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The influence of topography and tide on the habitat use of Harbour Porpoise.

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The influence of topography and tide on the habitat use of Harbour Porpoise

Abstract

The harbour porpoise is a highly mobile marine mammal, which presents a substantial challenge in the context of using marine protected areas (MPAs) for conservation. Cardigan Bay, West Wales, has been identified as an area of year-round importance for the species, and recognised as a location with the highest 10% predicted persistent high densities of harbour porpoise. Defining their habitat is problematic; primarily because of their highly mobile nature and their habitat use being directed by the availability and distribution of their prey. In the absence of prey data, associations between environment variables are often used as proxies of prey distribution. This study aimed to identify habitat preferences affecting the distribution of harbour porpoise and investigate the consistency of these results through time. Here, data gathered by the Sea Watch Foundation during vessel surveys in west Wales (May-October) across a 5-year time span (2009-2013) were used to examine temporal patterns in habitat use. Generalised additive models (GAMs) were used to analyse relative abundance of harbour porpoises in relation to environmental variables, e.g temperature, salinity, depth, maximum current speed. Results showed that survey variables influenced the model so future research should aim to minimize the effects of sea state and visibility in future research; sightings rates generally decreased with increasing sea state and in poorer visibility. Results also highlighted that harbour porpoise favoured areas of low current speed <0.1m/s and sightings were significantly higher in depths of 20m-50m. These oceanographic features can be used to predict distributions and inform further conservation efforts, such as providing evidence for the establishment of SACs for the species.

Keywords

Phocoena phocoena, Generalised additive models, Species–habitat relationships, Wales, Line transects

Introduction

Harbour porpoises are protected within Annex II of the EU Habitats Directive, which demands the designation of special areas of conservation (SACs) (Embling et al. 2010). Annex II species require the essential areas of their habitat to be designated as Sites of Community Importance (SCIs). These areas are then included in a network of protected sites across Europe known as Natura 2000 (Embling et al. 2010) and managed in accordance with the ecological needs of the species. For highly mobile marine species, it is not feasible to designate their entire range as a protected area; therefore, it is important to recognize areas which are most beneficial to the species' existence, for example feeding or breeding grounds (Hoyt 2005).

The status of harbour porpoise in the North Sea and adjoining waters has been a concern for many years. This concern has originated from the variety of threats that they face; risk from contaminants (Law et al. 1998, 2003; Morris et al. 2003; Barber et al. 2012; Mahfouz et al. 2014; IAMMWG et al. 2015; Torres et al. 2016) and disturbances (Arcangeli & Crosti 2009; Richardson 2012; IAMMWG et al. 2015; Pérez-Jorge et al. 2017), considerable bycatch during fishing operations (Clausen & Andersen 1988; Evans 1990a; Berggren 1994; Vinther 1999; IAMMWG et al. 2015), and decline in incidental sightings within coastal waters (Evans et al. 1986, 2003, 2015; Evans 1990b; Berggren & Arrhenius 1995a, 1995b).

The global population of harbour porpoise is estimated to be in excess of 700,000 individuals (Hammond et al. 2008). The species is found across the northern hemisphere, and in the Atlantic this species is distributed along the continental shelves from the Barents Sea down to the coastal areas of Northern Africa (Evans 2008a). In the UK, harbour porpoises are most abundant in Scotland, parts of Wales, for example Cardigan Bay, and Southern and Western Ireland (Evans & Prior 2012). Individuals seen within UK waters are believed to be members of a single population that ranges northwards from the Bay of Biscay (France) to Norway and Iceland (IAMMWG et al. 2015).

Prey distribution is one of the key factors that affects the distribution of harbour porpoise (Johnston et al. 2005; Sveegaard 2011; Mikkelsen et al. 2013; Tougaard et al. 2016). Other known environmental variables likely to affect cetacean distribution include tidal, seasonal, and diurnal factors (Johnston et al. 2005). Harbour porpoises are known to have a large energy requirement (Lockyer 2007) due to their high surface area to body ratio and female

individuals spend the majority of their lives simultaneously pregnant and lactating (Santos *et al.*, 2004; Goulton, 2012). It is therefore likely this species is distributed in areas of high food availability. Harbour porpoise feed on a wide variety of prey, including small schooling fish such as whiting, sprat and herring, and occasionally are known to eat polychaete worms and crustaceans (Rae 1965; Santos & Pierce 2003; Santos *et al.* 2004). Furthermore, the distribution of bottlenose dolphins may also impact on the distribution of harbour porpoise, as bottlenose dolphins are known to fatally interact with harbour porpoise, i.e bottlenose dolphins have been shown to attack and kill harbour porpoise (Ross & Wilson 1996; Evans 2008a; Boys 2017). Within Cardigan Bay specifically, fine scale temporal variations have been found between harbour porpoise and bottlenose dolphins with seasonal differences; with porpoise detections peaking in the winter and dolphins in the summer, diel; porpoise detection highest at night and dolphins after sunrise and tidal variation; porpoise detection highest at slack water, whereas dolphins were highest during ebb and before low tide (Nuuttila *et al.* 2017).

Seasonal movements of the species is likely a response to changes in the distribution and availability of prey (Hammond *et al.* 2002; Kindt-Larsen *et al.* 2016), and to varying oceanographic conditions such as sea surface temperatures (Lockyer 1995; Bräger *et al.* 2003; Goodwin & Speedie 2008). Other physical facts can also contribute such as current velocity, depth, bathymetric roughness, surface topography and gradient, and salinity. These can all result in events such as upwelling, water mixing and strong tidal streams, which are associated with areas of high biological production (Barlow 1988; Shanks 1988, 2007; Raum-Suryan & Harvey 1998; Carretta *et al.* 2001; Hastie *et al.* 2003; Hui 2006; Cox *et al.* 2018). Previous research has found depth is an important factor in explaining the distribution patterns of harbour porpoise, with preferences being found for deeper depths in association to prey type; 20-60m, and 50-150m in each respective research (Watts & Gaskin 1985; Carretta *et al.* 2001; Booth *et al.* 2013). Furthermore, research has found maximum tidal current to influence habitat use by the species. Their preference can vary with location and depends on a combination of topography and local tidal current speed variations. Research completed in the Bay of Fundy and Ramsey Sound found that the species occur in high densities within areas of maximum tidal speeds relative to the local area (Johnston *et al.* 2005; Pierpoint 2008), whereas research off the west coast of Scotland found distribution was best

explained with areas of high density being predicted in areas of low current relative to the local area (Embling et al. 2010). Embling et al. (2010) also went on to complete habitat models identifying areas of high use by harbour porpoises for marine protection, to identify areas of consistent high-density that could be designated as a Special Area of Conservation (SAC).

Harbour porpoise are the only cetacean species listed within the UK Biodiversity Action Plan (BAP) that are prioritised due to previous decline in UK waters (Bennett et al. 2001). Within Europe, harbour porpoise are listed in Annex IV of the EU Habitats Directive, and also within Annex II which requires the development of SACs (Natura 2000 sites), where suitable, due to their high vulnerability to anthropogenic threats (European Parliament & Council of the European Union 2008). As part of the Habitats Directive, the UK has an obligation to identify and evaluate threats to the conservation status of the harbour porpoise within UK waters (Evans & Anderwald 2016). Assessing the status and distribution of a species is vital to successfully identify conservation and management strategies (Kiszka et al. 2004). The West Wales Marine SAC was proposed in 2014 to protect the harbour porpoise and overlaps or encompasses two other SACs: Cardigan Bay SAC and Pen Llyn a'r Sarnau, that are designated to protect a number of different features such as bottlenose dolphins (*Tursiops truncatus*), bar-built estuaries, and Atlantic salt meadows (*Glaucopuccinellietalia maritima*).

Harbour porpoise are predominantly found in coastal habitats, which increases their vulnerability to human pressures. They face a wide range of anthropogenic threats, including bycatch, pollution, marine litter, prey depletion, climate change, and habitat loss (IAMMWG et al. 2015). Different forms of environmental change can result in temporal redistribution of animals instead of changes to the population size, such as changes in prey availability, acoustic noise, and change in shipping activity (Reijnders 1992; Carstensen et al. 2006; Sveegaard et al. 2012; van Beest et al. 2015). Increased knowledge of the habitat preference of individual marine species is critical for the successful implementation of spatial planning and management of human activities in core habitats of vulnerable species such as harbour porpoise.

One of the major challenges with assessing trends of abundance and distribution in cetaceans is the spatial scale that the surveys are completed over as surveys rarely cover the entire geographic range of the study population (Forney 2000; Silva et al. 2009; Cheney et al. 2012; Kaschner et al. 2012). Snapshot line transect surveys are used over wide areas to address this

(e.g. SCANS, (Hammond et al. 2013, 2017; Peltier et al. 2013)), but their high cost restricts the frequency of these surveys. This makes it difficult to define trends, especially with the limited knowledge of population structure (Evans & Prior 2012), such as the substructuring of populations (Andersen 1993; Walton 1997; Galatius et al. 2012). Large scale surveys, known as SCANS I, II, and III (Small Cetacean Abundance in the North Sea), were completed in 1994, 2005, and 2016 respectively (Hammond et al. 2013, 2017) to provide a broad scale estimate of small cetacean distribution and population estimates for conservation purposes. Due to the broad scale of these surveys they lacked the fine scale information required to determine favoured habitats for harbour porpoise (Evans & Prior 2012).

This study will focus on studying the habitat use of harbour porpoise within the proposed West Wales Marine SAC, which covers 7,376km² (NRW & JNCC 2017). Through previous habitat modelling the area was identified as an important summer habitat for harbour porpoise, with a small area in the south identified as a winter habitat for the species (NRW & JNCC 2017). The candidate SAC (cSAC) boundaries were designated through data modelling of an 18 year data series, and recognised as an area predicted to have the top 10% persistent high densities of harbour porpoise during the summer months (IAMMWG 2015; NRW & JNCC 2017). These models found an indication that harbour porpoises had a preference for water shallower than 40m, and a preference for tidal current speeds of 0.4-0.6m/s (NRW & JNCC 2017).

This study will focus on analysing Sea Watch Foundation data consisting of summer visual boat surveys from 2009 to 2013 carried out in Cardigan Bay. Boat surveys and habitat modelling have been applied to the 5-year dataset, 2009-2013, to determine trends in harbour porpoise habitat preference within Cardigan Bay. The aim of this study is to investigate a consistent habitat preference of harbour porpoise over time, and to discuss the results in the context of advising conservation and management requirements, and offers a frame of reference for the monitoring of habitat use variations for harbour porpoise within West Wales Marine SAC.

Materials and Methods

Study Area

The survey area encompasses the whole of Cardigan Bay (Figure 1), which is the largest embayment in the UK, extending over 100km from the western tip of the Llŷn Peninsula ($52^{\circ} 47'N, 004^{\circ} 46'W$) to St David's Head in the south ($51^{\circ} 54'N, 005^{\circ} 18'W$) (Lohrengel et al. 2017). Cardigan Bay is a relatively shallow bay covering 5,500km², with the deepest points reaching up to 60m. The Bay experiences seasonal variation in salinity, with water stratification ranging from 34.2‰ in the summer to 33‰ in the winter, and is influenced by fresh water input from rivers and estuaries in the bay, that cause localized reductions in salinity (NRW 2000; Ceredigion County Council et al. 2008). The Bay has a mainly semi-diurnal tide with a mean spring tide of between 4-5m and currents not exceeding 1.8 knots going northwards during the flood tide (Ceredigion County Council et al. 2008).

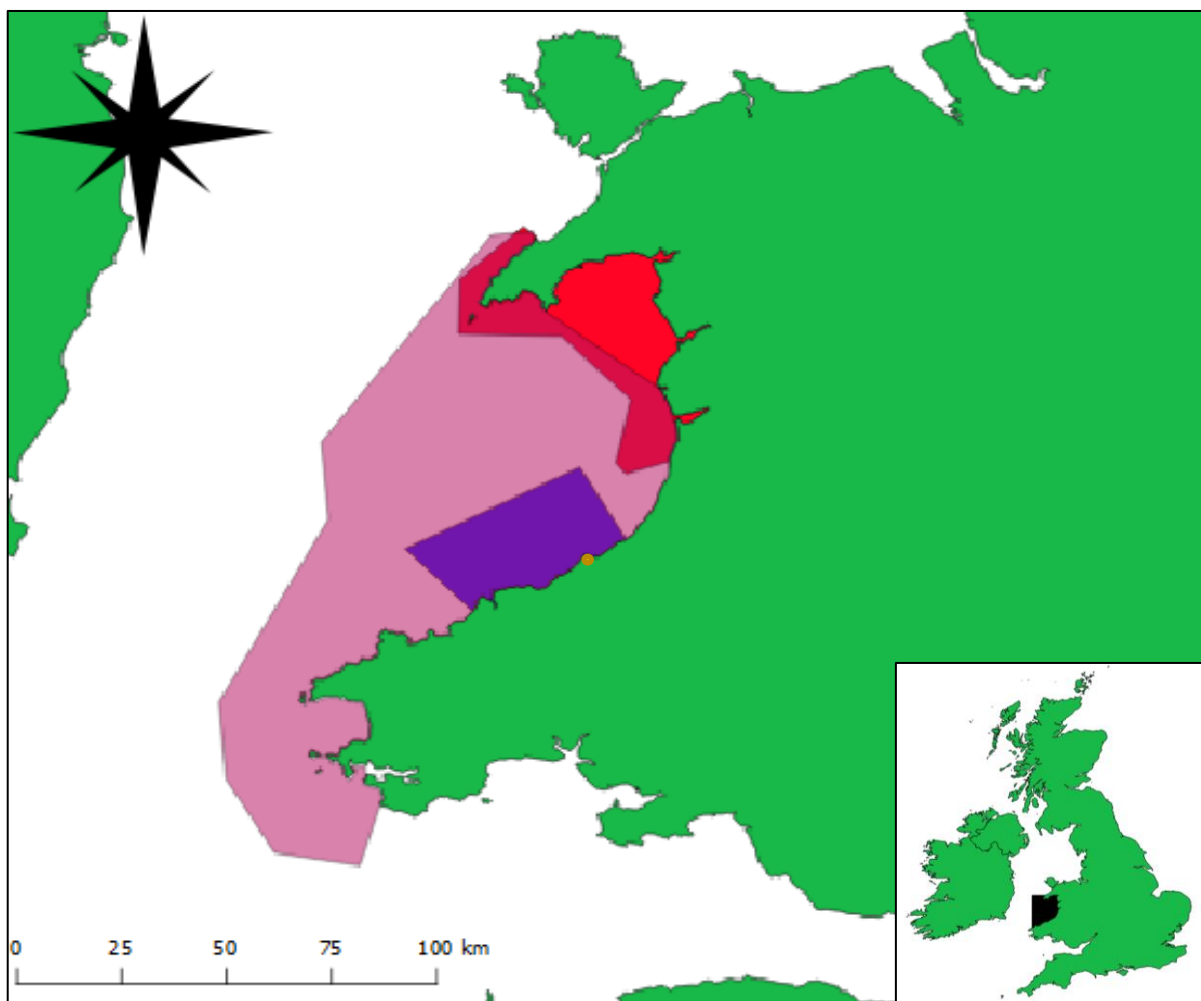


Figure 1 Study area in Cardigan Bay, West Wales, with SACs; Pen Llŷn a'r Sarnau SAC (red), Cardigan Bay SAC (blue), and candidate West Wales Marine (pink) highlighted. The orange circle shows the location of New Quay. A map of the British Isles with location of study area is also shown.

The Bay has a varying substrate composition that is driven by tidal currents. Areas that have strong currents are mainly formed of gravel, boulders and rocks, whereas areas that have a low current are mostly composed of mud. The coastal areas are predominantly composed of sand.

Harbour porpoise are the most common species within the Bay, present throughout the year. The bay is also home to Wales' only resident population of bottlenose dolphins (*Tursiops truncatus*), as well as hosting six other species of cetacean: minke whale (*Balaenoptera acutorostrata*), short beaked common dolphin (*Delphinus delphis*), Risso's dolphin (*Grampus griseus*), and occasionally long-finned pilot whale (*Globicephala melas*), fin whale (*Balaenoptera physalus*) and killer whale (*Orcinus orca*).

Under the European Union Habitat Directive 1992, member states must protect listed habitats and species by designating Special Areas of Conservation (SACs). In 2004, two SACs were established in Cardigan Bay.

In the north of Cardigan Bay there is Pen Llŷn a'r Sarnau SAC (figure 1) which is 1,460km² and covers sea, coast and estuary habitats. Pen Llŷn a'r Sarnau SAC's primary features for designation include: sandbanks, bar-built estuaries, coastal lagoons, large shallow inlets and bays, and reefs, other qualifying features include: mudflats, sandflats, *Salicornia*, Atlantic salt meadows (*Glauco-Puccinellietalia maritimae*), sea caves, bottlenose dolphins (*Tursiops truncatus*), Eurasian otters (*Lutra lutra*), and Atlantic grey seals (*Halichoerus grypus*) (NRW, 2000). Cardigan Bay SAC is in the southern end of Cardigan Bay (figure 1) and covers an area of 959km². Cardigan Bay SAC's primary designation feature is the bottlenose dolphins (*Tursiops truncatus*), with sandbanks, reefs, sea caves, sea lamprey (*Petromyzon marinus*) and European river lamprey (*Lampetra fluviatilis*) and Atlantic grey seals (*Halichoerus grypus*) all being other qualifying features (Ceredigion County Council et al. 2008).

West Wales Marine SAC is currently a candidate SAC (cSAC) which covers an area of 7,376km². It was first submitted for designation in December 2014. The cSAC is located between the Llŷn peninsula to the north and the Pembrokeshire coast to the south west (Figure 1). West Wales Marine SAC has been designated for the protection of harbour porpoises, hosting an estimated 5.4% of the UK Celtic and Irish Sea's Management Unit population (NRW & JNCC 2017).

The entire cSAC has been identified as an important area for harbour porpoises during the summer months, with a small area in the south identified as a winter habitat for the species. The cSAC boundaries were designated through data modelling of an 18 year data series, and recognised as an area predicted persistently high densities of harbour porpoise within the top 10% (NRW & JNCC 2017).

New Quay, west Wales, is a small, primarily tourist town approximately in the centre of the Cardigan Bay SAC, which offers prime locations for surveying marine mammals within the proposed SAC, being located at the coastal midpoint of the bay (Figure 1).

Data collection

The data were collected over a five-year period (2009-2013) during the summer months (May-October). Data were collected and analysed following methods described in Lohrengel and Evans (2015). Data was collected during both vessel-based line transect and dedicated 'ad libitum' surveys (Altmann 1974; Mann 2000). Line transects were completed following pre-determined transects throughout Cardigan Bay, using the vessels listed in Table 1, using a double platform of observers; two teams of two observers located in different positions on the boat. Primary observers were situated on the roof of the vessel, surveying with bare eyes from abeam (90°) on their side to 10° on the opposite side, with independent observers scanning the track line ahead using binoculars, focusing on 45° on their side to 10° on the other. Ad libitum surveys were run on a single platform (primary observers only) basis and followed no set routes but conformed to line transect data collection protocols in all other aspects.

Table 1 Vessels used for line-transect and ad libitum surveys in Cardigan Bay (Lohrengel & Evans 2015).

Vessel name	Length	Eye height (m)	Average speed (kn)	Engine type
Dunbar Castle II	9.7	3.5	5-6	120 hp diesel
MaChipe Seabrine	10	4.5	10	Twin 220 hp diesel
Highlander	10	4	10	Twin 370 hp diesel
Ermol V	11.5	2.5	6	Twin 128 hp diesel
Ermol VI	10.9	2.5	6	350 hp diesel
Bay Explorer	10	2.5	Variable	Twin 200hp petrol

Environmental conditions (sea state, swell, visibility) were recorded on effort forms (Appendix 1a) at 15-minute intervals, or if the conditions changed. Visibility was recorded within the following categories based on the distances listed within the brackets; 1 (<1km); 2 (1-5km); 3 (6-10km); 4 (>10km). A Garmin GPS 60 device was used to record the position and speed of the vessel every 15 minutes, and to log an automatically generated track. Other boat traffic and their activities were also recorded during each line of effort, noting the number and type of boats present.

On spotting a marine mammal the bearing of the sighting to the boat was logged using an angle board, with the bow of the vessel as point 0, and species, number of individuals, behaviours and group compositions recorded on a sighting form (Appendix 1b, Lohrengel & Evans 2015). Distance and bearing of the sighting were recorded to allow for estimation of the sighting coordinates during data entry. All volunteers completed a distance training session, and were tested regularly with a series of known distances (Lohrengel & Evans 2015).

Data were collected and analysed following methods described in Lohrengel and Evans (2015). Cetaceans are a protected species under the Conservation of Habitats and Species Regulations 2017 (Habitats Regulations) and as such it is an offence to approach or disturb wild animals. Only bottlenose dolphin groups were approached while on dedicated surveys, following guidelines indicated in the photo-identification licence which is granted to Sea Watch Foundation by Natural Resources Wales (Appendix 2). As harbour porpoise photo ID is

not beneficial due to the difficulty of identifying individuals, and because of the shy nature of harbour porpoise, they were not approached during data collection. Time spent approaching bottlenose dolphins for photo-ID was recorded as off-effort and not included in analysis.

Environmental variables

A range of environmental predictor variables were available relating to harbour porpoise relative abundance (Table 2). Tidal variables influence is known to be significant for the distribution of harbour porpoise (Johnston et al. 2005; Pierpoint 2008; Embling et al. 2010), so the spatially varying tidal variable; maximum tidal current speed, was included in the model, and calculated from FVCOM (Finite Volume Community Ocean Model).

Depth and bathymetric roughness have also been shown to be significant in predicting the distribution of harbour porpoise (Watts & Gaskin 1985; Carretta et al. 2001; Booth et al. 2013) and bathymetric roughness is also known to increase vertical mixing (Gille & Smith 2003). In this study depth and bathymetric roughness were provided by EMODNet (European Marine Observation and Data Network). Bathymetric roughness was calculated using the terrain ruggedness index (TRI) which is a measurement developed by Riley et al. (1999) to convey the amount of elevation difference between neighbouring cells (Moreno-Ibarra et al. 2009). Sea surface salinity, sea surface temperature and chlorophyll a were included to represent areas of tidal mixing fronts (Miller 2009), and primary production (Campbell et al. 2002), and were provided by EuroGOOS FOAM Shelf Seas – Atlantic Margin Model (AMM7).

Monthly average data for between April and October, 2009 to 2013, was used for the environmental features, where the mean value for each feature was estimated for each grid cell. The data sets were then processed to generate a corresponding grid for the environmental data at a resolution of 1km², half the segment size recommended by Hedley (2000) so that the environmental variables and survey conditions did not change appreciably within the cell.

Table 2 Summary statistics for the environmental variables for the five survey years. Mean and the standard deviation are given where the variables were normally distributed.

	2009	2010	2011	2012	2013
DISTANCE SURVEYED (KM)	1151	1472	738	1720	2049
NUMBER OF HARBOUR PORPOISE SIGHTINGS	54	28	21	70	99
NUMBER OF 1KM CELLS ANALYSED	1274	1397	1027	2289	2162
BOAT SPEED (KNOTS)					
RANGE	0.3-24.2	0.2-22	0.2-20	0.2-22	1-21
MEAN (SD)	9.57 (8.44)	7.47 (5.35)	6.58 (3.83)	8.76 (4.76)	8.54 (5.04)
SEA STATE					
RANGE	0-4	0-4	0-4	0-4	0-4
MEDIAN (SD)	1 (1.13)	0 (0.76)	2 (1.1)	1 (1.2)	0 (0.8)
VISIBILITY					
RANGE	2-4	3-4	0-4	1-4	1-4
MEDIAN (SD)	4 (0.15)	4 (0.76)	3 (1.1)	4 (0.7)	3 (0.4)
DEPTH (M)					
RANGE	-0.9 - -40.9	-0.9 - -94.4	-0.9 - -48.3	-0.9 - -45.1	-0.3- -105.7
MEAN (SD)	-15.3 (7.2)	-17.6 (11.6)	-18.6 (9.2)	-16.9 (8.7)	-27.8 (20.9)
BATHYMETRY ROUGHNESS (M)					
RANGE	0.08-9.52	0.19 - 15.04	0.23 -9.52	0.22 - 9.52	0.17-20.36
MEAN (SD)	2.59 (1.79)	2.77 (2.29)	2.39 (1.73)	2.04 (1.58)	2.24 (2.14)
SALINITY (PSU)					
RANGE	33.86-34.55	34.01-34.69	34.71-35.03	33.31 - 34.92	33.20-34.67
MEAN (SD)	34.26 (0.16)	34.45 (0.18)	34.90 (0.05)	34.28 (0.39)	34.17 (0.28)
CURRENT SPEED (MS⁻¹)					
RANGE	0.01-0.6	0.01 - 0.64	0.02 -0.20	0.02 - 0.20	0.01-0.64
MEAN (SD)	0.1 (0.04)	0.12 (0.08)	0.11 (0.04)	0.10 (0.03)	0.14 (0.08)
CHLOROPHYLL (MG/M³)					
RANGE	99.4-365	59.2-324.4	64.6-310.2	91.6-309.1	59 - 365.3
MEAN (SD)	209.3 (66.2)	187.7 (79.9)	199.7 (65.4)	218.1 (54.6)	254 (81.3)
TEMPERATURE (°C)					
RANGE	10.8-17.6	10.8 - 17.9	12.3-17.9	10.9 - 17.6	10.5-18.5
MEAN (SD)	15.5 (1.4)	15 (2.2)	16.7 (1.1)	14.8 (2.3)	14.6 (2.3)

Data processing

All data was overlaid and plotted using the software QGIS 2.18.26 (QGIS Team 2015). For each grid cell corresponding environmental data and sightings were joined and converted into the EPSG:32630- WGS 84 / UTM zone 30N Projection.

Effort data points were combined to form track lines using the Points2Line plugin. The track lines were intersected with their corresponding grid cell and the total amount of effort in metres calculated. Effort data was joined to the sightings and environmental data and isolated so only grid cells that contained effort data were retained for analysis.

Post joining, grid cells that contained data gathered in sea state above four were removed, as environmental conditions were deemed too poor to reliably spot harbour porpoise, due to their low detectability especially in rougher waters (Palka 1996; Teilmann 2003; MacLeod et al. 2008). Each grid cell effort distance was log transformed to allow for offsetting during analysis.

Data Analysis

Prior to beginning the modelling, a Spearman's rank correlations were estimated between all the variables. If there was a significant correlation ($p > 0.7$) the first of the variables that was chosen by the forward step-wise selection was conserved and any of the variables it was significantly correlated to were excluded from the model (Embling et al. 2010).

Generalised Additive Models (GAMs) were run to relate the presence and absence of harbour porpoise detected per 1km² cell to the survey and environmental variables for the years of data. GAMs relate predictor variables to data responses that can be non-normally distributed with non-linear smooth functions (Embling et al. 2010). They take the general form specified by Hastie & Robert (1990). The GAMs were fitted in R version 3.3.2 (R Team 2018), using the MGCV library (Wood 2018) where the degrees of freedom of the smooth functions or the predictor variables is decided within the model fitting process (Wood 2006; Embling et al. 2010). Within the MGCV the default smoothing spline that is used is a thin plate regression spline (TPRS). The TPRS allows the estimation of a smooth function with multiple predictor variables, without knowing the location of where the different splines join being needed (Embling et al. 2010). By using this method it eliminates the bias that are caused by estimating

the locations where the different splines join, which for smoothing in other methods is necessary. The smooth functions for each variable were limited to four degrees of freedom, to prevent excessive flexibility and model overfitting (Embling et al. 2010).

A stepwise addition of survey variables and then environmental variables to the null model (where no variables are predicting the distribution) was collected (forward step-wise selection) and the models were developed by selecting explanatory variables that minimizing the UnBiased Risk Estimator (UBRE) score. The UBRE score is the Poisson GAM equivalent of the Akaike information criterion (AIC) value, and balances the fit of the model with the number of parameters used to report the model (Embling et al. 2010; Wood 2017). First survey variables (sea state, visibility, and boat speed) were included in the model, so changes in detection probability could be accounted for, before adding environmental variables.

Results

Survey Results

A total of 7131km was surveyed in Cardigan Bay during the study period, during which 301 groups with a total of 557 harbour porpoise were detected (Table 2). There was a higher density of effort within Cardigan Bay SAC, than outside the SAC (Figure 2). Harbour porpoise detections were distributed mostly within the coastal region of the survey area, mainly concentrated within Cardigan Bay SAC. There were fewer detections in offshore locations (Figure 2).

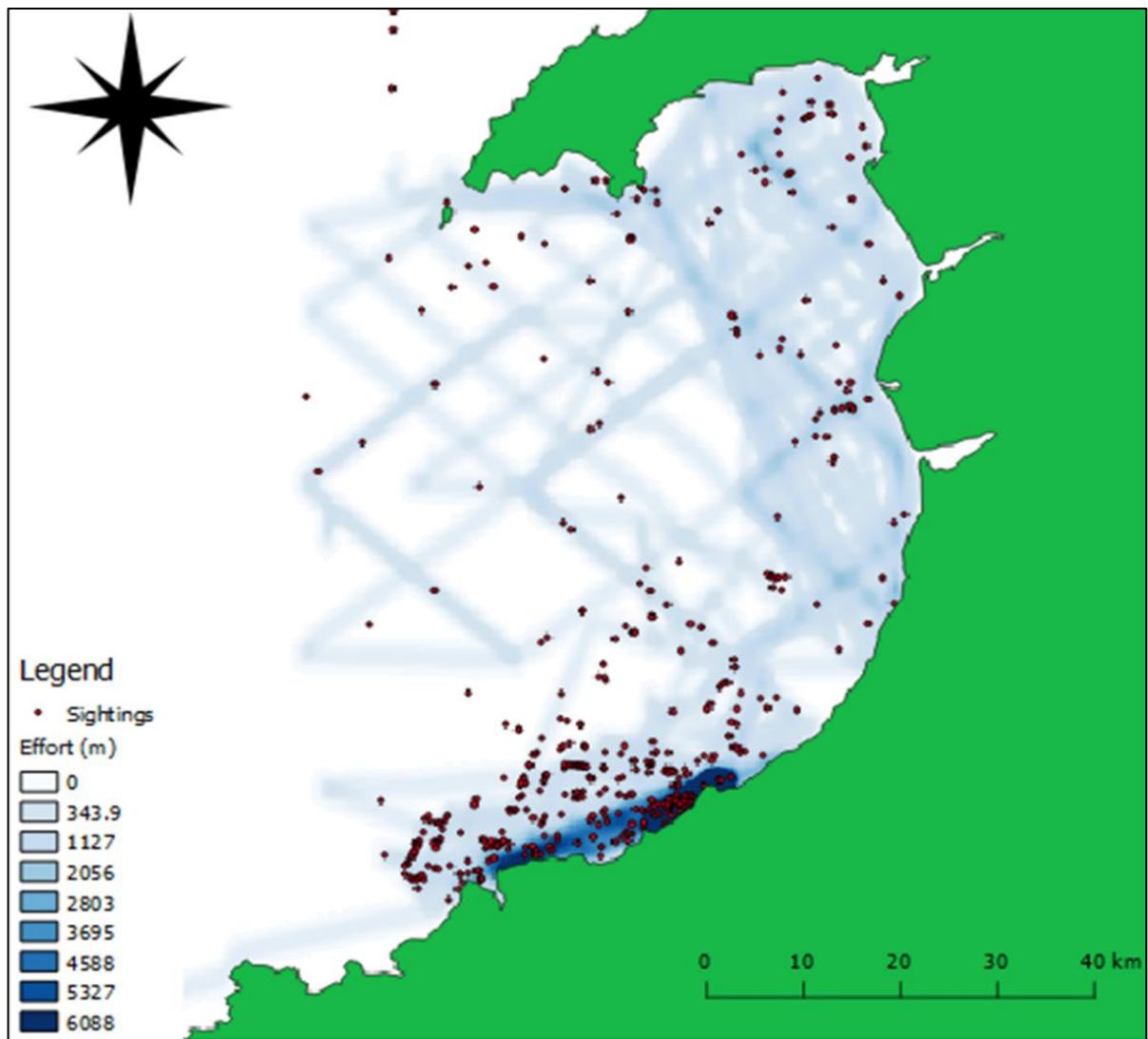


Figure 2 Map of effort intensity within Cardigan Bay, West Wales. Dark blue indicates areas of high effort intensity. Harbour porpoise sightings within Cardigan Bay are indicated by red dots (2009-2013). A map of effort intensity is included in Appendix 4.

Model Results

The optimal GAM model of presence/absence of harbour porpoises for all 5-years explained 7.35% of the deviance, the most important survey variable was sea state followed by visibility, which explained 2.8% and 0.95% respectively. Overall, within the five-year model the most important environmental predictor of harbour porpoise sightings was depth (1.28%), followed by bathymetric roughness (1.09%), current speed (0.63%), and chlorophyll a (0.6%) (Figure 4). Sightings were higher when the depth was between 50m and 20m, the bathymetric roughness was greater than 3m, and the current speed was less than 0.1m/s (Figure 4) (Table 3).

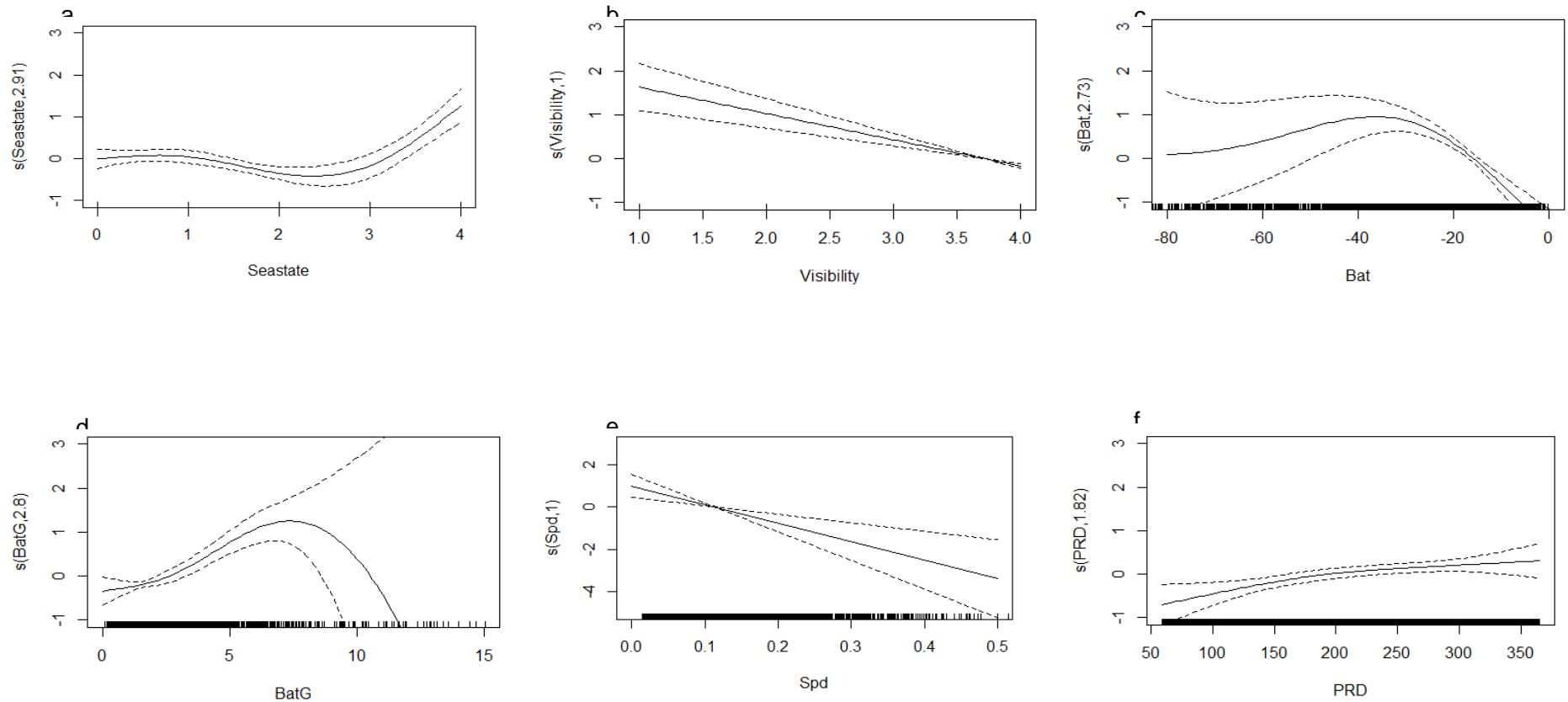


Figure 4 Relationships between visual detections of harbour porpoise groups and a) sea state, b) visibility, c) depth, d) bathymetric roughness, e) current speed and f) Chlorophyll a for all 1km segments within the five-year model (n=8149) The estimated 95% confidence intervals are shown by the dotted lines around the smooths.

Table 3 The results of the forward GAM model selection of the presence/absence of harbour porpoises per 1km cell for the five-year model. Variables have been displayed according to their importance in the model, first compensation for survey variables (sea state, vessel speed, and visibility). Smooths have been shown with the number of degrees of freedom in brackets. UBRE is the reduction in the UBRE score produced by the addition of each variable to the model, the first UBRE score in bold shows the starting UBRE score.

Order	Smooth (d.f.)	% Dev	UBRE	P value
1	Sea State (4)	2.8%	-0.67508	6.26×10^{-10}
2	Visibility (4)	+0.95%	-0.00245	1.06×10^{-9}
3	Depth (4)	+1.28%	-0.00357	1.48×10^{-10}
4	Bathymetric Roughness (4)	+1.09%	-0.00294	9.66×10^{-10}
5	Current Speed (4)	+0.63%	-0.00179	2.29×10^{-4}
6	Chlorophyll a (4)	+0.6%	-0.00213	2.37×10^{-3}
Total:		7.35%	-0.68796	

There was some variability in the habitat preferences found between years. During 2010 porpoise occurrence was higher with a sea surface temperature above 16.5°C ($p=0.22$, 3.45). Whereas in 2011, the optimal GAM model included sea state ($p=0.00171$, 9.96%), visibility ($p=0.02$, 4.34%) and salinity ($p=0.0058$, 4.6%) (Table 4) with occurrence being higher with a salinity around 34.85psu, explaining 6.5% of the deviance (Appendix 3.3).

In 2012 the optimal GAM model included sea state ($p=7.22 \times 10^{-10}$, 9.88%), visibility ($p=0.0345$, 0.62%), chlorophyll ($p=0.441$, 0.8%), and depth ($p=3.85 \times 10^{-5}$, 4%), presence was significantly higher when the depth was between 15m and 35m or chlorophyll was less than 225 mg/m³ (Appendix 3.4).

The 2013-based model included sea state ($p=3.25 \times 10^{-6}$, 4.74%), vessel speed ($p=0.0041$, 3.29%), bathymetry roughness ($p=2.08 \times 10^{-9}$, 5%) and salinity ($p=1.74 \times 10^{-4}$, 3.40%), explaining 16.4% of the deviance (Table 4), presence was higher in areas with bathymetric roughness of between 2.5m-7.5m or a salinity of 34psu.

Of the survey variables, sea state was the most crucial predictor of harbour porpoise detection rate in the each of the year models, except for 2010 and 2009, explaining between 2.8% and 10% of the deviance. Sightings within the 5-year GAM and 2011 model were higher within areas surveyed in a sea state <1 . In most cases there was higher porpoise sightings at low sea states and low boat speeds, though there was some variability in the relationship between years (Appendix 3). Visibility was the final survey variable measured and sightings were significant within the 2011 and 2012 model when visibility was less than category 2 (Appendix 3).

Table 4 The results of the forward GAM model selection of the presence/absence of harbour porpoises per 1km cell for 2009-2013. Variables have been displayed according to their importance in the model, first compensation for survey variables (sea state, vessel speed, and visibility). Smooths have been shown with the number of degrees of freedom in brackets. UBRE is the reduction in the UBRE score produced by the addition of each variable to the model, the first UBRE score in bold shows the starting UBRE score.

Order	2009			2010			2011			2012			2013		
	Smooth (d.f.)	% Dev	UBRE	Smooth (d.f.)	% Dev	UBRE	Smooth (d.f.)	% Dev	UBRE	Smooth (d.f.)	% Dev	UBRE	Smooth (d.f.)	% Dev	UBRE
1	Vessel speed (4)	3.85%	-0.647	Temperature (4)	3.54%	-0.803	Sea state (4)	9.96%	-0.685	Sea state (4)	9.88%	-0.676	Sea state (4)	4.74%	-0.650
2							Visibility (4)	+4.34%	-0.0116	Visibility (4)	+0.62%	-0.00149	Vessel speed (4)	+3.29%	-0.0114
3							Salinity (4)	+4.6%	-0.0101	Chlorophyll (4)	+0.80%	-0.00194	Bathymetry Roughness (4)	+5%	-0.0154
4										Depth (4)	+4.00%	-0.0120	Salinity (4)	+3.40%	-0.00929
5															
Total:		3.85%			3.54%			18.90%			15.30%			16.40%	

Discussion

This study shows that survey variables accounted for the majority of deviance within the models, varying from 3.85% in 2009 to the highest of 14.3% in 2011. Within the 5-year model survey variables accounted for 3.97% of the model's deviance, highlighting the importance of accounting for survey variables within models and attempting to collect data during sea states zero or one when harbour porpoise are most detectable and therefore absence data is most accurate (Palka 1996).

Visibility was a significant factor within the 2011 and 2012 models when the visibility was less than a category two (1-5km). This is contrary to most other species where higher visibility is usually related to higher likelihood of sightings (Williams et al. 2002; Evans 2008b; Leeney et al. 2012; Hammond et al. 2017). Harbour porpoise, however, have a low perpendicular sighting distance (Barlow et al. 2001) so a visibility of less than 5km is more than the perpendicular sighting distance of harbour porpoise, and above most calculated effective strip-widths for them (Buckland et al. 2001). Having a shorter distance to survey in poor visibility might therefore make it more likely for an observer to sight a porpoise, as they will be covering a smaller distance and the highly mobile and inconspicuous behaviours typical of harbour porpoise make them difficult to detect (Cox et al. 2017). Furthermore, harbour porpoise have a low detectability especially with increasing distance (Shucksmith et al. 2009).

Surprisingly, there was no consistent sea state which was significant within the models, especially with two one-year based models finding higher sea states significant for presence, sea state explained 9.88% and 4.74% of the deviance in 2012 and 2013 respectively (Table 4). This does not support previous research, which has found harbour porpoise to be harder to detect in rougher seas because of their small size, small group composition, active boat avoidance, and unobtrusive surface behaviours (MacLeod et al. 2008). Although some research has shown there to be no significant difference in sighting rates between sea state 2 and 3 (Teilmann 2003).

Vessel speed also affected detection and was significant within the 2009 and 2013 model with sightings being significant ≤ 5 knots and at 5 knots respectively. Embling et al. (2010) also found sighting rates decreased with increased vessel speed, and sightings were significant below 6 knots. Other research found harbour porpoise reacted negatively to boats, especially

at higher speeds, one study found 40% of negative responses were related to fast speeds (Oakley et al. 2017) and at faster speeds observers are more likely to overlook harbour porpoise due to their small size.

The five-year model found current speed to be significant, supporting previous research completed off the coast of Scotland (Embling et al. 2010), that harbour porpoises prefer areas of lower current speed. The first study of its kind to find a significance between area of low current speed and harbour porpoise preference in Cardigan Bay. This finding has not been supported by other research which has found high densities of harbour porpoises in areas of high current speed (Johnston et al. 2005; Pierpoint 2008; Marubini et al. 2009). However, like Embling et al. (2010), this study uses current speed as a spatial variable rather than a temporal variable like the previous studies. This highlights how species preference can vary with location and depend on a combination of topographic and local tidal current speed variations.

The five-year model also found depth to be significant between 20m and 50m, and the 2012 model for depths of 15m-35m. Previous research has found harbour porpoises to inhabit the deeper end of their range, 92m to 183m (Read & Westgate 1997), however, research completed in Skomer found that harbour porpoise occurrence was more likely at depths of 0m-60m (Isojunno et al. 2012). Within Cardigan Bay harbour porpoise inhabit the bay along with a resident bottlenose dolphin population, therefore they may use shallower areas of the bay as a means of avoidance as studies have shown bottlenose dolphins prefer habitats with greater depths (Ingram & Rogan 2002; Wilson et al. 2006)

Bathymetric roughness was significant within the 5-year model and the 2013 model, which found $\geq 3\text{m}$ and 2.5m-7.5m significant respectively. Bathymetric roughness has previously been found to affect harbour porpoise distribution (Watts & Gaskin 1985; Read & Westgate 1997; Bailey & Thompson 2009; Marubini et al. 2009; Isojunno et al. 2012; Scottish Natural Heritage 2016). It could be that the roughness and change in slope of the seabed causes upwelling of cold, nutrient rich waters which enhances marine productivity and increases the amount of predator-prey aggregations (Yen et al. 2004; Booth et al. 2013). The bathymetric roughness can also influence currents (Inall et al. 2008) and increase aggregations (Yen et al. 2004), which harbour porpoise can exploit for foraging.

Salinity was significant at around 34psu in the 2011 and 2013 model, this is generally the salinity found throughout the Bay during the summer, but salinity does decrease closer to the shore (CCW 2005), as the amount of fresh water increases (Gillibrand et al. 2003; CCW 2005). These areas of fresh water, which can create fresh water flume fronts, can lead to increased mixing and therefore, heightened productivity and increasing aggregations (Schwing et al. 2000; Yen et al. 2004). These areas of higher salinity could also be related to the harbour porpoise's bathymetric roughness preferences this study found, and in fact the areas preferred receive more upwelling of colder nutrient rich waters (Forney 2000).

Harbour porpoise avoidance of fresh water inlets, such as the river Dyfi (Figure 2), could also be related to avoidance of bottlenose dolphins. The river Dyfi is known for its salmon, which is a prey of choice for bottlenose dolphins (Pierce et al. 1990; Evans & Hinter 2012; Feingold & Evans 2014; Embling et al. 2015), future modelling could be completed to investigate if there is a significant effect of bottlenose dolphin distribution on habitat selection of harbour porpoises, as habitat partitioning has been previously studied between the marine species (Findlay et al. 1992; Weir et al. 2001; Gowans & Whitehead 2008).

Due to different funding and weather conditions throughout the dataset years different areas of Cardigan Bay received different levels of surveying. For example, within the Cardigan Bay SAC in the south of the bay extensive surveying was taken (Figure 3) compared to the outer bay where less surveys were completed. This may have produced a biased result as research effort has been more focused within the SACs because of their monitoring requirements (Cheney et al. 2012). Due to the lack of complete coverage of the survey area and the elusiveness of the study species, this has led to high zero inflation within the data set which could be dealt with using zero inflation models in further studies.

Although this five-year study provides some valuable information, further research is required. It is difficult to study these elusive marine mammals (Forney 2000), especially with primarily visual surveys. Completing acoustic line transect surveys alongside the visual line transect surveys may be better suited for the harbour porpoise. Furthermore, completing combined visual and acoustic surveys would allow for an assessment of how accurate current visual surveys are (Rankin et al. 2008), research has found acoustic detection rates to be more than twice that of visual sighting rates (Booth et al. 2013; Cucknell et al. 2017) and could therefore significantly improve the current understanding of harbour porpoise habitat use in

Cardigan Bay. Previous PAM (passive acoustic monitoring) research has been completed within the proposed SAC (Simon et al. 2010; Nuuttila et al. 2013, 2017, 2018), and could be used to improve habitat modelling to further support the application for SAC status.

Further modelling could also be completed including other environmental variables, such as substrate type, and a longer time series of data modelled to include winter distribution and account for major climate shifts.

Conclusion

Cardigan Bay supports important habitat features, providing ideal foraging and breeding regions for various species including the harbour porpoise. This study found harbour porpoises prefer low current areas, the second known study to find such information and the first within Cardigan Bay. This study has also confirmed the importance of depth and salinity for the harbour porpoise and opened questions for future study within this area for harbour porpoise. Whilst there is some variation between years, key factors have been highlighted and can be used for identifying potential conservation areas.

It is important to continue improving the knowledge of this elusive cetacean and developing a scientifically sound approach to monitoring cetacean populations is particularly important at this time, when the UK needs to develop an independent conservation strategy outside the framework of the EU Habitats Directive to conserve its marine wildlife.

It is vital to further study the harbour porpoise to be able to encourage the implementation of marine protection for them, especially with their high vulnerability to human activities.

The research undertaken in this project supports the designation of the West Wales SAC, and further work completed as part of the designation could greatly improve our knowledge of harbour porpoise.

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Appendix:

Appendix 1:

Survey forms used to collect data for a) the effort data during boat survey and b) the
sightings during boat surveys.

Appendix 2:

Photo-identification license from Natural Resources Wales outlining guidelines to Sea Watch Foundation.



Peter Evans
Sea Watch Foundation
Ewyn y Don
Bull Bay
Amlwch
Anglesey
LL68 0SD

Licence No: 71375:OTH:SA:2016

Valid From: 16th May 2016

Expiry: 31st March 2017

WILDLIFE AND COUNTRYSIDE ACT 1981 (AMENDED BY THE ENVIRONMENTAL PROTECTION ACT 1990) AND THE CONSERVATION OF HABITATS AND SPECIES REGULATIONS 2010

Licence to disturb wild animals and possess derivatives for scientific or educational purposes

This licence, granted under Section 16(3) (a) of the Wildlife and Countryside Act 1981 (amended by the Environmental Protection Act 1990) and under Regulation 53(2) (a) of the Conservation of Habitats and Species Regulations 2010, by the Natural Resource Body for Wales otherwise known as Natural Resources Wales, hereby authorises the person named above, hereinafter referred to as the "licensee" his accredited agents Katrin Lohrengel, Pia Anderwald, Daphna Feingold, Brett Stones, Gemma Veneruso, Kathy James, Mathew Clough, Sonia Doblado, Ben Murcott and James Waggitt (see condition 203.) and their assistants Jon Shaw, Winston Evans, Jonathan Evans, Mike Harris, Brett Stones, Dafydd Lewis, Nathan Enright, Graham Kennard, Tony Barber, Alan Giles and Jonathan James and Richard Dobbins (see condition 250.) to:

1. **possess** skin swabs for DNA analysis and stable isotope studies of diet;
2. **disturb** during the course of obtaining photo-identification as specified in the attached Protocol, the following wild animals in the following localities:-

Species

Locality

Targeted:

Bottlenose Dolphin
Risso's Dolphin

North Wales Coast, Anglesey, Menai Strait to Porth Dinllaen, Bardsey Island, Porth Dinllaen to Sarn Badrig, Sarn Badrig to Aberystwyth, Aberystwyth to Strumble Head, Pembrokeshire Islands, Celtic Deep, Strumble Head to St Anne's Head and St Ann's Head to Severn Estuary

Opportunist:

Fin Whale
Minke Whale
Humpback Whale
Killer Whale
Common Dolphin

- while the said wild animals are occupying any structure or place used by them for shelter or protection, at distances of up to and above 12km off-shore.

Ffôn/Tel 03000 654 974 / 03000 654 921

E-bost/Email: trwyddedrhwyogaeth@cyfoethnaturiolcymru.gov.uk or specieslicence@naturalresourceswales.gov.uk
www.cyfoethnaturiolcymru.gov.uk www.naturalresourceswales.gov.uk

Cyfoeth Naturiol Cymru / Natural Resources Wales, Maes y Ffynnon, Penrhos Gameidd, Bangor, Gwynedd, LL57 2DW

Croesewir gohebiaeth yn y Gymraeg a'r Saesneg Correspondence welcomed in Welsh and English

This licence is valid for the period as stated above and is granted subject to compliance with the conditions as specified. Anything done otherwise than in accordance with the terms of the licence may constitute an offence.



Signed for and on behalf of
Natural Resources Wales

CONDITIONS

Definitions

"NRW" is an abbreviation of the Natural Resources Body for Wales otherwise known as Natural Resources Wales

"EPS" is an abbreviation of European protected species

"Licence application" refers to the application form, method statement and any other supporting documents (where applicable).

200. While engaged in activities under this licence the Licensee shall carry a copy of the licence and must produce it to any police constable or employee of NRW, or other person authorised in writing by NRW, on demand.
202. The activities hereby licensed are restricted to the Licensee, accredited agents and assistants as specified on this licence.
203. No accredited agent of the Licensee shall act under this licence unless they are in possession of a letter appointing them as the duly accredited agent of the licensee for the purpose of this licence. The accredited agent shall carry with them the said letter and a copy of this licence and shall produce them to any police constable or employee of NRW, or other person authorised in writing by the NRW, on demand.
205. The Licensee must assume full responsibility for the conduct of any assistants and accredited agents employed under this licence.
207. Any disturbance to animals shall be kept to the absolute minimum required, so animals are not prevented from normal feeding or rest, nor disturbed during breeding or hibernation; unless permission has been granted by NRW to do otherwise. All reasonable steps must be taken to prevent accidental injury to any protected species. Equipment must be of a kind and used in a way which will avoid distress or injury.
208. Unless specified otherwise this licence does not authorise the intentional killing, taking or injuring of any protected species.
250. Any assistants employed under this licence must remain under the personal supervision of the Licensee or their accredited agents at all times. For the purposes of this licence, an assistant is classed as being any individual employed by the Licensee or accredited agent to operate vessels or any person or group of people who are invited to accompany the Licensee or their accredited agents in order that they may gather specific records/images or skin swabs for the purposes for which this licence has been issued. We would encourage skippers operating under this licence to become WISE accredited.
251. Prior to operating any activity under this licence, the licensee must liaise with the Marine Mammal Specialist (Thomas Stringell or Ceri Morris) at National Resources Wales, telephone 03000 653000.
252. Within four weeks after the expiry of this licence the Licensee shall submit to NRW copies of catalogued images and associated data obtained, subject to the terms and conditions of this licence. NRW has the Licensee's permission to store, copy, use, and release or publish any biodiversity records associated with the issue of this licence. Where NRW's policy on public access to data states that the information is sensitive, publication and public access will be restricted in accordance with both the Environmental Information Regulations (2004) and NRW's guidance on access to data on sensitive biodiversity features. Where NRW's policy on public access to data states that the information is exempt from general release, any such release will

be under restrictive licence conditions in accordance with NRW's guidance on [Ecological data exempt from general release under EIR / FOI](#). NRW may share the biodiversity records supplied with conservation organisations and research programmes selected by it. The licensee agrees that such third parties will have use of the images and associated data for the purposes of research programmes contributing to the conservation management of the species concerned; these purposes will include storage, copying, use, and publication where required. Please note that an inadequate return will prejudice future licence applications.

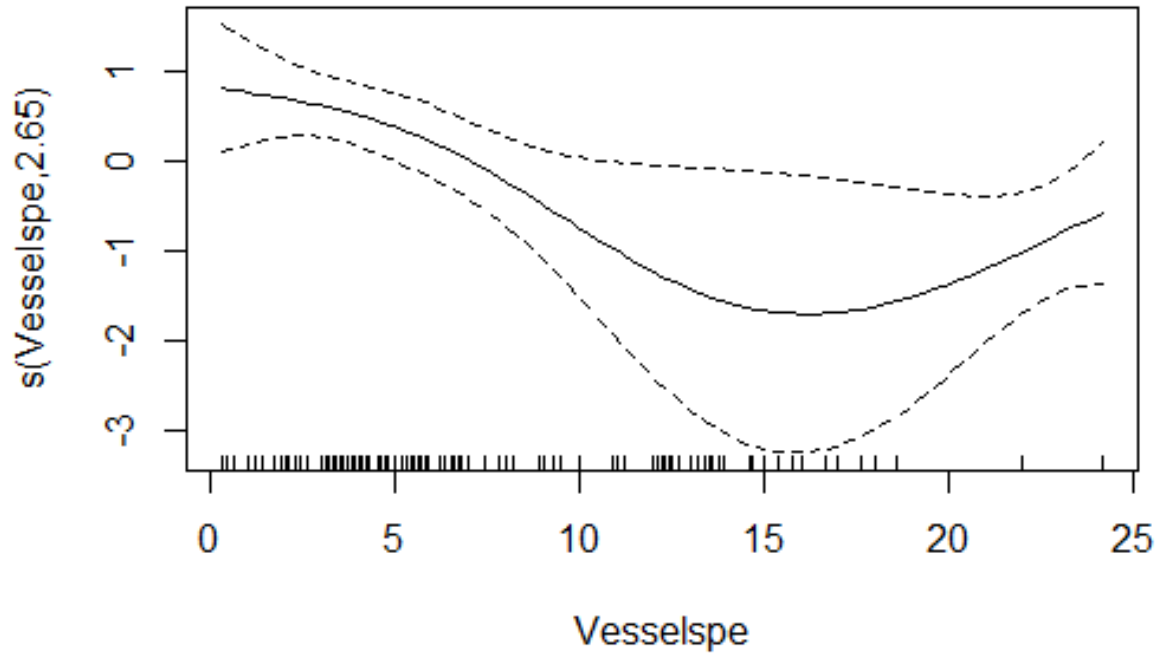
253. NRW acknowledges that intellectual property rights ownership for the biological records collected under this licence are unchanged by the issue of this licence. In all cases NRW will seek to acknowledge intellectual property and not use any biological records collected under licence beyond the purposes stated above. However, where the Licensee does not own the intellectual property rights to any part of the data or images collected under licence, they will ensure such arrangements as are required are put into place to allow NRW and third party conservation organisations and research programmes permission to store, copy, use, and release or publish any biodiversity records associated with the issue of this licence.
254. All activities carried out under the provisions of this licence shall adhere to the terms of the Protocols detailed in the attached Guidance Document. The Protocols detail the methods that must be used in order to obtain fit for purpose photographic identification images and associated data, and the behaviour that must be applied by the Licensee, their accredited agents or assistants when obtaining such images and associated data. Any breach of the terms of the Protocols may result in the immediate revocation of this licence.
255. Regular inshore Wildlife Watching trips (within 3 nautical miles of the shore) should only carry out one trip per day when the licence is invoked. This should be at a time agreed beforehand with the Marine Mammal Specialist (Thomas Stringell or Ceri Morris) at National Resources Wales, telephone 03000 653000.

NOTES

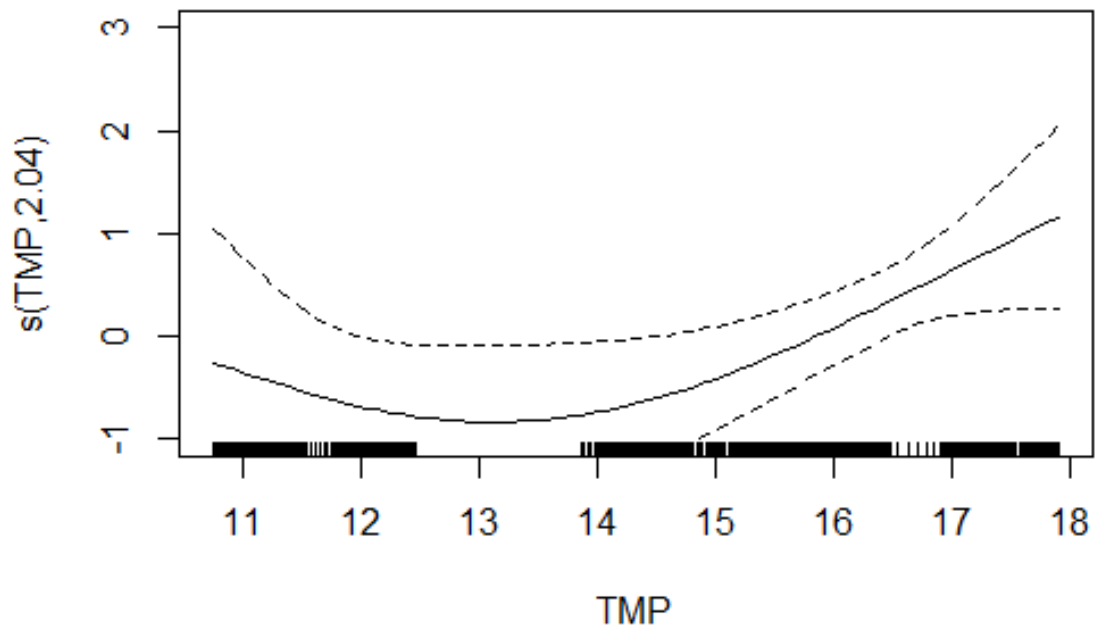
- N1. This licence authorises acts that would otherwise be an offence under The Conservation of Habitats and Species Regulations 2010. Failure to act within the purposes of this licence or failure to comply with the terms and conditions may mean that the licence cannot be relied upon and an offence is committed. Furthermore, under regulation 58 of the Conservation of Habitats and Species Regulations 2010 it is an offence to contravene or fail to comply with any condition of a licence issued on or after 21 August 2007. The maximum penalty upon summary conviction for an offence under the Regulations is a level 5 fine (£5000) and/or a six-month custodial sentence.
- N2. The Licensee is reminded that, in relation to conditions relating to Nationally Protected Species, anything done that is not under and in accordance with the terms of this licence may result in a criminal offence being committed under sections 1, 5, 6 (3), 7, 8, 9 (1 – 2), 9 (4 – 4A), 11 (1 – 2) and 13 (1) of the Wildlife and Countryside Act 1981.
- N3. This licence may be modified or revoked at any time by NRW.
- N4. Nothing in this licence confers any exemption from any legal provision contained in any Act, other than the Act(s) under which this licence is issued. Where appropriate licences should be obtained from the Home Office to fulfil the requirements of the Animals (Scientific Procedures) Act 1986.
- N6. The personal information on this licence will be kept and used by us in accordance with the Data Protection Act 1998. The licence will be permanently retained, as it is a legal document. We may discuss licence content with selected third parties. Other than stated above, we will not make the personal data on this licence available to third parties unless there is an overriding public interest. The Data Protection Act 1998 gives you the right to know what data we hold about you, how we use it, to which third parties it is disclosed, and that it is accurate. To exercise this right please contact the Data Protection Officer at NRW.
- N19. Licensees are expected to exercise the utmost care to avoid undue disturbance to the wild animals photographed under this licence. Failure to do so may result in revocation of this licence.

Appendix 3:

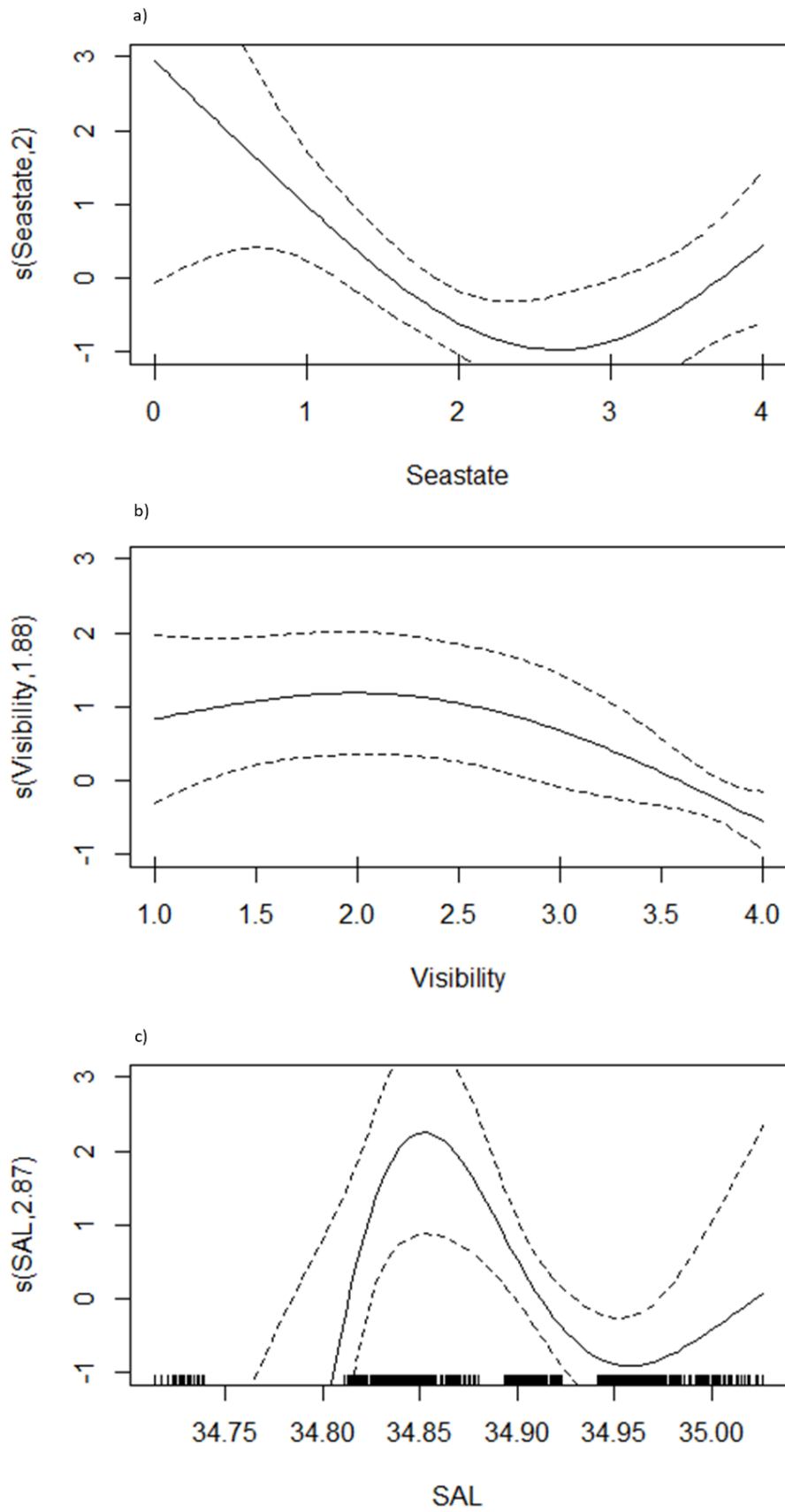
Best fit GAM model for each year between 2009-2013; 2009 (1), 2010 (2), 2011 (3), 2012 (4), and 2013 (5).



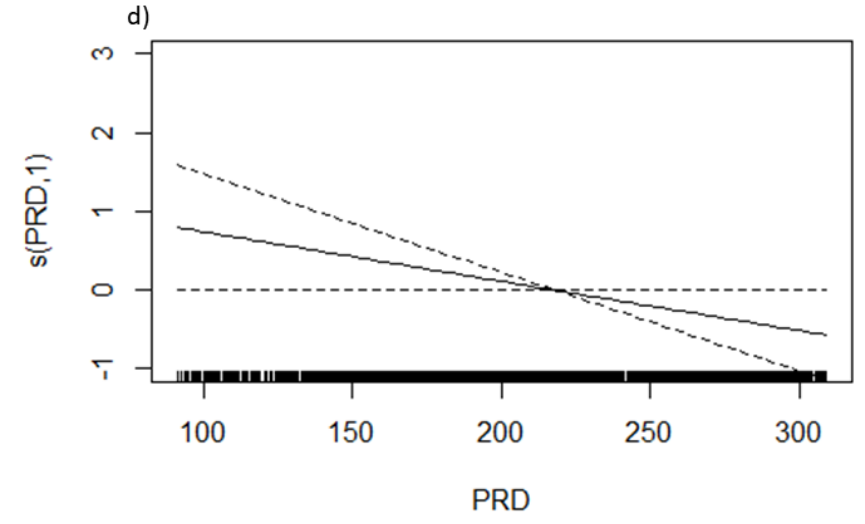
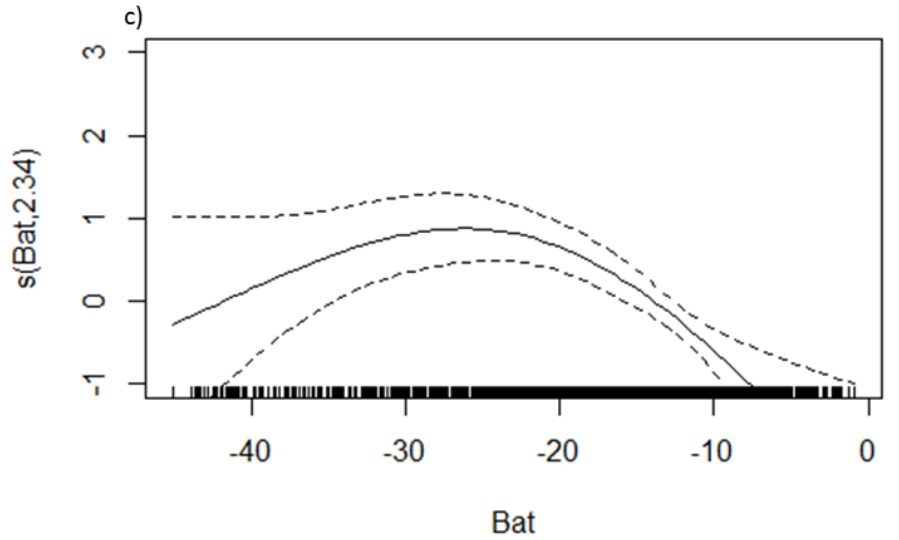
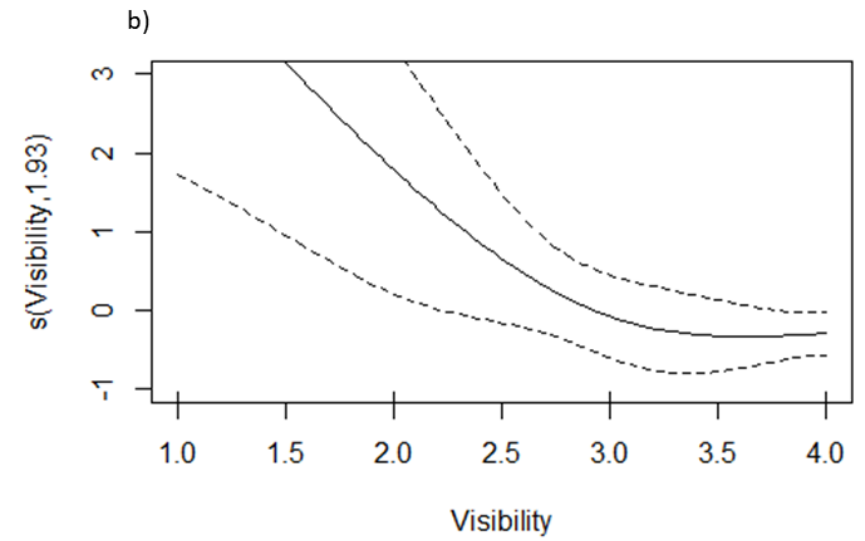
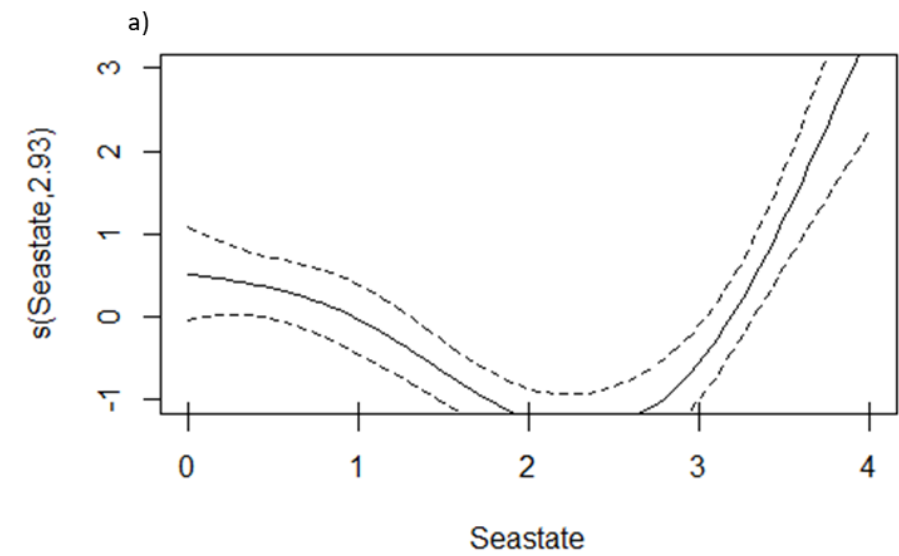
1) 2009 best fit model, showing a relationship between the visual detection of harbour porpoise groups and vessel speed.



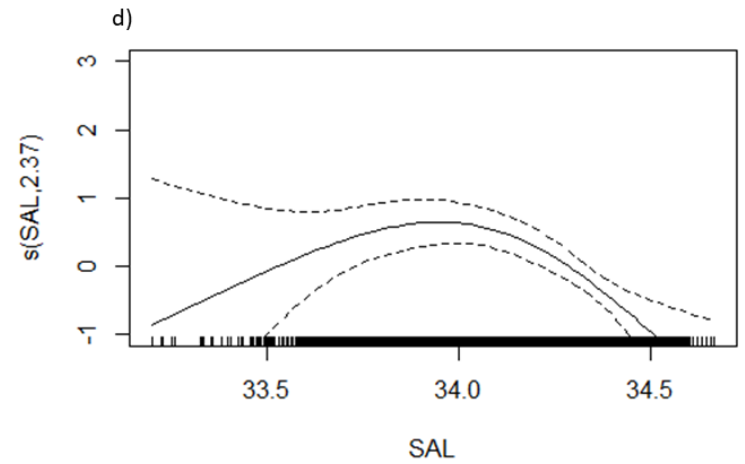
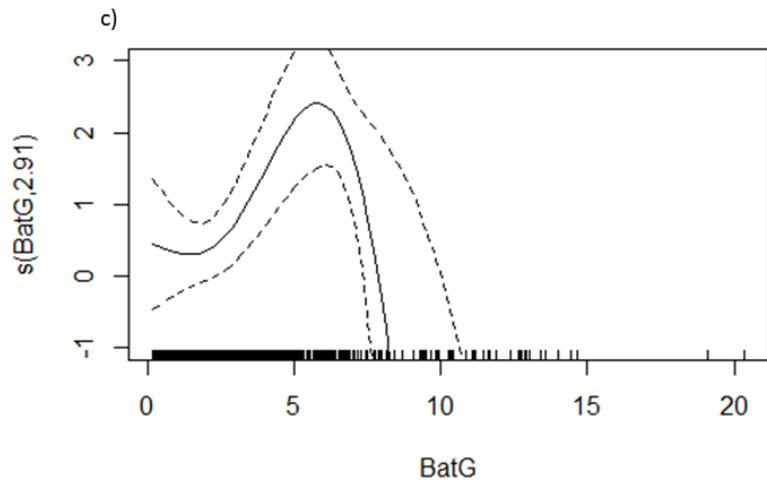
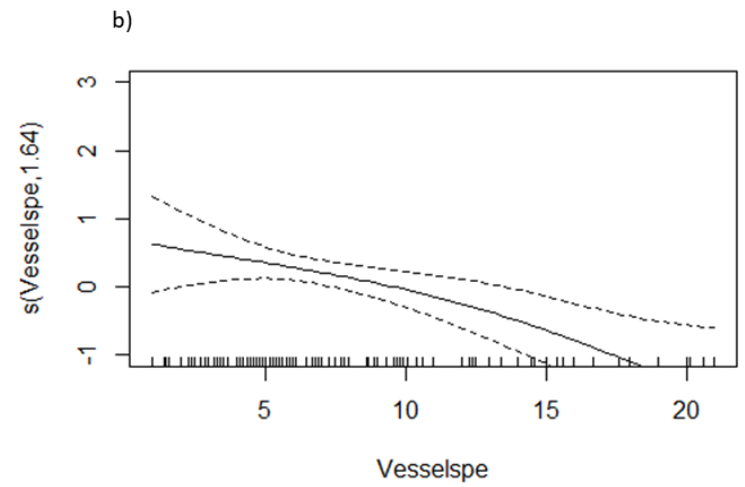
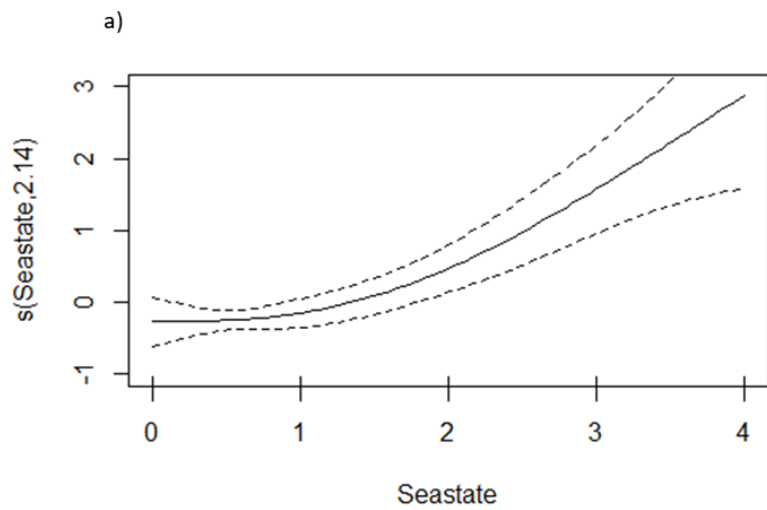
2) 2010 best fit model, showing a relationship between the visual detection of harbour porpoise groups and temperature.



3) 2011 best fit model, showing a relationship between the visual detection of harbour porpoise groups and a) sea state, b) visibility, and c) salinity.



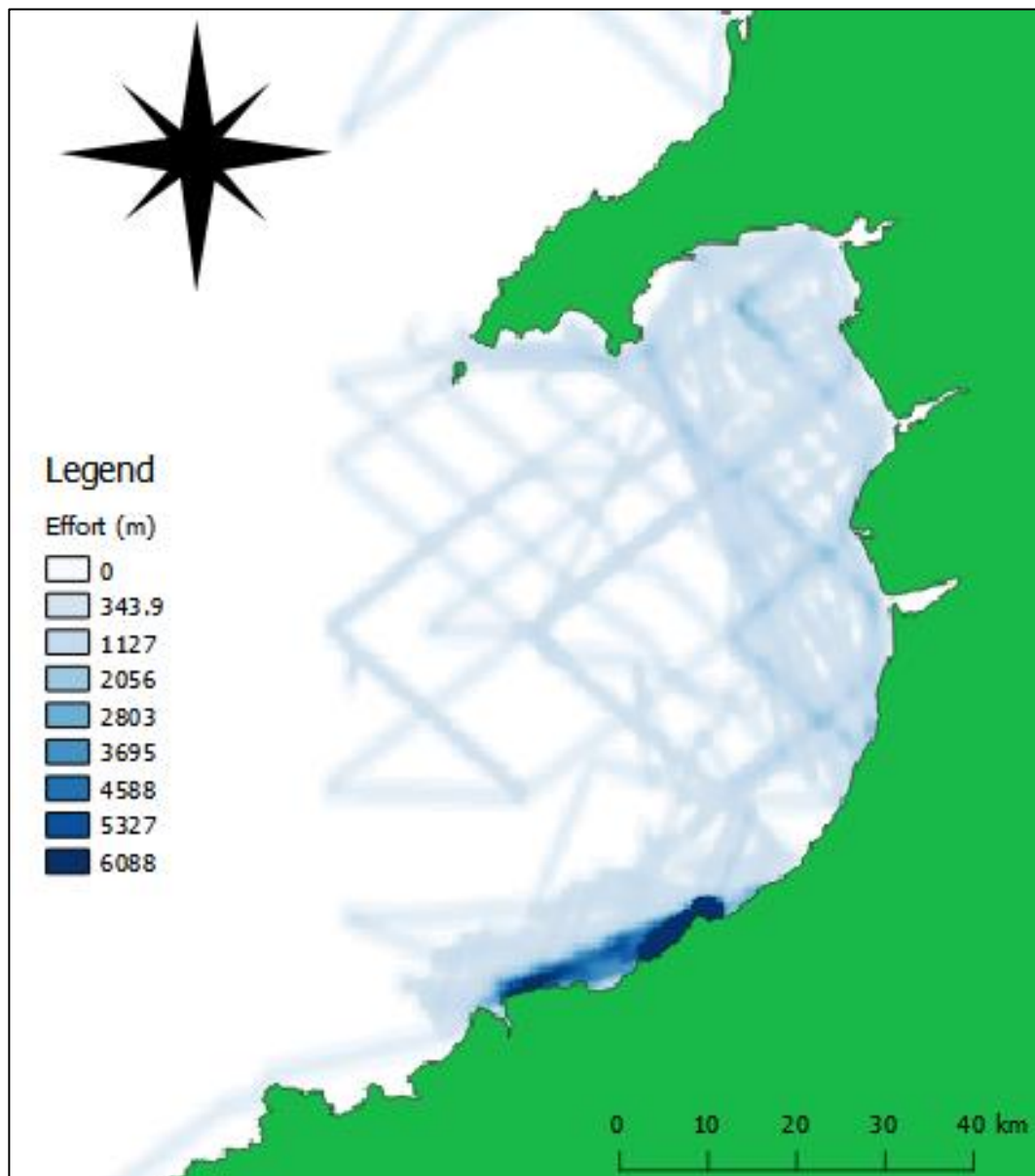
4) 2012 best fit model, showing a relationship between the visual detection of harbour porpoise groups and a) sea state, b) visibility, c) bathymetry, and d) chlorophyll a.



5) 2013 best fit model, showing a relationship between the visual detection of harbour porpoise groups and a) sea state, b) vessel speed, c) bathymetric roughness, and d) salinity.

Appendix 4:

Map of survey effort intensity.



Map of effort intensity within Cardigan Bay, West Wales. Dark blue indicates areas of high effort intensity.