CHAPTER 4

SEASONAL DISTRIBUTION OF HARBOUR PORPOISES (PHOCOENA PHOCOENA) AND RESPONSE TO OPERATIONAL OFFSHORE WIND FARMS IN THE BELGIAN NORTH SEA

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Abstract

Human activities at sea, such as shipping, fisheries, mariculture, and offshore renewable energy developments, potentially influence habitat use of marine mammals. In the Belgian part of the North Sea (BPNS), the most common marine mammal species is the harbour porpoise (Phocoena phocoena). In this study, we update the occurrence and seasonal distribution of this species in the BPNS and investigate the potential effect of operational offshore wind farms (OWFs). To do so, we used aerial survey data collected between 2009 and 2022 and analysed the spatio-temporal distribution of the harbour porpoise as a function of a selection of environmental drivers and anthropogenic stressors. The species' distribution followed a consistent seasonal pattern, with the highest densities in spring, but with a high interannual variability in abundance, with peaks in 2011, 2014 and 2018. Porpoise distribution was explained by latitude and longitude, with the species preferring the

western part of the BPNS, revealing a strong overlap with the Vlaamse Banken Special Area of Conservation (SAC). The distribution was also significantly negatively correlated with marine traffic intensity and distance to the closest OWF, but caution is needed in order not to overinterpret these correlations. Further studies are recommended to support or confute the findings of this study, and to better understand the interaction between natural factors, such as prey availability, and anthropogenic stressors driving the species distribution. The results of such studies may influence the management of future activities at sea and assist in conservation efforts.

1. Introduction

The rapid acceleration of human activities in, and exploitation of continental shelf areas has effects on marine mammals worldwide (e.g., Hawkins *et al.* 2017; Avila *et al.* 2018). For many species, essential habitats, including migration routes, feeding grounds and breeding areas, overlap with areas of intensive

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human activities, leading to a range of effects (Bearzi et al. 2019; Minton et al. 2021). The North Sea is a hotspot of anthropogenic activities, including shipping, fisheries, sand extraction, port development and rapidly increasing renewable energy production (Peschko et al. 2016; Nachtsheim et al. 2021). All of these activities have an effect on cetaceans, and potentially lead to habitat degradation or loss (e.g., Gilles et al. 2009), fisheries bycatch (e.g., Brownell et al. 2019), collisions with vessels (e.g., Schoeman et al. 2020) and disturbance due to noise pollution caused by marine traffic and offshore wind farm (OWF) development (e.g., Haelters et al. 2014; Verfuss et al. 2016; Wisniewska et al. 2018).

In the southern North Sea, including the Belgian part of the North Sea (BPNS), the most common marine mammal species is the harbour porpoise (*Phocoena phocoena*) (Haelters et al. 2011; Bouveroux et al. 2020; OSPAR 2023). Harbour porpoises are wideranging, highly mobile and energetically demanding small odontocetes that feed on a range of fish, such as sandeels, clupeids, gadoids, gobies and flatfish, and cephalopods (Haelters et al. 2012; Ransijn et al. 2019; Nachtsheim et al. 2021). After a strong decline in the 1960s, numbers of harbour porpoises have steadily increased in this region, likely as a result of a southward shift in distribution (Camphuysen 2011; Geelhoed et al. 2013; IJsseldijk et al. 2020). In the BPNS, animals can now be observed year-round, but their occurrence displays strong yearly fluctuations. There is a seasonal pattern with a peak from February to April (Haelters et al. 2013; Van Nieuwenhove et al. 2023); a similar seasonal pattern is observed in adjacent waters in the Netherlands and in the English Channel (Scheidat et al. 2012; Geelhoed et al. 2013; Gilles et al. 2016; Bouveroux et al. 2020). Within the BPNS, the density of animals was described as the highest in the south-western/ western part, and as higher further offshore vs inshore (Haelters et al. 2013). While the reasons driving a small-scale spatio-temporal distribution of harbour porpoises remain unclear, seasonal patterns may be driven by local prey availability (Haelters *et al.* 2011).

As a vulnerable species, the harbour porpoise is listed in Annexes II and IV of the European Union (EU) Habitats Directive (Council Directive 1992/43/EEC). As such, EU member states have the obligation to ensure its conservation through the implementation of, where needed, protection measures, supported by the necessary research and monitoring activities. Under the Marine Strategy Framework Directive (Directive 2008/56/EC), national and international indicators and targets are developed, including for marine mammals. Threats and mitigation measures are also discussed in the framework of the regional agreement ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas, 2009), concluded under the auspices of the Convention on the Conservation of Migratory Species of Wild Animals (CMS or Bonn Convention).

With the expansion of OWFs in the last decades in the North Sea (Xu et al. 2020; Degraer et al. 2022, 2021) and the planned ones for the next decade (Degraer et al. 2022, 2023), the investigation of responses of harbour porpoises to OWFs during their construction and operational phases is of high importance in the frame of reaching conservation objectives. Studies using aerial survey and passive acoustic monitoring (PAM) have shown that OWF construction (and more in particular, pile driving of foundations) causes disturbance and largescale (temporal) displacement and avoidance reactions (e.g., Carstensen et al. 2006; Dähne et al. 2013; Thompson et al. 2013; Haelters et al. 2014; Brandt et al. 2018). Sound mitigation measures have been developed, tested and used in practice with positive results: a temporal ban on piling limits the number of animals exposed where seasonally differences occur in animals present, and measures such as single and double bubble curtains and ramp-up procedures reduce the number of animals exposed to loud noise,

the risk of physical damage to animals and the spatial extent of disturbance (Lucke *et al.* 2011; Dähne *et al.* 2017; Rumes & Degraer 2020; Rumes & Zupan 2021).

The potential negative or positive effects of operational OWFs on harbour porpoises have, in comparison to acute effects due to piling, received less attention. Studies have investigated if harbour porpoises were attracted to operational windfarms, were indifferent to them or if they avoided them, but contrasting behavioural responses lead to the question remaining largely unanswered (e.g., Blew et al. 2006; Tougaard et al. 2006a, 2006b; Scheidat et al. 2009, 2011; van Polanen Petel et al. 2012; Teilmann & Carstensen 2012; Dähne et al. 2014; Vallejo et al. 2017; Collier et al. 2022). Behavioural responses may be site-specific, as the interplay between positive effects (i.e., high habitat quality, artificial reef effect for prey species, sheltering effect, effect of a diminished ship traffic) and negative effects (i.e., low habitat quality, noise disturbance) would yield different outcomes, depending on the underlying ecological features (Tougaard et al. 2005; Scheidat et al. 2011; Haelters et al. 2013). Potential responses could also be masked by a natural distribution, independent of the presence of offshore wind turbines.

In the BPNS, eight OWFs, totalling 399 turbines, became operational over the course of 15 years (Rumes et al. 2022) and an additional zone for offshore renewable energy has been designated in the national marine spatial plan (MSP 2020-2026). However, no assessment specifically aimed at elucidating potential effects of operational OWFs on harbour porpoise distribution and abundance, has been undertaken. Also, given future developments, it is useful to update information on the species' presence in the BPNS. The aim of this study is to analyse the spatio-temporal distribution of harbour porpoises in Belgian waters as a function of a selection of environmental drivers and anthropogenic stressors using aerial survey data. Specifically, this study aimed at analysing

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distribution patterns with special attention to the influence of operational OWFs.

2. Material and methods

2.1. Study area

The BPNS is located in the southwestern part of the North Sea basin (Figure 1); it has a surface of 3454 km². The area is physically, geologically, and ecologically heterogeneous, consisting of a shallow sandbank system that classifies as Habitat 1110 ("sandbanks permanently covered with seawater") under the European Habitats Directive. The habitat hosts a rich and highly productive benthic ecosystem (Pecceu et al. 2021). Offshore, predominantly in the northwestern part of the area, gravel beds occur that formerly hosted oyster beds (Habitats directive Habitat 1170; "reefs"). Within the soft sediment, aggregations of the polychaete worm Lanice conchilega are widely dispersed; also, these aggregations were classified under habitat type 1170. The habitats present act as nursery areas for fish, cephalopods and crustaceans (Houziaux et al. 2008). The presence of habitat types 1110 and 1170 are the background for the delimitation, in 2012, of a Special Area of Conservation (SAC) of approximately 1.112 km² (the Vlaamse Banken) in the western part of Belgian waters (Pecceu et al. 2016).

In the eastern part of the BPNS, close to the border with Dutch waters, an area of 238 km² was allocated to the production of renewable energy. Between 2009 and 2022, eight OWF were constructed, totalling 399 turbines with a total capacity of 2.26 GW (timeline and current status described in Rumes *et al.* 2022). The area is located between two major shipping lanes in the Southern North Sea (Figure 1). Due to its proximity to the English Channel and to large ports, such as those of Antwerp and Rotterdam, the BPNS and its surrounding waters have one of the busiest shipping traffic worldwide (Schallier & Van Roy 2015; Putland *et al.* 2022).



Figure 1. Overview of all harbour porpoise sightings during dedicated aerial surveys (2009-2022) outside of periods with piling operations in Belgian waters. Red tracks represent the line transects as planned. OWFs are colour coded based on the year they became operational. An average monthly route density map (number of vessels detected by AIS in a grid cell of 1×1 km each month) is shown underneath, on top of which is the latest shipping lanes plan as revised in the MSP (2020–2026).

2.2. Aerial surveys

Highly standardized and dedicated aerial surveys were carried out following the line-transect sampling strategy (Buckland et al. 2001). Surveys followed predefined track lines 5 km apart and perpendicular to the coastline to follow an onshore-offshore gradient (Figure 1). For practical reasons, part of the westerly survey tracks is located in French waters. A detailed description of the survey design and data collection are given by Haelters (2009) and Haelters et al. (2013). During the flight, sightings were recorded at non-predefined distances from the track line. Group sizes and presence of calves were noted. To calculate the perpendicular distance of each animal from the track (x), the altitude (h) was recorded, together with the angle (θ) between the horizon and the perpendicular line from the track to the animal, using a hand-held Suunto clinometer PM-5/360PC. The distance of the animal from the trackline was calculated with the Eq. 1: $\chi = h * \tan(90^\circ - \theta)$.

The aircraft used was a Norman Britten Islander equipped with two bubble windows, accommodating two observers. Flight altitude was kept constant at 600 feet (183 m) and groundspeed was 100 knots (185 km/h). Data on ground speed, altitude, time, GPS-position and heading were recorded with a high temporal frequency (every second). Given the high availability of the aircraft, flights were only performed during good observation conditions (sea state ≤ 2 and visibility > 2 km). Preferably, surveys were completed within one day, but if this was not possible, the tracks were completed in a subsequent flight, in most

cases less than a few days later, thus assuming a similar species abundance and distribution in both flights. Survey flights were always combined with regular coastguard tasks: tracks were temporarily interrupted to record and document detections of e.g., oil slicks or shipping navigation violations.

Analyses of the data were carried out using Distance 7.5 Release 1 (Thomas *et al.* 2010). Given the highly standardized nature of the surveys, all observations could be pooled to obtain one detection function. A half-normal detection function with cosine adjustments was selected on the basis of the lowest Akaike Information Criterion (AIC; Thomas *et al.* 2010).

From the detection model, an effective half strip width (E(1/2)SW) of 147.97 m (137.93-158.74) could be estimated, using 2926 observations of in total 3552 animals during 40 surveys. As not all animals were seen by the observers (perception bias), and as some animals were not visible at or near the surface, given that they were too deep (availability bias), a g(0) was applied as estimated for similar surveys (g(0): 0.364;Hammond et al. 2021). Using different values of g(0) would influence the absolute value of density and abundance estimates but would not change the relative distribution or encounter rate (animals observed/effort). Hence, as the aim of this study was to investigate variability in abundance and density distributions, the use of partially corrected observations is as informative (as seen in Vallejo et al. 2017).

In this study, 40 aerial surveys performed between 2009 and 2022 were considered. Surveys with a deviating track or a different technical setup (1 bubble window instead of 2) were excluded from the analysis (3 surveys) and in some cases consecutive surveys that were carried out over a very short period were combined and considered as one survey, with some or all tracks being flown more than once. This resulted in 31 full coverage surveys. Of these, surveys that were carried out during or very shortly (\leq 48 hrs) after piling operations in Belgian or Dutch waters (e.g., Borssele) were excluded from the analyses, reducing the number of surveys considered to a total of 21. The surveys were analysed for the purpose of assessing factors that could influence harbour porpoise distribution and abundance, and especially with a focus on possible effects of operational OWFs.

2.3. Data processing in QGIS

2.3.1. Seasonal maps of observed estimated densities

A squared grid of resolution 5x5 km was created to cover the entire surveyed area. The grid was aligned as much as possible with the surveyed transects to maximize the evenness of the survey effort across grid cells. For each survey, the total length of the flight track and the total number of observed individuals in each grid cell were calculated. To only retain representatively surveyed grid cells for each survey, grid cells with a surveyed effort smaller than 3.75 km were excluded from the dataset, corresponding to a threshold of 75% coverage of the grid cell dimension (length of 5 km). The survey effort (hereafter called "observed km²") was calculated as the length of the flight track in the grid cell (hereafter called "transect length") multiplied by the total effective strip width (295.94 m). Grid cells which were not representatively surveyed, or which fell outside the surveyed area, were assigned a N/A value. For each representatively surveyed grid cell, the encounter rate was calculated as the number of harbour porpoises observed per km surveyed (ind/km). The estimated density (D) was calculated as the number of individuals observed per observed km², the latter multiplied by g(0) (0.364) (Eq. 2):

$$D_{grid cell} = \frac{No. of ind_{grid cell}}{Transect \ length_{grid cell} * ESW * g(0)}$$

Estimated density distribution maps were produced for each survey. After visual scrutiny, the estimated density distributions were averaged at grid cell-level for each season to obtain seasonal distribution maps, except for winter where surveys were too scarce in number. In winter, given that observation conditions are usually unfavourable, mostly due to short days and a low hanging sun leading to a lot of glare, only two surveys were performed. Seasonal distribution maps were preferred over an overall map as strong seasonal patterns are known for the species in Belgian waters (Haelters et al. 2011, 2013) and in the North Sea in general (Gilles et al. 2009, 2016). The averaging exercise followed the assumption of a spatial symmetric distribution in different surveyed years but during the same season, similarly to what was done by Gilles et al. (2009). Furthermore, the individual survey detection curves were verified to be similar, as done in Scheidat et al. (2008). To quantify and visualize the variability in total number of observations in the same grid cell across years, estimated density standard deviation (SD) maps were computed for each season. This choice was justified by the scope of the study, which aimed at understanding and visualizing relative abundances and spatial distribution of harbour porpoises in Belgian waters rather than obtaining exact absolute numbers and density values at a relatively small spatial scale for this highly mobile species.

2.3.2. Calculation of explanatory variables

Several environmental and anthropogenic factors were considered for the investigation of potential drivers influencing the relative distribution of harbour porpoises in the BPNS. Information on each observation of position (latitude, longitude, corrected for distance to the aircraft), season and year were available from the survey data. A bathymetry map with a resolution of 115×115 m was downloaded from the opensource Map Viewer of the European Marine Observation and Data Network (EMODnet; https://emodnet.ec.europa.eu/geoviewer/). Depth values were extracted at each corrected observation position using the plugin 'point sampling tool'. Monthly route density maps for the period 2019-2022 (i.e., maximum time interval available) with 1×1 km resolution were downloaded from EMODnet Map Viewer.

Monthly route density maps represent the total number of vessels of all types detected in each grid cell in a given month using the Automatic Identification System (AIC), and account as a proxy of marine traffic. All monthly maps were averaged to obtain an overall proxy map for marine traffic and shipping intensity (Figure 1). Shipping intensity values were extracted at each observation location using the plugin 'point sampling tool'. To quantify the potential attraction or avoidance effect of OWFs on harbour porpoises, the distance of each observed individual from the closest OWF (i.e., the closest turbine) was calculated using the function 'distance to the nearest hub'. As different OWFs became operational in different years, distances of observations made in a specific year were calculated exclusively with respect to the turbines present at the time, following the development timeline presented in Rumes et al. (2022; Figure 2). Finally, the underlying seafloor habitat type was considered as a proxy for other ecological factors driving the species distribution. The seafloor habitat classification in Pecceu et al. (2021) was used as it considered sandbanks, the probability of the occurrence of aggregations of Lanice and the occurrence of gravel beds (Habitats 1110 and 1170 in the Habitat Directive). It further subdivided sandbank habitats into five types of macrobenthic communities, and Habitat type 1170 into gravel beds and the probability of the occurrence of aggregations of Lanice conchilega (for a total of seven benthic community types, hereafter called 'habitat type'). To obtain a habitat type for each grid cell, grid cells were assigned to the classification with the highest coverage percentage. Grid cells where the habitat type was not available (e.g., for the parts of the tracks over French waters) were classified as 'unknown'. For the grid cells where no individuals were observed during a specific survey, all explanatory variables were calculated from the grid cell centroid coordinates.

2.4. Statistical analysis

Due to the spatial nature of the data, two separate sets of statistical analyses were done:



Figure 2. A. Grid area (red) of 1475 km² up to 15 km from all turbines in surveyed Belgian waters selected for the spatio-temporal analysis of the potential influence of operational OWFs on the distribution of harbour porpoises. **B**. Timeline of the sequence of OWFs becoming operational in the BPNS between 2009 and 2022 with associated yearly harbour porpoise sightings made during aerial surveys, and underlying bathymetry map. From 2019 onwards, one track directly over the OWF was not flown anymore for safety reasons (see Fig. 1).

(1) a spatio-temporal analysis of the potential influence of environmental and anthropogenic factors on the overall distribution of harbour porpoises in the BPNS; (2) a spatiotemporal analysis of the potential influence of operational OWFs on the distribution of harbour porpoises in the area surrounding, and including, the OWF area.

Operational OWFs in the BPNS are highly clustered and localized at the eastern part of the BPNS, along the border with the Dutch EEZ and neighbouring the most westerly Dutch OWFs. As such, they have a strong spatial correlation with other environmental features and gradients such as latitude, longitude and depth when considered at the overall BPNS level (Figure 1). Moreover, wind farms are located in the eastern part of Belgian waters, while porpoises naturally occur in higher densities in more westerly waters, as documented by previous literature (Haelters et al. 2011, 2013), with results indicating a higher sighting rate in more westerly waters within the BPNS (Figure 1). To reduce such spatial correlation and to produce a meaningful assessment of the potential effect of operational OWFs on harbour porpoise distribution, the area of interest in the latter statistical analysis was reduced to 1475 km² (59 of 255 grid cells), as such covering a surface defined by a 15 km radius surrounding the OWF area (Figure 2). The area east of the OWF area was not selected as it covered Dutch waters with no survey effort.

All statistical analyses were performed in Rstudio (ver. 4.1.1; Rstudio Team 2020). Both data from response and exploratory variables were inspected for correlation, outliers, normality and homoscedasticity prior to the modelling exercise following the protocol from Zuur *et al.* (2010). The response variable used in both analyses was the sighting rate (ind/nm) in each grid cell per survey (transformed into integer counts for the modelling exercise). As it is often the case with species distribution count data (Dénes *et al.* 2015), especially when derived from visual surveys (Zipkin *et al.* 2014; Vallejo *et*

al. 2017), the data were zero-inflated. Zeroinflation occurs when the number of zeros is excessive compared to the integer counts and influences the modelling of a Poisson regression causing overdispersion (Yang et al. 2017). Zeros divide into true zeros (i.e., the animal is absent) and false zeros (i.e., due to observed error, sampling error, or wrong survey design; Zuur et al. 2009). Therefore, zero-inflated (ZINB) and zeroaltered negative binomial regression (ZANB) models were used and tested. The difference stands in how the zeros are handled, but both apply two different distributions to the data: a logistic distribution to the zeros and a negative binomial distribution to the counts (Zuur et al. 2009). ZINB models were built with the function zeroinfl (package pscl), while ZANB models were built with the function hurdle (package pscl). Backward stepwise model selection was done separately for both models based on the AIC. Model selection between the best ZINB and ZANB models was based on AIC scores. Models were validated by assessing the residuals' normality, the residuals versus fitted values, and the residuals versus each covariate. For all analyses, an alpha threshold of p=0.05was used for statistical significance.

3.Results

3.1. Seasonal distribution

A total of 2738 harbour porpoises were observed during the 21 aerial surveys considered for this analysis (Table 1). The average sighting rate (number of animals observed per 100 nautical miles surveyed) was much higher in spring (54.93 ± 87.14) than in summer (16.58 ± 33.61) or autumn (10.60 ± 26.58) (mean \pm SD) (Wilcoxon Rank Sum Test p-value < 0.0001 for both pairs). The sighting of (presumed) mother-calf pairs was, as can be expected giving the calving season (May–July), highest in summer (54 out of 84 calves observed). The observed average group size was 1.12 in spring, 1.30 in summer, and 1.29 in autumn.

Table 1. Overview of aerial surveys used in this study with associated features, including the survey year, the season, total on task effort in nautical miles, the total number of harbour porpoises observed, the number of calves, the average group size and the average sighting rate expressed as observed individuals per 100 nautical miles surveyed (mean \pm SD). Surveys with asterisks (*) indicate surveys that are the result of a combination of surveys undertaken within short timeframes.

Year	Season	Survey effort (nm flown)	No. of individuals	No. of calves	Average group size	Sighting rate (ind/100 nm)
2009	Spring	275.35	13	0	1.08	4.32
2010	Winter	347.04	51	0	1.30	14.74
2010	Spring*	344.50	59	0	1.04	15.60
2010	Summer	346.29	38	2	1.28	10.13
2011	Spring*	1118.09	646	0	1.24	56.64
2011	Winter	327.89	100	2	1.79	29.84
2012	Spring	348.02	196	1	1.14	53.42
2012	Autumn	344.32	40	0	1.28	11.15
2014	Spring	333.71	331	0	1.09	94.48
2014	Autumn*	728.15	64	0	1.32	8.13
2016	Spring	333.30	104	0	1.05	29.86
2017	Summer	357.78	116	21	1.25	30.49
2017	Autumn	302.23	21	2	1.07	6.98
2018	Spring	359.81	404	0	1.15	108.62
2018	Summer	287.46	41	6	1.28	12.73
2019	Summer*	706.64	93	12	1.23	12.38
2020	Autumn	325.37	37	0	1.19	9.94
2021	Summer	315.49	52	10	1.49	16.31
2021	Autumn	323.96	52	7	1.58	13.47
2022	Spring	334.66	235	21	1.19	64.94
2022	Autumn	284.66	45	0	1.32	14.51
Total (n = 21)/average		8444.76	2738	84	1.26	30.33

The strong seasonal difference in estimated density is associated with a strong seasonal spatial distribution pattern (Figure 3). Although the total number of observations made in each grid cell varied across years in the same season, the spatial pattern of the observations did not differ, and seasonal maps of mean densities could be achieved. In spring, both observations and estimated density distribution followed a clear pattern, with a relatively high density offshore and in the western part of Belgian waters, continuing into adjacent French waters. In this area, estimated densities reached average values of 8 individuals per km². Observations and estimated densities were low in coastal waters within the first 12 nautical miles, except for the coastal area

off Nieuwpoort. In summer, the distribution gradients were less defined and homogeneous, but still revealed higher estimated densities in offshore waters, especially in the western part of the BPNS. Estimated densities per grid cell ranged from 0 to 4.1 individuals/ km². Most mother-calf pairs were observed in the western part of the BPNS. Several grid cells showed a higher variability in density over different years. In autumn, observations and estimated densities were spread across the BPNS without a clear distributional pattern. Most mother-calf pairs were seen offshore, and relatively many animals were observed in waters close to shore. In autumn, the highest estimated density per grid cell was 2.7 individuals/km².



Figure 3. Seasonal density distribution maps of harbour porpoises (ind/km²) (left) and associated variability (right) in the survey area in spring (March–May), summer (June–August), and autumn (September–November), calculated as mean between 2009 and 2022. Grid cell size: 5×5 km. Black dots indicate every observation; red stars indicate calves.

3.2. Factors influencing overall harbour porpoise distribution in the BPNS

The variability in the overall harbour porpoise distribution in the BPNS, represented by sighting rate (ind/nm) per grid cell, was statistically significantly explained by the season, the year, the latitudinal and longitudinal coordinates and their interaction, depth and marine traffic (Table 2). Predicted values in function of scaled explanatory variables and predicted regression curves are shown in Figure 4. Sighting rate (ind/nm) showed significant variability in function of years (overall p-value < 0.0001), with higher rates in 2011, 2014 and 2018. Significant variability was also found in function of season, with spring significantly different (p-value < 0.0001) from summer and autumn, which did not differ from each other.

Table 2. ZINB regression model with best performance used to describe overall distribution of sighting rates (ind/nm) in the BPNS as a function of broad-scale environmental and anthropogenic factors. Model estimated coefficients for the count model part are presented as mean \pm SE. Chi-Square values and p-values are shown for each explanatory variable selected by the model.



Figure 4. Negative binomial regression lines fitted by the best selected ZINB model between predicted sighting rates (fitted values) and each statistically significant explanatory variable for A) the analysis of the overall distribution of harbour porpoises in the BPNS, and B) the analysis of the distribution of harbour porpoises in the SUPPONE on areas as a function of distance to operational turbines, and other environmental drivers.

Table 3. ZINB regression model with best performance used to describe distribution of sighting rates (ind/nm)
as a function of their distance to operational OWF and other local environmental factors, in the selected area of
2125 km ² surrounding and including all OWF concession areas. Model estimated coefficients for the count model
part are presented as mean \pm SE. Chi-Square values and p-values are shown for each explanatory variable selected
by the model.

		Negative binomial part (counts)			Zero-inflated part (zeros)		
Response variable	Explanatory variable	Est. coeff. (mean ± SE)	Chi- Square	p-value	Est. coeff. (mean ± SE)	Chi- Square	p-value
Sighting rate (ind/nm)	Distance to OWF	$\textbf{-0.18} \pm 0.11$	2.47	0.116	_	_	-
	Latitude	_	_	_	1.04 ± 0.21	44.97	<0.0001
	Longitude	$\textbf{-}0.36\pm0.05$	34.44	<0.0001	0.47 ± 0.19	41.59	<0.0001
	Interaction Lat*Long	_	_	_	-1.36 ± 0.22	38.06	<0.0001
	Season-Spring	0.75 ± 0.11	91.84	<0.0001	-1.60 ± 0.24	52.05 < 0.	<0.0001
	Season-Summer	0.27 ± 0.15		0.068	-0.25 ± 0.28		0.356
	Year	0.88 ± 0.65	97.97	<0.0001	-3.54 ± 0.66	124.63	<0.0001

Spatially, the overall distribution was significantly explained by latitude, longitude and their interaction. Sighting rate (ind/nm) increased with increasing latitude (p-value = 0.004) and decreasing longitude (p-value < 0.0001). Habitat type was highly correlated with depth and latitudinal and longitudinal coordinates, and therefore could not be tested in the same model. Habitat type was tested in an alternative competing model, but it did not significantly explain variability in density (data not shown). Finally, marine traffic significantly affected the overall distribution (p-value < 0.0001), with species density being higher with lower traffic intensity.

3.3. Effect of operational offshore wind farms on harbour porpoise distribution

The distribution of harbour porpoises in the vicinity of the OWFs in the BPNS was represented by sighting rates (ind/nm) per grid cell in a selected area of 1475 km² comprising and extending beyond the OWF concession areas. The spatio-temporal distribution could be explained by distance to the closest OWF, as well as by season, year, latitudinal and longitudinal coordinates, and their interaction (Table 3, Figure 4). The distance of each observation from the closest OWF (i.e., turbine) did not significantly explain part of the variability in the observed distribution despite the variable was retained in the best model (p-value = 0.116), with sighting rates marginally decreasing with increasing distance to the OWF. Sighting rates in the selected area varied from 0 ind/nm to 5.56 ind/ nm per grid cell, and distances ranged from 42 m to 35 km. The remaining variability was significantly explained by the environmental factors, in line with the results of the analyses over the entire survey area. Sighting rate was significantly different among years (overall p-value < 0.0001), with higher rates in 2011, 2014 and 2018. Significant variability was found in function of season, where sighting rate was higher in spring (p-value = 0.0001) but similar in summer and autumn. Finally, the distribution was significantly explained by longitude and by the interaction between latitude and longitude. The sighting rate increased with decreasing longitude (p-value < 0.0001).

4.Discussion

Data were collected in a highly standardised way, as such allowing for analyses on a larger spatial scale, such as the southern and central North Sea (Gilles *et al.* 2016) and even the whole of the North Sea and adjacent Atlantic Ocean (Waggit *et al.* 2019). While the surveys conducted here were conducted on a relatively small spatial scale, they were conducted, compared to large-scale surveys such as SCANS surveys (Hammond *et al.* 2021), with a relatively high spatio-temporal resolution, as such allowing for, for instance, finer-scale temporal and spatial analyses.

4.1. Seasonal and interannual variability

Dedicated marine mammal surveys conducted between 2009 and 2022 revealed a clear seasonal and interannual variability in the abundance of harbour porpoises. Porpoises could be observed year-round, but the highest numbers were observed in spring. In spring, mean sighting rate was 54.9 ind/100 nm and mean estimated density was 2.78 ind/km². In summer, abundances were lower, but sightings of calves were most common, as females give birth in late spring or early summer (Gilles et al. 2009). Animals were mostly sighted alone or in small groups, leading to a small average group size (1.26 individuals). Observations are in line with those of Bouveroux et al. (2020) who recorded the highest numbers in the eastern English Channel in winter, and Haelters et al. (2013) and Scheidat et al. (2012), who recorded the highest abundances in winter and early spring in Belgium and the Netherlands. Due to reasons explained above, very few surveys were conducted in winter, but acoustic monitoring between 2010 and 2018 in the BPNS confirm this trend (Haelters et al. 2016; Augustijns 2018). Seasonal trends in relative spatial distribution were consistent across all surveys, but the number of sightings varied interannually, as also reported by Haelters et al. (2013). These variations are potentially the consequence of the small spatial scale of this analysis and the highly mobile nature of the species, but they may also be caused by large-scale natural variations in distribution, possibly instigated by changes in the distribution and abundance of the most important prey species (Hammond et al. 2013; Dähne et al. 2014; Geelhoed & Scheidat 2018).

4.2. Patterns in distribution

The seasonal distribution maps (Figure 3) display the standard deviation in sighting rate

recorded in each grid cell across years. As it is based on a large number of data and as the resulting density distribution shows a similar pattern throughout the years, it is probable that this distributional pattern is the consequence of a combination of environmental and anthropogenic factors. Instead, the summer and autumn maps should be treated with more caution, and they could partly be the result of animals passing through the area, with an ad hoc location that is influenced to a lesser extent by local environmental conditions or effects of anthropogenic activities. Nevertheless, the observed spatial distribution in this study is in accordance with what is already known for the species in Belgian waters (Haelters et al. 2011, 2013). Harbour porpoises could be observed throughout the surveyed area. Coastal waters, within the 12 nautical mile zone, had the lowest sighting rate during the study period. A strong longitudinal gradient in distribution was confirmed in this study, with relatively high sighting rates in the northwestern/western part of the study area, near and beyond the border with the French EEZ. This distribution was especially apparent in late winter and spring. In summer however, and more noticeably in autumn, animals were more evenly distributed across the BPNS.

The harbour porpoise is a highly mobile species with an extensive range within the North Sea. It feeds opportunistically on a large number of prey species. Therefore, the array of ecological and anthropogenic factors and their interactions driving the species' spatio-temporal distribution are hard to unravel (Gilles et al. 2016). Large-scale studies performed in one season and with a low temporal resolution, such as the SCANS surveys (Hammond et al. 2013, 2017) and small-scale surveys performed with a higher frequency, such as the ones described here, both have their value in unravelling spatiotemporal patterns, as a first step towards understanding the drivers of the patterns. For the harbour porpoise, a small, warmblooded mammal that lives in a relatively cold environment, the availability of food is key to its survival (Kastelein et al. 1997; IJsseldijk, 2021). Therefore, one should be able to explain, at least partly, its occurrence and distribution by the distribution and availability of its preferred prey (Lambert et al. 2016; Ransijn et al. 2019; Nachtsheim et al. 2021). In turn, prey distribution is influenced by several underlying ecological factors (Skov & Thomsen 2008; Ransijn et al. 2019). Given the frequently very high densities recorded locally in the survey area in this study, this area should be considered as forming part of a highly valuable area for the species, with also in adjacent French and nearby Dutch waters frequent records of high densities of porpoises (Geelhoed & Scheidat 2018; Bouveroux et al. 2020).

In this study, statistical analyses revealed that latitude, longitude and their interaction accounted for a large part of the distribution variability of harbour porpoises. These factors act as proxies for underlying ecological gradients that are not directly accounted for in the analysis (IAMMWG 2015). Harbour porpoises inhabit dynamic shallow waters of continental shelves which host suitable habitat conditions for feeding (Skov & Thomsen 2008; Lambert et al. 2016). Water current speed was not included in this study, although in studies it was reported to be a significant driver for the presence of porpoises, as stronger currents can promote primary productivity and prey abundance (Bouveroux et al. 2020). In the BPNS, prey distribution may be influenced by the underlying benthic habitat type. Habitat type was considered in the analyses but did not significantly explain variability in harbour porpoise distribution, potentially because of the very different spatial resolution by which habitat type and porpoise distribution are described, and/or because of the fact that part of the diet of porpoises consists of fish that are pelagic, or at least partially pelagic (e.g., sandeels), as such independent of the habitat type used in the analysis. However, as part of the diet of porpoises consists of pelagic fish species, with an occurrence partly independent of local benthic habitat type, local concentrations and seasonal movement patterns of porpoises may be the consequence of the presence and migration of these prey species.

Independently of the considerations mentioned above, it is clear that at least in late winter and spring porpoises occurred in a relatively high density in the western and northwestern part of the study area, with a strong overlap with the Vlaamse Banken SAC (MSP 2020-2026). This SAC was established in 2012 to protect an ecosystem of sandbanks that included Habitat 1110 and 1170, and to conserve some of the richest remnants of gravel beds in Belgian waters known to occur in their gullies (the Hinder Banks) (Houziaux et al. 2008; Pecceu et al. 2016, 2021; Montereale-Gavazzi et al. 2023). The area is known to sustain a complex food web that includes species of commercial interest, and it is therefore subject of a sustained exploitation by fisheries (Pecceu et al. 2021).

4.3. Influence of shipping

Marine traffic is the primary source of underwater noise pollution worldwide and it is known to cause behavioural responses in cetaceans (e.g., Gomez *et al.* 2016; Avila *et al.* 2018; Pirotta *et al.* 2018). Harbour porpoises have been seen to fluke, dive and interrupt foraging and even echolocation when encountering noisy vessels (Wisniewska *et al.* 2018). Noise avoidance and behavioural changes in foraging may particularly be affecting the species' fitness and survival as it extensively uses echolocation for its incessant feeding pace (Wisniewska *et al.* 2018).

In this study, shipping intensity was found to significantly explain the distribution of porpoises, with a decline in sighting rate with increasing shipping traffic. The highest densities of porpoises were found within and around the Vlaamse banken SAC which is void of shipping lanes, and therefore has lower traffic intensities compared to other areas.

However, such results should be considered carefully, as other factors could affect this relationship. For instance, as the data on shipping relies on AIS detections, the anchorage area in front of Ostend is overrepresented. Moreover, the area around the port of Zeebrugge has a very high shipping density, and a low harbour porpoise density, but the latter could also be due to a less suitable habitat, with for instance a higher turbidity and/or a lower density of suitable prey species.

4.4. Influence of operational OWFs

Underwater noise generated by operating OWF is another source of anthropogenic noise of which the effect on marine mammal behaviour is still unclear. While marine mammals may be attracted to operational OWFs because of a higher food availability due to artificial reef effects and the absence of fishing, they may also avoid the area because of the increased underwater noise from the turbines and the vessel traffic in their surroundings (Tougaard et al. 2005; Scheidat et al. 2011; Haelters et al. 2013). In the Netherlands, an increase in the number of harbour porpoises was detected by acoustic devices inside the operational OWF Egmond aan Zee (OWEZ; Scheidat et al. 2009, 2011). The increase in food availability and/or a sheltering effect from fisheries disturbance were proposed as a possible explanation for this. In contrast, no differences were detected inside vs outside the operational OWF Prinses Amalia windfarm (van Polanen Petel et al. 2012). Similar results were obtained with aerial surveys over the Borssele OWF, where no conclusive support for either avoidance or attraction was found (Collier et al. 2022). In Denmark, no difference in number of animals was detected by acoustic devices inside and outside the OWF Horns Reef, with a complete recovery to baseline levels observed within one year of the operational phase (Tougaard et al. 2006b; Blew et al. 2006). In contrast, a long-term negative effect from the construction extending into the operational phase on the species' occurrence was suspected for the OWF Nysted: acoustic detections had returned to baseline levels in the nearby reference area after two years, but

within the OWF itself they had not recovered after 10 years (Tougaard et al. 2006a; Teilmann & Carstensen 2012). In the UK, no difference in the number of harbour porpoises between the preconstruction and the operational phase was observed during ship surveys at the Robin Rigg OWF in UK (Vallejo et al. 2017). The quick return of animals after the construction phase ended was hypothetically linked to habitat quality: animals may display a shortened avoidance behaviour if the habitat is of high quality for feeding. In Germany, the operational OWF Alpha Ventus did not seem to affect harbour porpoise distribution, which was apparently driven by a large-scale natural variation (Dähne et al. 2014). Overall, contrasting results have been potentially linked to site-specificities such as differences in OWF features, or underlying ecological aspects driving the harbour porpoise response (Scheidat et al. 2009; van Polanen Petel et al. 2012), underlining the importance of regionspecific investigations.

As OWFs are densely clustered and localised in the eastern part of the BPNS, at the border with the Dutch EEZ, they have a strong spatial correlation with other environmental gradients in the BPNS such as latitude, longitude and depth. The results of our analysis revealed that variability in harbour porpoise distribution was not significantly explained by the distance of each observation to the closest OWF, despite the variable being retained in the best model with marginally higher sighting rates at decreasing distances from the turbines. A similar density of harbour porpoises outside and within the OWF area could, in theory, be due to the trade-offs between the introduced underwater noise of operational wind turbines and the availability of suitable prey. However, the results presented here may have been confounded by presumptions and analytical constraints. Although the analysis was performed in a selected area to avoid the covariates of spatial distribution affecting the results, the natural gradient in the distribution of harbour porpoises across the BPNS may still have influenced the analysis. As discussed above, porpoises were generally distributed according to an east-west gradient, and perhaps favour more westerly waters, independently of the presence of OWFs. Furthermore, the survey track directly above the OWFs could not be flown from 2019 onwards. The lower coverage of the OWF area may have influenced the analysis. All in all, this study cannot come to conclusion about the effect of operational OWFs on the occurrence of harbour porpoises in Belgian waters. This may be due to the method being not very suitable. Visual aerial surveys typically generate data in a low temporal and spatial resolution, but over a wide area, and are as such considered suitable to assess distribution and abundance patterns of highly mobile species. However, as operational OWFs generate relatively low underwater noise levels, and as underwater noise levels are also generated through other activities, it is likely that effects play at a smaller spatial scale than can be detected through aerial surveys (which remain useful for assessing activities potentially generating widerranging effects, such as piling). Using passive acoustic monitoring with a sufficiently dense distribution of sensors within and outside OWFs, tagging animals or performing digital aerial surveys in a higher temporal and spatial resolution (Williamson et al. 2016; Collier et al. 2022) may be more suitable methods to reveal effects.

Despite the limitations of the analyses, the results presented in this study contribute valuable information to the discussions on the potential implications of current and future OWF development and other human activities at sea for the harbour porpoise wellbeing.

5. Conclusions

The aerial survey data collected between 2009 and 2022 revealed a seasonal pattern in the presence of harbour porpoises in the survey area, with the highest densities recorded during late winter and spring. They also revealed a high temporal variability, with years with very high and years with much lower densities. The results of the analyses, although conducted on a small scale considering the high mobility of the species and its wide dispersal, still clearly showed that in spring harbour porpoises were most common in the northern and western part of the survey area, with especially in the northwestern part frequently very high densities. The study also suggests that shipping intensity was a factor negatively influencing densities on a local scale.

The density of harbour porpoises near operational wind turbines was relatively low. The background for this could have been natural, while it could also have been partly caused by the presence of wind turbines and the related activities in and near the wind farm. It was concluded that the use of aerial surveys, in the way they were conducted, is probably not the best method to reveal possible smallscale changes in porpoise distribution due to the presence of offshore wind turbines. Changes in distribution outside and inside an OWF area may be hard to distinguish from larger scale spatio-temporal variability driven by larger scale environmental gradients.

The results of this study are useful for informing the management of current and future activities in Belgian waters, such as fisheries and renewable energy development, and provide a basis for appropriate measures needed in light of the ever-increasing human presence at sea.

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