PrePARED Report No. 001

Using modelled sandeel distribution maps to characterise spatio-temporal variation in the occurrence and foraging behaviour of harbour porpoises around offshore windfarms

PrePARED

Predators + Prey Around Renewable Energy Developments

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PrePARED Report

Using modelled sandeel distribution maps to characterise spatio-temporal variation in the occurrence and foraging behaviour of harbour porpoises around offshore windfarms

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Summary

Assessment and mitigation of the cumulative impacts of offshore windfarm developments remain constrained by knowledge gaps on the links between the distribution of marine mammals and their prey. Using passive acoustic monitoring techniques and the outputs of a recently developed sandeel distribution model, we investigated how prey density and the presence of windfarms influenced spatio-temporal variation in occurrence and foraging behaviour of harbour porpoises (*Phocoena phocoena*) in the Moray Firth, NE Scotland. We found a consistent positive predator-prey relationship in this area, which matched the seasonal presence of prey in the water column. Analyses also suggest that the installation of wind turbine structures may have modified predator-prey interactions and highlight how additional work within the OWEC funded PrePARED project can be used to better understand this effect.

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1. Introduction

The harbour porpoise is the most widespread and commonly occurring cetacean in the North Sea (Hammond et al. 2002). Given its listing under Annex II of the Habitat Directive, this species has been a key receptor in Environmental Impact Assessments (EIA) for offshore windfarm developments across the North Sea. Underpinning these assessments is the need for robust data on spatio-temporal variation in porpoise densities. This information is used in combination with underwater noise modelling (see Faulkner et al. 2018) to assess and mitigate potential individual and population level impacts of noise from windfarm construction activities (King et al. 2015; Nabe-Nielsen et al. 2018).

Whilst focussed surveys at some developments have provided local estimates of porpoise densities, most project assessments are based upon broader-scale data such as those collected during co-ordinated international large-scale visual surveys conducted during the summers of 1994, 2005, 2016 and 2022 (eg. Hammond et al. 2002; Hammond et al. 2013). Such data may be used to provide estimates of average densities within large survey blocks or to create spatial distribution maps by modelling each species' association with different environmental variables (Waggitt et al. 2020). It seems reasonable to assume that the environmental variables retained in these models provide a proxy of prey availability. However, efforts to test predator-prey associations more directly are often constrained by uncertainties over both the predator's diet and the distribution of potential prey. Critically, this also constrains our understanding of likely temporal changes in predicted distributions of key receptors. This may also be because sparse data have been pooled across time periods to generate distribution models (Carter et al. 2022; Waggitt et al. 2020) because surveys were restricted to a particular season (eg. Hammond et al. 2002; Hammond et al. 2013), or because longer term changes in environmental conditions may result in changes in prey distribution (Perry et al. 2005).

In the context of cumulative impacts of offshore windfarm developments, another potential driver of change in predator and prey distribution is the installation of new structures in the marine environment. There is growing evidence that these structures can modify ecosystems (Degraer et al. 2020; Methratta and Dardick 2019; Reubens et al. 2014), introducing hard substrate that becomes colonised by epibenthic organisms, attracting fish and other predators such as marine mammals (Fernandez-Betelu et al. 2022; Russell et al. 2014). Thus, baseline distributions and foraging patterns of marine predators may be modified by the presence of new windfarms, and the consequences of those changes need to be considered in assessments for subsequent developments in adjacent areas.

Although harbour porpoises are opportunistic feeders, with diet in the North Sea varying seasonally, a key prey species during summer months is the lesser sandeel (*Ammodytes spp*) (Ransijn et al. 2021; Santos et al. 2004). Sandeels exhibit complex seasonal and diel behaviour patterns, spending most of the year buried in sediment and emerging between April and August to feed in the water column (Henriksen et al. 2021; Reebs 2002; Winslade 1974). During that feeding season, sandeels form large schools in the water column during the day, returning to the seabed at dusk or once they are satiated (van Deurs et al. 2011; Winslade 1974). As the feeding season progresses, the proportion of sandeels in the water column during the day decreases, while the proportion of buried sandeels increases (Greenstreet et al. 2006). Burying in the seabed is considered an anti-predator behaviour (Scharf et al. 2006), although data on the winter diet of seals (Prime and Hammond 1990; Tollit and Thompson 1996) suggest that some marine mammals may continue to exploit sandeels even when they are buried in the sediment. Limited data on harbour porpoise diet in winter suggests that seasonal changes in sandeel availability may result in porpoises switching to alternative prey (Santos et al. 2004), and potentially using alternative foraging habitats.

Given the ecological importance of sandeels to a wide range of predators, the Scottish Government Marine Directorate recently produced probability of occurrence and density maps of sandeels across the North and Welsh seas (Langton et al. 2021). These maps present the predicted spatial variation of sandeels whilst buried in the sediment. Predictions are based on the relationship between observed sandeel density and aspects of the seabed (i.e., sediment type, the slope of the seabed, the overall water depth). However, it is unknown how well the predictions reflect sandeel distribution when they emerge to feed in the water column and are thus available to predators. A key aim of the PrePARED project is to assess the performance of Langton et al. (2021) model output in predicting the distribution and behaviour of top predators, such as harbour seals and harbour porpoises.

In this report we investigate whether spatio-temporal variation in the occurrence and foraging behaviour of harbour porpoises around Moray Firth windfarm sites are related to relative sandeel density predicted by the Langton et al. (2021) model. To achieve this, we used a long-term passive acoustic monitoring (PAM) dataset that included baseline data collected before windfarm farm construction commenced, and recent post-construction data collected around windfarm structures that have been in place for 2-5 years.

This PrePARED project task has three specific objectives: 1) to investigate whether there is a spatial relationship between porpoise occurrence or foraging behaviour and sandeel distribution in summer, when sandeels are known to be important prey; 2) to assess if this relationship varies temporally, in relation to expected seasonal variation in the availability of sandeels in the water column; 3) to assess if the introduction of offshore windfarm structures into this environment modified these predator-prey relationships.

2. Methods

2.1 Study area and data availability

This study was conducted in the Moray Firth (NE Scotland), within three windfarm sites: Beatrice, Moray East and Moray West (Figure 1). Between 2009 and 2022, PAM data were collected using echolocation click detectors (CPODs, www.chelonia.co.uk), throughout various stages of windfarm consenting, construction and operation. A map showing the spatial and temporal pattern of these data is provided in Supplementary Material (Figure S.1). Field data collection methods are described in detail in Graham et al. (2019) and Benhemma-Le Gall et al. (2021).

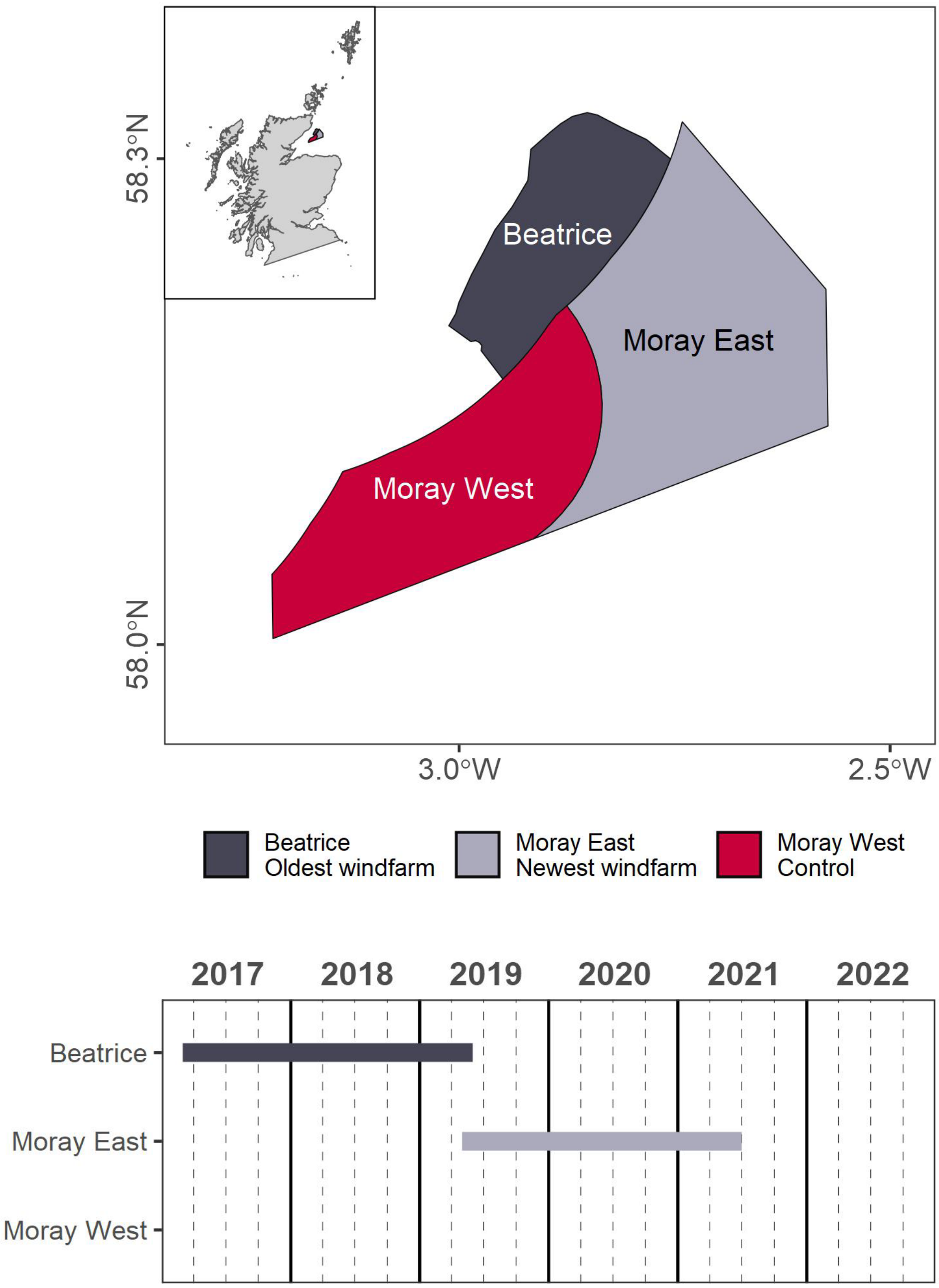

Figure 1: Map showing the location of the windfarm sites (dark grey: Beatrice Offshore windfarm, light grey: Moray East windfarm, red: Moray West windfarm), including a timeline of their construction.

Beatrice Offshore windfarm was built between March 2017 and May 2019. Moray East Offshore windfarm construction started in May 2019 and finished in September 2021. Beatrice and Moray East were fully operational in 2019 and 2021 respectively. The construction of Moray West Offshore windfarm started in October 2023, and there were no structures nor construction activities within this site during the 2022 surveys.

To address the objectives within this study, our analyses used data collected during 2009, 2010, 2011 (pre-construction years) and 2022 (a post-construction year for Beatrice and Moray East, and pre-construction year for Moray West). We therefore excluded all periods when major construction activities were carried out, as pile-driving noise can modify harbour porpoise distribution (Benhemma-Le Gall et al. 2021; Graham et al. 2019).

For objectives 1 and 3, we used data collected during July and August of 2009, 2010, 2011 and 2022. Within this period, 103 PAM deployments were made within the windfarm sites, resulting in a total of 3,982 CPOD data days (Table 1 and Figure 2). For objective 2, we used pre-construction CPOD data that were collected throughout July 2010 to October 2011. Within this period, 122 PAM deployments were made within the windfarm sites, resulting in a total of 6,529 CPOD data days (Table 2 and Figure 3).

Table 1: Summary table including the total number of CPOD locations and cumulative data days by year in each of the three windfarm sites in July and August 2009, 2010, 2011 and 2022.

	2009		**2010**		**2011**		**2022**	
	CPOD locations	Data days	CPOD locations	Data days	CPOD locations	Data days	CPOD locations	Data days
Beatrice	2	92	5	219	3	175	37	1248
Moray East	1	46	4	155	2	124	18	648
Moray West	5	238	6	266	5	288	12	523

Table 2: Summary of CPOD data within the three windfarm sites between July 2010 and October 2011, including total number of deployment locations and cumulative CPOD data days by quarter.

January-March (Q1)		**April-June (Q2)**		**July-September (Q3)**		**October-December (Q4)**	
CPOD locations	Data days	CPOD locations	Data days	CPOD locations	Data days	CPOD locations	Data days
16	1603	13	1104	17	2002	17	1820

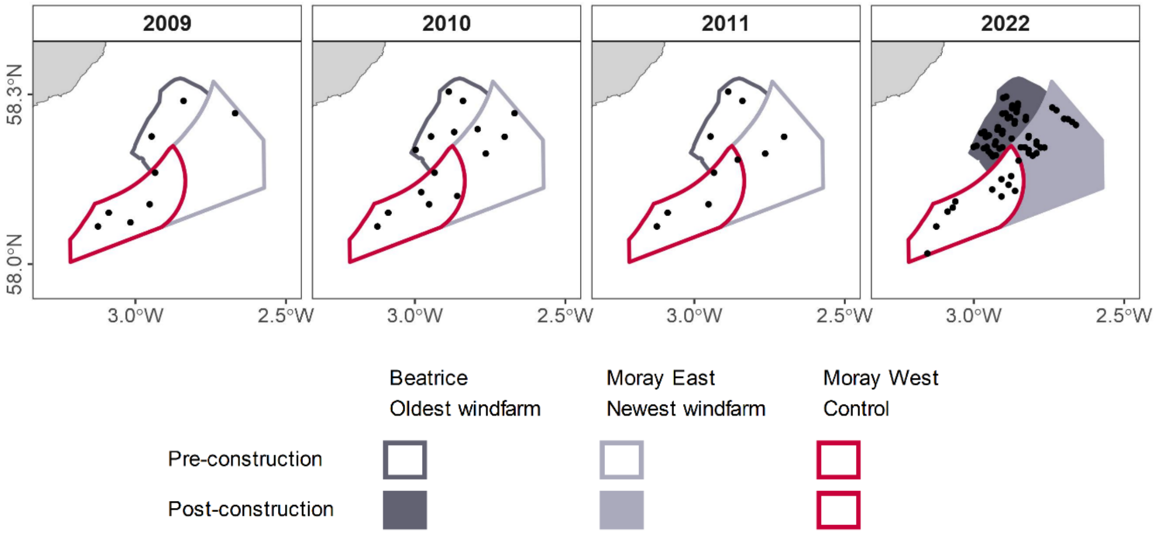

Figure 2: Locations of CPODs deployed (black dots) within the three windfarm sites (dark grey: Beatrice offshore windfarm; light grey: Moray East offshore windfarm; red: Moray West offshore windfarm) per year (2009, 2010, 2011, 2022), during July and August. The construction of Beatrice and Moray East finished in 2019 and 2021 respectively.

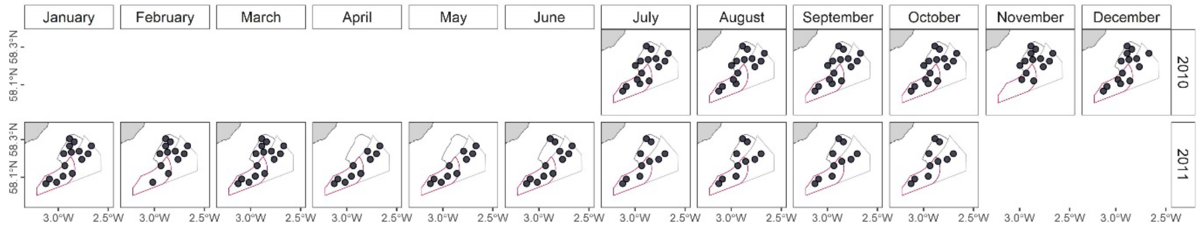

Figure 3: CPOD deployment locations (black dots) within the studied area between 2010 and 2011 divided by month. Map includes the borders of the three windfarm sites (lines).

2.2 Predator occurrence and foraging behaviour

We used CPOD data to assess the spatio-temporal variation in harbour porpoise occurrence (a proxy for distribution; see Brookes et al. 2013) and foraging behaviour. Echolocation click data were extracted from CPODs using the CPOD custom software (cpod.exe v2.044). Following the manufacturer’s guidelines only echolocation clicks classified as Narrow Band High Frequency (NBHF) of high and moderate quality by the built-in “KERNO” classifier were included in the datasets.

To save CPOD memory in noisy environments, we set a maximum number of recorded clicks (scan limit) to 4096 clicks per minute. When the scan limit is reached, CPODs stop recording for the rest of the minute and start again at the next minute. Therefore, increased ambient noise levels can impact the performance of CPODs both by decreasing their recording time and causing a masking effect. Following the methodology developed by Branstetter et al. (2018) and in line with other recent studies from this area (Fernandez-Betelu et al. 2024) we minimized false negative detections resulting from noise by discarding all hours with more than 100,000 recorded clicks and hours where the scan limit had been reached in more than 2 mins. We removed a total of 4,107 h of data (~ 2 %) from the analyses due to excessive background noise (either hours with more than 100,000 recorded clicks or hours where the scan limit had been reached in more than 2 mins).

We extracted the hourly presence/absence of porpoise echolocation click detections to estimate porpoise hourly occurrence. We then used the click detections to infer harbour porpoise foraging behaviour from the presence of echolocation buzzes (Pirotta et al. 2014). We calculated inter-click intervals (ICIs) between consecutive echolocation clicks and fitted a Gaussian mixture-model with the component distribution (k) set to three. This divided ICIs into three groups: 1) “long ICIs” which correspond to pauses between distinct click trains, 2) “regular ICIs”, ICIs within regular click trains and 3) “buzz ICIs”, click trains with a high repetition rate, which correspond to echolocation buzzes. Porpoises may use echolocation buzzes for both foraging behaviour and social communication (Clausen et al. 2011; Sørensen et al. 2018). However, in line with previous work (Benhemma-Le Gall et al. 2021; Todd et al. 2022; Williamson et al. 2017) we assumed that identified buzzes provided a proxy for foraging behaviour. Foraging positive hours were defined as those hours in which at least one echolocation click train had been labelled as a buzz (Brough et al. 2020; Pirotta et al. 2014; Trabue et al. 2022).

2.3 Prey distribution

The Langton sandeel distribution model (Langton et al. 2021) predicts sandeel probability of occurrence and density across the North Sea (250 x 250 m grid resolution), based on environmental variables that include sediment type, seabed slope, and depth (Figure 4). Here, we extracted the predicted sandeel density value from the grid cell in which each CPOD was deployed. Langton et al. (2021) model was based on survey data from the Firth of Forth, Scotland, collected between 1998 and 2003 during winter, when sandeels are expected to be buried all day (Reeves 1994). Importantly, the model provides a fixed density value per grid cell, which does not reflect either the interannual variation in regional stock size or the seasonal variability in sandeel occurrence in the water column. The extent to which this constrains inferences from different analyses that draw upon these model predictions is explored in our discussion. Sandeel density values for each CPOD location were scaled by substracting the mean value for the whole dataset and dividing them by the standard deviation.

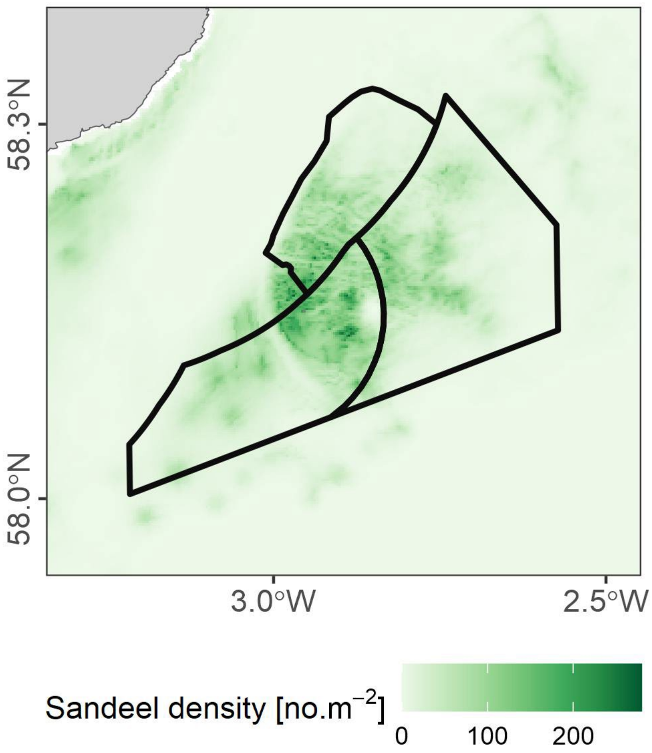

Figure 4: Predicted sandeel density (Langton et al. 2021) overlayed on the boundaries of Beatrice, Moray East and Moray West windfarm.

2.4 Objective 1: Is the spatial variation in harbour porpoise occurrence and foraging behaviour in summer related to Langton et al. (2021) predictions of sandeel density distribution?

To assess the spatial relationship between porpoise and sandeel density, we modelled the hourly presence/absence of harbour porpoise occurrence and foraging behaviour in relation to local predicted sandeel density using generalized linear mixed models (GLMMs; Bolker et al. 2009). We included deployment unique identifier and Julian day within each location as random effects to account for both a lack of temporal variation in the prey density data and any device-specific differences in detection probability. To further assess the consistency of this relationship over time, we also modelled the hourly presence/absence of harbour porpoise occurrence and foraging behaviour in relation to the interaction between predicted sandeel density and year (2009, 2010, 2011, 2022).

To ensure that samples were balanced between pre-construction and post-construction years, these analyses used data from July and August (Figure 2), which also overlaps with the months when sandeels are most likely to be predated by porpoises in this region (Santos et al. 2004).

2.5 Objective 2: Do the relationships between harbour porpoise occurrence and foraging behaviour and sandeel density change seasonally?

To assess whether relationships between porpoises and sandeels varied in line with seasonal changes in prey behaviour, which affects their availability, we modelled the hourly presence/absence of harbour porpoise occurrence and foraging behaviour in relation to the interaction between predicted sandeel density, season (as quarters; Q1: Jan-Mar, Q2: Apr-Jun, Q3: Jul-Sep, Q4: Oct-Dec) and diel cycle (day/night). We included diel cycle as an explanatory variable as there could be an important interaction with daylight when considering seasonal changes in prey availability. We included location within season as a random effect to improve model residuals. To investigate seasonal differences in more detail, we ran the same models including predicted sandeel density, diel cycle (day/night) and calendar month (Jan-Dec), instead of season (Q1/Q2/Q3/Q4), as explanatory variables in interaction. These analyses were restricted to pre-construction years when data were collected year-round between July 2010 and October 2011 (Figure 3).

2.6 Objective 3: Do relationships between harbour porpoise occurrence and foraging behaviour and sandeel density change following the installation of wind turbine foundations?

To investigate the effect of the presence of windfarm structures on the relationship between porpoises and sandeel density, we modelled the hourly presence/absence of harbour porpoise occurrence and foraging behaviour in relation to the interaction between predicted sandeel density, construction period (2009, 2010, 2011 vs 2022) and windfarm site (Beatrice, Moray East, Moray West). We included deployment unique identifier and Julian day within each location as random effects to control for any device-specific differences in detection probability and to improve the overall model residuals. As for objective 1, these analyses used data from CPOD deployments collected in July and August.

All models were fitted using generalized linear mixed-effects models (Bolker et al. 2009) with a binomial family distribution and the *probit* link function, using the R package ‘lme4’ (Bates et al. 2015). The best model was chosen based on the lowest Akaike Information Criterion (AIC; Burnham and Anderson 2002; Sakamoto et al. 1986). We performed model averaging when the difference between the lowest AIC scoring models was less than 2, to better account for parameter uncertainty and to plot confidence intervals of averaged parameter estimates (Anderson and Burnham 2004). Tukey Honestly Significant Difference tests (Tukey HSD; Tukey 1991) were conducted as a post-hoc test to identify significant differences between group means. We checked residual plots with the R package ‘DHARMa’ (Hartig 2017). All data processing and statistical analyses were performed in R v4.2.2 (R Core Team 2022).

3. Results

3.1 Objective 1: Is the spatial variation in harbour porpoise occurrence and foraging behaviour in summer related to Langton et al. (2021) predictions of sandeel distribution?

Harbour porpoises were detected every day for a median of 13 hours per day.

During July and August, the probability of both harbour porpoise occurrence (Figure 5A) and foraging behaviour (Figure 5B) increased with increasing predicted sandeel density. This positive relationship was found in all years of the study (Supplementary Material Fig. S.2).

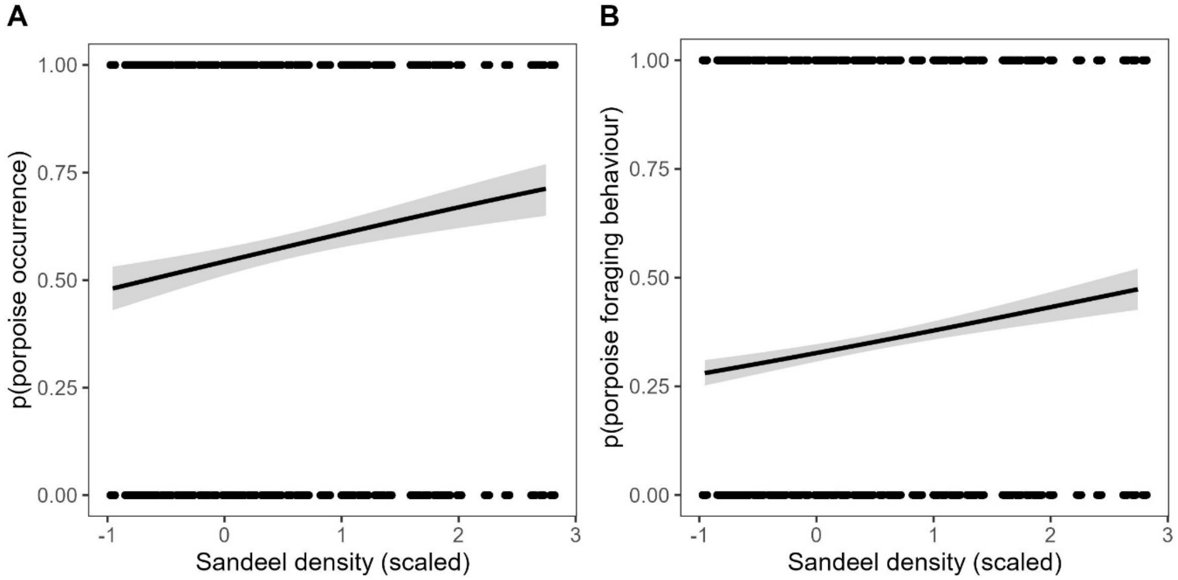

Figure 5: Predicted harbour porpoise occurrence (A) and foraging behaviour (B) (black line) in relation to predicted sandeel density during July and August. Shaded areas are the 95% confidence intervals for the fixed effects only. Raw data points, representing the hourly presence (1) or absence (0) of harbour porpoises in relation to predicted sandeel density, are denoted by black dots. Predictions extracted from the models with the lowest AIC (Model 1 for both occurrence and foraging behaviour, Supplementary Material Table S.1).

3.2 Objective 2: Do the relationships between harbour porpoise occurrence and foraging behaviour and predicted sandeel density change seasonally?

Harbour porpoise occurrence was best explained by the interaction between predicted sandeel density, diel cycle, and season (see Supplementary Material Table S.1 for model selection tables). The relationship between harbour porpoise occurrence and predicted sandeel density exhibited seasonal variation (Figure 6A). In Q2 and Q3 (April to September), porpoise occurrence increased with predicted sandeel density both during the day and at night. However, during Q1 and Q4 (October to March), no significant increase in porpoise occurrence was observed in relation to predicted sandeel density, during either the day or at night. Similar results were obtained when we used month instead of season as an explanatory variable (Supplementary Material Figure S.3).

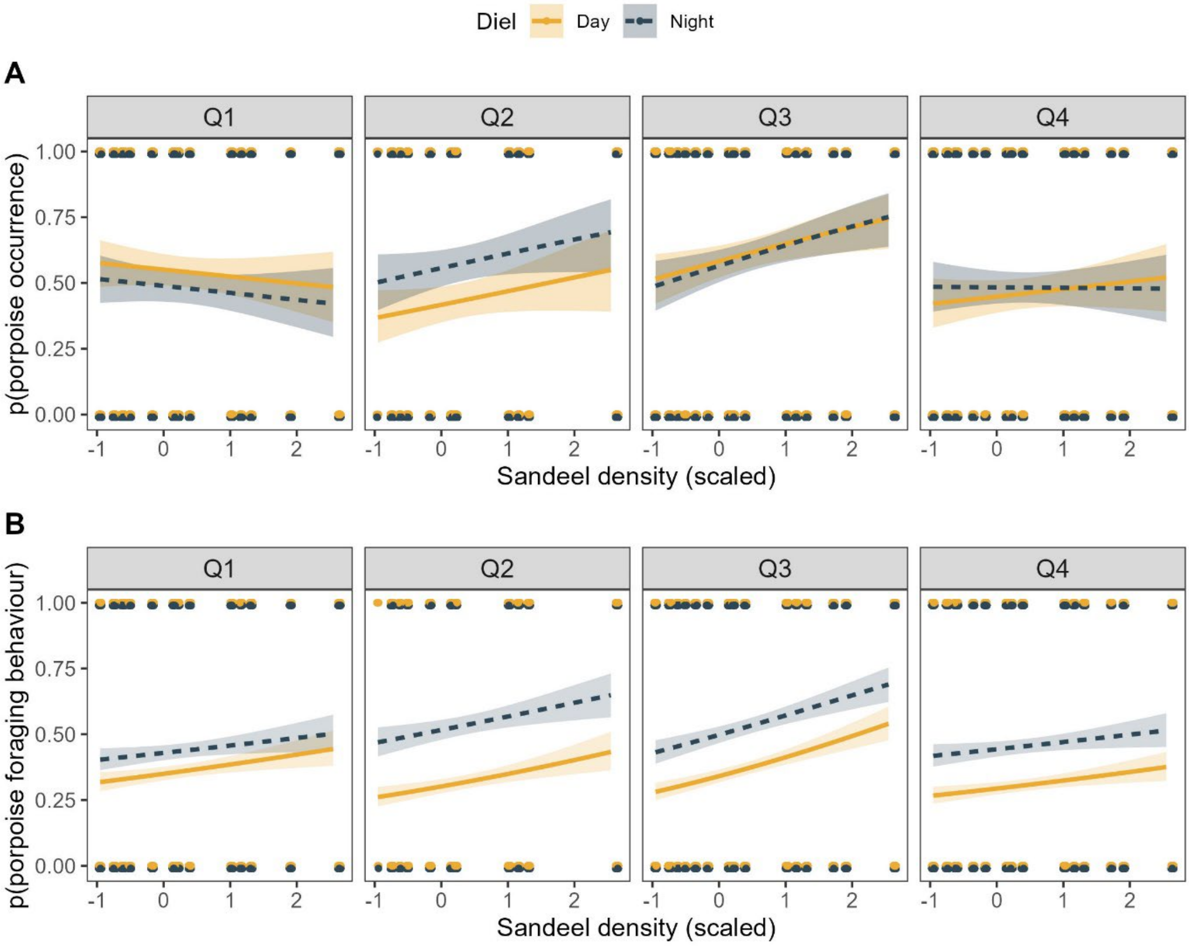

Figure 6: Predicted harbour porpoise occurrence (A) and foraging behaviour (B) in relation to predicted sandeel density by season (Q1: Jan-Mar, Q2: Apr-Jun, Q3: Jul-Sep, Q4: Oct-Dec) and diel cycle (day: yellow continuous line; night: dark blue dashed line) between July 2010 and December 2011. Shaded areas are the 95% confidence intervals for the fixed effects only. Raw data points, representing the hourly presence (1) or absence (0) of harbour porpoises in relation to predicted sandeel density, are denoted by dots, coloured in blue for night and yellow for day. Predictions extracted from the models with the lowest AIC (Model 1 for both occurrence and foraging behaviour, Supplementary Material Table S.1).

Harbour porpoise foraging behaviour was best explained by the interactions between predicted sandeel density and season, diel cycle and sandeel density and diel cycle and season (Supplementary Material Table S.1). Two models with ΔAIC < 2 were averaged (the confidence intervals of the averaged estimates are available in Supplementary Material Figure S.6). Porpoise foraging behaviour increased with predicted sandeel density both during the day and at night throughout the whole year (from Q1 to Q4). In Q1 and Q4 (October to March), the increase in foraging behaviour with predicted sandeel density was less apparent (Figure 6B). Overall, the probability of foraging behaviour was higher at night than during the day during all quarters. Like porpoise occurrence, similar results were obtained using month instead of season as an explanatory variable (Supplementary Material Figure S.4).

3.3 Objective 3: Do relationships between harbour porpoise occurrence and foraging behaviour and predicted sandeel density change following the installation of wind turbine foundations?

Harbour porpoise occurrence was best explained by the interactions between construction period and predicted sandeel density, construction period and windfarm site, and predicted sandeel density and windfarm site (Supplementary Material Table S.1).

During the pre-construction period (2009-2010-2011), the probability of harbour porpoise occurrence increased with predicted sandeel density in all windfarm sites (Figure 7A). However, in the 2022 post-construction dataset, the results differed across the three windfarm sites. In Beatrice, the oldest windfarm, there was a positive increase in porpoise occurrence with predicted sandeel density, but the relationship was less apparent than during the pre-construction period. In Moray East, the newest windfarm (< 2 years old), the relationship became non-significant or slightly negative. In Moray West, the control site, the relationship between porpoise occurrence and predicted sandeel density remained positive.

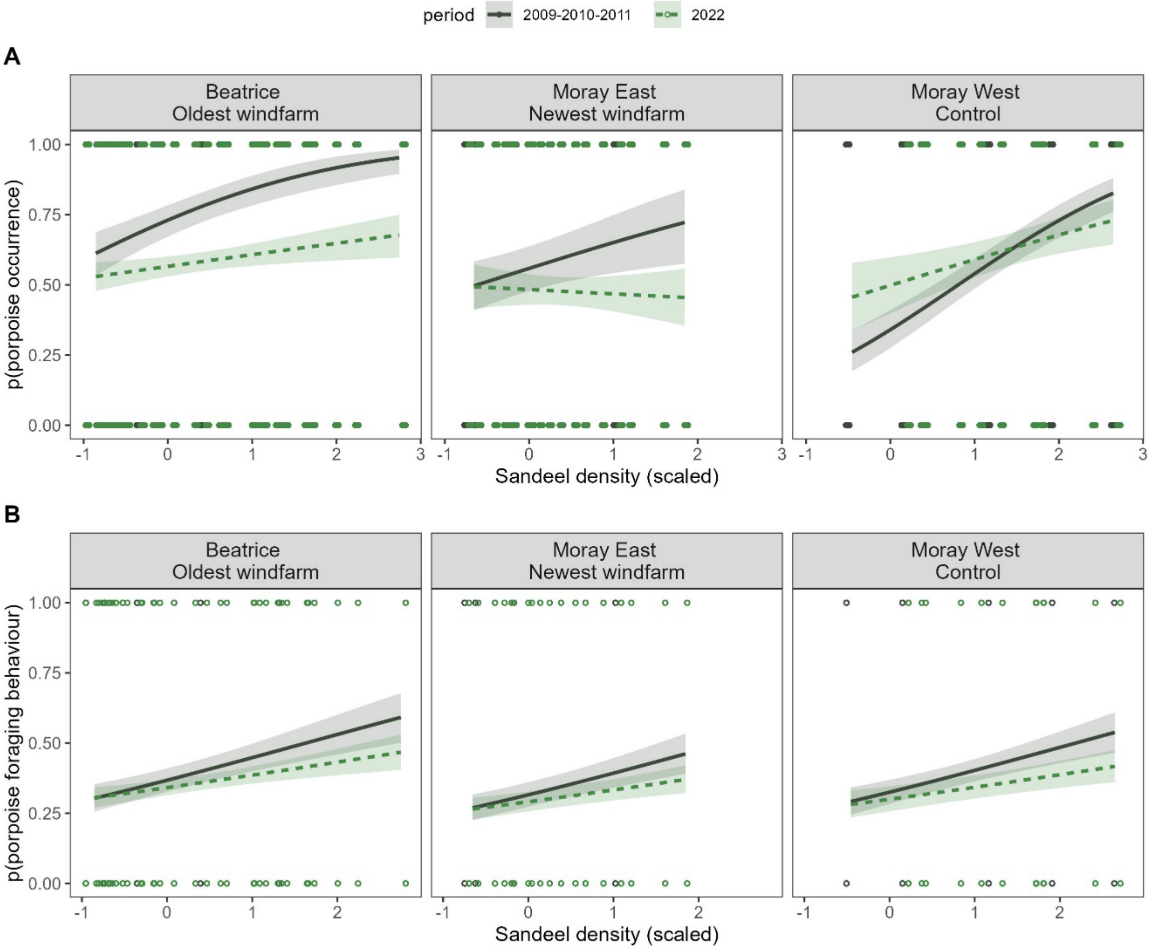

Figure 7: Predicted harbour porpoise occurrence (A) and foraging behaviour (B) in relation to predicted sandeel density by construction period (pre-construction, 2009-2010-2011: dark grey dashed line; post-construction, 2022: green continuous line) and windfarm site during July and August. Shaded areas are the 95% confidence intervals for the fixed effects only. Raw data points, representing the hourly presence (1) or absence (0) of harbour porpoises in relation to predicted sandeel density, are denoted

by dots. Predictions extracted from the models with the lowest AIC (Model 1 for both occurrence and foraging behaviour, Supplementary Material Table S.1).

Harbour porpoise foraging behaviour was best explained by the interaction between predicted sandeel density and construction period (Supplementary Material Table S.1). Two models with ΔAIC < 2 were averaged (the confidence intervals of the averaged estimates are available in Supplementary Material Figure S.7). The probability of foraging behaviour increased with predicted sandeel density during both pre- and post-construction periods (Figure 7B).

4. Discussion

This study showed that during the summer (July and August) there was a positive relationship between harbour porpoises and the predicted lesser sandeel densities from the model developed by Langton et al. (2021). We demonstrated that predicted buried sandeel density influenced both the occurrence and foraging behaviour of porpoises, highlighting the potential for incorporating these new broad-scale data on sandeel density into harbour porpoise distribution models. However, the relationship was not consistent throughout the year, and followed the seasonal pattern of sandeel presence in the water column. Interestingly, our findings suggest that the presence of offshore windfarm structures may have weakened the relationship between porpoises and sandeel density.

This positive relationship between predicted sandeel density and both harbour porpoise occurrence and foraging behaviour was consistent during July and August in all four study years (Figure 5). Previous work in the same study area investigated the relationship between harbour porpoise detections and seabed characteristics, finding high porpoise detections in sandy shallow areas (Williamson et al. 2017), where the windfarms were built. However, Williamson et al. (2017) also found localised differences in detections which could not be explained by sediment type or depth, and hypothesized that this pattern could be driven by prey distribution. Here, we showed that increases in harbour porpoise occurrence and foraging behaviour were related to predicted sandeel density, providing evidence for Williamson et al. (2017) hypothesis. Based on porpoise stomach contents, fisheries surveys and telemetry data, Ransijn et al. (2021) also found a positive relationship between harbour porpoise and sandeel distribution in the southern North Sea. Similarly, information on sandeel fishing grounds was included as a predictor of modelled porpoise distribution using sightings from visual surveys in the central and southern North Sea (Gilles et al. 2016). By applying these different methodologies, our results and those from Ransijn et al. (2021) and Gilles et al. (2016) highlight the importance of sandeels for harbour porpoise across the entire North Sea.

Sandeels follow a seasonal cycle where they spend the winter months buried in the sand and the summer months foraging in the water column during the day (Henriksen et al. 2021; Reebs 2002; Winslade 1974). Given that this behaviour may influence sandeel availability for porpoises, we tested whether association between porpoises and predicted sandeel densities followed similar seasonal and diel patterns. We found that the positive relationship between porpoise occurrence and foraging behaviour with predicted sandeel density was only present between April and September (Q2 and Q3; Figure 6). These findings align with studies investigating the stomach content of harbour porpoises in Scottish waters, which also revealed seasonal variation in the importance of sandeels, reaching a peak between April and September (also Q2 and Q3; Santos et al. 2004). Coupled with Santos et al. (2004)'s findings, our results suggest that sandeels may not be accessible to porpoises when they are buried in the sand. In contrast, in Icelandic waters, sandeels were found in the stomach content of harbour porpoises throughout the winter (Víkingsson et al. 2003). Harbour porpoises are opportunistic foragers, thus the seasonal differences in foraging on sandeels may also be due to differences in the availability of alternative prey (Santos et al. 2004). Methodological limitations may also have influenced our ability to detect harbour porpoises if they altered their foraging behaviour in response to those seasonal changes in sandeel behaviour. Harbour porpoise echolocation clicks, and foraging buzzes are highly directional (Koblitz et al. 2012; Wisniewska et al. 2015). Therefore, if porpoises were foraging on buried sandeels, and directing their clicks towards the seabed, this could have affected the detection probability of CPODs that were deployed three meters above the seabed.

Unlike the seasonal cycle, the diel patterns of porpoises did not align with expected patterns of burying and schooling behaviour of sandeels. Our analyses revealed that porpoise occurrence and foraging activity increased with predicted sandeel density both during the day and at night (Figure 6). Notably, from April to June, porpoise occurrence was higher at night than during the day. Similarly, from April to December, porpoise foraging activity was also higher at night. Since sandeels remain buried during the night, sandeel density alone cannot fully explain the observed diel patterns of porpoises. A number of fish species predate on sandeels, some of them during the night, and their distribution is also likely to correlate with those of sandeels (Engelhard et al. 2008). One explanation for the positive relationship between porpoises and sandeel density at night is that porpoises are foraging on predatory fishes that are also attracted to sandeel habitat. Alternatively, the simplicity of the methodology used to categorize the diel cycle into two groups (day/night) might have misclassified crepuscular behaviour as either day or night, thus leading to a misinterpretation of porpoise and sandeel diel patterns. Future work investigating the diel behaviour of these animals may need to take this into consideration.

Numerous PAM studies across the North Sea have detected higher nocturnal foraging activity of harbour porpoises (Carlstrom 2005; Holdman et al. 2019; Nuuttila et al. 2018; Schaffeld et al. 2016; Williamson et al. 2017; Wisniewska et al. 2016). Increased echolocation activity during the night has also been observed around man-made structures (Brandt et al. 2014; Fernandez-Betelu et al. 2022; Todd et al. 2009; Todd et al. 2022). All these studies suggested that changes in prey abundance or behaviour throughout the day and night could be driving the diel behaviour of porpoises. However, studies with captive porpoises that were exclusively fed during the day still detected an increase in echolocation detections during the night, suggesting that the diel behaviour may not solely be driven by prey but could also be influenced by changes in light availability (Osiecka et al. 2020). Conversely, Linnenschmidt et al.

(2013) reported diel patterns in acoustic behaviour in only one out of three tagged harbour porpoises. Uncertainties over the drivers of diel changes in harbour porpoise acoustic behaviour, and the extent to which changes in behaviour may affect detection probability (Macaulay et al. 2023) prevent us making definitive conclusions on the relationship between sandeel density and porpoises throughout the diel cycle in this area.

Our analyses also suggest that the relationship between porpoises and sandeels may be moderated by the introduction of windfarm structures. Prior to windfarm construction (2009-11), the probability of harbour porpoise occurrence increased with sandeel density across the three windfarm sites. However, in 2022, after the construction of two of the three windfarms, the positive relationship was weaker at one of the windfarm sites and absent at the second (Figure 7). Definitive conclusions are constrained as there was only a single year of post-construction data. Nevertheless, observed differences between the pre-construction (2009-2010-2011) and post-construction (2022) years indicate that there may be changes in prey species distribution and/or composition associated with the presence of the wind turbine foundations. It is recognised that subsea structures may modify local species composition and relative fish abundance (Claisse et al. 2014; Degraer et al. 2020; Methratta and Dardick 2019), leading to increased densities of both benthic and pelagic fish (Coates et al. 2014; Lefaible et al. 2018). Furthermore, early results from related studies within PrePARED suggest that the abundance of gadoids and flatfish is higher within constructed windfarms compared to reference areas (Bicknell & Witt Unpublished data). Such changes in prey populations may modify the positive relationship between porpoise occurrence and sandeel density observed in the pre-construction data. For example, increased abundance of some prey species due to the presence of structures may result in porpoises switching to alternative prey where these are more abundant within windfarm sites. Furthermore, food web models estimate that predatory fish such as saithe, whiting and mackerel have an important top-down effect on forage fish such as sandeels (Engelhard et al. 2014). If the relative abundance of fish that are sandeel predators increased inside the windfarm sites, it may have caused an increase in the interspecific competition for this prey species. Alternatively, the installation of turbines may have altered the sandy habitat required by sandeels, potentially leading to local decreases in sandeel abundance. However, previous work at Horns Rev I in Denmark found no decrease in sandeel density after construction, instead highlighting interannual fluctuations in sandeel density within both impact and control areas (van Deurs et al. 2012). Similarly, post-construction monitoring of sandeels at the Beatrice Windfarm found no evidence of negative impacts of construction, with observed densities higher than during baseline surveys (Beatrice Offshore Windfarm Ltd. 2021). This also reflects the likely importance of larger scale interannual variation in stock size in predator-prey relationships.

4.1 Conclusions and next steps

Overall, our study provides evidence that the sandeel model developed by Langton et al. (2021) can inform models used to predict spatial variation in the occurrence and foraging behaviour of harbour porpoises, at least during summer months. At the same time, our results highlight limitations that need to be considered when using this approach. First, the Langton et al. (2021) model provides relative density values that do not reflect known interannual variation in the absolute abundance of sandeel stocks (ICES 2023) or seasonal burying behaviour of sandeels (Henriksen et al. 2021; Reebs 2002; Winslade 1974). Second, the model is based on fixed environmental variables (such as sediment type and slope) and does not consider potential changes in those variables caused by the installation of man-made structures, such as windfarms. Finally, the Langton et al. (2021) model predicts spatial variation in sandeel densities within the sediment, resulting in additional complexities when linking these prey fields to the behaviour of predators that are thought to forage on sandeels within the water column.

Thus, while the Langton et al. (2021) model appears well-suited for modelling predator occurrence, additional investigations are required to confirm some of our key results and to address these limitations. We suggest that ongoing work within the PrePARED project could be used to support these investigations in the following ways:

1) Additional post-construction CPOD data could be used to further investigate the effect of the presence of wind turbines on the relationship between sandeels and porpoises. Our results suggest an effect of structure presence (Figure 7); however, our analyses were limited to just one year of post-construction data. Therefore, we could not attribute these findings to either the presence of the windfarm or the natural variability in sandeel stocks, which could also affect the relationship between sandeels and porpoises. To prevent us from suggesting misleading impacts caused by wind turbines, we suggest analysing PAM data that will become available from late August 2023 (before the start of construction at Moray West in October 2023), which will extend our post-construction dataset to two years.

2) Data collected during PrePARED fisheries acoustic surveys could be used to compare the predicted sandeel densities in the sediment from Langton et al. (2021) model to the spatial distribution of sandeels in the water column. These comparisons could be based on the acoustic surveys performed in 2022 and 2023, with potential for additional data collection in 2024.

3) Porpoise dose-response curves for pile driving noise have been based on data collected during the Beatrice piling campaign (Graham et al. 2019). However, it is recognised that responses to disturbance are likely to be context dependent (Ellison et al. 2012) and, for example, may vary in relation to local prey abundance. CPOD data collected during the Moray West piling campaign could be used to generate context-specific dose response curves by incorporating local predicted sandeel density as a co-variate in the analyses.

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Supplementary Material

Figure S.1: CPODs deployed between 2009 and 2022 within the three windfarm sites divided by year and month.

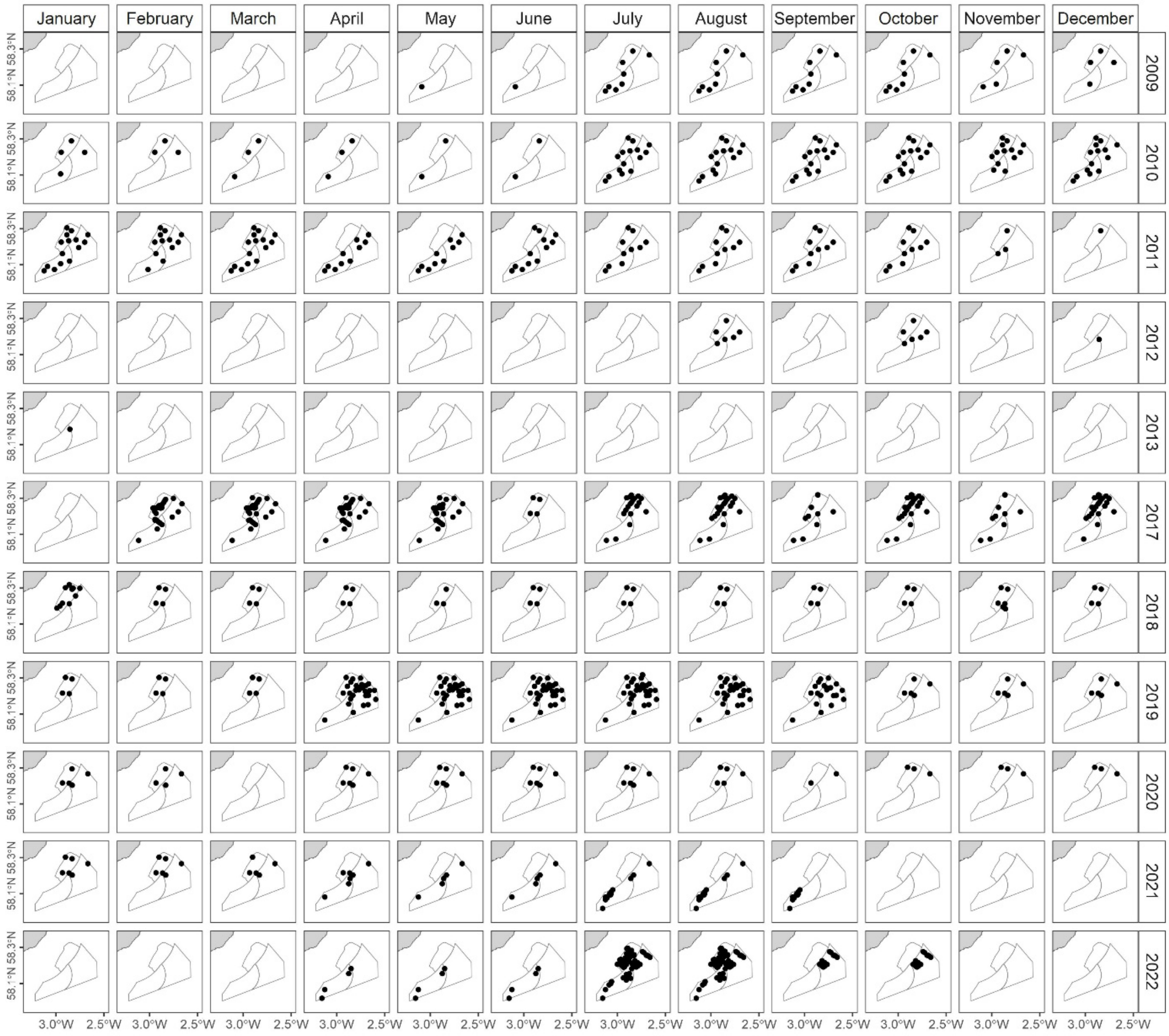


Figure S.2: Predicted harbour porpoise occurrence (A) and foraging behaviour (B) in relation to the interaction between sandeel density and year (2009, 2010, 2011 and 2022) in July and August. Shaded areas are the 95% confidence intervals for the fixed effects only. Pairwise comparisons did not reveal significant differences in the probability of porpoise occurrence between years (Tukey HSD $p > 0.05$ for all comparisons). For the probability of porpoise foraging behaviour, pairwise comparisons revealed significant differences between 2009 and all other years (Tukey HSD < 0.01), while all remaining comparisons did not yield significant results (Tukey HSD > 0.05 for all remaining comparisons).

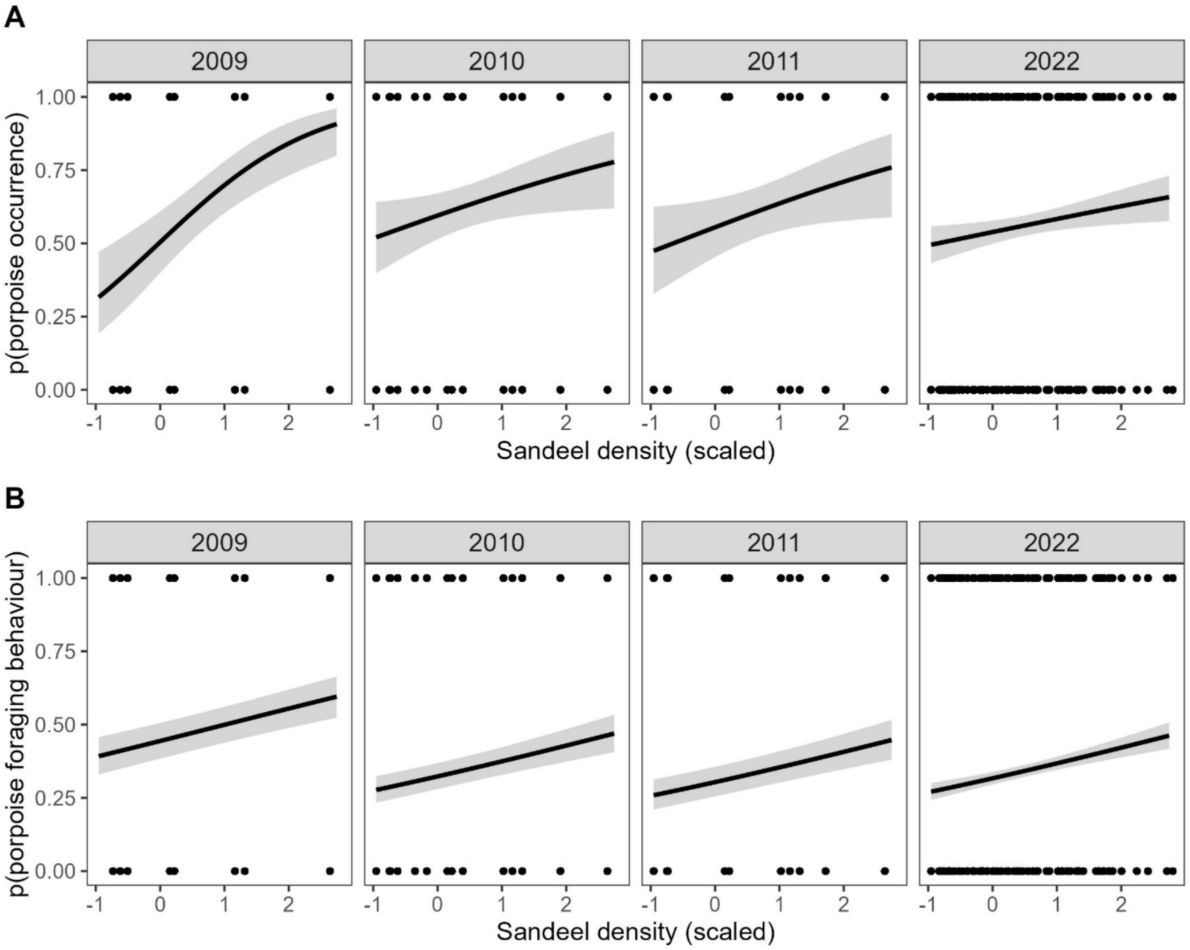
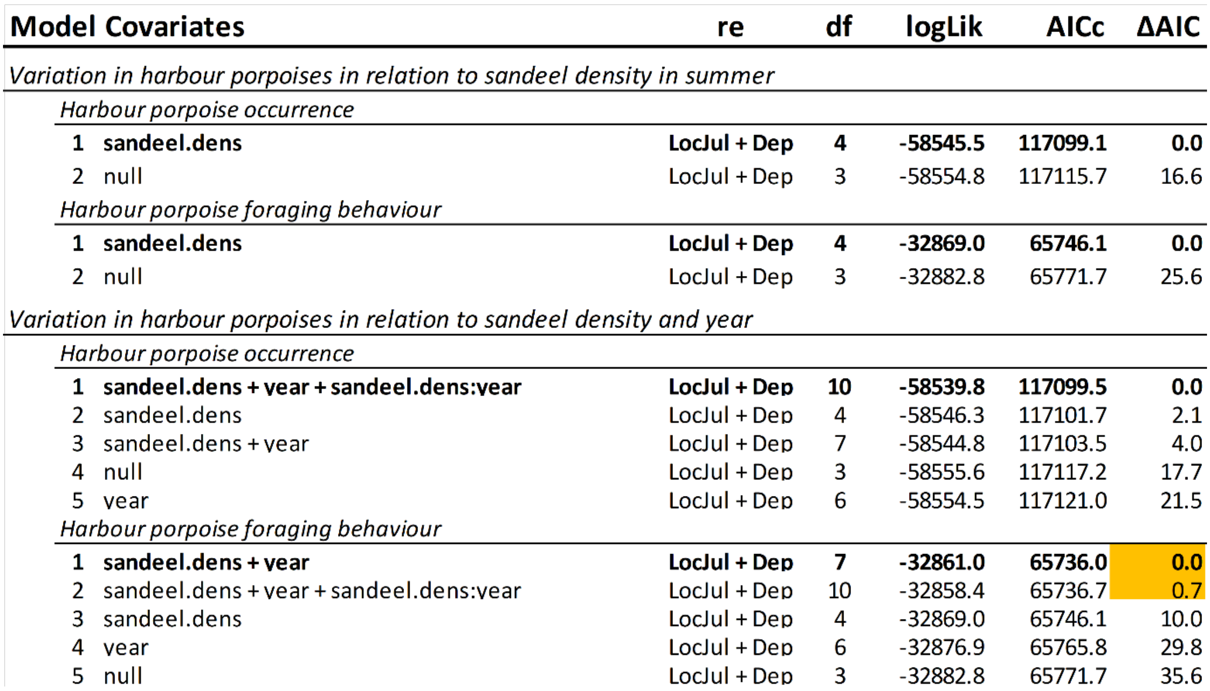


Table S.1: Model selection table for all the generalised linear models performed in this study (6 best supported models for each hypothesis) based on AIC. Table headings refer to: Covariates (different combination of explanatory variables and their interactions for each model; “+“ refers to additive and “:” to the interaction), df (degrees of freedom), logLik (log-likelihood), AICc (second-order Akaike Information Criterion) and ΔAIC (difference in AIC score between the best model and the model being compared). List of covariates includes: sandeel.dens (sandeel density scaled), year (2009, 2010, 2011, 2022), diel (day/night), season (quarters: Q1, Q2, Q3, Q4), month (from January to December), period (pre-/post-construction) and windfarm (Beatrice, Moray East, Moray West). Random effects column includes: LocJul (julian day within location), Dep (deployment unique identifier) and LocSeas (location within season).

Models that were averaged are highlighted in yellow (see Supplementary Material Figures S.5, S.6 and S.7).



	Model Covariates	**re**	**df**	**logLik**	**AICc**	**ΔAIC**
Variation in harbour porpoises in relation to sandeel density in summer						
Harbour porpoise occurrence						
1	**sandeel.dens**	**LocJul + Dep**	**4**	**-58545.5**	**117099.1**	**0.0**
2	null	LocJul + Dep	3	-58554.8	117115.7	16.6
Harbour porpoise foraging behaviour						
1	**sandeel.dens**	**LocJul + Dep**	**4**	**-32869.0**	**65746.1**	**0.0**
2	null	LocJul + Dep	3	-32882.8	65771.7	25.6
Variation in harbour porpoises in relation to sandeel density and year						
Harbour porpoise occurrence						
1	**sandeel.dens + year + sandeel.dens:year**	**LocJul + Dep**	**10**	**-58539.8**	**117099.5**	**0.0**
2	sandeel.dens	LocJul + Dep	4	-58546.3	117101.7	2.1
3	sandeel.dens + year	LocJul + Dep	7	-58544.8	117103.5	4.0
4	null	LocJul + Dep	3	-58555.6	117117.2	17.7
5	year	LocJul + Dep	6	-58554.5	117121.0	21.5
Harbour porpoise foraging behaviour						
1	**sandeel.dens + year**	**LocJul + Dep**	**7**	**-32861.0**	**65736.0**	**0.0**
2	sandeel.dens + year + sandeel.dens:year	LocJul + Dep	10	-32858.4	65736.7	0.7
3	sandeel.dens	LocJul + Dep	4	-32869.0	65746.1	10.0
4	year	LocJul + Dep	6	-32876.9	65765.8	29.8
5	null	LocJul + Dep	3	-32882.8	65771.7	35.6

Model Covariates		re	df	logLik	AICc	ΔAIC
Relationship between harbour porpoises and sandeel density across the seasonal and diel cycles						
Harbour porpoise occurrence						
1	**diel + sandeel.dens + season + diel:sandeel.dens + diel:season + sandeel.dens:season + diel:sandeel.dens:season**	**LocSeas**	**17**	-100670.9	**201375.7**	**0.0**
2	diel + sandeel.dens + season + diel:sandeel.dens + diel:season + sandeel.dens:season	LocSeas	14	-100690.5	201409.0	33.2
3	diel + sandeel.dens + season + diel:sandeel.dens + diel:season	LocSeas	11	-100693.8	201409.5	33.8
4	diel + sandeel.dens + season + diel:season + sandeel.dens:season	LocSeas	13	-100692.3	201410.5	34.8
5	diel + sandeel.dens + season + diel:season	LocSeas	10	-100695.6	201411.2	35.5
6	diel + season + diel:season	LocSeas	9	-100697.0	201412.1	36.3
Harbour porpoise foraging behaviour						
1	**diel + sandeel.dens + season + diel:sandeel.dens + diel:season + sandeel.dens:season**	**LocSeas**	**14**	**-51789.0**	**103606.0**	**0.0**
2	diel + sandeel.dens + season + diel:sandeel.dens + diel:season	LocSeas	11	-51792.1	103606.3	0.3
3	diel + sandeel.dens + season + diel:sandeel.dens + diel:season + sandeel.dens:season + diel:sandeel.dens:season	LocSeas	17	-51787.6	103609.2	3.2
4	diel + sandeel.dens + season + diel:season + sandeel.dens:season	LocSeas	13	-51794.8	103615.7	9.7
5	diel + sandeel.dens + season + diel:season	LocSeas	10	-51798.4	103616.9	10.9
6	diel + season + diel:season	LocSeas	9	-51814.8	103647.6	41.7
Relationship between harbour porpoises and sandeel density across the diel cycle per month						
Harbour porpoise occurrence						
1	**diel + sandeel.dens + month + diel:month + diel:sandeel.dens + month:sandeel.dens + diel:month:sandeel.dens**	**Dep**	**49**	**-99775.9**	**199649.8**	**0.0**
2	diel + month + sandeel.dens + diel:month + month:sandeel.dens	Dep	37	-99848.3	199770.7	120.9
3	diel + month + sandeel.dens + diel:month + diel:sandeel.dens + month:sandeel.dens	Dep	38	-99848.2	199772.5	122.7
4	diel + month + sandeel.dens + diel:month + diel:sandeel.dens	Dep	27	-100061.0	200176.0	526.2
5	diel + month + sandeel.dens + diel:month	Dep	26	-100065.3	200182.6	532.8
6	diel + month + diel:month	Dep	25	-100066.4	200182.9	533.1
Harbour porpoise foraging behaviour						
1	**diel + sandeel.dens + month + diel:month + diel:sandeel.dens + month:sandeel.dens + diel:month:sandeel.dens**	**Dep**	**49**	**-51457.7**	**103013.4**	**0.0**
2	diel + sandeel.dens + month + diel:month + diel:sandeel.dens + month:sandeel.dens	Dep	38	-51471.0	103018.1	4.7
3	diel + sandeel.dens + month + diel:month + month:sandeel.dens	Dep	37	-51477.4	103028.8	15.4
4	diel + sandeel.dens + month + diel:month + diel:sandeel.dens	Dep	27	-51520.4	103094.9	81.5
5	diel + sandeel.dens + month + diel:month	Dep	26	-51533.0	103118.0	104.6
6	diel + month + diel:month	Dep	25	-51544.5	103139.0	125.6

	Model Covariates	re	df	logLik	AICc	ΔAIC
Relationship between harbour porpoises and sandeel density linked to the installation of wind turbines						
Harbour porpoise occurrence						
1	**period + sandeel.dens + windfarm + period:sandeel.dens + period:windfarm + sandeel.dens:windfarm**	**LocJul + Dep**	**12**	**-58512.9**	**117049.9**	**0.0**
2	period + sandeel.dens + windfarm + period:sandeel.dens + period:windfarm + sandeel.dens:windfarm + period:sandeel.dens:windfarm	LocJul + Dep	14	-58512.0	117052.0	2.1
3	period + sandeel.dens + windfarm + period:sandeel.dens + period:windfarm	LocJul + Dep	10	-58516.6	117053.3	3.4
4	period + sandeel.dens + windfarm + period:windfarm + sandeel.dens:windfarm	LocJul + Dep	11	-58520.2	117062.4	12.5
5	period + sandeel.dens + windfarm + sandeel.dens:windfarm	LocJul + Dep	9	-58525.5	117069.0	19.1
6	period + sandeel.dens + windfarm + period:sandeel.dens + sandeel.dens:windfarm	LocJul + Dep	10	-58524.6	117069.1	19.2
Harbour porpoise foraging behaviour						
1	**sandeel.dens + windfarm + period + period:sandeel.dens**	**LocJul + Dep**	**8**	**-32862.9**	**65741.8**	**0.0**
2	period + sandeel.dens + windfarm	LocJul + Dep	7	-32864.5	65743.1	1.3
3	period + sandeel.dens + windfarm + sandeel.dens:windfarm	LocJul + Dep	9	-32862.9	65743.8	2.0
4	period + sandeel.dens + windfarm + period: sandeel.dens + sandeel.dens:windfarm	LocJul + Dep	10	-32862.0	65743.9	2.1
5	period + sandeel.dens + windfarm + period: sandeel.dens + period:windfarm	LocJul + Dep	10	-32862.0	65744.0	2.2
6	period + sandeel.dens + period: sandeel.dens	LocJul + Dep	6	-32866.2	65744.3	2.5

Figure S.3: Predicted harbour porpoise occurrence in relation to sandeel density by month (Jan-Dec) and diel cycle (day: yellow continuous line; night: blue dashed line) between July 2010 and December 2011. Shaded areas are the 95% confidence intervals for the fixed effects only. Predictions extracted from the model with the lowest AIC (Model 1, Supplementary Material Table S.1).

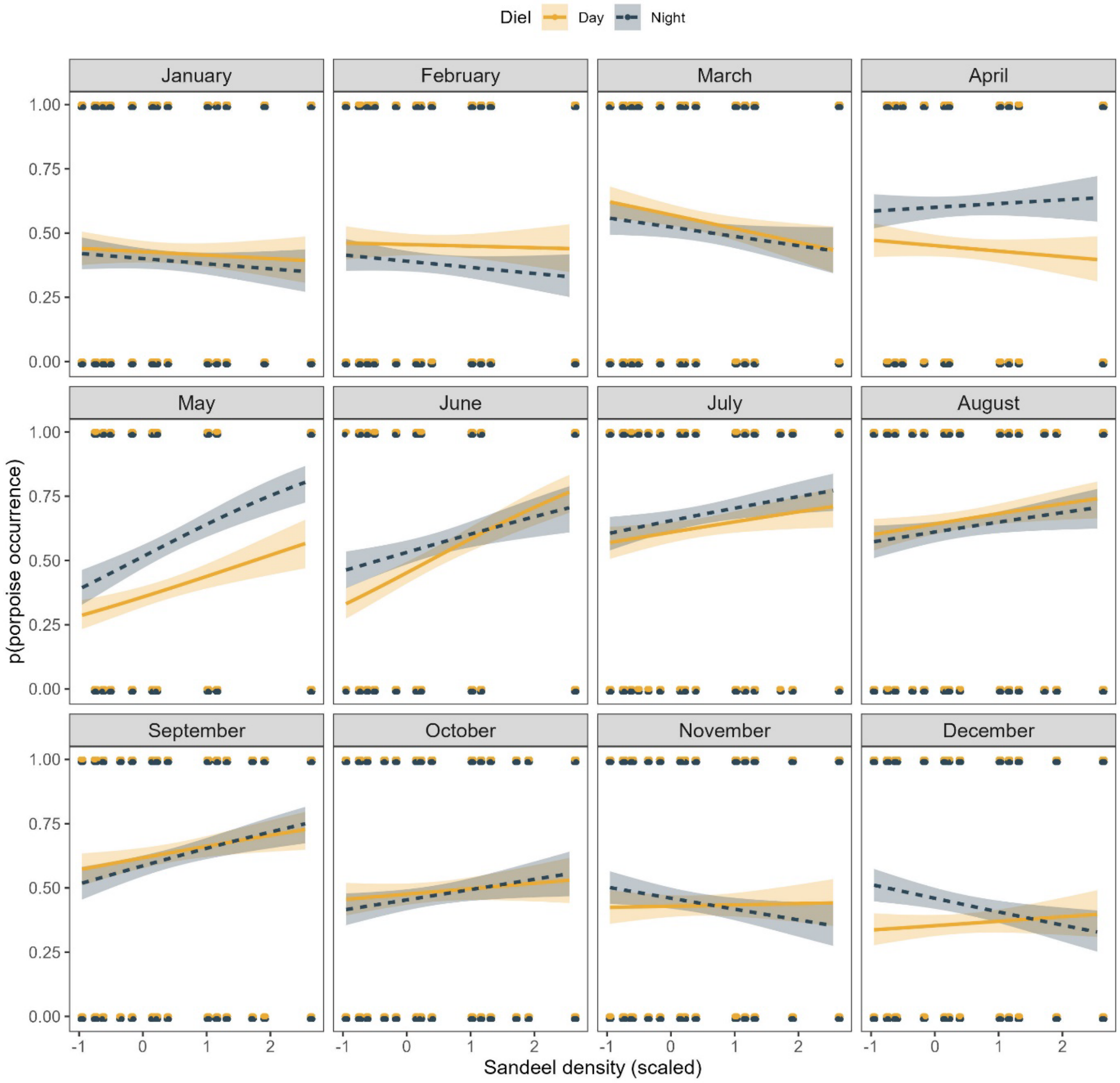


Figure S.4: Predicted harbour porpoise foraging behaviour in relation to sandeel density by month (Jan-Dec) and diel cycle (day: yellow continuous line; night: blue dashed line) between July 2010 and December 2011. Shaded areas are the 95% confidence intervals for the fixed effects only. Predictions extracted from the model with the lowest AIC (Model 1, Supplementary Material Table S.1).

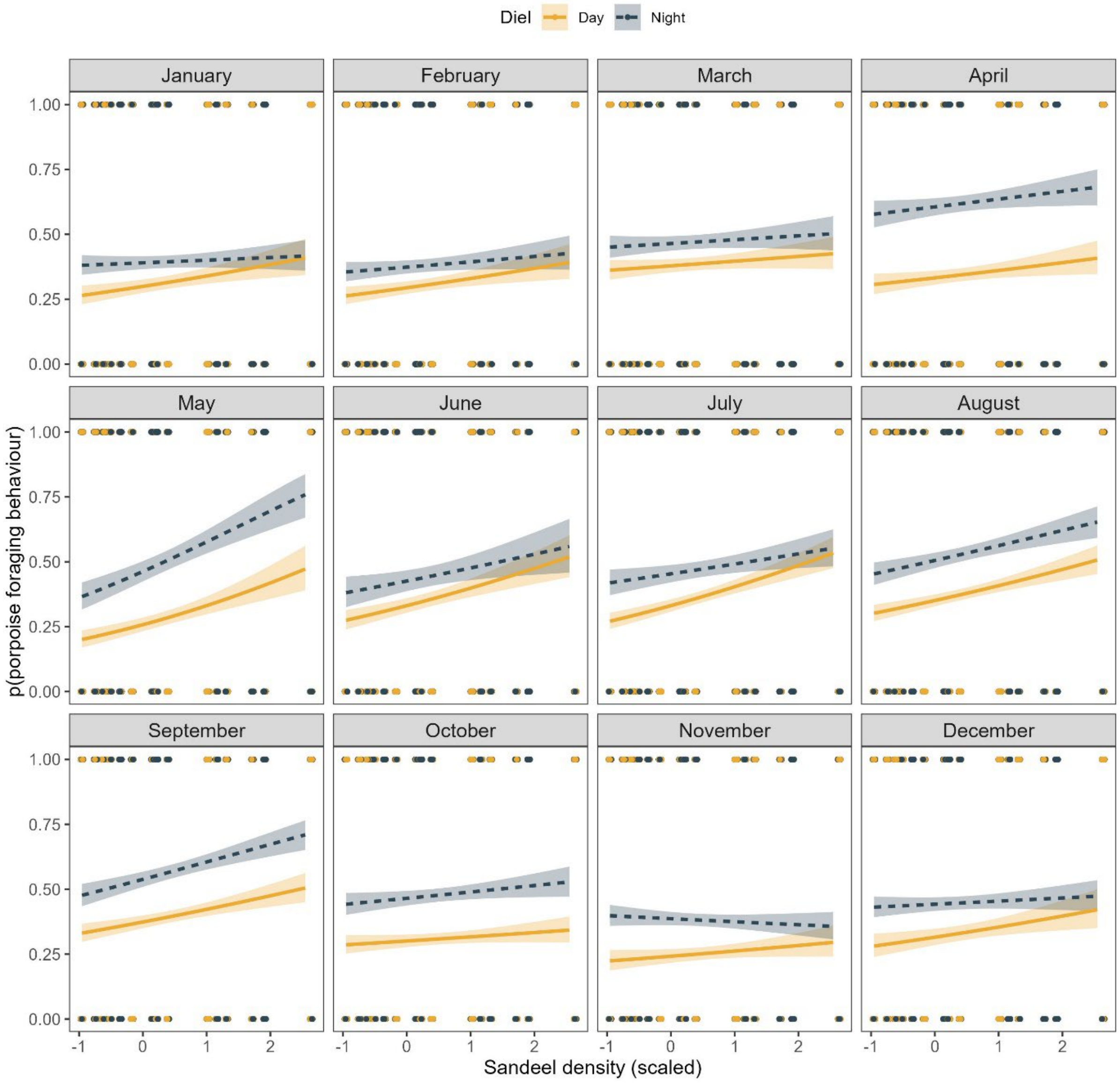


Figure S.5: Model-averaged confidence intervals (95% CI) estimated from Models 1 and 2 (Supplementary Material Table S.1) assessing the probability of harbour porpoise foraging activity in relation to sandeel density and year.

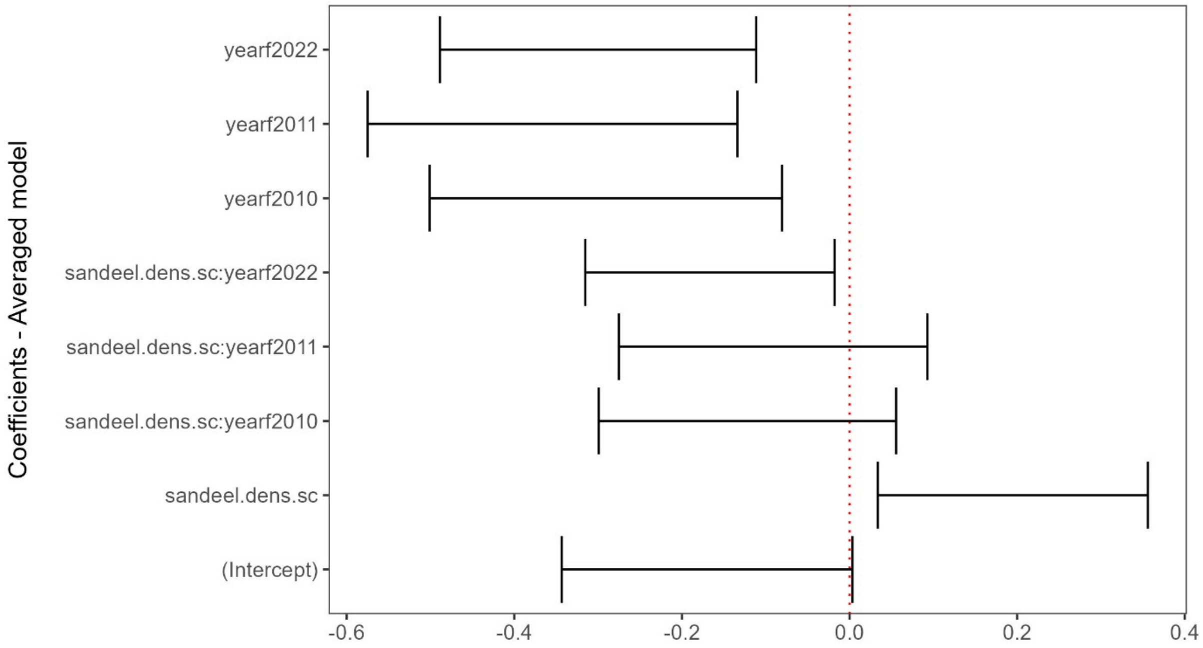


Figure S.6: Model-averaged confidence intervals (95% CI) estimated from Models 1 and 2 (Supplementary Material Table S.1) assessing the probability of harbour porpoise foraging behaviour across the seasonal and diel cycles.

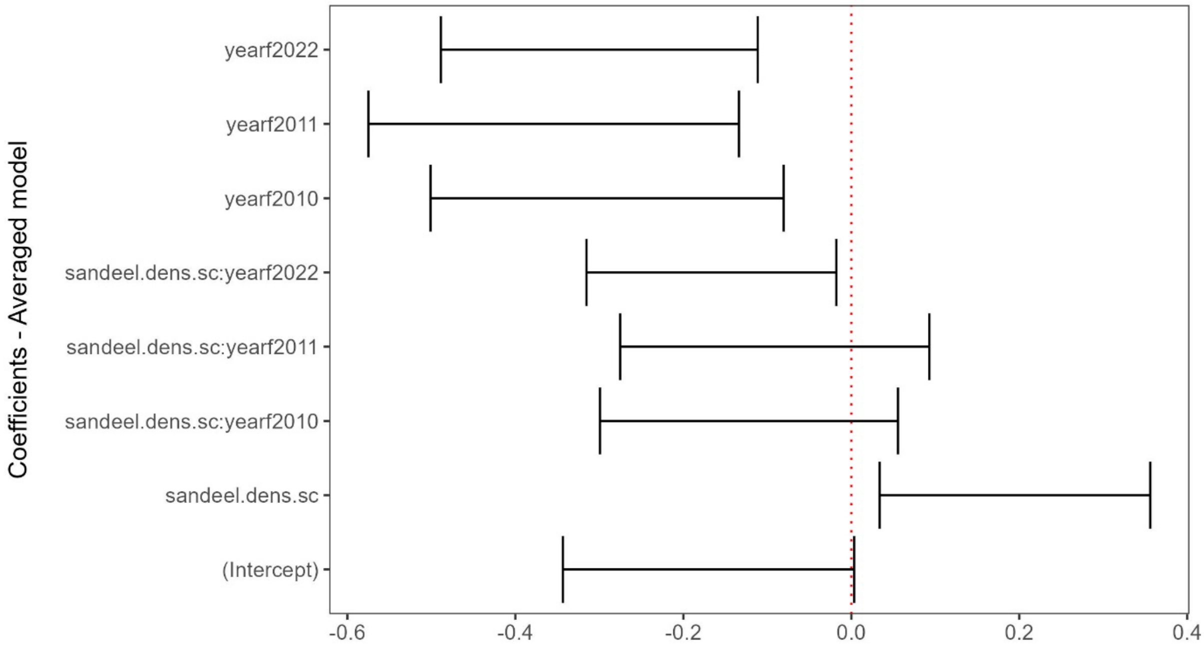


Figure S.7: Model-averaged confidence intervals (95% CI) estimated from Models 1 and 2 (Supplementary Material Table S.1) assessing the probability of harbour porpoise foraging behaviour in relation to sandeel density linked to the installation of wind turbines.