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Habitat modelling of the harbour porpoise (*Phocoena phocoena*) in southwest UK: effects of depth, slope, and tidal state

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Abstract

The harbour porpoise, *Phocoena phocoena*, is a widespread cetacean species in the Northeast Atlantic, with a year-round distribution around the UK. The south-west experiences the highest bycatch rates in the UK and is the main threat to *P. phocoena* populations. Yet here there is limited information on their abundance, distribution, and habitat preferences. This study aims to understand harbour porpoise species-habitat relationship in the UK south-west, which may be used to inform conservation management and sustain valuable populations. From boat-based visual surveys conducted over summers 2017-2019 from Plymouth to St Marys in the Scilly Isles, habitat modelling using generalised additive models (GAMs) were used to analyse harbour porpoise occurrence in relation to variables including seabed depth, slope, and tidal state. A total of 197 harbour porpoises were spotted over 111 hours and 35 minutes survey time. The best model explained 15.7% of the deviance with variables sea state, month, depth, slope, and time of day as significant predictors. A low sea state, in the month of August, and at 35-60m depth all resulted in increased sighting rate, as well as regions of higher slope and at 10-12am. These results suggest seasonal movement patterns, reliance on static bathymetric features, and diurnal changes in surfacing behaviour. This study has successfully identified important predictors of *P. phocoena* distribution within a previously understudied area, to aid towards the species conservation particularly in terms of management and reduction of bycatch.

Keywords: Harbour porpoise, habitat modelling, species-habitat relationship, seasonal variation, UK

Introduction

Cetaceans are a diverse group of marine mammals that inhabit every one of the world's oceans. They live in a variety of habitats, from the polar regions (e.g. beluga whale *Delphinapterus leucas*) to tropical waters (pantropical spotted dolphin *Stenella attenuate*) and temperate seas (Risso's dolphin *Grampus griseus*) (Ballance 2009). Their morphology is largely diverse, with sizes ranging from <1m for a vaquita calve (*Phocoena sinus*) up to 33m for a blue whale adult (*Balaenoptera musculus*). Their geographical ranges can remain extremely local, such as the vaquita occupying just a few hundred square km in the northern Gulf of California, or they can migrate throughout all the world's oceans, like the killer whale (*Orcinus orca*), making it the most wide-ranging mammal on Earth with exception to humans (Ballance 2009).

Amongst this diversity, all cetaceans provide ecosystem services that have a wide range of positive effects on the health of the planet and the economy. For example, by being at high trophic level cetaceans act as ocean sentinels, with their overall health status reflecting that of their ecosystem over large temporal and spatial scales, which can even provide early warning for potential human health hazards (Moore 2008; Bossart 2011). Cetaceans can increase primary productivity through recycling of macro and micro-nutrients (Roman & McCarthy 2010), they act as biological controllers, and enhance biodiversity (Tavares *et al.* 2019). They also hold notable economic value within the tourism industry through marine mammal watching (O'Connor *et al.* 2009) which in many coastal communities is a main contributor of income and employment (Parsons *et al.* 2003). Moreover, they are effective flagship species, bringing public and media attention to conservation issues with high fundraising potential (Sergio *et al.* 2008).

One particular group of cetaceans is the porpoise family, *Phocoenidae*; consisting of 7 species within 3 genera: *Phocoenoides*, *Phocoena*, and *Neophocaena*. The harbour porpoise *Phocoena phocoena*, is one species which inhabits much of the Northern hemisphere, mainly the North Atlantic, European waters, and parts of the North Pacific (Teilmann & Sveegaard 2019) making it the widest ranging porpoise species. In the European continental shelf, comprehensive abundance estimates of 470,000 individuals (Hammond *et al.* 2017) has contributed to the status of *P. phocoena* European populations as being of least concern (Braulik *et al.* 2020). However, Black Sea and Baltic Sea populations are endangered and critically endangered, respectively (Braulik *et al.* 2020), due to pressures such as hunting, bycatch, and chemical pollution (Carlén *et al.* 2021). In UK waters*, P. phocoena* has wide-spread distribution (Hammond *et al.* 2017) that is year-round, with areas like the west of Scotland containing some of the highest densities within Europe (Evans & Wang 2008; Hammond *et al.* 2013).

Despite their high ecological value, cetaceans are subject to increasing and cumulative anthropogenic impacts that have adverse effects on species and ecosystems. Worldwide, cetaceans can face direct impacts from human activities such as hunting, as well as indirect impacts from increasing pressures of climate change, prey depletion, habitat degradation, and pollution (Halpern *et al.* 2019). For the harbour porpoise, the largest threat is from fisheries with high levels of accidental catches, also known as bycatch. Of which, *P. phocoena* are most susceptible to static gill and tangle nets (Camphuysen & Siemensma 2015). In the UK, bycatch levels in areas such as the Celtic Sea (Tregenza *et al.* 1997) and North Sea

(Northridge & Hammond 1999) have been considered as unsustainable for the harbour porpoise population as they surpass impact levels of 1% as set by the International Whaling Committee (IWC). Moreover, noise pollution is understood to severely effect cetacean functioning, since sound is imperative for many ecological functions such as communication and locating food, which human induced noise can mask (Parsons *et al.* 2010). Anthropogenic noise can come from many sources, not restricted to shipping (Wisniewska *et al.* 2016), military activities (Evans & England 2001), wind farm construction (Tougaard *et al.* 2009), and seismic surveys (Sarnocińska *et al.* 2020). The effects of noise disturbance can include behavioural changes, stress, and temporary or permanent hearing damage (Parsons *et al.* 2010). Furthermore, chemical pollutants in the marine environment can accumulate in cetaceans to dangerously high levels due to their long-life span and high trophic level (Siebert *et al.* 1999; Parsons *et al.* 2010). These can have severe effects on many biological functions, such as reproductive and immune suppression, resulting in increases in disease-related deaths (Parsons *et al.* 2010).

In order to mitigate these threats, conservation methods can be put in place through legislation. One method is the designation of Special Areas of Conservation (SACs) as directed by the European Union Habitats Directive 1992. An SAC is translated as a ‘site of Community importance where necessary measures are applied to maintain, or restore, to a favourable conservation status, the habitats of populations of the species for which the site is designated’ (EU Habitats Directive 92/43/EEC 1992). As of 2019, *P. phocoena* has 5 SACs around England, Wales, and Northern Ireland and one to the west of Scotland. There are other international treaties, such as the Convention on Biological Diversity (CBD) that led to the creation of a UK post-2010 Biodiversity Framework with priority actions for reduction in bycatch levels. Also, the Bonn Convention; specifically, the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS) which sets for all small cetaceans to reach Favourable Conservation Status (FCS) through ambitious targets to minimise bycatch levels to zero (Camphuysen & Siemensma 2015). How these treaties set to reduce bycatch will involve reporting of all bycatch and stranding events, and direct research and mitigation on ways to reduce bycatch itself (Camphuysen & Siemensma 2015).

Understanding abundance and distribution of species is necessary to emplace management measures for their protection. There has been a reasonable level of research conducted into identifying the abundance and distribution of *P. phocoena* at both international (Hammond *et al.* 2017) and regional scales around the UK (Weir *et al.* 2007; Oakley *et al.* 2016; Nuuttila *et al.* 2017). These studies provide baseline understanding of population levels, providing information on their conservation status, to report to treaties such as the Habitats Directive and the Marine Strategy Framework Directive (Hammond *et al.* 2017). This also means that data on bycatch levels can be put into a population context and risk levels can be assessed. Once this baseline understanding is in place, further research can be used to understand the drivers behind species associations and their habitat. With the use of habitat modelling, studies can explain species presence and absences across space and time. This is an area of research that is being used to aid conservation of a wide range of species (Jeong *et al.* 2011; Kunwar *et al.* 2021) including cetaceans (Cañadas *et al.* 2005; Panigada *et al.* 2008). Through knowledge on species-habitat relationships, habitat models can inform real conservation practices such as recommendations for protected area designations (Cañadas *et al.* 2005; Embling *et al.* 2010), often by identifying species high-use areas that are considered as priority for conservation efforts.

Habitat modelling of *P. phocoena* around the UK has been fragmented, with many studies occurring on the west coast of Scotland (Booth 2010; Embling *et al.* 2010; Marubini *et al.* 2009), which is known to have some of the highest densities of *P. phocoena* in Europe (Evans & Wang 2008; Hammond *et al.* 2013). One area that is lacking in research for habitat modelling and baseline understanding of abundance and distribution, is the south west coast of the UK. Limited studies have indicated a small population of *P. phocoena* in south west UK waters, or one that is spread over a larger area (Goodwin & Speedie 2008). Although, more recent international surveys have noted shifting distributions of *P. phocoena* from northern North Sea to the south (Hammond *et al.* 2013) and increased abundance in the English Channel (Hammond *et al.* 2017), where in 1994 there were no sightings (Hammond *et al.* 2002).

The southwest UK coast is known to have the highest bycatch rates within the UK (Calderan & Leaper 2019) and has been the leading cause of cetacean strandings along the south coast of Cornwall (Leeney *et al.* 2008). Investigating *P. phocoena* species-habitat relationship within southwest UK could be integral to reducing conflict between the species and capture fisheries, and aid towards conservation targets set by agreements such as ASCOBANS. Knowledge on their habitat preferences can also be used to mitigate other anthropogenic threats, which collectively could enhance movement towards a sustainable population. This will help to conserve the vital ecosystem services that cetaceans like *P. phocoena* provide, such as nutrient cycling and environmental awareness in society (Tavares *et al.* 2019). This study will aim to investigate the effect of environmental variables including depth, slope, and tidal state on *P. phocoena* occurrence along the southwest UK coast, to begin to fill the gap on understanding their species-habitat relationship.

Methodology

Survey area and design

The survey area ranged from 50.42°N to 49.83°S and -4.10°E and -6.38°W, along the southwest coast of the UK, from the edge of Devon (port of Plymouth), past the south coast of Cornwall to the Isles of Scilly (port of St Marys) (figure 1).

Four boat-based surveys took place across three consecutive summers on board the motor—sailing yacht *Take the Helm*. The first two surveys took place in August 2017 and 2018; in 2019 there was a survey in both June and July. Each survey was four to six days duration, depending on weather restrictions which also meant some surveys did not cover the entire coastline within the survey area. The survey design was a zig-zag line transect (Buckland *et al.* 2001), up to approximately 6 nm from the shore, chosen to cover the area as evenly as possible (see figure 1).

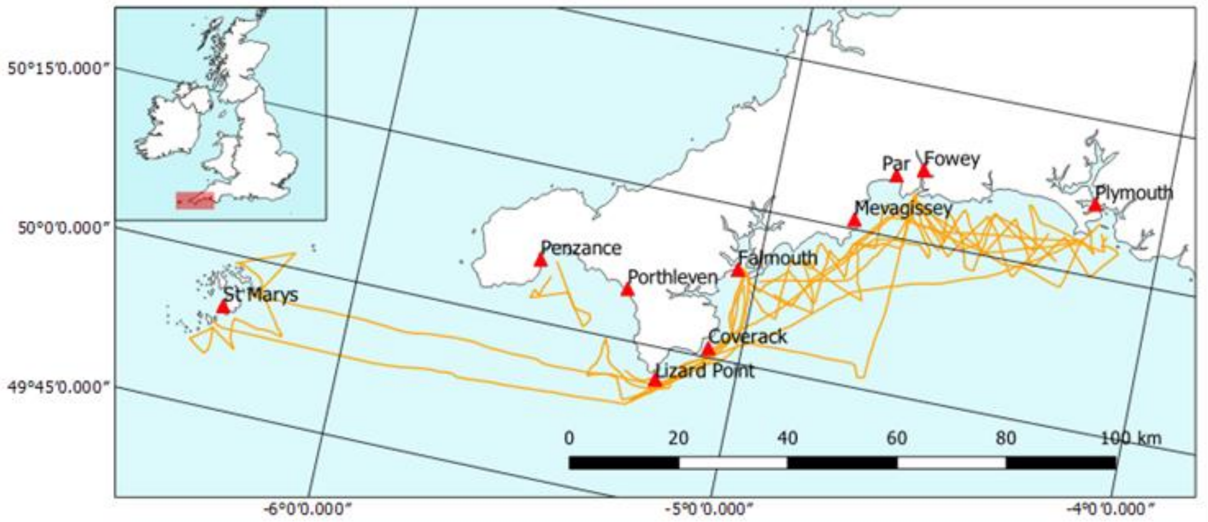

Figure 1: Survey area along the southwest coast of the UK. Orange lines indicate the line transect whilst on effort, covered between 2017-2019. Red triangles indicate port locations. Made with QGIS (QGIS.org 2021).

Sightings of all animals were recorded, including seabirds and other cetaceans. A sighting was classed as an event where 1 or more individuals were spotted. Individuals were detected by eye by volunteer observers under the supervision of an experienced observer, and species identification backed up with 7x50 binoculars. For the survey technique, methods used by Embling *et al.* (2010) were adopted; 2 observers searching from the front deck -5° to 90° of the transect line on either side of the vessel, switching sides every 30 minutes, and employing hourly watch changes to avoid observer fatigue. Once spotted, distance and bearing to individuals were recorded using angle boards and binoculars reticules. Species, number of individuals in a group, behaviour, latitude, longitude, time, sea state and engine on/off were also noted using the CyberTracker data logger. In bad weather periods it was necessary for observers to go off effort, such as when sea state levels became too rough. Any data collected during off effort was excluded from analysis.

Survey variables

Survey variables were investigated with respect to *P. phocoena* sightings as they are known to affect sighting rate. Sea state and engine on/off were therefore recorded every 15 minutes, or every time there was a change on survey. Too high a sea state can have severe effects on porpoise sight-ability, particularly above Beaufort state 3 (Clarke 1982) with ideal sighting conditions being $\leqslant$1. Noise from the engine may also deter porpoises from the boat (Palka & Hammond 2001). Boat speed was kept at a constant 6 knots with engine on/off depending on whether sail was sufficient.

Environmental data

Environmental variables were chosen due to previously being identified as important drivers of *P. phocoena* distribution. Such as depth, of which *P. phocoena* generally associates with 20-200m in shelf waters (Carretta *et al.* 2001; Embling *et al.* 2010; Isojunno *et al.* 2012). For this study, seabed depth data was obtained from GEBCO Compilation Group (2020) 15 arc second global grid (figure 2). From this, seabed slope was calculated (figure 3) using Raster Analysis in QGIS version 3.12.2

(QGIS.org 2021). Slope is another important predictor as *P. phocoena* is often found in regions of steeper topography (de Boer *et al.* 2014).

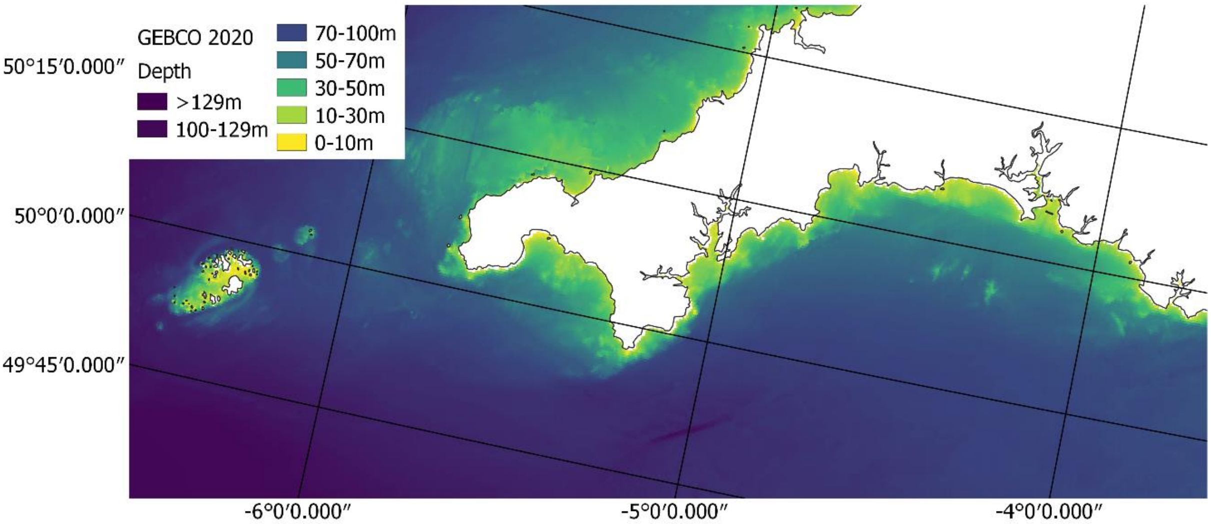

Figure 2: Depth of survey area along southwest coast of the UK. Data collected from GEBCO Compilation Group (2020). Map made with QGIS (QGIS.org 2021).

Tidal state is one tidal variable known to affect *P. phocoena* distribution, as they often associate with particular tide times depending on location (Marubini *et al.* 2009; Jones 2012). Tidal state was calculated from the date on survey, time of day, and location of nearest port. The nearest port to each data point was determined using the ‘Join Attributes by Nearest’ function in QGIS.

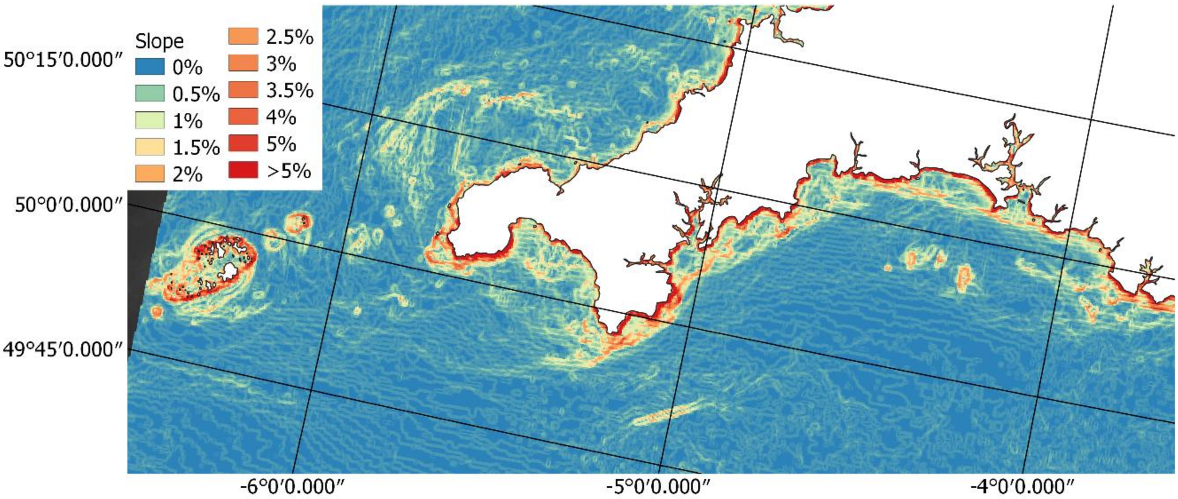

Figure 3: Slope of seabed in survey area, southwest coast of UK. Slope calculated and map made in QGIS (QGIS.org 2021).

Tide times for each port per day were taken from Tide Plotter version 5.8. From this, tidal state could be calculated as a continuous variable between 0 and 1 using the equation:

$$\frac{x - LW_1}{LW_2 - LW_1}$$

where x= time of data bin, LW_1= time of previous low water, LW_2= time of next low water.

Roughly, this equates to tidal state as: 0-0.1 being the first half of low water slack tide; 0.1-0.3 is flood tide; 0.3-0.6 is high water slack tide; 0.6-0.9 is ebb tide; and 0.9-1 is the second half of the low water slack tide (Embling *et al.* 2010). Time of day and month were also considered as temporal variables in the models. Harbour porpoise surfacing behaviour has been shown to change depending on time of day (Westgate *et al.* 1995), thereby altering their detectability. Month has also been a significant predictor in harbour porpoise abundance (Weir *et al.* 2007; Bouveroux *et al.* 2020). Surveys in June and July were treated as the same month due to proximity in time of the surveys. All data were processed into 5-minute bins, where for every 5 minutes environmental and survey variables were taken at the beginning of each bin and the number of harbour porpoises spotted within each 5 minutes were accumulated.

Modelling

Analysis of data took place using R version 3.5.2 (R Core Team 2018). Before modelling, collinearity between variables was tested by using a correlation analysis. Pairs of variables that give a value of r>0.7 have strong collinearity and one must be excluded from the model to prevent inflated or underestimated standard errors and p-values (Booth *et al.* 2013). There was no strong collinearity between variables, so all were put forward for use in the GAMs.

Poisson generalised additive models (GAMs) with a log link function were used to analyse the number of harbour porpoises in each 5-minute bin against the environmental and survey variables. GAMs are often used for interpreting ecological interactions between predictor variables and observations because they do not impose limitations on underlying relationships and can fit non-normal data (Hastie *et al.* 2005). The MGCV library was used as it reduces overfitting of GAMs (Wood 2006) and smooths were restricted to ⩽4 degrees of freedom unless the variables used a cyclic smooth (i.e. tide state and time of day). Month and engine on/off were treated as factor variables where all other variables were treated as smooths, including sea state. Forward stepwise selection was carried out by addition of environmental and survey variables to the null model (no predictor variables). Sea state was added first to ensure changes in detection probability are accounted for (Teilmann 2003) before remaining variables were added. Addition of variables were based on reducing the UBRE score if p<0.05 and they explained at least 1% deviance.

Results

A total of 197 harbour porpoises were sighted over annual summer surveys between 2017 and 2019, covering 111 hours and 35 minutes survey time (table 1). The highest number of sightings occurred in 2017, of which there were 116 individuals spotted in 35 hours and 15 minutes survey time. In contrast, the longest survey time was in 2019 lasting 56 hours and 20 minutes but spotted less than half the number in 2017, with 43 individuals (table 1).

Over the 3 years *P. phocoena* sightings were relatively evenly distributed between Plymouth and Lizard Point (figure 4). The transect line which continued from Lizard Point straight to St Marys (in 2019 only) continued to spot *P. phocoena*, but with an increase in sightings on the east side of the Scilly Isles. Surveys along the coast from Lizard Point to Penzance were fragmented in 2018 due to weather restrictions and in 2017 only reached halfway between Lizard Point and Porthleven. Neither year produced sightings of harbour porpoise north of Lizard Point (figure 4).

Ideal sighting conditions of sea state ⩽1 were high in both 2017 and 2019 but with a large drop in 2018 to only 16.3% of the survey time (table 1). 'Engine on' was consistently above 70% of the survey time across all 3 years with a particularly high percentage in 2019 of 98.8%. For environmental variables, over 3 annual surveys depth along the transect line had a range of 0-82m. Slope of the seabed ranged from 0-6.46% (table 1).

Table 1: Survey and environmental statistics for all surveys 2017-2019.

	2017	**2018**	**2019**	**Total**
Month	August	August	June/July	
No. harbour porpoises sighted	116	38	43	197
Time on effort (hours:minutes)	35:15	20:00	56:20	111:35
% Sea state ⩽1	69.4	16.3	63.6	
% Engine on	79.7	71.3	98.8	
Depth (m)				
Median (IQR)	46 (15)	48 (27)	55 (24)	
Range	66	62	82	
Slope (%)				
Median (IQR)	0.48 (0.76)	0.34 (0.68)	0.33 (0.69)	
Range	5.69	6.33	6.46	
Tidal State				
Median (IQR)	0.68 (0.64)	0.63 (0.59)	0.59 (0.51)	
Range	0.99	0.99	0.99	
Time of day (decimal hrs)				
Median (IQR)	13.42 (3.54)	11.88 (4.67)	11.92 (5.19)	
Range	9.58	13.17	13.08	

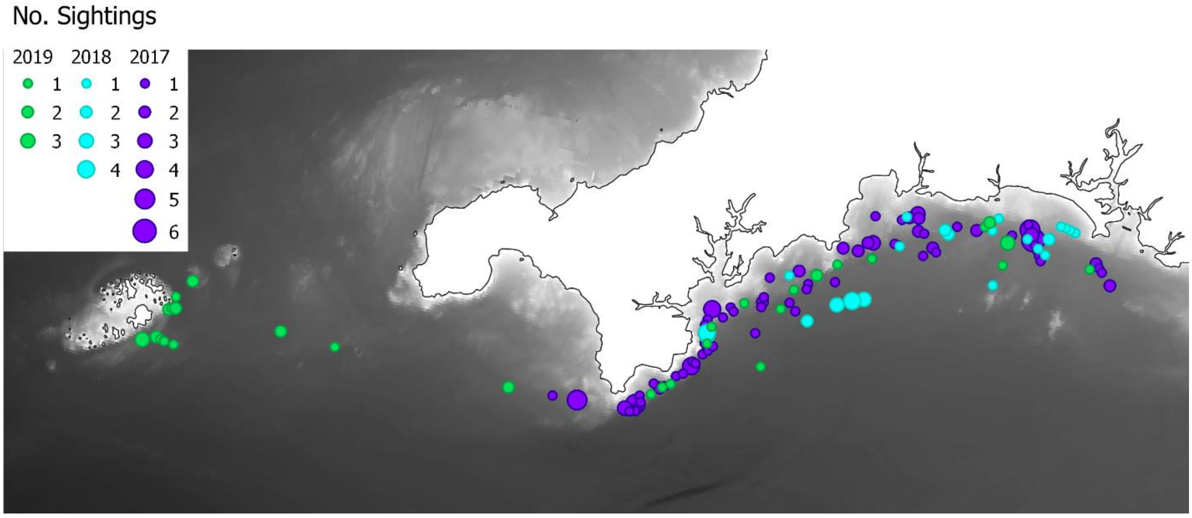

Figure 4. Locations of *P.phocoena* sightings across 2017-2019 surveys. Circle size indicates how many individuals were spotted at that location per year.

The best model following forward-stepwise selection included sea state (1 d.f., p<0.001), month (2 d.f., p<0.001), depth (2 d.f., p<0.001), slope (2 d.f., p<0.05), and time of day (4 d.f., p<0.05). This model explained 15.7% of the deviance (table 2). Sea state was the most important variable, displaying a significant decrease in *P. phocoena* sightings at sea states greater than 1 (figure 5a). After accounting for this in the model, month was the most significant predictor of harbour porpoise sightings. This gave a 3.5x increase in mean number of harbour porpoises sighted in August compared to June/July (figure 5b). The next most significant variable was depth, with a higher probability of porpoise sightings between 35 and 60m (figure 5c). Slope of the seabed between 1 and 3.5% also resulted in increased sighting rate (figure 5d). And significantly more harbour porpoises were sighted at times between 10 and 12am (figure 5e).

Table 2. Results of forward stepwise GAM model selection of the number of harbour porpoises in each data bin, for all surveys 2017-2019. Variables are in order of importance, starting with sea state to compensate for changes in detection. UBRE reduction shows the starting UBRE score in bold, and then the reduction caused by the addition of each variable to the model.

Order	**Smooth (d.f.)**	**UBRE reduction**	**Deviance explained (%)**
1	Sea state (1)	**-0.2729**	2.88
2	Month (2)	-0.0622	+8.52
3	Depth (2)	-0.0118	+2.10
4	Slope (2)	-0.0057	+1.10
5	Time of day (4)	-0.0027	+1.10
Total			15.70

When modelled alone, tidal state showed harbour porpoise preferences around 0.6-0.75, which equates to the first half of ebb tide. But it was not significant in the full model as it dropped out of the model selection after compensating for sea state.

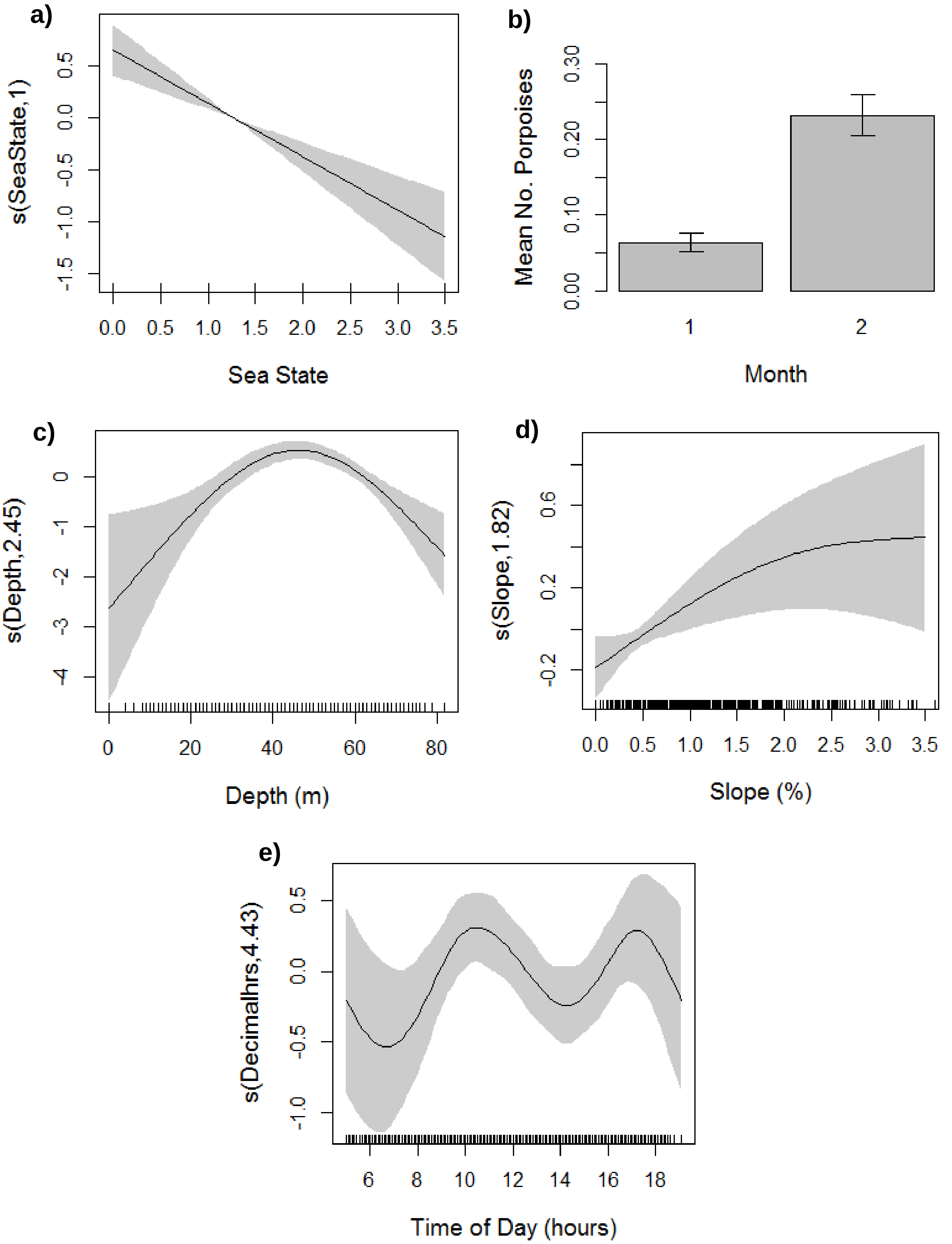

Figure 5: Relationships between significant variables on harbour porpoise sighting rate from 2017-2019. GAM plots (a) sea state, (c) depth, (d) slope and (e) time of day were produced via individual models. The shaded areas in GAMs indicate 95% confidence intervals. Rug plots at the bottom of GAMs show the actual data. Key in (b), 1= June/July, 2= August.

Discussion

The present study has successfully created a habitat model displaying the relationship between harbour porpoise distribution and environmental variables in south west UK waters. Knowledge on *P. phocoena* species-habitat relationships can provide information for conservation methods, such as mitigating bycatch in high-use areas. The present model best explains *P. phocoena* distribution with variables sea state, month, depth, slope, and time of day, explaining a total of 15.7% of the deviance. From accounting for changes in detection probability due to survey effects, I found a significant decrease in harbour porpoise sightings above sea state 1. This concurs with other studies that show a negative relationship between harbour porpoise abundance and increasing sea state (Palka 1996; Teilmann 2003), likely due to reduced observer efficiency (Palka 1996). Two out of three years on survey had considerably good weather conditions with a high proportion of survey time with sea state $\leqslant$1. As opposed to the 2018 survey, where sea state frequently went above 3 and meant there was decreased time on effort. The low number of *P. phocoena* sightings found in 2018 may be due to the reduction in survey effort, but also the large reduction in time in sea state $\leqslant$1 which will have negatively affected sighting rate.

Following adjustment in detection probability with changing sea state, month was the most significant predictor of harbour porpoise sighting rate. I found sightings to be higher in August compared to June/July. This study is the first in the region to describe differences in harbour porpoise abundance and distribution between months, as previous studies such as Goodwin & Speedie (2008) and Hammond *et al.* (2017) provide only a snapshot in time. At least for summer months, this study describes a temporally dependant distribution of *P. phocoena*, which may be due to seasonal variation of diet or changes in prey availability (Santos & Pierce 2003). Because of their high energy requirements (Lockyer 2007), harbour porpoise movements are often linked to prey availability and distribution (Read & Westgate 1997; Sveegaard *et al.* 2012a; Sveegaard *et al.* 2012b). Knowledge on seasonal prey movements in the study area are currently unknown and can be difficult to collect, therefore their influence on driving *P. phocoena* movement into the area, particularly during August, can only be assumed.

Increases in harbour porpoise abundance during the late summer months is seen in other locations around the UK, including eastern Scotland (Weir *et al.* 2007), western Scotland (Booth *et al.* 2013) and Wales (de Boer *et al.* 2014). However, the integrity of this pattern has been questioned due to better survey conditions (Booth *et al.* 2013). Nevertheless, seasonal movements and aggregations of *P. phocoena* have been clearly documented throughout the North Sea (Gilles *et al.* 2009; Gilles *et al.* 2016). It seems the Southern Bight of the North Sea experiences peak *P. phocoena* abundance during winter and spring, with lower abundance in summer months (Gilles *et al.* 2016; Bouveroux *et al.* 2020). It may that some individuals spread south westerly into the English Channel and towards the present study area during the summer, primarily for foraging or movement towards other foraging sites, resulting in increased abundance in August. Although, there is also apparent movement to offshore North Sea areas in summer months (Gilles *et al.* 2016). It should also be noted that I have limited replicates for each monthly period (August and June/July), with two years of data for August and just one year for June/July in 2019. There is a chance that overall harbour porpoise numbers could have been low in 2019 due to interannual variability (see Marubini *et al.* 2009), rather than low numbers observed specifically in June/July. Further surveys will need to be carried out to confirm monthly effects on their distribution within the survey area. On the other hand, with seasonal differences in abundance and distribution of *P. phocoena* being well documented (Gilles *et al.* 2009; Gilles *et al.* 2016; Zein *et al.* 2019; Bouveroux *et al.* 2020), and many places around the UK observing increases in abundance throughout the summer (Weir *et al.* 2007; Booth *et al.* 2013; de Boer *et al.* 2014), it is likely that the present study has captured the same trend.

As well as seasonal differences, *P. phocoena* distribution is often associated with bathymetric features. This includes depth, although preferences can vary between regions. Generally, on shelf waters they inhabit waters of 20-200m, with a lower preference for those exceeding 100m (Northridge *et al.* 1995; Carretta *et al.* 2001; Evans *et al.* 2003; Isojunno *et al.* 2012). Although, there are studies with more porpoises than expected in deeper depths (Raum-Suryan & Harvey 1998) and in mid-deep waters, 50-150m (Marubini *et al.* 2009; Booth *et al.* 2013). In the present study, there was a significant increase in harbour porpoise sightings between 35-60m. With the present study having a mean depth of 48.5m and maximum of 82m along the transect line, the data is restricted to depths <82m. Similar results were found by Carretta *et al.* (2001) who surveyed up to 90m and *P. phocoena* exhibited preferences 20-60m. This is opposed to areas like the west coast of Scotland, where the study area by Booth *et al.* (2013) in part reached depths of >200m and showed 50-150m as significant for harbour porpoise presence. Differences in porpoise depth preference could therefore be largely driven by topographical differences between regions (Carretta *et al.* 2001), providing there is sufficient prey abundance and/or quality within that area. Additionally, it may be preferable to restrict dive depths to shallower portions of the water column with sufficient prey quality, to reduce energy expenditure compared with diving to deeper waters of their range (Cox *et al.* 2018). This could explain the drop in abundance >60m in the present study area, similar to decreases at greater depths observed in other studies (Carretta *et al.* 2001; Marubini *et al.* 2009; Booth *et al.* 2013).

Slope is another bathymetric feature that is often found to influence harbour porpoise distribution. Slope >0.5% and <3.5% was found to be significant in the present study. This is backed up by several studies that also indicated a lesser preference for areas <0.5% (Isojunno *et al.* 2012; Booth *et al.* 2013; de Boer *et al.* 2014; Jones *et al.* 2014), with few exceptions (Raum-Suryan & Harvey 1998). Slopes >3.5% and up to 15% have also been significant (Booth *et al.* 2013; Jones *et al.* 2014; de Boer *et al.* 2014). In this study, slope was restricted to a maximum of 6.5% and with limited data in regions >3.5%. Defining areas of higher slope within the study area may be limited by resolution of the data that is too large to detect the fine-scale changes in bathymetry. Despite this, my results support harbour porpoise preference for sloped areas >0.5% and can be explained as higher slope is often associated with greater productivity (Yen *et al.* 2004), therefore attracting top predators. This is supported by Stalder *et al.* (2020) who found that higher slope determined increased use of area-restricted movements by *P. phocoena*, indicative of increased foraging activity (Gurarie *et al.* 2016).

For temporal effects, the present study found a significant increase in sightings between 10 and 12am. Diel variations in sighting rates have been shown in other studies (Isojunno *et al.* 2012; Jones 2012) as well diel changes in acoustic behaviour (Benjamins *et al.* 2017; Nuuttila *et al.* 2017). Many studies have found acoustic activity of porpoises to be higher at night-time (Cox *et al.* 2001; Carlström 2005; Benjamins *et al.* 2017; Nuuttila *et al.* 2017). Isojunno *et al.* (2012) linked increased sighting rate at day/night transition phases with increased acoustic activity at night-time, although direct links between these are not always made (Linnenschmidt *et al.* 2013). Moreover, sighting and acoustic rates have displayed different seasonal peaks at larger temporal scales (Booth *et al.* 2013), suggesting no linear relationship. Without acoustic data in this study, any relationship cannot be determined. It may be more likely that increased sightings between 10-12am are due to other behavioural changes independent of acoustic activity. Changes in surfacing behaviour may be linked to increased foraging at the surface and fewer dives. Diurnal patterns in diving behaviour seem to be variable, with some studies finding porpoises diving deeper at night-time (Westgate *et al.* 1995), others observing a pattern in only some individuals (Linnenschmidt *et al.* 2013), or no diurnal pattern at all (Otani *et al.* 1998).

Unlike other selected environmental variables, the present study found no significant relationship between tidal state and harbour porpoise sighting rate. Previously, tidal state has been an important predictor of harbour porpoise distribution, although the exact relationship can vary between regions (Johnston *et al.* 2005; Pierpoint 2008; Marubini *et al.* 2009). For example, in western Scotland, Marubini *et al.* (2009) found more sightings during times of high tide. In South Wales, Isojunno *et al.* (2012) found more sightings at the start of ebb tide, and Pierpoint (2008) found more sightings throughout the entire ebb phase. Differences in tidal preference can vary over spatial scales 10s kilometres, as shown by studies that cover the same region but differ ~50km in north/southward ranges (Marubini *et al.* 2009; Embling *et al.* 2010; Booth *et al.* 2013). Furthermore, peak acoustic detections with tidal regime have even been shown to differ between moorings <600m apart (Benjamins *et al.* 2017). It is possible that in the present study, having covered large spatial scales (100s kilometres), multiple areas with differing tidal preferences were crossed. Therefore, the scale we have covered may have been too large to detect the fine scale spatial differences in tidal preference.

The habitat model within the present study has successfully identified key predictor variables and accounted for 15.7% of the deviance. However, there is notably some unexplained distribution of *P. phocoena* that the model has not accounted for. It may be that the study has missed a key driver of harbour porpoise populations in the area, or that the unexplained distribution is due to missing fine scale habitat preferences, such as tidal state and high slope. Survey limitations mean that we are also reliant on spotting individuals at the surface, which can be affected by dive duration, behaviour, and swimming speed (Buckland *et al.* 2001) as well as visual survey conditions. Although, inclusion of sea state in the model has mediated some survey effects. Despite some unexplained deviance, I have successfully determined key environmental variables as significant predictors within the study area. This knowledge can be used to aid conservation measures, particularly focussing on reducing bycatch to meet targets of agreements such as ASCOBANS. It may be suitable for restrictions on gillnet use, for example, to be in place during later summer months when their abundance is highest. Bycatch rates can also overlap with water depth (Bjørge *et al.* 2013), therefore targeting fishing outside of frequently used depths may be suitable.

Conclusions

From a total of 111 hours and 35 minutes survey time, 197 harbour porpoises were spotted along the southwest coast. The best model included sea state, month, depth, slope, and time of day as significant predictors of harbour porpoise occurrence and explained 15.7% deviance. A low sea state, in the month of August, and at 35-60m depth all resulted in increased sighting rate, as well as regions of higher slope and at 10-12am. These results account for survey effects, suggest seasonal movement patterns, reliance on static bathymetric features, and diurnal changes in surfacing behaviour. Habitat modelling in the present study has enabled deeper understanding of habitat use by *P. phocoena*, within an area where minimal studies on their abundance, distribution, and habitat preferences have previously been carried out. This research may also be used to aid towards the species conservation such as through management and reduction of bycatch.

Future work

Further work should focus on continued summer surveys to understand interannual variability and confirm increased abundance in August compared to June/July. Deeper understanding of species-habitat relationships means we can make more informed decisions and recommendations for conservation with the aim of ensuring sustainable populations. This will enable secured provision of vital ecosystem services from cetaceans like *P. phocoena*, including biological control, enhanced biodiversity (Tavares *et al.* 2019), and ecotourism (O’Connor *et al.* 2009).

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