Environmental Drivers of Harbour Porpoise (*Phocoena phocoena*) Distribution in the Irish Sea

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Running page head: drivers of harbour porpoise distribution

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Abstract

Understanding spatiotemporal variation in cetacean distributions is critical for improving their protective status and area management, as well as preventing habitat loss caused by increasing anthropogenic threats. In the Irish Sea, hotspots in the distribution of highly mobile and widely abundant harbour porpoises (*Phocoena phocoena*) are relatively well known, but information on the underlying ecological causes is scarce. This study used a collated sightings dataset by the Sea Watch Foundation, from aerial and vessel- based surveys from April to September, 1990 to 2019, to perform habitat association models in four different study areas: the Celtic Deep, Cardigan Bay, North Anglesey, and the Irish Sea Front. Generalised linear models were used to analyse porpoise presence and absence in relation to a set of environmental and survey variables; it was identified that the probability of sighting increased the more time was spent and area covered in the survey. Predominantly, all relationships with the chosen environmental variables were weak but nevertheless significant; porpoises most often occurred when annual temperature variance was <9 °C and depth ranged between 20 - 90 m. Seabed roughness, average salinity, and thermal stratification also indicated preference for particular areas, serving as proxies for localised habitat heterogeneity and subsequent prey availability. The study found that commonly accepted environmental factors from existing literature applied to harbour porpoises in the Irish Sea. These provided valuable insight to their distribution and inferred that porpoises were most likely to occur where prey was abundant and easy to catch.

Keywords:

Phocoena phocoena, Irish Sea, habitat association models, generalised linear models, species-habitat relationships, stratification, fronts, long-term dataset

1 Introduction

One of the smallest of cetacean species, the harbour porpoise (*Phocoena phocoena*), occupies cold temperate and subarctic waters of the Northern hemisphere (Reid et al. 2003, Jefferson et al. 2015, Evans 2020). It is primarily a shelf-species, with a distribution from Alaska south to California in the North Pacific, and from north-west Greenland, Iceland and northern Norway south to the west European coast, and Senegal (Evans 2020). Porpoises inhabit most of the northern European shelf seas, but occur in low numbers in the Baltic Proper (Carlén et al. 2018) and within the Mediterranean Sea are regular only in the northern Aegean Sea (Frantzis et al. 2003, Fontaine 2016). As the most frequently sighted cetacean in the UK, high abundances are reported in parts of Scotland (Embling et al. 2009, Marubini et al. 2009, Brookes et al. 2013, Booth et al. 2013), Wales (Pierpoint, 2001, Shucksmith et al. 2009, Baines & Evans 2012, Nuuttila et al. 2017), Ireland (Berrow et al. 2010, Berrow et al. 2014), southern North Sea and English Channel, and the Bay of Biscay (Lambert et al. 2017, Laran et al. 2017, Bouveroux et al. 2020). In the Irish Sea, porpoises are common and widespread, with clusters of sightings around the Isle of Man, the Mull of Galloway, the north coast of Anglesey, western end of the Llŷn Peninsula and south-west Wales (Pierpoint 2001, Baines & Evans 2012, Feingold & Evans 2014).

As a species that is commonly found in coastal waters, the harbour porpoise is thereby frequently subject to a series of threats (Evans 2020). Whilst feeding on commercially important species like cod (*Gadus morhua)*, hake (*Melanogrammus aeglefinus*), turbot (*Scophthalmus maximus*), plaice (*Pleuronectes platessa*) and sole (*Solea solea*) (Leopold 2015), it often suffers accidental capture in bottom set gill nets and pelagic trawls (Evans 2020). The severe injuries through entanglement are often fatal - 17% of porpoise strandings between 1991 and 2010 in the UK were thought to be bycatch (Deaville & Jepson 2011). A further 15% were found starved, possibly caused by diminishing prey resources linked to climate change (MacLeod et al. 2007) as studies indicate range shifts of several prey species and their predators (Evans & Waggitt 2020a). Development in offshore infrastructures, such as marine renewable energy devices, pose a threat to porpoises, which make use of tidal stream habitats for foraging (Waggitt et al. 2018). Noise pollution, stemming from offshore constructions and vessel traffic, can impair their hearing and mask communication with others (Rumes et al. 2017). Porpoises have been observed to avoid construction-related activities (Carstensen et al. 2006, Brandt et al. 2018, Gall et al. 2021) as well as recreational vessel traffic (Evans et al. 1994, Oakley et al. 2017), affecting their behaviour, possibly causing displacement of the area.

To implement effective conservation areas, detailed research on a species' life history, distribution and abundance is required (Cañadas et al. 2008). For highly mobile and widely distributed cetaceans such as the harbour porpoise, information of this nature can be challenging to obtain. Extensive research has found seasonal and regional variations of its habitat (e.g. Gilles et al. 2016, Laran et al. 2017, Nuuttila et al. 2017), showing higher abundances in shallower water (30- 150 m) (Evans et al. 2003, Shucksmith et al. 2008, Embling et al. 2009, Marubini et al. 2009, Booth et al. 2013, Lambert et al. 2017, Isojunno et al. 2012, Williamson et al. 2017) with variations in seabed topography (Isojunno et al. 2012, Brookes et al. 2013, Stalder et al. 2020) influencing the local tidal regime. Major upwelling regions that are biologically productive, such as oceanic fronts or energetic tidal currents, attract species of prey, thereby providing favourable habitat (e.g. Weir & O'Brien 2000, Embling et al. 2009, Marubini et al. 2009, Shucksmith et al. 2009, Sveegaard et al. 2012, Waggitt et al. 2018, Bouveroux et al. 2020). Porpoises are highly influenced by the spatio-temporal distribution and availability of their prey which include sandeel (ammodytidae), sprat (*Sprattus sprattus*), herring (*Clupea harengus*), whiting (*Merlangius merlangus*) and other fish species (Santos & Pierce 2003, Santos et al. 2004, Sveegaard et al. 2012a, Evans 2020), emphasising our limited understanding of the complexity of dynamic marine environments (Embling et al. 2012).

Predictive species modelling is a useful statistical tool to facilitate the understanding of bio-physical coupling underlying cetacean distribution (Redfern et al. 2006). A species' distribution can be predicted by the inclusion of environmental variables based on habitat features with which the species associates (Kaschner et al. 2006). However, the limitations and costs of obtaining cetacean data and the wide-ranging spatio- temporal variability of environmental factors in the marine ecosystem make it a challenging field of study (Redfern et al. 2006). Habitat models increasingly have been applied in species and habitat management and conservation biology (Guisan & Zimmermann 2000, Cañadas et al. 2008, Nuuttila et al. 2015, Gall et al. 2021, Williamson et al. 2021). Despite the status of harbour porpoise as a protected species in Europe under the EU Habitats Directive 92/43/EEC (1992), no designated area in UK waters was assigned in relation to its status until very recently due to limited information on the species' "physical and biological factors essential to their life and reproduction" (The Conservation Regulations 1994) (Evans & Prior 2012). The use of habitat models (Evans et al. 2015, Heinänen & Skov 2015), however, initiated the designation of five Special Areas of Conservation (SAC), of which three lie within the Irish Sea: the North Channel north-west of the Isle of Man, North Anglesey Marine, and West Wales Marine, from the northern Llŷn Peninsula to Pembrokeshire in the south-west (JNCC, 2019).

Due to their small size and thereby lack of energy storage (Lockyer 2003), porpoises are predominantly driven by the need to feed constantly and must therefore be near abundant food sources (Read & Hohn 1995, Johnston et al. 2005, Wisniewska et al. 2016). Hence, environmental factors that influence prey distribution indirectly drive porpoise abundance. In order to build habitat association models predicting the presence or absence of porpoises, temperature variance, average salinity, depth, seabed roughness, stratification, and current speed (see Table 2 for supporting evidence) are used as environmental variables. Based on these factors, inferences can be made concerning the distribution of porpoises and their preferred prey. Further included as an explanatory variable is the abundance of bottlenose dolphin (*T. truncates*) known to attack porpoises (often fatally), possibly to reduce prey competition (Ross & Wilson 1996, Deaville et al. 2018, Williamson et al. 2021).

In order to predict differences in porpoise distribution, four focal areas have been chosen within the boundaries of the Irish Sea, characterised by different environmental features. The study aimed to explore which features drive porpoise presence and if areas of oceanic fronts and productive upwelling provide favourable habitat. Through the use of habitat association models it was possible to explore a range of distinctive dynamic and static environmental variables that can inform further the conservation management of porpoises in comparable habitats.

2 Methods

2.1 Study area

Protected from strong winds and currents from the Atlantic (Howarth 2005), the Irish Sea exhibits a relative homogeneous bathymetry, with the exception of the deeper St. Georges Channel (Vincent et al. 2004) and shallower bays in the east (Howarth 2005). Much of the Irish Sea benthic substrate is composed of sand with two large regions of mud, the Western Irish Sea Mud Belt and in the Celtic Deep (Ward *et al.*, 2015). Nutrients are being carried in highly saline currents from the St. George’s Channel in a northward direction (Howarth, 2005). Two important frontal upwelling systems are found at each end of the Irish Sea, the northern Irish Sea front and the southern Celtic Sea front (Simpson & Hunter 1974). Here, upwelling of nutrients cause high concentrations of plankton which in turn cause temporary prey aggregations (Pingree et al. 1978, Wolanski & Hamner 1988). Within the Irish Sea, fish of the clupeid (Atlantic herring, sprat), gadidae (Atlantic cod, whiting), ammodytidae and gobiidae family are the common diet of harbour porpoises (Evans & Shepherd 2001) together with haddock, plaice and sole they are widely abundant in the area (Heesen et al. 2015).

Four study areas were identified *a priori*, based on representative geographical features and the abundance of harbour porpoise: (1) the west of Pembrokeshire stretching out into the Celtic Deep (51°30’N to 52°00’N, 5°00’W to 6°30’W); (2) Cardigan Bay ranging from St. David’s Head in the south to the Llŷn Peninsula in the north (52°00’N to 53°00’N, 4°00’W to 5°0’W); (3) coastal waters of north Anglesey (53°40’N to 53°10’N, 4°00’W to 5°0’W) and (4) the Irish Sea front between the east coast of Ireland and the west coast of the Isle of Man (53°04’N to 54°10’N, 4°30’ W to 6°0’W) (Fig. 1).

2.2 Surveys

Through the collaboration with Sea Watch Foundation, a multi-sourced, long-term dataset of harbour porpoise and bottlenose dolphin sightings from dedicated surveys was provided (Table S1). For details of porpoise sighting locations, see Fig. 2. Sightings data were collated from a range of organisations that conducted line transects using vessels and airplanes between 1990 and 2019, with the exception of WWT surveys, that followed the European Seabirds at Sea (ESAS) protocol. The sources JNCC and SCANS2 were making use of both aerial and vessel survey techniques; CE and WWT were exclusively airplane based, providing data in the four study regions, covering 27573 km (1350 km^2) of the total effort, with speeds ranging from 79.7- 152.9 knots. The majority (~70%) of effort provided vessel-based data (HORIZON, IWDG, JNCC, MANW, MWDT, SCANS 2, SWF, WDC) that covered 63038 km (9195 km^2) with speeds ranging from 0- 28.4 knots.

For each study area, it was decided *a priori* which data source and survey years produced a homogeneous dataset of sightings. In order to avoid potential seasonal bias in sightings, only summer data from April to September were used in this study. Corrections for the two different survey efforts were achieved by including survey variables effort *HRBP_EF* (km^2), platform speed *speed* (knots) and survey time *Hr* (hr) in the generalised linear models (GLM).

2.3 Environmental data

The environmental variables used in the habitat models are listed in Table 1 and were selected based upon their presence in the study area and their ecological explanation for the presence of harbour porpoises in previous research (Table 2).

2.4 Data analysis

R! Studio (R version 4.0.2) (R Core Team, 2020) was used for statistical analysis. Harbour porpoise counts were converted to presence (=1) and absence (=0) due to high zero inflation (93%) in the response variable. ArcMap (v. 10.7.1) was used for mapping species and environmental data by converting points to raster data with a spatial resolution of 2.5 x 2.5 km.

Model fitting. The collinearity between the explanatory environmental variables was tested separately for each study area. If two variables had a strong positive or negative correlation (threshold: Spearman's rho > 0.7), only one of the variables was used in the modelling process. In some study areas, more than two ecologically important variables were highly correlated. In this case, the linearity of the scatterplot determined whether one or both variables could be included in the model: a straight line, indicating very strong collinearity, suggested to exclude one variable. Collinearity varied much between study areas, preventing to proceed using the same survey variables in all areas.

For the modelling process, the survey variables *HRBP_EF*, *Hr* and *speed* were used in all models, but the environmental variables for each area were chosen *a priori*, based on the presence and variation of the explanatory variable. The presence and absence of harbour porpoises at each study site was modelled using GLM with a logit-link binomial distribution. Using backward stepwise selection, the lowest AIC (Akaike Information Criterion) score, as well as a non-significant *p*-value (>0.05) caused one variable to drop until all explanatory variables remained with a significance level <0.05. The final model was then plotted using 'visreg' package (Breheny & Burchett, 2017) where the inverse link function is applied to plot the prediction model (Zuur et al. 2007).

If the calculated probability of sighting a harbour porpoise in association with an environmental variable was not well explained ie. modelled using a linear function (due to its ecological explanation), then a generalised additive model (GAM) was used. GAMs were modelled with the 'mgcv' package (Wood, 2006) using the degrees of freedom as a smoothing parameter (Zuur et al. 2007), whereby a maximum number of degrees of freedom was set to 4 to avoid overfitting (Embling et al. 2009, Marubini et al. 2009). The stepwise backward selection process for all study areas is detailed in the supplementary data (Table S6-S9).

Outliers. In the study area in North Anglesey, four values where salinity was ≤32.5 gl^{-1} were removed. The records were marked as porpoise absences and deviated from the mean of 34.4 ± 0.007 SE gl^{-1}. In the Celtic Deep area, values ≥ 0.5 hrs (n = 14) deviated significantly from the mean of 0.09 hrs ± 0.001 SE (range from 0.004 - 2.57) and were removed; a histogram shows the uneven data distribution (Fig. S5 in supplementary data).

3 Results

3.1 Correlations

There were strong negative correlations (r > 0.7) between current speed and stratification in all study regions indicating a tendency for weaker currents where stronger stratification occurs. At the Irish Sea Front, in North Anglesey and Cardigan Bay, the average salinity decreased with increasing annual temperature variance whereas in the Celtic Deep, average salinity increased with seabed depth. There was a strong negative relationship between annual temperature variance and seabed depth in North Anglesey and Cardigan Bay whilst in the latter study area, the temperature variance decreased with high current speeds; these in turn were amplified in greater seabed depths. In Cardigan Bay, survey effort (km^2) was also positively related to the surveying time (see correlation matrices Table S1- S5 and pairplots Fig. S1- S4 in supplementary data).

3.2 Models

3.3 Survey variables

Moderately weak and positive relationships were found with *HRBP_EF* (Pd = 1.66 at the Irish Sea Front; Pd = 0.77 in North Anglesey; Pd = 1.37 in Cardigan Bay) and a strong relationship with *Hr* (Pd =5.24 in North Anglesey; Pd = 3.95 in the Celtic Deep). Response curves from the GLMs between the probability of harbour porpoise presence and the latter two survey variables are shown in Fig. 3 and Fig. 4. In the Celtic Deep study region, the variable *HRBP_EF* was eliminated in the second step in the process of stepwise model selection due to a low AIC and non-significant *p*-value ($p = 0.264$) (see Table S9 in supplementary data).

When including the survey variable *Hr* in the modelling process, the estimation values were negative, implying that the probability of presence increases if less time is spent surveying (Pd = -0.93 at the Irish Sea front; Pd = -2.11 in Cardigan Bay). If relationships with *Hr* were negative, then the variable was excluded from the model. This resulted in an increase, rather than a decrease of the final AIC. The variable *speed* was significant in all areas but North Anglesey, with exceedingly weak but significant relationships (Pd = 0.003 at the Irish Sea Front; Pd = -0.01 in Cardigan Bay; Pd = -0.01 in the Celtic Deep) (Fig. 5).

3.4 Environmental variables

In the region of the Irish Sea Front, most sightings were recorded in Manx waters, south-west of the Isle of Man, and between Holyhead and Dublin where a visible survey strip indicates the possible use of a ferry as platform of opportunity. Only a few sightings were recorded in the central area between (Fig. 2), although survey effort in the Irish Sea frontal region was high (2964 km^2 coverage). As a result of the stepwise model selection, *BAT* was included in the model despite a *p*-value above the threshold of 0.05 (*BAT*, $p = 0.0559$). By retaining *BAT*, the other significant environmental variables that predicted porpoise presence around the Irish Sea Front were *AnTPV* and *HU3* (Table 3). The probability of sighting a porpoise was higher (Pd = -0.19) when the annual temperature variance was low (between 6 - 9 °C) as visualised in Fig. 8 a. Sightings were also recorded on North Ireland's west coast, where temperature variance was >9 °C. The relationships between porpoise presence and water depth were negative with a low estimation value (Pb = -0.003), but with slightly higher probabilities of presence in moderate water depths of >30 m and <90 m as indicated by the GAM curve (Fig. 7). Porpoises avoided areas beyond this depth, although there a few sightings west of Anglesey (Fig. 8b). Possibly, this is due to the stratification that is present in this area (Fig. 8c), with predictions to increase (Pd = 0.1) where the stratification parameter SI ranged between >1.5 and 3, and peaked at ~ 2 (Fig. 7).

In the study region of North Anglesey, harbour porpoises were predominantly recorded near the coastline with fewer sightings further offshore. The headlands create variations of the seabed, to which porpoises had a preference to, as indicated by a positive relationship with *FEA* (Pb = 0.09) (Table 4). The response curve in Fig. 9 showed higher probabilities when seabed roughness was >7 m, this is also reflected in Fig. 10 where there was a preference for habitats with steeper sloped seabed. Salinity levels varied from east to west of the coastline, providing a range of values where porpoises were recorded. This is reflected in a negative relationship with *AnSAL* (Pb = -0.42) (Table 4) where most porpoise presences were recorded around mean salinity levels of 34.4 gl^{-1} ± 0.007 SE. Lower levels were recorded on the east coast of the Isle of Anglesey where the Menai Strait influences these (Fig. 10).

In Cardigan Bay, survey effort (= 5386 km^2) and porpoise sightings (n = 2309) were the highest of all four study areas, with clusters of sightings in the south of Cardigan Bay, the main area where Sea Watch Foundation conducts its surveys. The probabilities of presence showed negative relationships with *AnTPV* (Pd = -0.22) and *BTND1* (Pd = -0.08) (Table 5). The chance of porpoise presence diminished with increasing annual temperature variance, but in areas where the sea temperature varied less than ~ 10° C, the probability of finding porpoises increased (Fig. 11). Clearly, less sightings were recorded where temperature variance was <10 °C, with most sightings in areas of low temperature variance in the south and west of the Llŷn Peninsula (Fig. 12). The presence of just a few bottlenose dolphins in Cardigan Bay reduced this chance significantly (Fig. 11), although the number of observations where both species occurred simultaneously was limited (see presences rug plot in Fig. 11) and was reflected in a low estimation value.

In the south-eastern Irish Sea, porpoise presence was mainly recorded in the area west of Pembrokeshire, with only a few sightings further west in the Celtic Deep. Probabilities of porpoise sightings in this area were estimated to have a negative relationship with *AnTPV* (Pd = -0.65) and *BAT* (Pd = -0.02) (Table 6). Annual temperature variance ranged only from 7.3 - 10.5 °C, but higher porpoise presence was predicted when temperatures varied less than ~9 °C (Fig. 13); this was also indicated on the map in Fig. 14a, where no sightings were recorded in areas of temperature variance >9 °C. The habitat association with depth is plotted in Fig. 13, showing a declining probability with increasing depth. A preference for shallower depths (20- 60 m) is clearly visible in Fig. 14b, although few sightings were recorded in deeper depths of ~120 m in the Celtic Deep.

4 Discussion

This study was the first to examine habitat associations with harbour porpoises (*P. phocoena*) in four different regions within the Irish Sea. To address this gap in knowledge, a 29-year dataset of collated porpoise sightings was used in a linear modelling approach with a range of dynamic and static environmental variables. The aim was to determine the environmental factors driving species presence in each study area, and identify whether regions with specific environmental features such as tidal upwelling or oceanic fronts would provide favourable habitat. The combined use of aerial and vessel data required effort correction using survey variables, of which survey time and area cover were the most important variables with the strongest relationships. Logically the probability of encountering an animal will increase the more time is spent and the greater the area covered. Platform speed was retained in some models, but probability values near to zero indicated little relevance. Relationships with environmental variables and porpoise presence were predominantly highly significant, with small estimation values indicating insufficient number of sightings or to the variables not being fully sampled.

Annual temperature variance explained porpoise distribution in the Irish Sea, Cardigan Bay and in the Celtic Deep. Although the estimates were low, they were highly significant at all three sites, with the models indicating a preference for areas where temperature variance was below 9- 10 °C. Previous studies (e.g Gilles et al. 2016, Bouveroux et al. 2020, Stalder et al. 2020) predominantly used short-term sea surface temperatures instead of temperature variance in their habitat models, thus limiting the comparison of temperature values with this study. The result of the present study, however, is in line with the findings of Waggitt et al. (2020) who also used temperature variance and found that 10 °C was where probabilities of porpoise presence was highest in the North- East Atlantic. Temperature variance can be used as an indirect driver of thermal stratification, which in turn is correlated with locally enhanced productivity (Pingree et al. 1978). There is evidence that the distribution of some porpoise prey species such as cod, herring and sprat is linked to particular temperatures and/or salinity values (Akimova et al. 2016); all of these are seasonally abundant in the Irish Sea (Marine Ecosystems Research Programme, unpublished data).

Fluctuations in temperature gradients are associated with frontal regions such as the seasonal Irish Sea Front, prevalent during spring/ summer as a result of mixing of slack water and tidal streams (Simpson & Hunter 1974, Pingree & Griffiths 1978). Previously recognised as a hotspot for porpoises (Weir & O’Brien 2000), the present study found small but significant relationships between the probability of porpoise presence and areas of stratification from the Irish Sea Front, but this did not apply for the Celtic Sea Front. Associated with fronts are zones of convergence and upwelling causing high concentrations of bio-productivity to occur (Pingree et al. 1978, Wolanski & Hamner 1988), attracting secondary and tertiary predators. A more recent observation at the Celtic Sea Front, however, did not find higher prey (sprat, herring, sardine) densities at the frontal system, but in adjacent waters that were either shallow and mixed, or deep and stratified (Waggitt et al. 2018). Instead, porpoises preferred areas of less stratified waters (Scott et al. 2010), giving indication to why porpoise presence in the present study had no relationship to stratification in the Celtic Deep, but instead to shallower depths and lower temperature variance.

As expected, habitat associations with shallower water depths of between 20- 90 m, with some individual sightings in deeper regions, were present at the Irish Sea Front and in the Celtic Deep. The probability estimates were extremely low with values near to zero, but highly significant in the Celtic Deep, and just above the significance threshold at the Irish Sea Front. The two regions are dominated by steep bathymetric slopes of the St. Georges Channel, rising to shallow coastal areas. Many other studies have found habitat preferences for shallower waters (30- 60 m) (Evans et al. 2003, Reid et al. 2003, Shucksmith et al. 2008, Embling et al. 2009, Isojunno et al. 2012, Williamson et al. 2017), although travel to deeper regions is not uncommon for harbour porpoise (Goodwin & Speedie 2008, Marubini et al. 2009, Booth et al. 2013). Porpoise dives were shown to be around mean depths of ~30 m (Westgate et al. 1995, Teilmann et al. 2007) despite deeper waters being available. The choice for shallower waters may be linked to the distribution and proximity of abundant prey of high nutritional quality (Macleod et al. 2003, Johnston et al. 2005, Spitz et al. 2012), thereby reducing the energy spent foraging for prey species (Stephens et al. 2007). For example, herring tends to be more abundant in the water column between 25- 45 m (Reid 1999) whereas cod and whiting (*Merlangus merlangus*) occur across a range of depths between 20- 200 m (Zheng et al. 2001).

In coastal systems, tidal currents are important drivers of ecosystems and have frequently been shown to influence porpoise occurrence (Pierpoint 2008, Marubini et al. 2009, Embling et al. 2009, Shucksmith et al. 2009, Benjamins et al. 2016, Lambert et al. 2017, Waggitt et al. 2018). It was therefore unexpected that current speed showed no relationship in the habitat model in the coastal waters of North Anglesey. Other tide related changes are temperature and salinity, of which the latter best described porpoise habitat preference in this study area. Wide ranging values of salinity were measured in the study area due to the openness to the Irish Sea in the west and the Menai Strait in the east. The latter receives a freshwater influx from rivers in the north-east (Afon Ogwen) and south-west (Afon Seiont) (Natural Resources Wales 2018), and through strong tides in the narrow strait, it reduces the salinity levels on the north-east coast of Anglesey. In the present study, there were no indications of preference for a particular level of salinity; the probability of sightings was slightly higher in less saline waters, although the majority of presences were in waters between 33.5 - 34.4 gl^{-1}. Previous studies have found habitat associations with both high and low salinities (Ijsseldijk et al. 2015, Stalder et al. 2020). It is therefore unlikely that salinity alone is driving porpoise presence. Instead, porpoises may be following the distributions of their prey, of which some species such as sprat are positively correlated with salinity (Akimova et al. 2016) or whiting and cod that generally prefer salinity levels between 33 - 35 ‰ (permille) (Pehrson et al. 2009).

Of all four study regions, North Anglesey exhibits the most heterogeneous seafloor roughness, with headlands causing strong tidal currents and eddies to appear along the North Wales coast (Shucksmith et al. 2009, Waggitt et al. 2018). Despite no relationship between porpoises and current speed, a habitat association with the variation of seabed slopes or roughness was found. In line with previous findings, habitat heterogeneity in the form of seabed complexity were important drivers of porpoise distribution, particularly in areas with steeply sloped bathymetry (e.g. Skov & Thomsen 2008, Isojunno et al. 2012, Jones et al. 2014). Habitat diversity provides niches for a wide range of species and therefore slope alone does not determine the distribution of a species (Tews et al. 2003). Geodiversity, in this study represented as seabed roughness, associates with species richness and consequently prey availability (Jones et al. 2014).

This study shows that the environmental variables found in the literature relevant to harbour porpoise also applied in the Irish Sea. In contrast to the initial expectation, harbour porpoises in the Irish Sea were not associated with tidal upwelling and only to one of two frontal regions. Instead, heterogenous environmental conditions favoured the distribution of porpoise prey, dictating their occurrences. Pendleton et al. (2020) suggested using prey itself as an explanatory variable instead of dynamic environmental proxies that fluctuate over time. Sourcing accurate prey data over long time periods, as in the present study, may be difficult, but if conducting studies are made at smaller spatio-temporal scales, hydro-acoustic prey surveys could be conducted, as described in Johnston et al. (2005). Large spatio-temporal studies, however, require knowledge of local mechanisms of bio-physical coupling, so that environmental factors as proxies can be applied, and inferences on the species' habitat preferences can be made.

Due to high collinearity amongst the explanatory variables, using a predetermined set of variables may have limited the study by overlooking important relationships with variables that were not included. This also relates to the paucity of relevant sediment data, which was hypothesised to have a significant relationship in Cardigan Bay where substrates are heterogeneous. With regards to the heterogeneity of sightings data, the study was initially set out using porpoise densities which had already been determined having calculated effective strip widths and the probability of detection along the track-line (PGH Evans, personal communication, 13 August). The highly zero-inflated dataset, however, demanded a presence only approach, omitting valuable information on abundances. Further research is needed where harbour porpoise density is applied to models, and all explanatory variables, including substrate type, are applied across the study regions.

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7 TABLES

Table 1 Explanatory variables used in this study for predictive statistical modelling (adapted from Waggitt et al. 2020); ranges are calculated from the combined subsets of the study areas.

Variable	Unit	Range	Description	Source
Speed	knots	0 – 152.9	Speed of the survey platforms	all
Hr Hours of survey effort	hr	0 – 3.9	Hours of survey effort	
HRBP_EF Harbour porpoise survey effort	km^2	0 – 4.1	km^2 of survey effort for harbour porpoise	
AnTPV Annual temperature variance	°C	6.4 – 15.6	Variance in temperature between 0 - 150 m depth	FOAM AMM7 model
AnSAL Average salinity	°C	28.2 – 35.1	Mean salinity from 2019	
CUR Current	ms^{-1}	0.1 – 2.1	Mean tidal currents from 2019	
HU3 Hunter- Simpson Stratification Index	Hunter - Simpson parameter SI	0.3 – 4.8	Gradients of thermal stratification calculated using $SI = \log_{10}(h/u^3)$, where h is depth (m) and u is current speed (ms^{-1}) (Simpson & Hunter 1974)	derived from *CUR* and *BAT*
BAT Depth	m	1.0– 134.7	Depth	EMODNet-bathymetry
FEA Seabed roughness	m	0.4 – 17.2	Gradients in depth, calculated using the main difference between the focal cell and its neighbouring cells. Strong gradients indicate areas of uneven seabed including bank-systems, shelf- edges, slopes, and trenches	derived from BAT and a Terrain Ruggedness Index (based on Wilson et al. 2006)
BTND1 Number of bottlenose dolphins	counts	0 - 70	Number of sightings of bottlenose dolphins	SWF, WDC, WWT

Table 2 List of explanatory variables and their ecological reasoning used in this study for predicting habitat associations with harbour porpoises in the Irish Sea. Studies in recent literature that found environmental relationships with harbour porpoise distribution.

Variable	Ecological explanation	Evidence found in literature
AnTPV	Temperature and its effect on local productivity affects favoured pelagic fish prey items such as herring that may be associated with major upwelling zones and fronts.	Gilles et al. 2016; Stalder et al. 2020, Goodwin & Speedie 2008
AnSAL	Salinity is used as proxy for resource availability because particular prey species may have preferred salinity ranges, some favouring open ocean environments and other ones receiving freshwater input.	Hedger et al. 2004, Edren et al. 2010, van Beest et al. 2018, Stalder et al. 2020
CUR	Currents transport nutrients and planktonic organisms leading to high productivity including prey aggregations; tidal regimes with favourable topography can enhance feeding efficiency.	Pierpoint 2008, Marubini et al. 2009, Embling et al. 2009, Benjamins et al. 2016, Lambert et al. 2017, Waggitt et al. 2018
HU3	Oceanic frontal systems with stratified water masses, associated with major upwelling zones causing high primary production, are hotspots for prey aggregations and recorded abundance of small cetaceans including porpoises.	Johnston et al. 2005, Skov & Thomsen 2008, Sveegaard et al. 2012, Gilles et al. 2016, Weir & O'Brien 2000
BAT	Porpoises are primarily observed in shelf seas, with relatively shallow depths (mainly 30-60 m, although depths exceeding 100 m have been recorded.	Evans et al. 2003, Skov & Thomsen 2008, Marubini et al. 2009, Isojunno et al. 2012, Booth et al. 2013, Lambert et al. 2017, Williamson et al. 2017, Nielsen et al. 2018
FEA	The topographical variability of the seabed may be linked to prey availability through provision of shelter and nutrient upwelling.	Isojunno et al. 2012, Booth et al. 2013, Brookes et al. 2013, Stalder et al. 2020
BD_presence	Bottlenose dolphins are known to attack harbour porpoise where they co-occur, possibly to reduce competition for prey; in Cardigan Bay, both species occur sympatrically but rarely occur concurrently.	Ross & Wilson 1996, Simon et al. 2010, Boys, 2015, Deaville et al. 2018, Williamson et al. 2021, Nuuttila et al. 2017

Table 3 Summary output of the final model calculating habitat associations with harbour porpoises in the study region at the Irish Sea front between 1990 and 2016. Standard error (SE) and *p*-value at 0.05 significance level are indicated (0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’)

Model parameter	**Estimate**	**SE**	***p***
Intercept	-1.81	0.60	0.003**
HRBP_EF	1.66	0.12	< 0.001***
speed	0.003	0.00	0.003**
AnTPV	-0.19	0.08	0.012 *
BAT	-0.003	0.00	0.056 .
HU3	0.14	0.06	0.032 .

Table 4 Summary output of the final model calculating habitat associations with harbour porpoises in the study region of North Anglesey between 2002 and 2018. Standard error (SE) and *p*-value at 0.05 significance level are indicated (0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’)

Model parameter	**Estimate**	**SE**	***p***
Intercept	10.53	7.16	0.142
HRBP_EF	0.77	0.24	< 0.01**
Hr	5.24	0.82	< 0.001***
AnSAL	-0.42	0.21	0.045 .
FEA	0.09	0.03	< 0.001***

Table 5 Summary output of the final model calculating habitat associations with harbour porpoises in the study region of Cardigan Bay between 2001 and 2019. Standard error (SE) and *p*-value at 0.05 significance level are indicated (0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’)

Model parameter	**Estimate**	**SE**	***p***
Intercept	-0.43	0.27	0.1
HRBP_EF	1.37	0.08	< 0.001***
speed	-0.01	0.00	< 0.001***
AnTPV	-0.22	0.02	< 0.001***
BTND1	-0.08	0.02	< 0.001***

Table 6 Summary output of the final model calculating habitat associations with harbour porpoises in the study region west of Pembrokeshire and the Celtic Deep between 2004 and 2016. Standard error (SE) and *p*-value at 0.05 significance level are indicated (0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’)

Model parameter	**Estimate**	**SE**	***p***
Intercept	3.39	2.4	0.170
speed	-0.01	0.00	0.081 .
Hr	3.95	1.35	0.003**
AnTPV	-0.65	0.30	0.030*
BAT	-0.02	0.004	< 0.001***

8 FIGURES

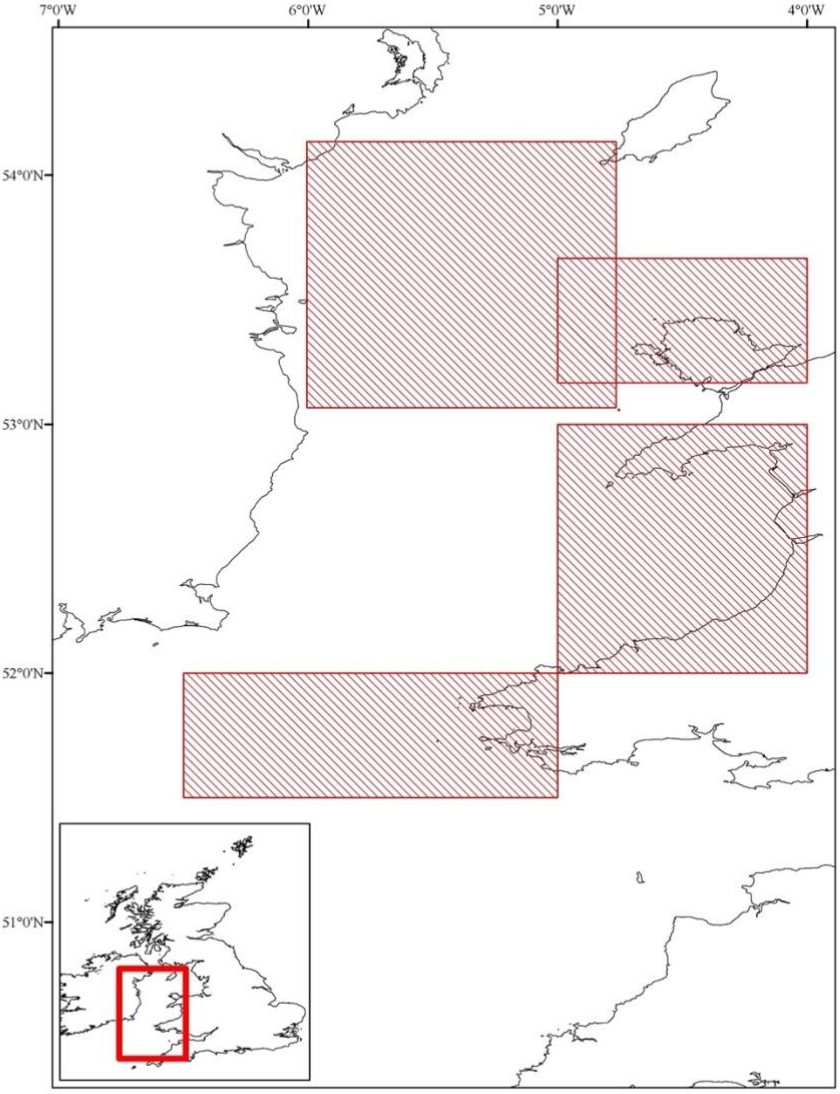

Fig. 1 Four study areas (hatched) within the boundaries of the Irish Sea. From south to north: the west of Pembrokeshire and the Celtic Deep; Cardigan Bay; the north coast of the Isle of Anglesey and the Irish Sea Front.

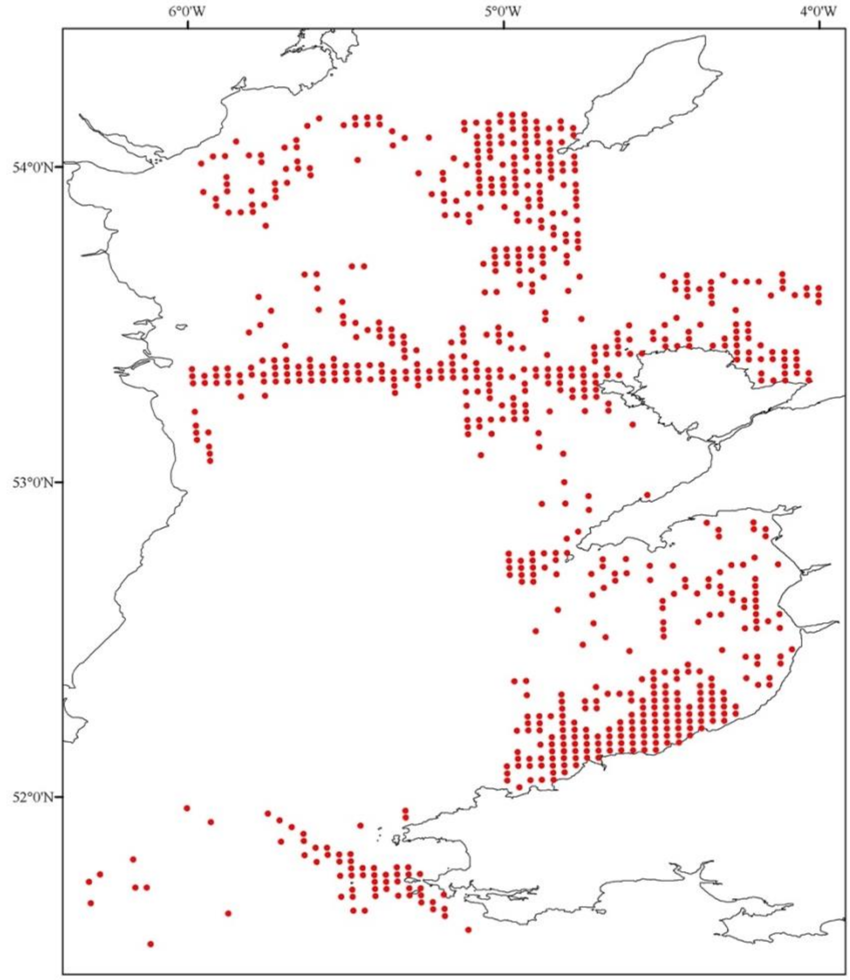

Fig. 2 Map of all cells with porpoises present (red dots) within four survey areas in the Irish Sea.

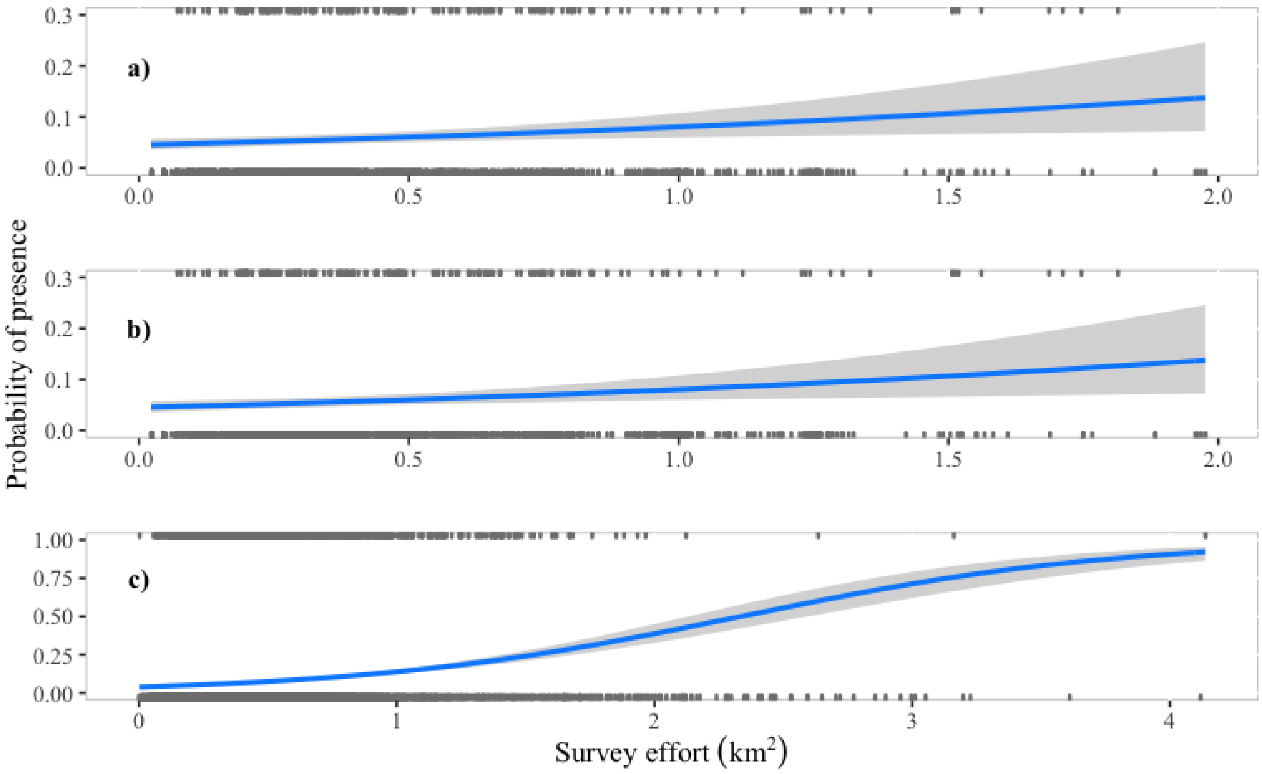

Fig. 3 Response curves from the GLM showing how the probability of presence changes in response to the survey variables *HRBP_EF* (=survey effort in km^2) in study regions a) the Irish Sea front b) North Anglesey and c) Cardigan Bay with 95% confidence intervals (grey shaded) and rug plots indicate presence (0) and absence (1) of harbour porpoises.

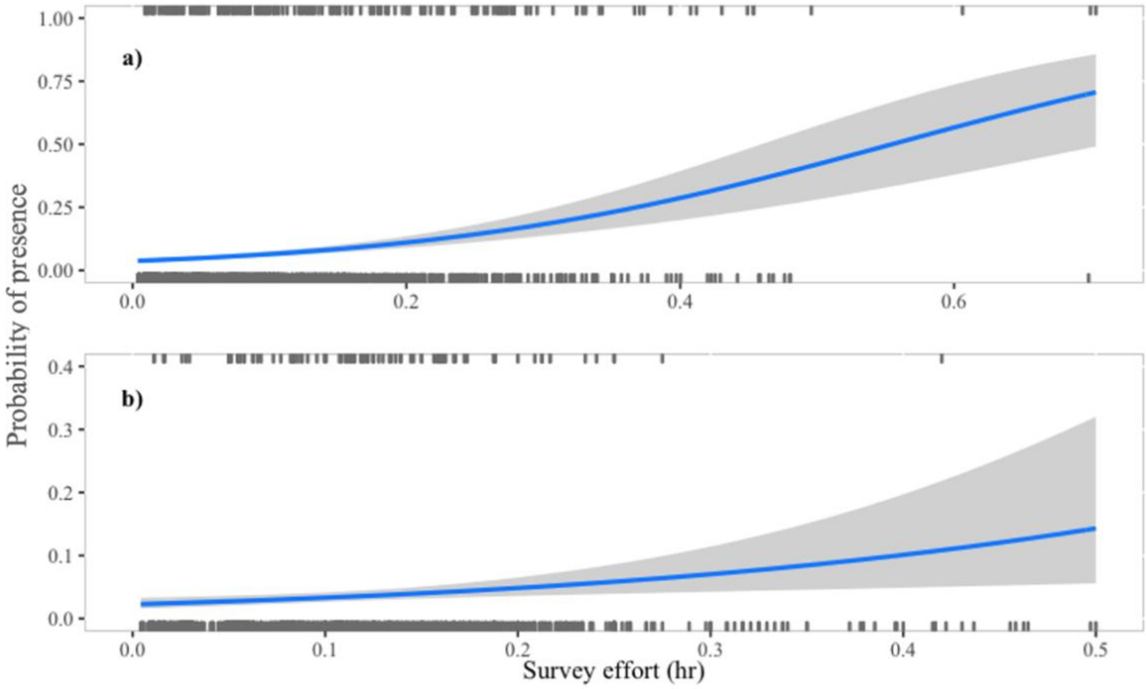

Fig. 4 Response curves from the GLM showing how the probability of presence changes in response to the survey variable *Hr* (= hours of survey effort) in a) North Anglesey and b) the Celtic Deep. 95% confidence intervals are grey shaded and rug plots indicate presences (0) and absences (1) of harbour porpoises.

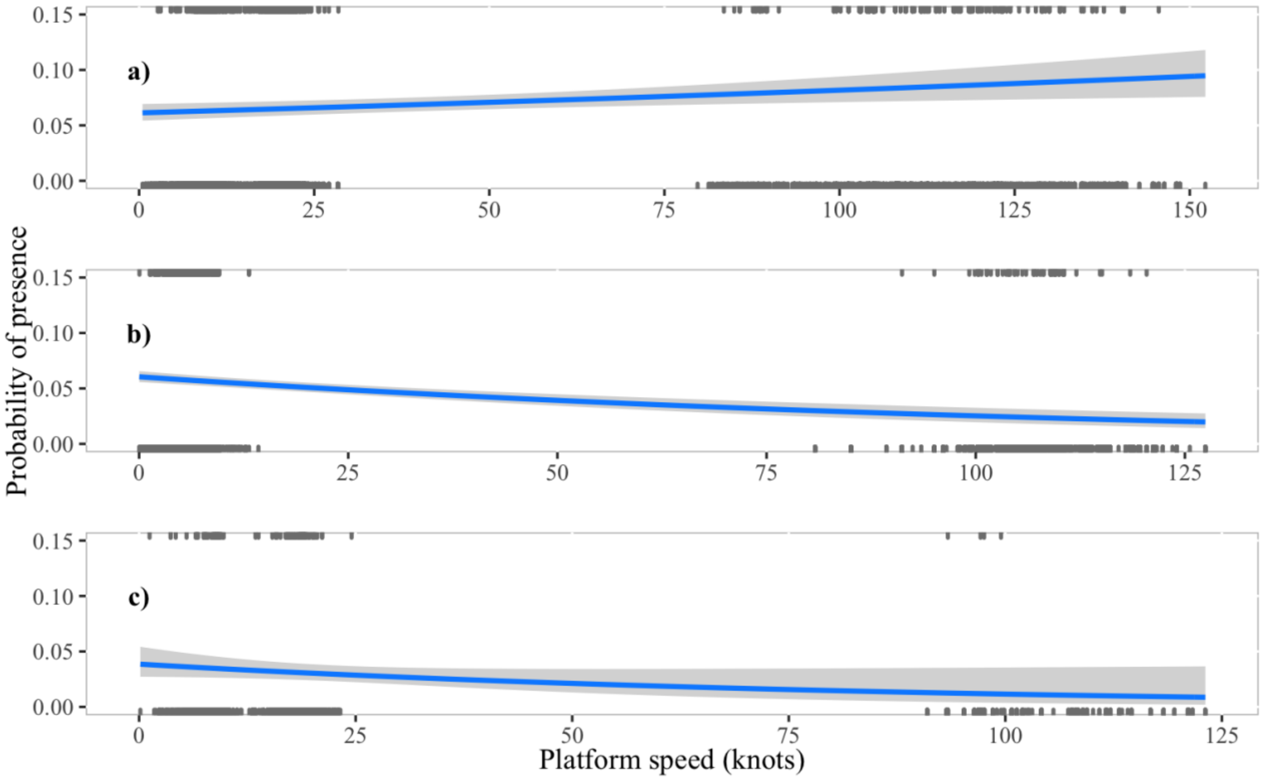

Fig. 5 Response curves from the GLM showing how the probability of presence changes in response to the survey variable *speed* (= platform speed) in a) the Irish Sea front b) Cardigan Bay and c) Celtic Deep. 95% confidence intervals are grey shaded and rug plots indicate presences (0) and absences (1) of harbour porpoises.

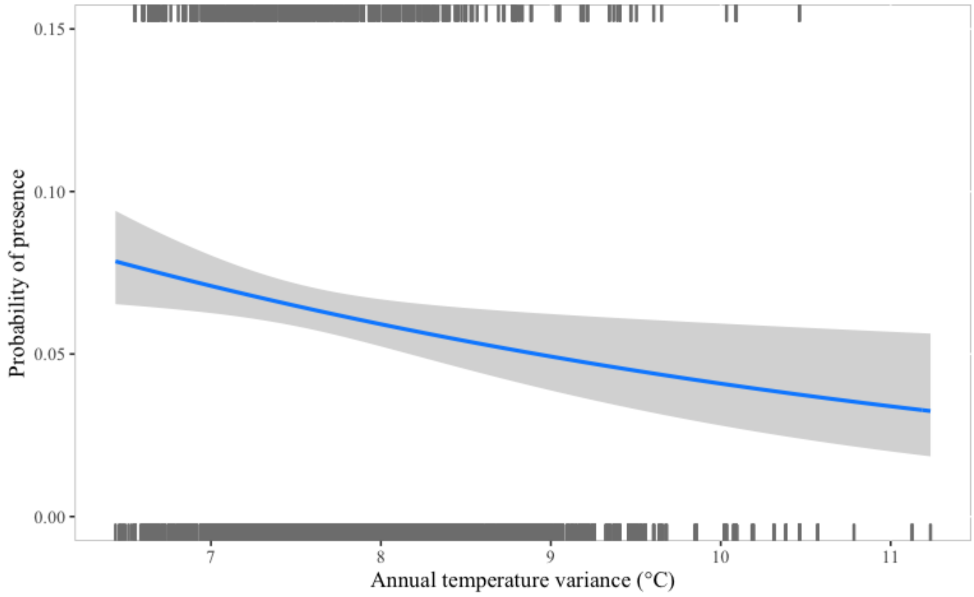

Fig. 6 Response curves from the GLM showing how the probability of presence changes in response to the environmental variable annual temperature variance *AnTPV* at the Irish Sea Front from April to September 1990 to 2018. 95% confidence intervals are grey shaded and rug plots indicate presences (0) and absences (1) of harbour porpoises.

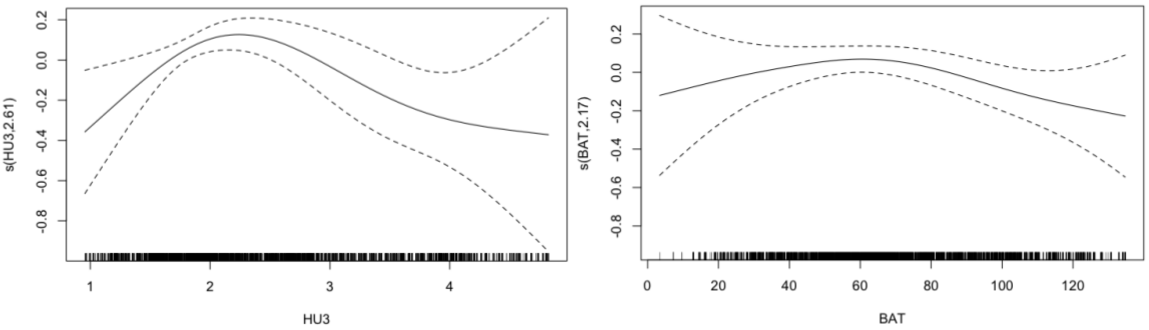

Fig. 7 GAM model outputs of Hunter – Simpson stratification index (*HU3*, df = 2.76) (left) and depth (in meter) (*BAT*, df = 2.17) in the Irish Sea Front from April to September 1990 to 2018; dotted line represents 95% confidence interval.

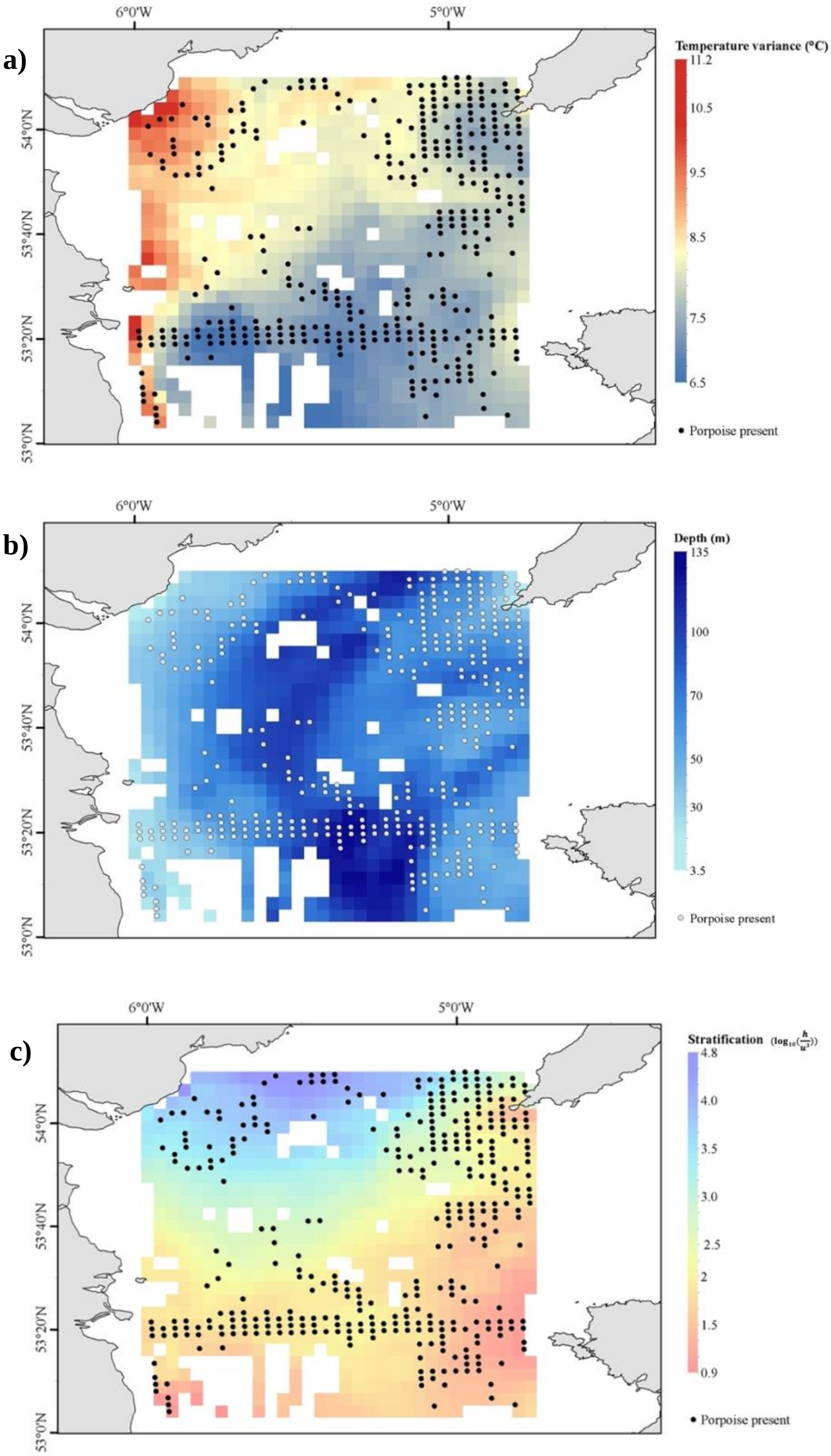

Fig. 8 Environmental variables a) annual temperature variance *AnTPV*, b) seabed depth *BAT* and c) Hunter-Simpson stratification *HU3*, mapped with cells where harbour porpoises (*P. phocoena*) (n = 690) were present in the study region of the Irish Sea front from April to September 1990 to 2018.

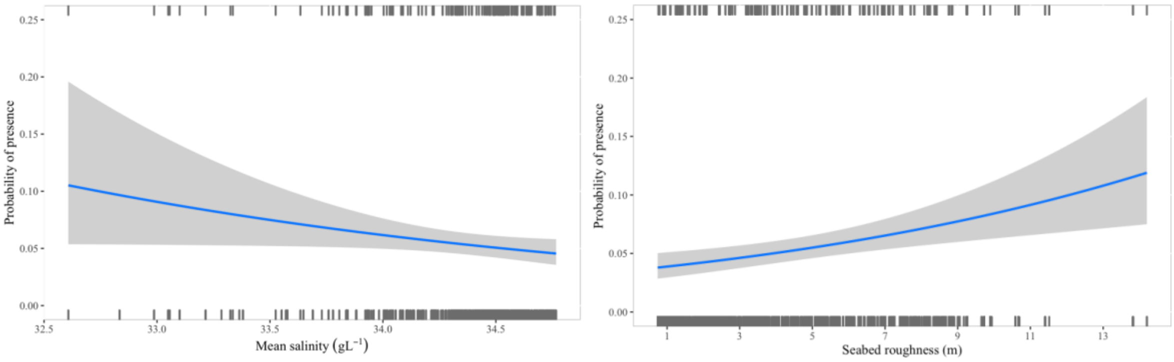

Fig. 9 Response curves from the GLM model showing how the probability of presence changes in response to the environmental variable mean salinity and seabed roughness in North Anglesey between 2002 and 2018. 95% confidence intervals are grey shaded and rug plots indicate presences (0) and absences (1) of harbour porpoises.

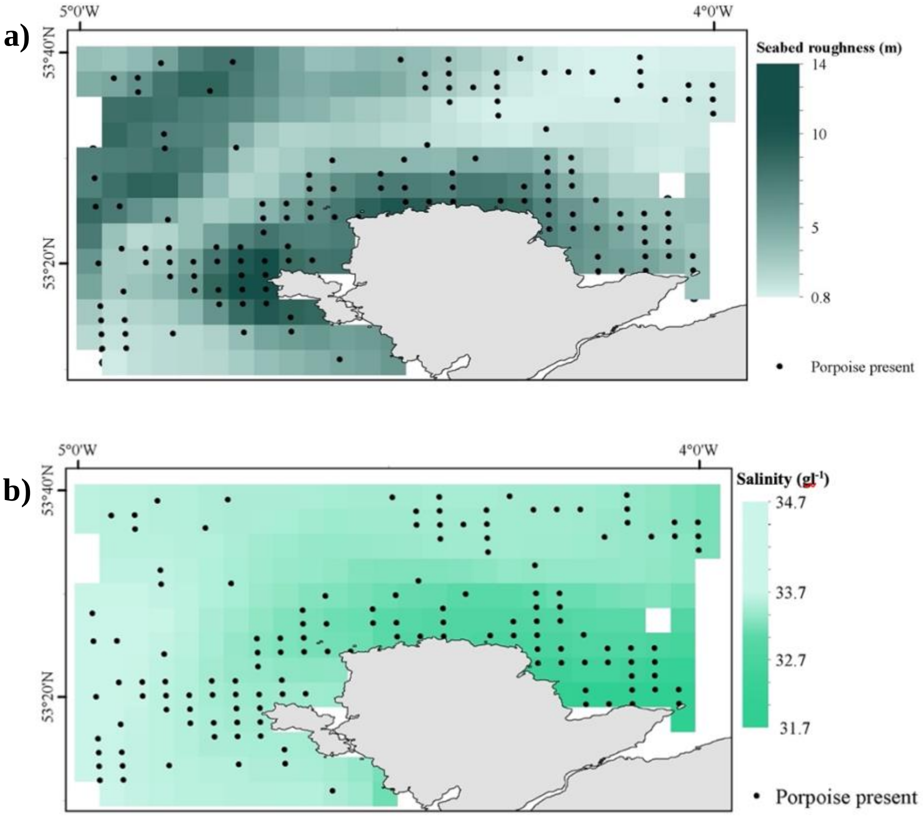

Fig. 10 Environmental variables a) average salinity *AnSAL* and b) seabed roughness *FEA* mapped with cells where harbour porpoises (*P. phocoena*) (n = 217) were present in the study region in the study region of North Anglesey from April to September between 2002 and 2018.

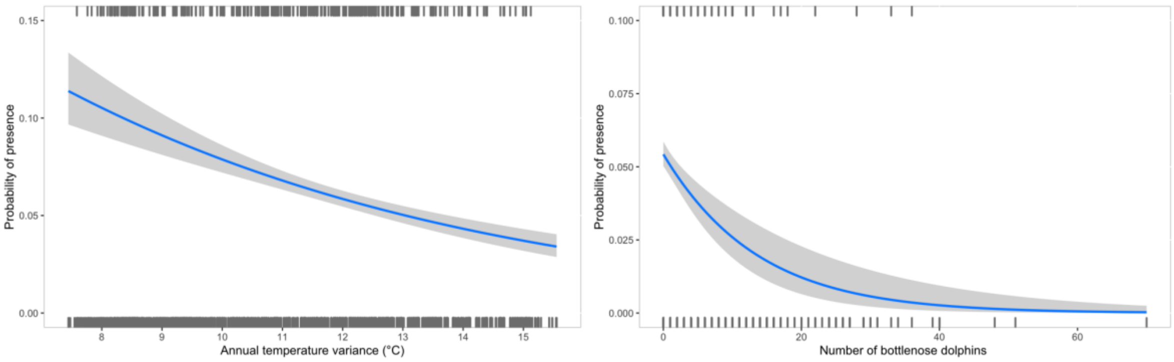

Fig. 11 Response curves from the GLM showing how the probability of presence changes in response to the environmental variable annual temperature variance *AnTPV* (left) and the count of bottlenose dolphins *BTND1* (right) in Cardigan Bay from April to September between 2001 and 2019. 95% confidence intervals are grey shaded and rug plots indicate presences (0) and absences (1) of harbour porpoises.

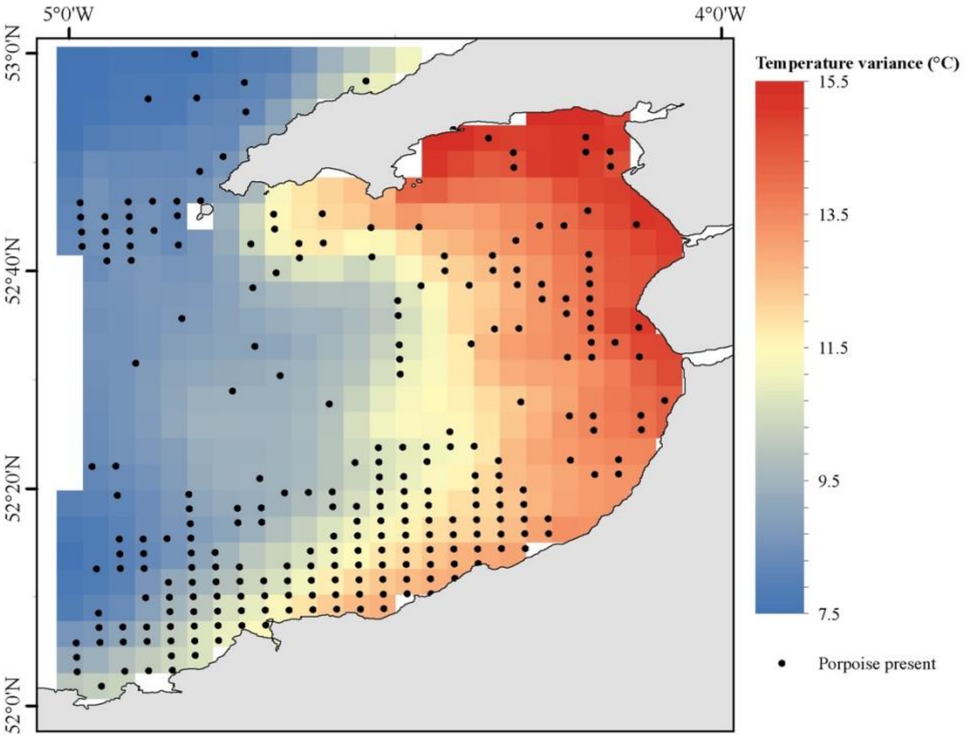

Fig. 12 Environmental variable annual temperature variance *AnTPV* mapped with cells where harbour porpoises (n = 1004) were present in the study region of Cardigan Bay from April to September between 2001 and 2019.

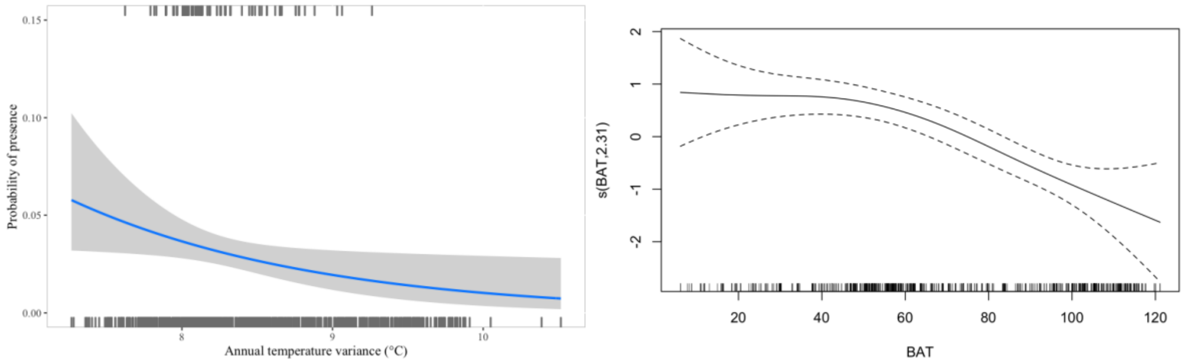

Fig. 13 Response curves from the GLM (left) and GAM (right). The curves show how the probability of presence changes in response to the environmental variables, annual temperature variance *AnTPV* and depth *BAT* (in meter) west of Pembrokeshire and in the Celtic Deep, between 2004 and 2016. 95% confidence intervals are grey shaded and rug plots indicate presences (0) and absences (1) of harbour porpoises.

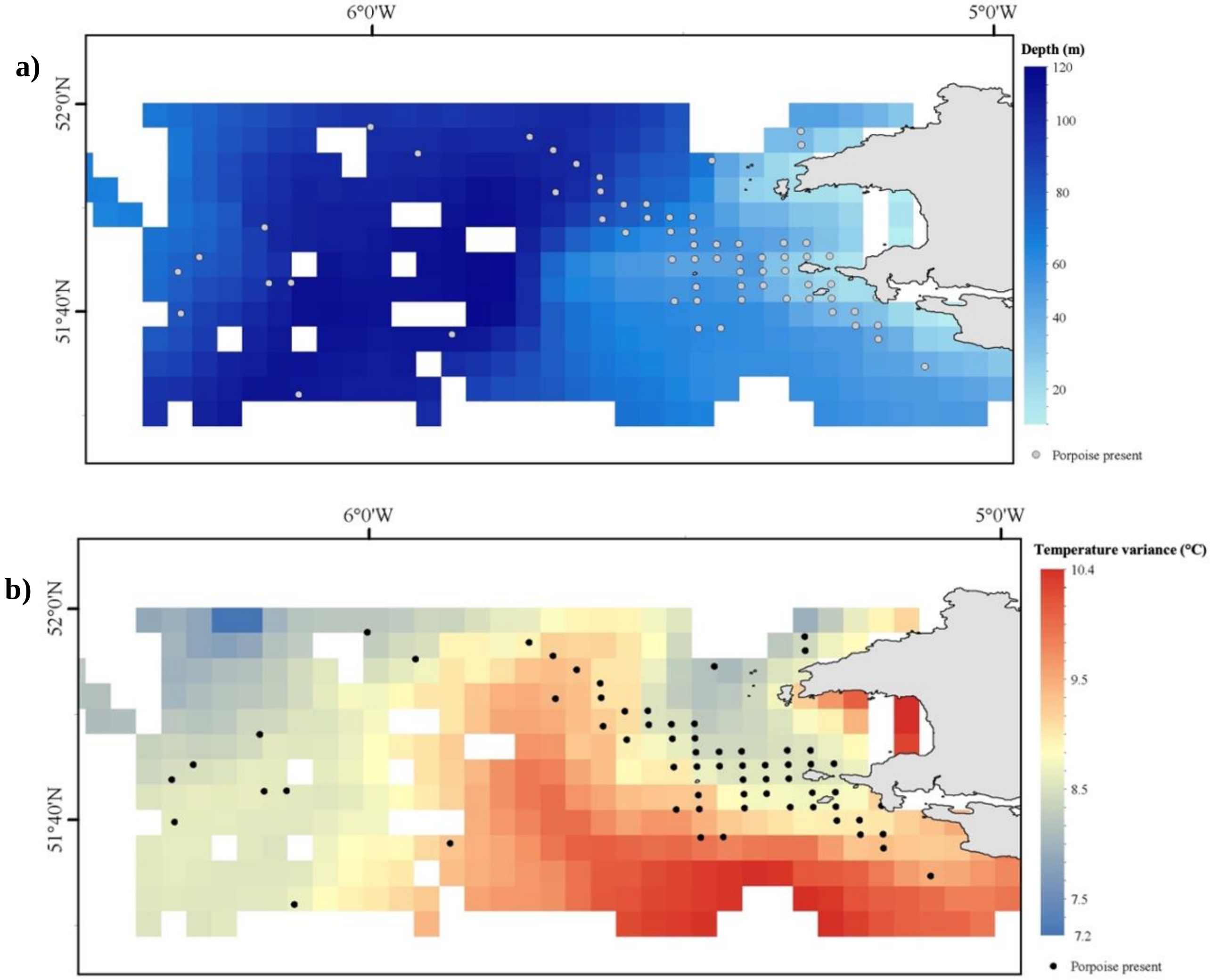

Fig. 14 Environmental variables a) depth *BAT* and b) annual temperature variance *AnTPV* mapped with cells where harbour porpoises (n = 100) were present in the study region west of Pembrokeshire and the Celtic Deep from April to September between 2004 and 2016.

9 SUPPLEMENTARY DATA

Table S1 Overview of choice of sources and subset of survey years per study area in the Irish Sea: CE = Crown Estate; HORIZON; IWDG = Irish Whale and Dolphin Group; JNCC = Joint Nature Conservation Committee; MANW = Marine Awareness North Wales; MWDT = Whale and Dolphin Trust; SCANS = Small Cetacean Abundance in the North and Adjacent Seas (July 2005); SWF = Sea Watch Foundation; WDC = Whale and Dolphin Conservation; WWT = Wildfowl and Wetlands Trust

Source / **Study area**	**CE**	**HORIZON**	**IWDG**	**JNCC**	**MANW**	**MWDT**	**SCANS 2**	**SWF**	**WDC**	**WWT**	**Subset of survey years**
Irish Sea Front	✓	-	✓	✓	-	✓	✓	✓	-	✓	‘90 – ‘16
North Anglesey	✓	✓	✓	-	✓	-	-	✓	-	✓	‘02 – ‘18
Cardigan Bay	-	-	-	-	-	-	-	✓	✓	✓	‘01 – ‘19
Celtic Deep	-	-	✓	-	-	-	✓	✓	-	✓	‘04 – ‘16

	CE	HORIZON	IWDG	JNCC	MANW	MWDT	SCANS 2	SWF	WDC	WWT	***Total***
Survey length (km)	18,006	1,112	16,330	4,413	772	2,389	439	37,421	652	9,073	***90,612***
Area coverage (km^2)	427	146	3,116	290	114	347	35	5,065	115	887	***10,545***

Table S2 Correlation matrix of environmental variables in the Irish Sea frontal region (ISF). Spearman's rho correlation factor is marked in bold if >0.7. Abbr.: speed = platform speed; Hr = survey hours; HRBP_EF = survey effort; AnTPV = annual temperature variance; AnSAL = average salinity; CUR = current speed; HU3 = Simpson-Hunter Stratification; BAT = depth to seabed; FEA = seabed roughness

	Speed	Hr	HRBP_EF	AnTPV	AnSAL	CUR	HU3	BAT
Hr	-0.36							
HRBP_EF	-0.17	0.17						
AnTPV	0.24	0.03	-0.15					
AnSAL	-0.21	0.02	0.10	**-0.77**				
CUR	-0.06	-0.10	0.17	-0.50	0.63			
HU3	0.15	0.09	-0.16	0.47	-0.53	**-0.92**		
BAT	-0.18	0.09	0.06	-0.45	0.67	0.17	0.03	
FEA	-0.10	-0.01	0.06	-0.24	0.30	0.10	-0.01	0.33

Table S3 Correlation matrix of environmental variables in the study region of North Anglesey (NA). Spearman's rho correlation factor is marked in bold if >0.7. Abbr.: speed = platform speed; Hr = survey hours; HRBP_EF = survey effort; AnTPV = annual temperature variance; AnSAL = average salinity; CUR = current speed; HU3 = Simpson-Hunter Stratification; BAT = depth to seabed; FEA = seabed roughness

	Speed	Hr	HRBP_EF	AnTPV	AnSAL	CUR	HU3	BAT
Hr	-0.61							
HRBP_EF	-0.34	0.46						
AnTPV	-0.29	0.27	-0.10					
AnSAL	0.30	-0.30	0.13	**-0.96**				
CUR	-0.29	0.15	0.17	-0.52	0.45			
HU3	0.48	-0.33	-0.21	0.25	-0.19	**-0.87**		
BAT	0.38	-0.35	-0.02	**-0.75**	0.69	0.37	0.08	
FEA	-0.50	0.29	0.18	0.15	-0.10	0.25	-0.43	-0.29

Table S4 Correlation matrix of environmental variables in the study region of Cardigan Bay. Spearman’s rho correlation factor is marked in bold if >0.7. Abbr.: speed = platform speed; Hr = survey hours; HRBP_EF = survey effort; AnTPV = annual temperature variance; AnSAL = average salinity; CUR = current speed; HU3 = Simpson-Hunter Stratification; BAT = depth to seabed; FEA = seabed roughness; BD_presence = bottlenose dolphin presence

	Speed	Hr	HRBP_EF	AnTPV	AnSAL	CUR	HU3	BAT
Hr	-0.34							
HRBP_EF	-0.11	**0.71**						
AnTPV	-0.31	0.21	0.06					
AnSAL	0.10	0.00	0.07	**-0.73**				
CUR	0.24	-0.23	-0.11	**-0.81**	0.41			
HU3	-0.06	0.10	0.04	0.52	-0.17	**-0.81**		
BAT	0.36	-0.27	-0.12	**-0.84**	0.51	**0.82**	-0.39	
FEA	-0.13	0.16	0.10	-0.12	0.09	0.25	-0.45	-0.10
BD_presence	-0.14	0.48	0.29	0.13	0.00	-0.15	0.10	-0.17

Table S5 Correlation matrix of environmental variables in the study region west of Pembrokeshire and the Celtic Deep. Spearman’s rho correlation factor is marked in bold if r > 0.7. Abbr.: speed = platform speed; Hr = survey hours; HRBP_EF = survey effort; AnTPV = annual temperature variance; AnSAL = average salinity; CUR = current speed; HU3 = Simpson-Hunter Stratification; BAT = depth to seabed; FEA = seabed roughness

	Speed	Hr	HRBP_EF	AnTPV	AnSAL	CUR	HU3	BAT
Hr	-0.35							
HRBP_EF	-0.09	0.42						
AnTPV	0.35	-0.09	-0.11					
AnSAL	-0.41	0.20	-0.04	-0.25				
CUR	0.00	-0.07	0.28	-0.32	-0.29			
HU3	-0.09	0.11	-0.23	0.23	0.60	**-0.89**		
BAT	-0.25	0.13	-0.04	0.06	**0.84**	-0.31	0.65	
FEA	0.04	-0.01	0.04	-0.06	-0.53	0.16	-0.43	-0.64

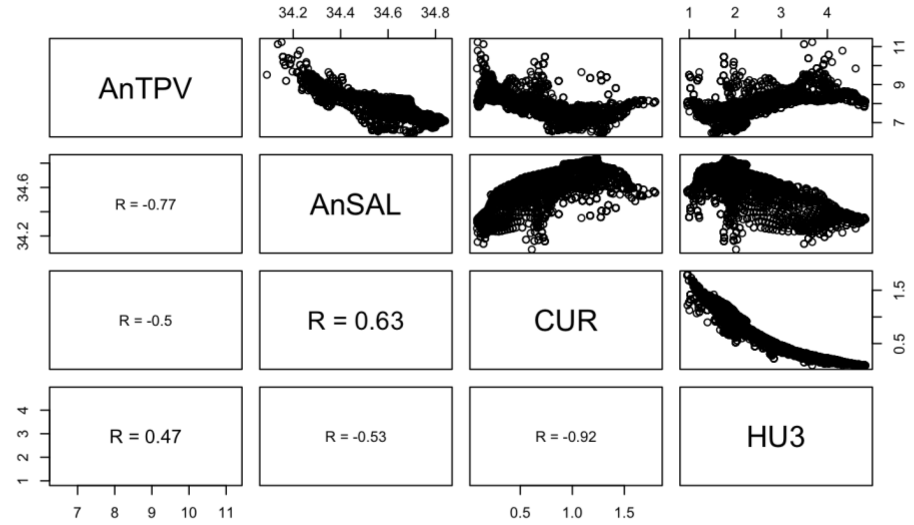

Fig. S1 Pairplot of highly (r > 0.7) correlated environmental variables in the Irish Sea frontal region (ISF); Spearman’s rho is indicated as number in the panels below the variable name and a scatterplot above. Abbr.: AnTPV = annual temperature variance; AnSAL = average salinity; CUR = current speed; HU3 = Simpson-Hunter Stratification.

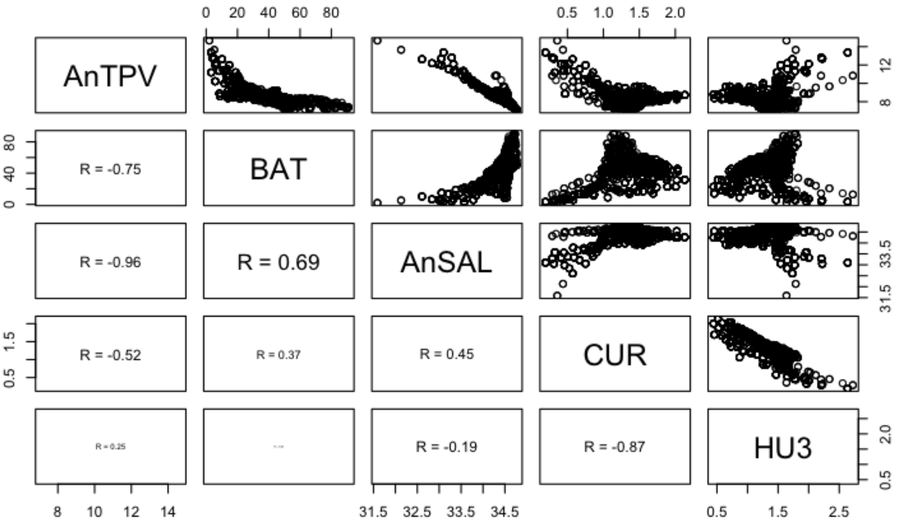

Fig. S2 Pairplot of highly (r > 0.7) correlated environmental variables in the study region of North Anglesey (NA); Spearman's rho is indicated as number in the panels below the variable name and a scatterplot above. Abbr.: AnTPV = annual temperature variance; BAT = depth to seabed; AnSAL = average salinity; CUR = current speed; HU3 = Simpson-Hunter Stratification.

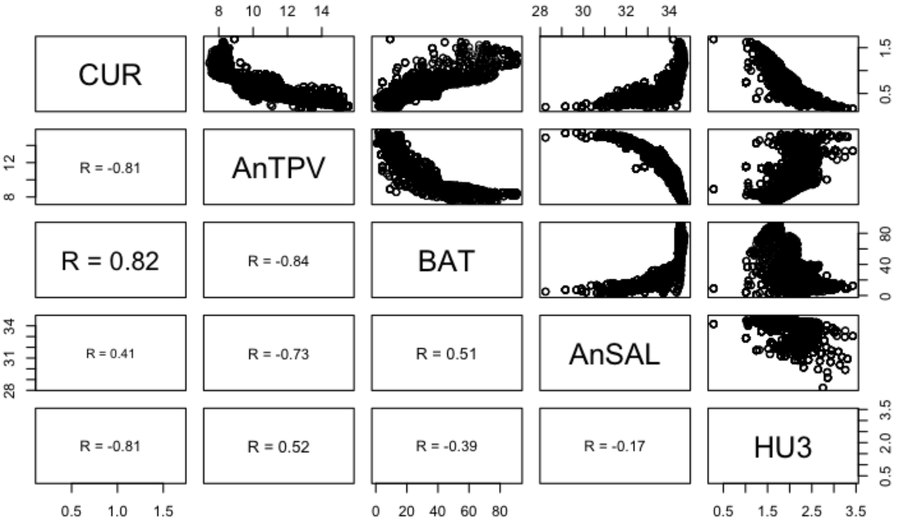

Fig. S3 Pairplot of highly (r > 0.7) correlated environmental variables in the study region of Cardigan Bay (CB); Spearman's rho is indicated as number in the panels below the variable name and a scatterplot above. Abbr.: CUR = current speed; AnTPV = annual temperature variance; BAT = depth to seabed; AnSAL = average salinity; HU3 = Simpson-Hunter Stratification.

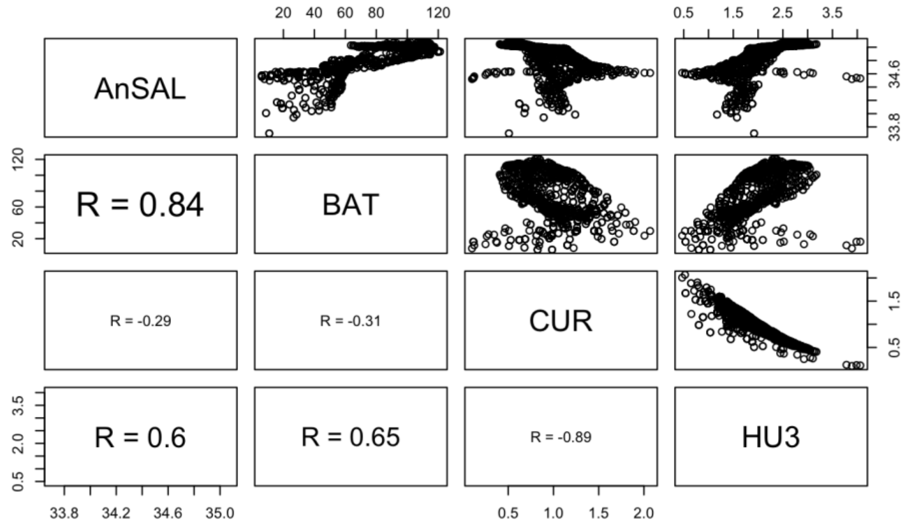

Fig. S4 Pairplot of highly (r > 0.7) correlated environmental variables in the study region west of Pembrokeshire and the Celtic Deep (CD); Spearman's rho is indicated as number in the panels below the variable name and a scatterplot above. Abbr.: AnSAL = average salinity; BAT = depth to seabed; CUR = current speed; HU3 = Simpson-Hunter Stratification.

Table S6 Results of backward stepwise GLM model selection of the environmental variables for the presence of harbour porpoises in the region of the Irish Sea front between 1990 and 2016. The lowest AIC and non-significant (p ≥ 0.05) p-value are in bold, indicating the exclusion of the variable in the proceeding step. Abbr.: HRBP_EF = survey effort; AnTPV = annual temperature variance; BAT = depth to seabed; FEA = Seabed roughness; HU3 = Simpson-Hunter Stratification. Note: the negative estimation value *Hr* was removed prior to step 1, therefore affecting the final AIC.

HP_presence ~ Hr + HRPB_EF+ speed + AnTPV + BAT + FEA + HU3

Start: AIC = 4471.9

	Step 1		Step 2	
	AIC	*p*	AIC	*p*
HRPB_EF	4697.3	<0.001	4695.90	<0.001
Speed	4481.1	<0.01	4480.9	<0.01
AnTPV	4479.6	<0.01	4478.7	0.01
BAT	4474.8	0.1	4475.9	0.06
HU3	4477.4	0.03	4476.9	0.03
FEA	**4474.3**	**0.2**		

Final AIC = 4474.3

Table S7 Results of backward stepwise GLM model selection of the environmental variables for the presence of harbour porpoises in the region of North Anglesey between 2002 and 2018. The lowest AIC and non-significant ($p \geq 0.05$) p-value are in bold, indicating the exclusion of the variable from the final model. Abbr.: HRBP_EF = survey effort; AnSAL = average salinity; FEA = Seabed roughness; CUR= current speed; BAT = depth to seabed.

HP_presence ~ HRBP_EF + Hr + FEA + AnSAL+ speed+ CUR + BAT

Start: AIC = 1396.6

	Step 1		Step 2		Step 3		Step 4	
	AIC	*p*	AIC	*p*	AIC	*p*	AIC	*p*
HRPB_EF	1405.3	<0.001	1391.8	<0.001	1402.0	<0.01	1400.9	<0.01
Hr	1430.2	<0.001	1418.5	<0.001	1431.6	<0.001	1430.8	<0.001
FEA	1400.7	0.01	1392.5	<0.001	1404.8	<0.001	1402.8	<0.001
AnSAL	1396.6	0.08	1385.6	0.02	1396.1	0.02	1395.0	0.05
speed	1396.8	0.07	1383.1	0.09	**1393.3**	**0.14**		
CUR	1394.8	0.25	**1381.0**	**0.36**				
BAT	**1394.2**	**0.41**						

Final AIC = 1393.3

Table S8 Results of backward stepwise GLM model selection of the environmental variables for the presence of harbour porpoises in the study region of Cardigan Bay between 2001 and 2019. The lowest AIC and non-significant ($p \geq 0.05$) p-value are in bold, indicating the exclusion of the variable from the final model. Abbr.: HRBP_EF = survey effort; AnTPV = annual temperature variance; BAT = depth to seabed; AnSAL = average salinity; BTND1 = bottlenose dolphin count. Note: the negative estimation value *Hr* was removed prior to step 1, therefore affecting the final AIC.

HP_presence ~ HRBP_EF + speed + Hr + AnTPV + BTND1 + BAT + AnSAL

Start: AIC = 6851.5

	Step 1		Step 2		Step 3	
	AIC	*p*	AIC	*p*	AIC	*p*
HRPB_EF	7176.7	<0.001	7175.0	<0.001	7175.8	<0.001
speed	6987.9	<0.001	6986.0	<0.001	6984.1	<0.001
AnTPV	6954.2	<0.001	6980.3	<0.001	7021.4	<0.001
BTND1	6967.1	<0.001	6965.2	<0.001	6963.6	<0.001
AnSAL	6937.0	0.68	**6935.2**	**0.64**		
BAT	**6937.0**	**0.75**				

Final: AIC = 6935.2

Table S9 Results of backward stepwise GLM model selection of the environmental variables for the presence of harbour porpoises in the study region west of Pembrokeshire and the Celtic Deep between 2004 and 2016. The lowest AIC and non-significant ($p \geq 0.05$) p-value are in bold, indicating the exclusion of the variable from the final model. Abbr.: Hr = survey effort; HRBP_EF = survey effort; AnTPV = annual temperature variance; HU3 = Simpson-Hunter Stratification; BAT = depth to seabed; FEA = seabed roughness.

HP_presence ~ speed+ Hr + AnTPV + BAT+ FEA+ HRBP_EF + HU3

Start: AIC = 790.5

	Step 1		Step 2		Step 3		Step 4	
	AIC	*p*	AIC	*p*	AIC	*p*	AIC	*p*
speed	780.0	0.020	792.2	0.022	790.9	0.031	790.2	0.047
Hr	778.0	0.062	790.9	0.046	793.8	0.006	793.9	0.006
AnTPV	779.0	0.033	791.0	0.043	791.0	0.029	791.4	0.023
BAT	792.3	0.000	809.7	0.000	810.0	0.000	819.3	<0.001
FEA	776.6	0.144	788.9	0.161	**788.3**	**0.153**		
HRPB_EF	776.1	0.207	**788.2**	**0.264**				
HU3	**775.0**	**0.498**						

Final: AIC = 788.3

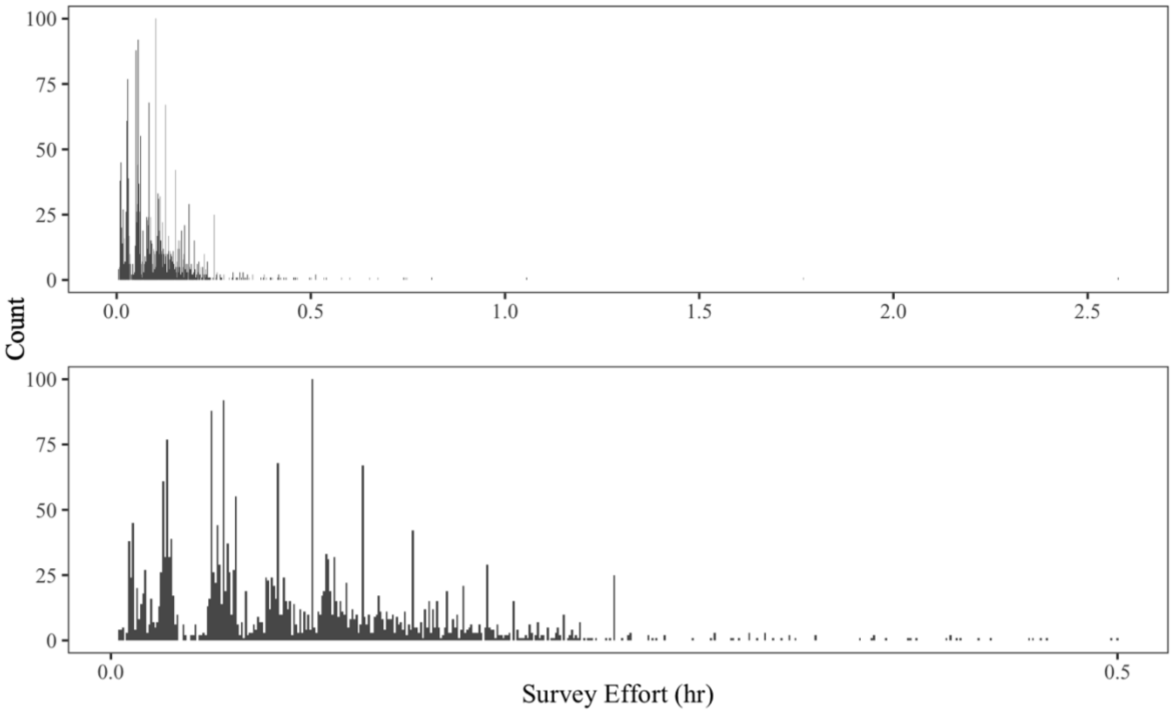

Fig. S5 Histogram of survey effort in hours in the in the study region west of Pembrokeshire and the Celtic Deep between 2004 and 2016. Top panel shows the full data range (0 – 2.58 hrs), the lower panel shows the data range when outliers >0.5 were removed (n = 14) (0 – 0.5 hrs).