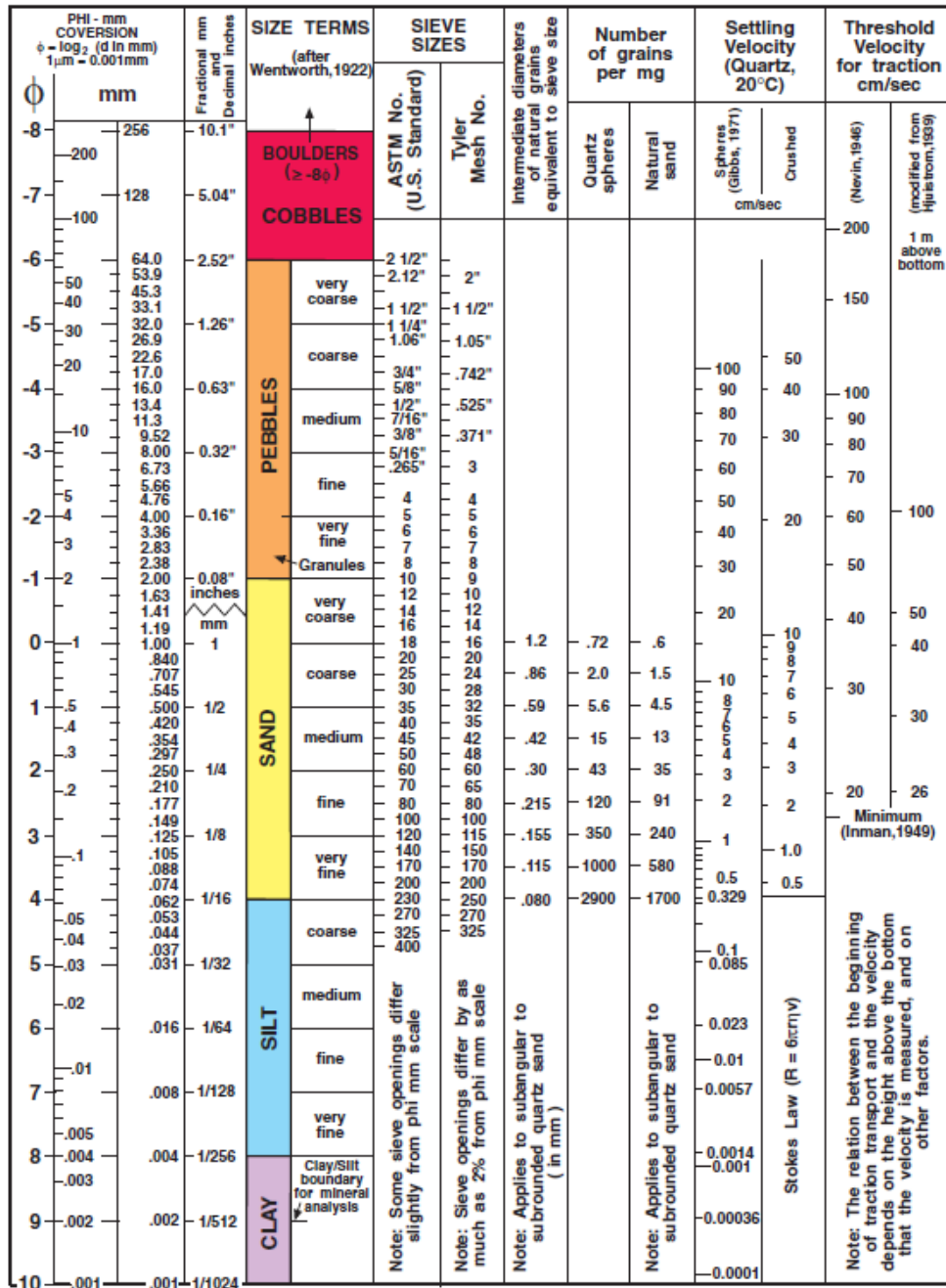
- Scott, M.D., Wells, R.S., and Irvine, A.B. (1990). A long-term study of bottlenose dolphins on the west coast of Florida. In: Leatherwood, S., Reeves, R.R. (eds), *The Bottlenose Dolphin*, Academic Press. San Diego, CA, pp. 235-244.
- Selzer, L.A., and Payne, P.M. (1988). The distribution of white-sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) vs. environmental features of the continental shelf of the northeastern United States. *Marine Mammal Science*, 4, 141-153.
- Simon, M., Nuuttila, H., Reyes-Zamudio, M.M., Ugarte, F., Verfuss, U., and Evans, P.G.H. (2010). Passive acoustic monitoring of bottlenose dolphin and harbour porpoise, in Cardigan Bay, Wales, with implications for habitat use and partitioning. *Journal of the Marine Biological Association of the United Kingdom*, 90(8), 1539-1545.
- Smith, H.C., Pollock, K., Waples, K., Bradley, S., and Bejder, L. (2013). Use of the robust design to estimate seasonal abundance and demographic parameters of a coastal bottlenose dolphin (*Tursiops aduncus*) population. *PLoS ONE*, 8(10), 76574.
- Smith, H., Frère, C., Kobryn, H., and Bejder, L. (2016). Dolphin sociality, distribution and calving as important behavioural patterns informing management. *Animal Conservation*, 19(5), 462-471.
- Soldevilla, M.S., Wiggins, S.M., and Hildebrand, J.A. (2010). Spatial and temporal patterns of Risso's dolphin echolocation in the Southern California Bight. *Journal of Acoustic Society America*, 127, 124–132.
- Stewart, A.J.A., John, E.A., and Hutchings, M.J. (2000). The world is heterogeneous: ecological consequences of living in a patchy environment. In Hutchings, M.J., John, E.A. and Stewart, A.J.A (eds), *The Ecological Consequences of Environmental Heterogeneity*, Springer-Verlag. New-York, pp. 1-8.
- Tezanos-Pinto, G., Baker, G.S., Russell, K., Martien, K., Baird, R.W., Hutt, A., Stone, G., Mignucci-Giannoni, A.A., Caballero, S., Endo, T., Lavery, S., Oremus, M., Olavarría, C., and Garrigue, C. (2009). A Worldwide Perspective on the Population Structure and Genetic Diversity of Bottlenose Dolphins (*Tursiops truncatus*) in New Zealand. *Journal of Heredity*, 100(1) 1, 11–24.
- Traganza, E.D., Redalije, D.G., and Garwood, R.W. (1987). Chemical flux, mixed layer entrainment and phytoplankton blooms at upwelling fronts in the California coastal zone. *Continental Shelf Research*, 7, 89–105.
- Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Berghe, E.V., and Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, 466, 1098–1101.
- Torres, L.G., Read, A.J., and Halpin, P. (2008). Fine-scale habitat modeling of a top marine predator: do prey data improve predictive capacity? *Ecological Application*, 18(7), 702-17.

- Tyne, J. A., Johnston, D. W., Rankin, R., Loneragan, N. R., and Bejder, L. (2015). The importance of spinner dolphin (*Stenella longirostris*) resting habitat: implications for management. *Journal of Applied Ecology*, 52(3), 621-630.
- Wells, R.S., and Scott, M.D. (2002). Bottlenose dolphins. In: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (eds), *Encyclopedia of Marine Mammals*, Academic Press. San Diego.
- Wells, R.S., Irvine, A.B., and Scott, M.D. (1980). The social ecology of inshore odontocetes. In: Herman, L.M. (eds), *Cetacean Behavior: Mechanisms and Functions*, John Wiley & Sons. New York, NY, pp. 263-318.
- Wiens, J.A. (1989). Spatial scaling in ecology. *Functional Ecology*, 3,385–397.
- Wilson, B., Thompson, P.M., and Hammond, P.S. (1997). Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth Scotland. *The Journal of Applied Ecology*, 34,1365–1374.
- Worm, B., Sandow, M., Oschlies, A., Lotze, H.K., and Myers, R.A. (2005). Global patterns of predator diversity in the open oceans. *Science*, 309, 1365–1369.
- Yen, P.P.W., Sydeman, W.J., and Hyrenbach, K.D. (2004). Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *Journal of Marine Systems*, 50: 79–99.
- Zanardo,harwood N., Parra, G.J., Passadore, C., and Möller, L.M. (2017). Ensemble modelling of southern Australian bottlenose dolphin *Tursiops* sp. distribution reveals important habitats and their potential ecological function. *Marine Ecology Progress Series*, 569, 253-266.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., and Smith, G.M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer Science and Business Media. 580pp.

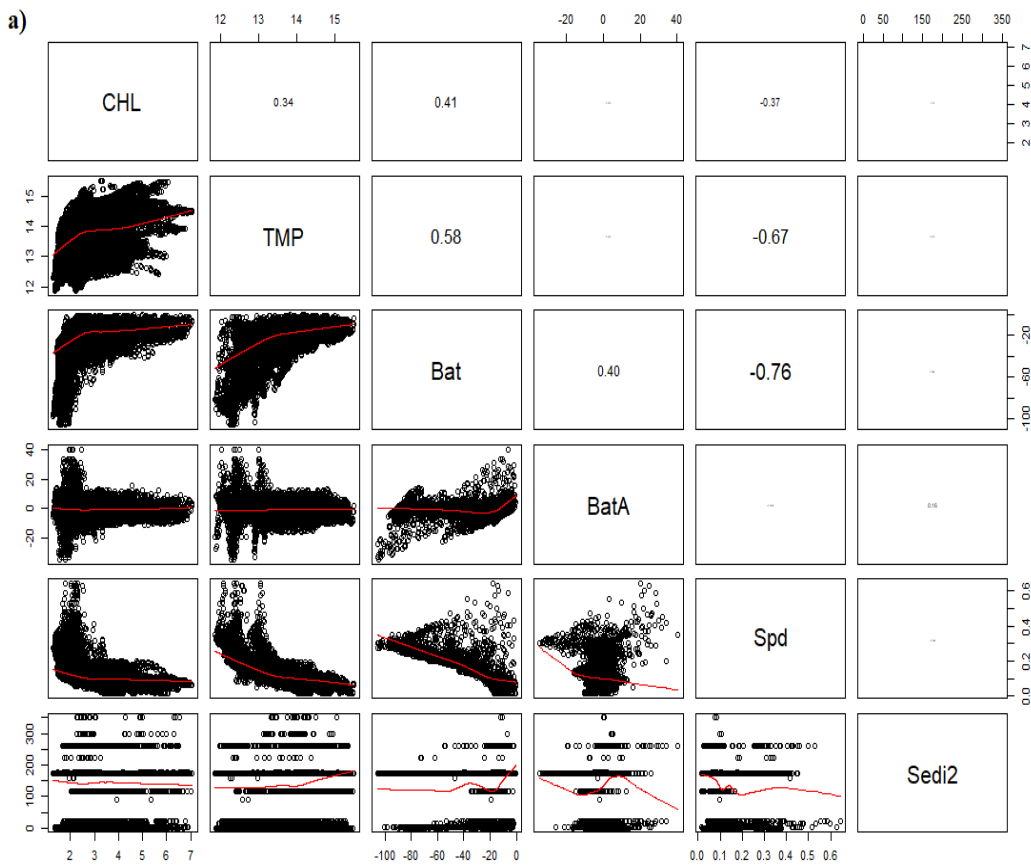
APPENDIX I. Vessels used to conduct surveys in Cardigan Bay**Table 3-**Vessels used for distance-sampling and dedicated non-line transect in Cardigan Bay over a period of 13 years. *CB SAC- Cardigan Bay SAC, **NCB= Northern Cardigan Bay. *** only used for the dedicated non-line transect surveys.

Vessel Area name surveyed	Length (m)	Eye height (m)	Speed (kn)	Engine type
Dunbar Castle II CB SAC*	9.7	3.5	5-6	120 hp diesel
Ma Chipe Seabrin NCB**	10	4.5	10	Twin 220hp diesel
Pedryn NCB**	11.7	3.0	10-12	Twin 350hp diesel
Severn Guardian CB SAC*	18.3	5.5	10	Twin Volvo D9-MH
Highlander NCB**	10	4	10	Twin 370hp diesel
Bay Explorer *** CB SAC*	10	2.5	Variable 1	200hp
Celine NCB**	10.6	2.0	6	30hp diesel
Scorpius NCB**	8.99	2.4	10	230hp diesel
Ermol V NCB**	11.5	2.5	6	Twin 128hp diesel
Ermol VI NCB**	10.9	2.5	6	350hp diesel

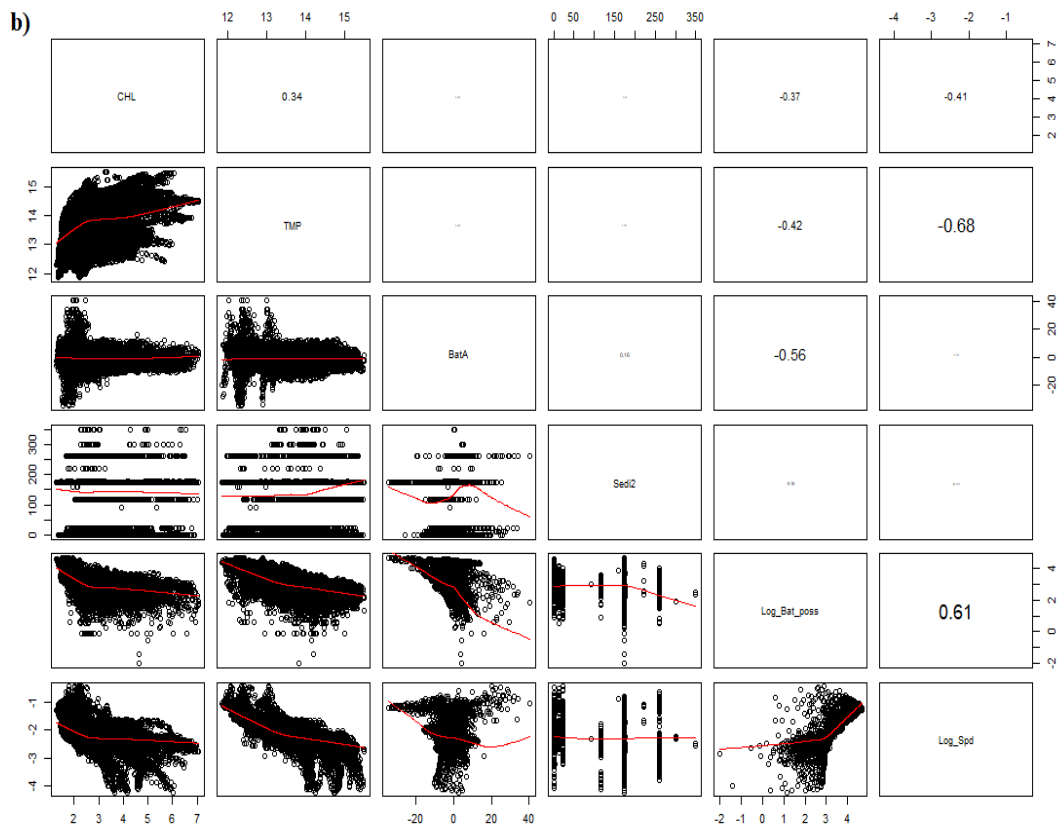
APPENDIX II. Krumbein phi scale used to categorize sediment into different types based on their grain size.



APPENDIX III. The plot represent the Pearson correlation test performed on six environmental variables, which are sediment size (Sedi2), bathymetry (Bat), bathymetry anomaly (Bat A), sea surface temperature (SST), and chlorophyll *a* (CHL). Two environmental variables are correlated when their Pearson coefficient (r) beyond the ranges $-0.5 < r < 0.5$. The test results showed correlation between TMP and Spd ($r = -0.61$); and between Bat and Spd ($r = -0.76$) respectively (a). To reduce the influence of extreme values the bathymetry and SST were log transformed (b), however the test results showed a correlation between Bathymetry anomaly and bathymetry (-0.56). Environmental predictors: Spd and BatA were removed from the models.



Habitat preference of bottlenose dolphin

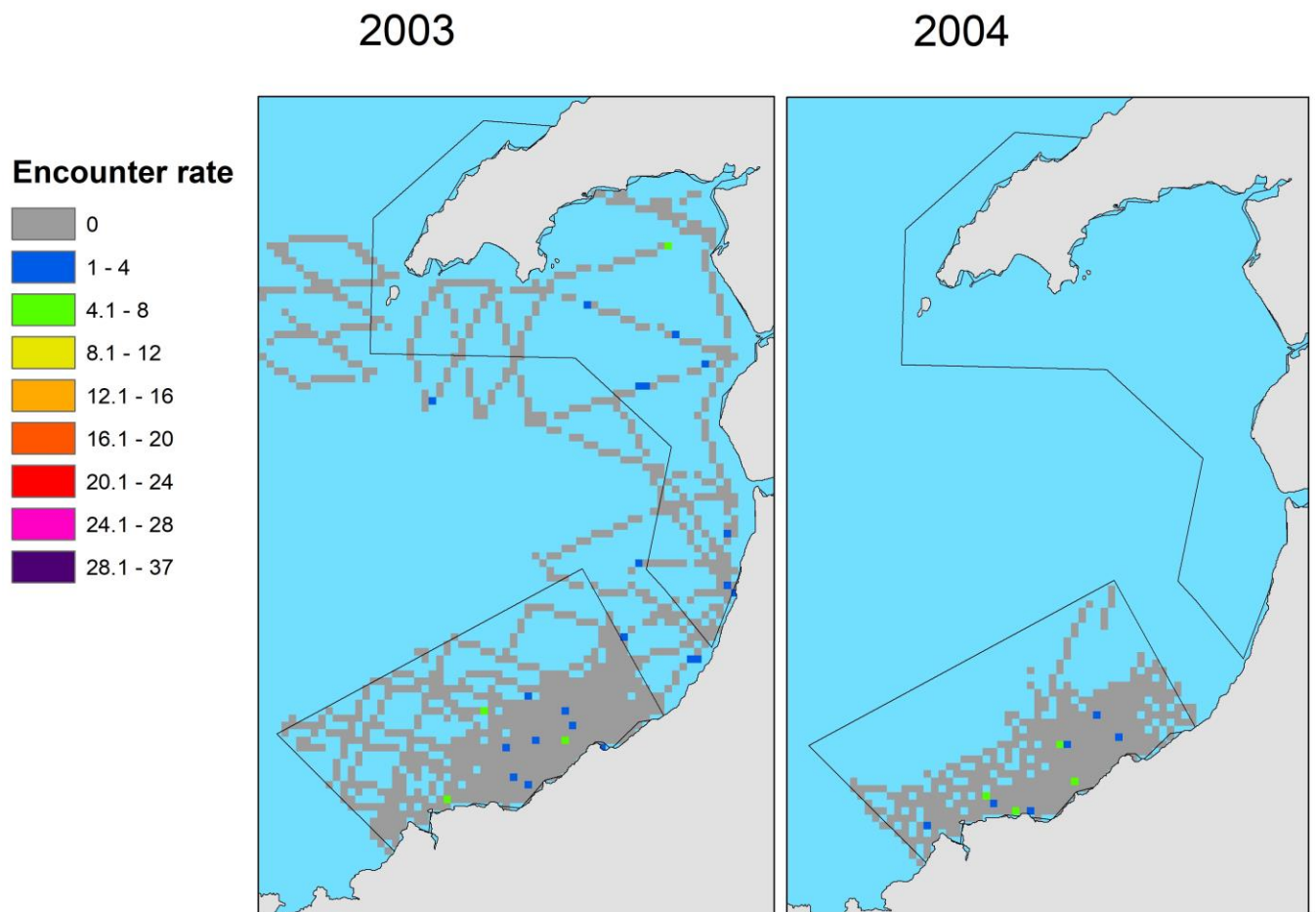


Habitat preference of bottlenose dolphin

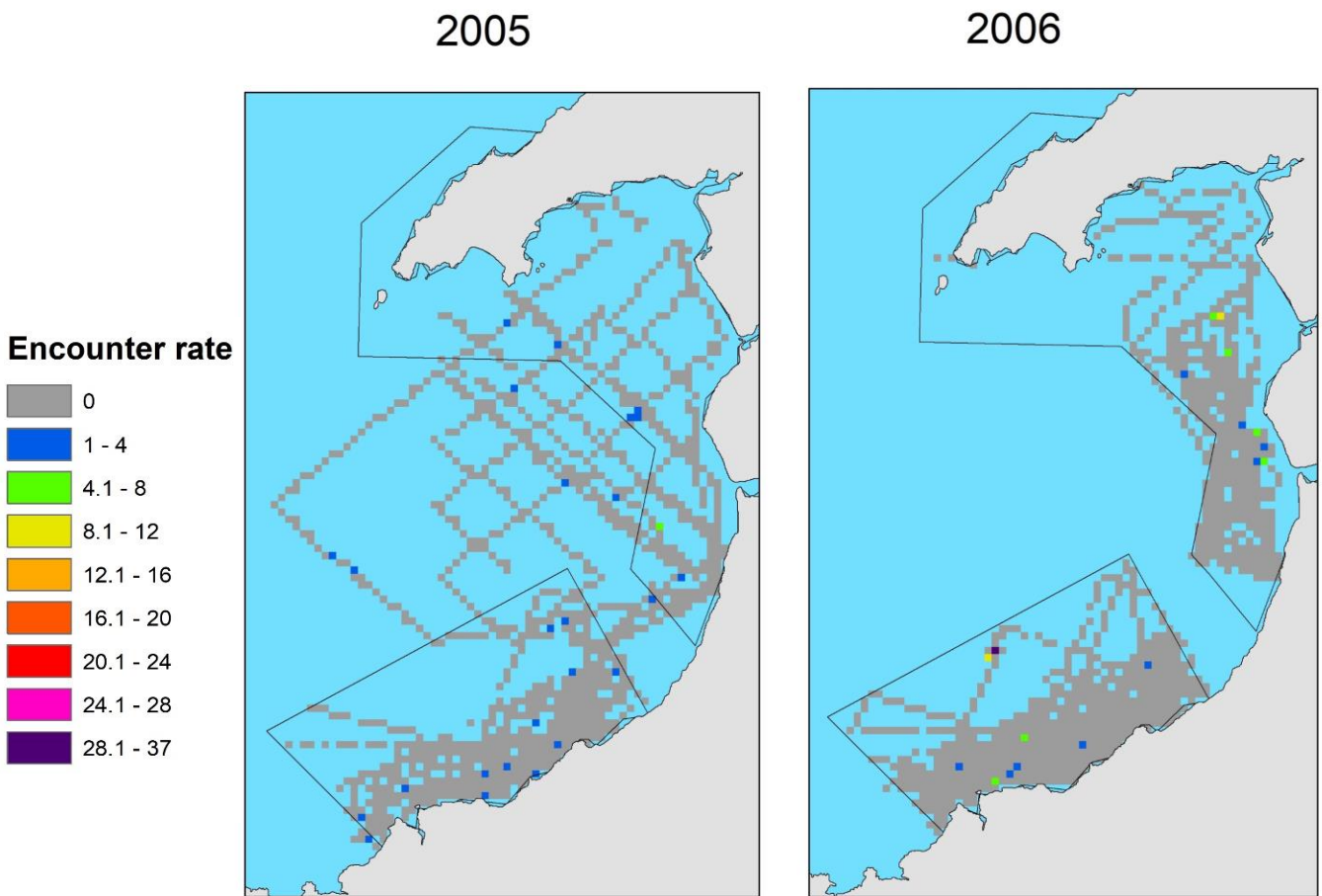
APPENDIX IV. Table of binomial model (presence/absence) and negative binomial model (density) performance values. The red squares are highlighting the models with the lowest AIC values which were the final models and variables chosen to run the analysis.

Model Name	Code name	Data input code	AIC value
Binomial Model	M1	<-gam(BTND2~s(Bat,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13317.02
	M2	<-gam(BTND2~s(CHL,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	14005.98
	M3	<-gam(BTND2~s(Sedi2,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13849.68
	M4	<-gam(BTND2~s(TMP,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	14000.21
	M5	<-gam(BTND2~s(BatA,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13827.42
	M6	<-gam(BTND2~s(Spd,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13857.81
	M7	<-gam(BTND2~s(Bat,k=3)+s(Sedi2,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	12890.99
	M8	<-gam(BTND2~s(Bat,k=3)+s(CHL,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13319.01
	M9	<-gam(BTND2~s(Bat,k=3)+s(BatA,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13318.66
	M10	<-gam(BTND2~s(CHL,k=3)+s(Sedi2,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13734.16
	M11	<-gam(BTND2~s(CHL,k=3)+s(TMP,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13906.72
	M12	<-gam(BTND2~s(TMP,k=3)+s(Sedi2,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13737.59
	M13	<-gam(BTND2~s(CHL,k=3)+s(BatA,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13712.53
	M14	<-gam(BTND2~s(Bat,k=3)+s(CHL,k=3)+s(Sedi2,k=3)+s(BatA,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	12891.05
	M15	<-gam(BTND2~TMP+s(CHL,k=3)+s(Sedi2,k=3)+s(BatA,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13341.29
	M16	<-gam(BTND2~s(Spd,k=3)+s(CHL,k=3)+s(Sedi2,k=3)+s(BatA,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13054.93
	M17	<-gam(BTND2~s(Sedi2,k=3)+TMP+Bat+offset(DOL_EF),family=binomial,data=Bnd)	12807.46
	M18	<-gam(BTND2~s(Spd,k=3)+s(CHL,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13825.87
	M19	<-gam(BTND2~s(Spd,k=3)+s(Sedi2,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13540.10
	M20	<-gam(BTND2~s(Spd,k=3)+s(BatA,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13498.27
	M21	<-gam(BTND2~s(BatA,k=3)+s(TMP,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13695.54
	M22	<-gam(BTND2~s(BatA,k=3)+s(Sedi2,k=3)+offset(DOL_EF),family=binomial,data=Bnd)	13465.01
	M23	<-gam(BTND2~Bat+s(Sedi2,k=3)+s(CHL,k=3)+TMP+offset(DOL_EF),family=binomial,data=Bnd)	12807.44
Model Name		Data Input	AIC
Negative Binomial	M25	gam(BTND~s(CHL,k=3)+s(Sedi2,k=3)+Bat+s(BatA,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8148.307
	M26	<-gam(BTND~s(CHL,k=3)+s(Sedi2,k=3)+TMP+s(BatA,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8201.73
	M27	<-gam(BTND~s(CHL,k=3)+s(Sedi2,k=3)+s(Spd,k=3)+s(BatA,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8174.54
	M28	<-gam(BTND~s(CHL,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8240.37
	M29	<-gam(BTND~TMP+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8287.28
	M30	<-gam(BTND~Bat+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8198.74
	M31	<-gam(BTND~s(Spd,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8243.10
	M32	<-gam(BTND~s(Sedi2,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8257.96
	M33	<-gam(BTND~s(BatA,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8254.52
	M34	<-gam(BTND~s(CHL,k=3)+s(BatA,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8218.347
	M35	<-gam(BTND~s(CHL,k=3)+s(Sedi2,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8215.576
	M36	<-gam(BTND~s(CHL,k=3)+s(TMP,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8238.798
	M37	<-gam(BTND~s(CHL,k=3)+s(Bat,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8164.947
	M38	<-gam(BTND~s(CHL,k=3)+s(Sedi2,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8215.576
	M39	<-gam(BTND~s(CHL,k=3)+s(Spd,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8207.332
	M40	<-gam(BTND~s(Sedi2,k=3)+s(Spd,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8208.306
	M41	<-gam(BTND~s(TMP,k=3)+s(Sedi2,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8258.424
	M42	<-gam(BTND~s(BatA,k=3)+s(Sedi2,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8236.096
	M43	<-gam(BTND~s(BatA,k=3)+s(Sedi2,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8236.096
	M44	<-gam(BTND~s(BatA,k=3)+s(TMP,k=3)+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8256.037
	M45	<-gam(BTND~s(CHL,k=3)+s(Sedi2,k=3)+Bat+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8159.228
	M46	<-gam(BTND~s(CHL,k=3)+s(Sedi2,k=3)+TMP+Bat+offset(log(DOL_EF)),family=negbin(2.0318),data=Bnd2)	8153.681

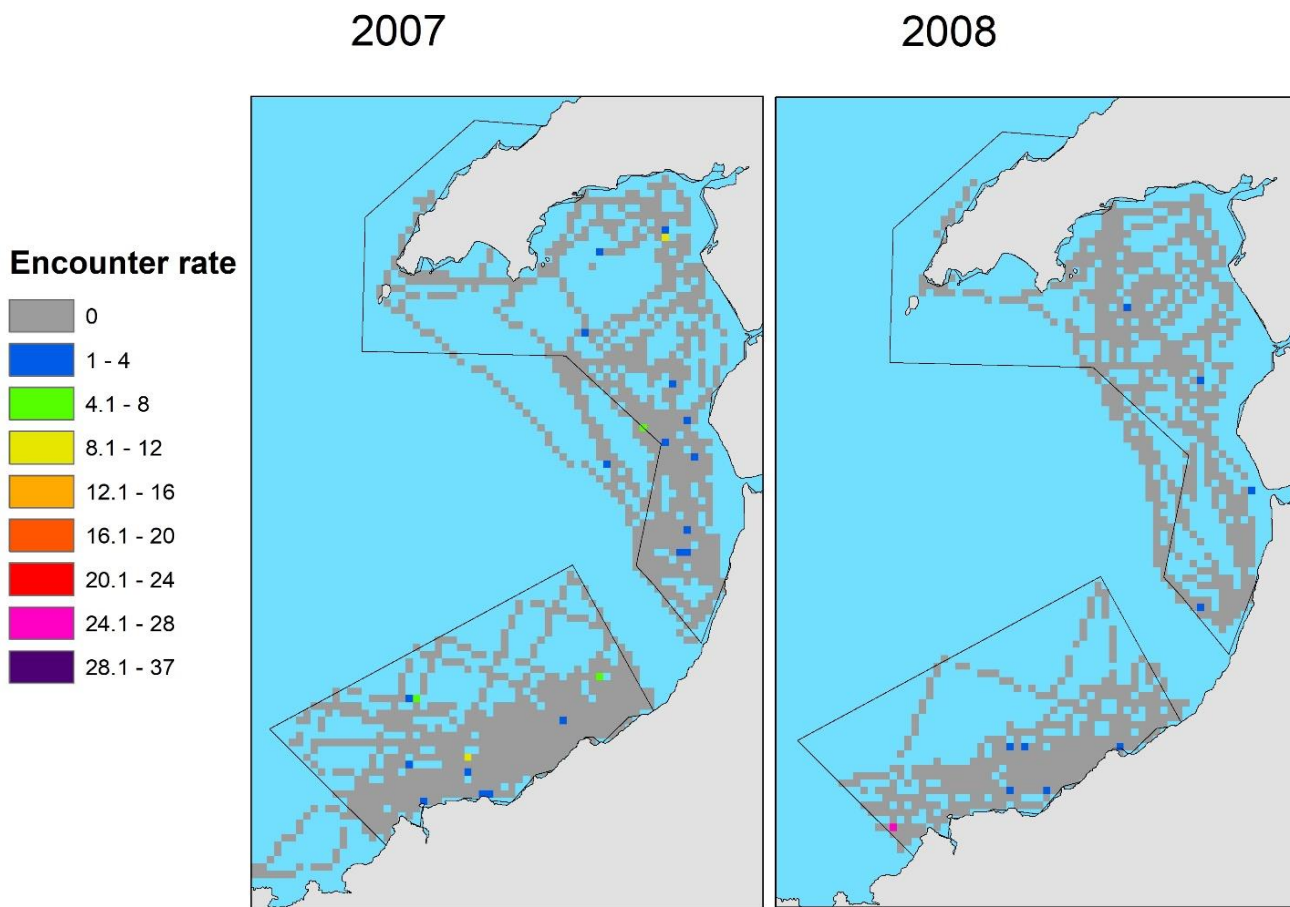
APPENDIX V. Map representing bottlenose dolphin encounter rate (number of dolphin per km travelled) in Cardigan Bay from 2003-2016.



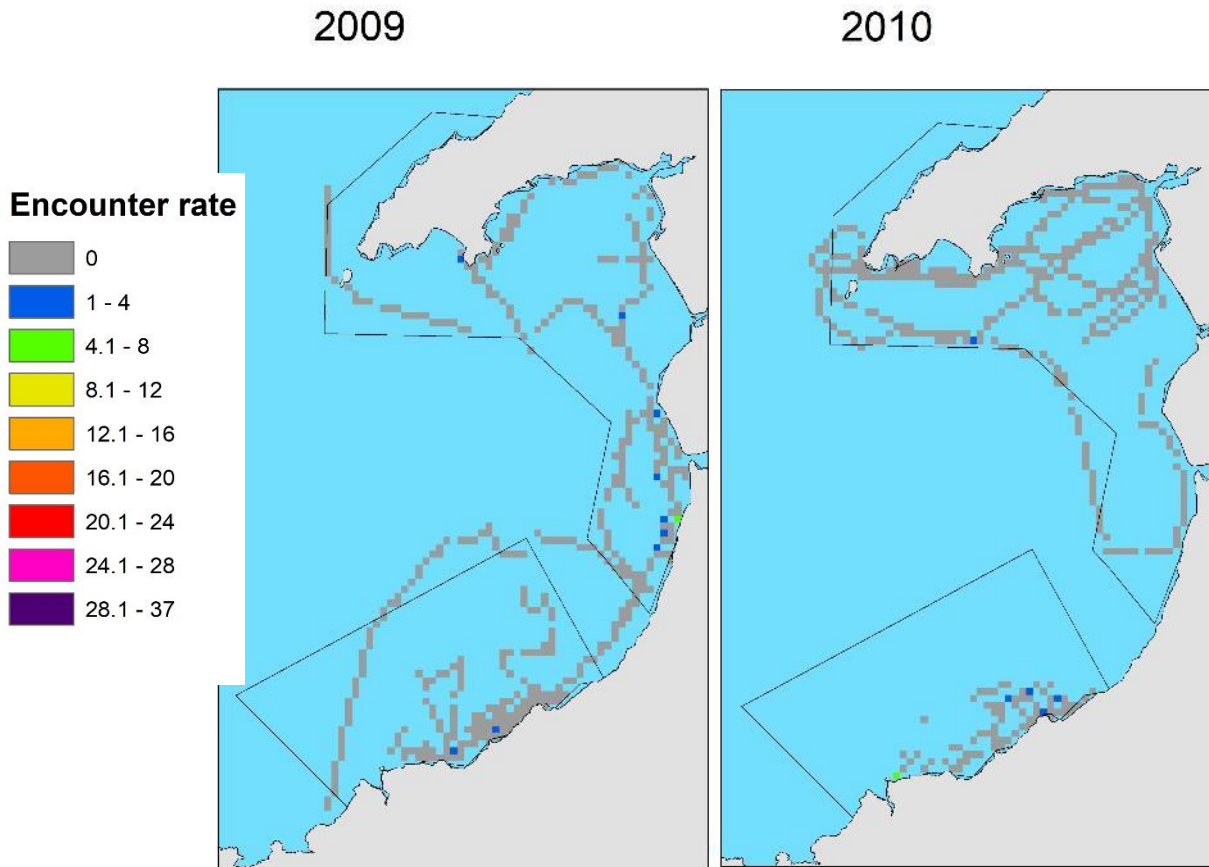
Habitat preference of bottlenose dolphin



Habitat preference of bottlenose dolphin



Habitat preference of bottlenose dolphin

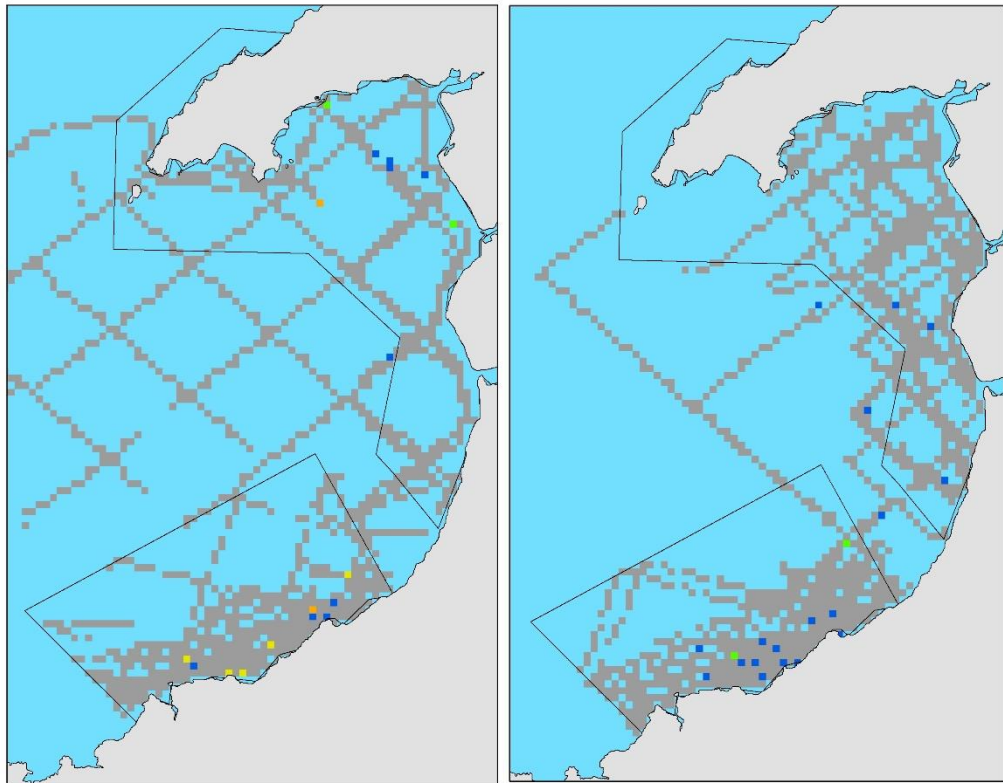
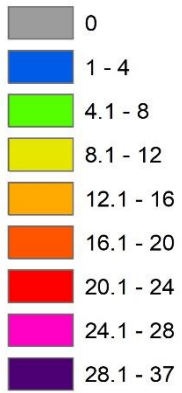


Habitat preference of bottlenose dolphin

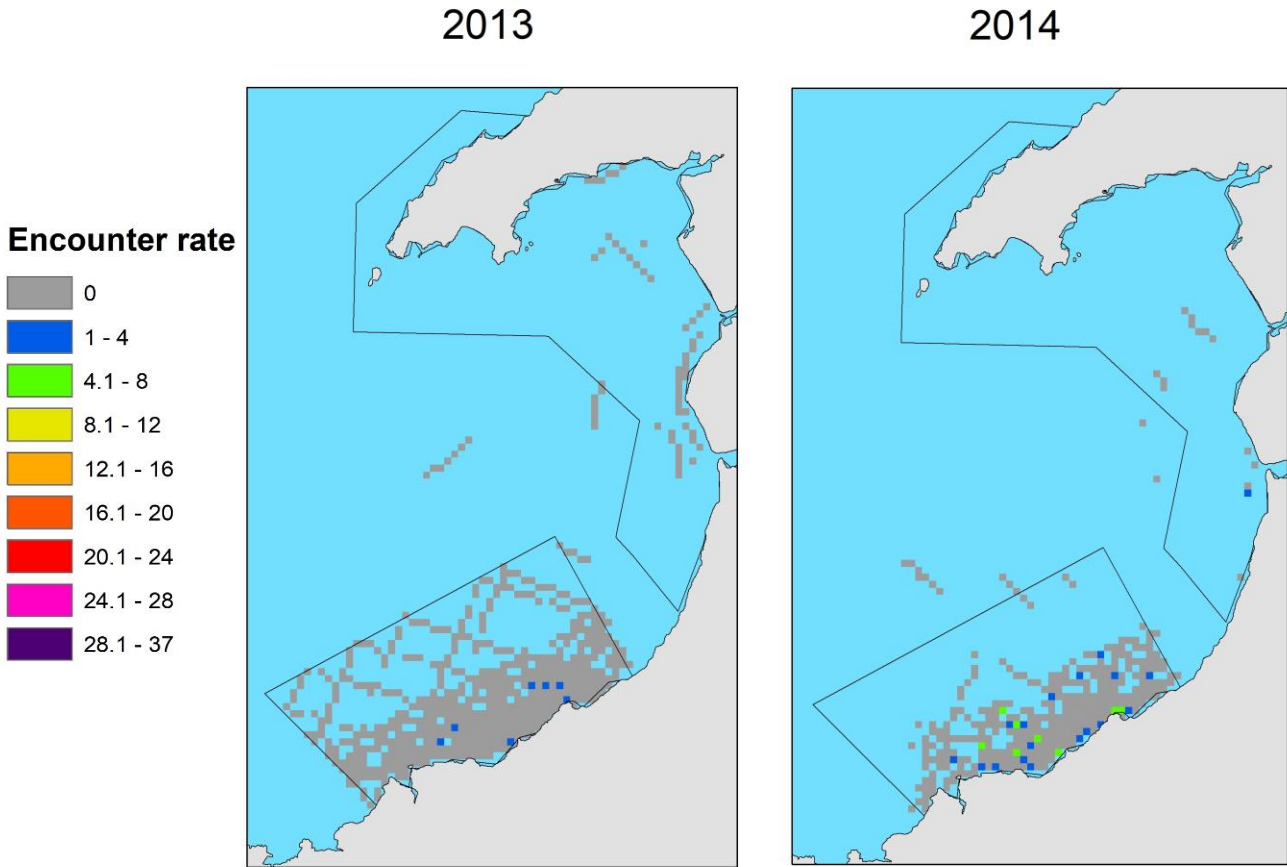
2011

2012

Encounter rate



Habitat preference of bottlenose dolphin



Habitat preference of bottlenose dolphin

