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Research article

Northern gannets (*Morus bassanus*) are strongly affected by operating offshore wind farms during the breeding season

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ABSTRACT

Northern gannets (*Morus bassanus*) have been ranked as one of the most vulnerable species in terms of collision with offshore wind farm (OWF) turbines, and strong avoidance of OWFs has been documented for this species. Gannets increasingly encounter OWFs within the ranges of their largest breeding colonies along the European coasts. However, information on their actual reactions to OWFs during the breeding season is lacking. We investigated the possible effects of OWFs located 23–35 km north of the colony on Helgoland in the southern North Sea on breeding gannets. GPS tags were applied to 28 adult gannets breeding on Helgoland for several weeks over 2 years. Most gannets (89%) predominantly avoided the OWFs in both years, but 11% frequently entered them when foraging or commuting between the colony and foraging areas. Flight heights inside the OWFs were close to the rotor-blade zone, especially for individuals predominantly avoiding the OWFs. Gannets preferred distances of 250–450 m to the turbines when being inside the OWF. A point process modelling approach revealed that the gannets resource selection of the OWF area compared with the surroundings (outside OWF = up to 15 km from the OWF border) was reduced by 21% in 2015 and 37% in 2016. This study provides the first detailed characterisation of individual reactions of gannets to OWFs during the breeding season and one of the first comprehensive studies of OWF effects on this species based on telemetry data. The documented effects need to be considered during the planning processes for future OWFs, especially those located close to large seabird breeding colonies.

1. Introduction

Seabirds increasingly encounter offshore wind farms (OWFs) in European waters, especially over the past 10–15 years (Perveen et al. 2014; Windeurope 2020; Bórawski et al. 2020). Seabirds such as northern gannets (*Morus bassanus*, hereafter gannet), depend on offshore areas for foraging, and also for resting and moulting (Schreiber and Burger 2001). It is therefore necessary to study and understand the potential OWF effects, especially during the breeding season when birds have a restricted foraging range and choice of foraging habitats, and are under increased pressure to find enough prey to raise their offspring (Orians and Pearson 1979). However, few studies have explicitly investigated the reactions of seabirds towards OWFs during this stage of their life cycle (Masden et al. 2010; Thaxter et al. 2015, 2018).

Seabirds show different behavioural reactions towards OWFs ranging from complete avoidance to attraction (Drewitt and Langston, 2006; Furness et al. 2013; Dierschke et al. 2016). As a wide-ranging seabird species, gannets can encounter OWFs with increasing frequency in range of their largest breeding colonies along the European coasts (Grecian et al. 2012; Bradbury et al. 2014). Their flight height and manoeuvrability make gannets one of the most vulnerable species in terms of collision with turbines (Garthe and Hüppop, 2004; Furness et al. 2013). In Scottish waters, it was predicted that the gannet population on the Bass Rock could be affected due to a relatively high number of predicted collisions with future OWFs (Cleasby et al. 2015). Furthermore, strong avoidance of OWFs was found for gannets in most studies (reviewed in Dierschke et al. 2016). At the Blight Bank OWF for example, an 85% reduction in gannet density was detected in the OWF (Vanermen et al. 2015), while a study at the Alpha Ventus OWF in German waters found a reduction of 75% inside the OWF (Welcker and

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Nehls 2016). Displacement and collision effects of OWFs may thus have different consequences for gannets in terms of habitat loss and direct mortality.

Although some knowledge on the general avoidance of OWFs by gannets is available, very little is known on the individual reaction and movement patterns in and around the OWFs, the behaviour of the gannets close or inside the OWFs as well as their flight height compared to the turbine height. GPS tracking can generate valuable data on fine- and large-scale habitat use and behaviours (Garthe et al. 2007; Thaxter et al. 2018), as well as changes in these with regard to changing environmental conditions (Garthe et al. 2011; Paredes et al. 2014). However, few studies to date have used GPS tags to investigate effects of operating OWF on seabirds (Thaxter et al. 2015, 2018; Garthe et al. 2017a; Peschko et al. 2020). In a recent pilot study, for example, Garthe et al. (2017a) showed that three gannets equipped with GPS tags largely avoided the operating OWFs north of Helgoland. Based on flight heights collected before OWF construction, Cleasby et al. (2015) predicted the possible collision risk of breeding gannets with respect to future OWFs.

Three wind farms, covering an area of 105 km^2, are currently operating only 23–35 km north of Helgoland. However, the only gannet colony in the southern North Sea is located on Helgoland, highlighting the need to assess the possible effects of these nearby OWFs on the local gannet population. We therefore applied GPS tags on adult gannets for several weeks during two consecutive breeding seasons to generate a unique, extensive, and detailed dataset of gannet movements and behaviours to address the following questions: Do gannets breeding on Helgoland react to the presence of OWFs close to their colony? Are gannets displaced or attracted by the OWFs and can we quantify their reactions? Are there individual differences between the birds' reactions towards the OWFs? How do the gannets behave in the vicinity of or inside the OWFs in terms of foraging and flight heights? Do they behave similarly in consecutive years? We approached these questions by visualizing and quantifying the reactions of gannets towards OWFs based on recorded foraging trips, behaviours, and altitudes. We also applied a state-of-the-art modelling approach for telemetry data (spatio-temporal point process model; PPM) to investigate if resource selection of the OWF area was reduced in comparison with the areas outside the wind farm.

2. Materials and methods

2.1. Fieldwork and data collection

Gannets were caught on the island of Helgoland (54°11′ N, 7°55' E) in the south-eastern North Sea. Gannets started to breed on Helgoland in 1991 and the colony increased to 1071 breeding pairs in 2017 (Dierschke et al. 2018). Using a noose pole, we caught 28 incubating or chick-rearing gannets during the breeding seasons in 2015 and 2016. GPS devices were attached to the base of the four central tail feathers using TESA® tape (Beiersdorf AG GmbH, Hamburg, Germany). Sixteen gannets each received a Bird Solar GPS logger (e-obs GmbH, Munich, Germany, 39 g), eight were equipped with OrniTrack-25 loggers (Ornitela, Vilnius, Lithuania, 25 g), and four with both a CatLog-S GPS logger (Catnip Technologies, Hong Kong SAR, China) and a precision temperature–depth (PTD) logger (Earth and OceanTechnologies, Kiel, Germany, CatLog-S plus PTD: 64 g). The attached devices represented 0.8%–1.9% of the mean gannet body mass of 3286 g (Wanless and Okill 1994), which was well below the recommended threshold of 3% (Phillips et al. 2003). Although attachments to the tail may have negative effects on flight behaviour (Vandenabeele et al. 2014), most pairs successfully incubated their eggs and/or raised their chicks, similar to non-handled nests. The mean handling time was 17 min, and the birds were released in close proximity to their nest. Eggs were observed during the handling period to prevent nest predation. Individuals were either re-caught after 3–4 weeks to remove the devices, or the devices fell off during moulting. All GPS devices recorded the date, time, and geographic position with a sampling interval of 2–5 min. When the battery was low, the solar devices reduced the sampling interval to 15–30 min. In 2016, at each regular sampling interval, the e-obs devices were additionally programmed to record positions continuously for 15 s to generate reliable flight-height measurements (see below). The Bird Solar GPS devices transmitted data via a UHF connection to a base station, and the OrniTrack-25 devices transmitted data via GSM. Recapture was thus only mandatory for CatLog-S devices.

Gannet catching and tagging were conducted in accordance with the German Protection of Animals Act and with the permission of the Ministry of Energy, Agriculture, the Environment, Nature and Digitalization (file number V 242-7224.121-37).

2.2. Foraging trips

We did not interpolate the birds' positions because we focused on their reactions to OWFs and therefore chose to use the original data points, representing the true positions of the individuals. Some devices recorded at 1-s intervals during different periods of the data collection and we excluded these data points from the trip identification, the behavioural analysis and the statistical modelling, but used them for the analyses of flight heights and the distance of the birds to the single turbines. Based on the number and duration of tracks passing through the OWFs, we classified birds which have entered the OWFs on more than three occasions and stayed for more than 30 min inside the OWFs during each occasion as 'attracted' to the OWFs. The remaining birds were classified as 'predominantly avoiding individuals'.

All trips with a duration of >20 min and ≥1 km distance from the nest were classified as foraging trips, using an R code provided by Lascelles et al. (2015) which also estimated the duration (h) and total and maximum distance (km) of the foraging trips. We applied linear mixed models (LMM; R-package lme4 (Bates et al. 2015)) to test if the duration (h) and total and maximum distance (km) differed between the years, controlling for by-individual variability. Subsequently we performed a likelihood ratio test for the full compared to the null model applying an ANOVA.

To find out if there was an overall difference in the amount of trips crossing and positions in the OWFs between the years, we calculated the percentage of trips and positions within the OWFs for each individual bird. We estimated the percentage of trips inside the OWF for trips with > 3 positions in the OWF and the overall percentage of positions inside the OWFs. We then applied LMMs to test if the percentage inside the OWF changed depending on the year, controlling for by-individual variability. Subsequently we performed a likelihood ratio test for the full compared to the null model applying an ANOVA. We furthermore grouped the results in different categories: 0%, 0.01–10%, $>$ 10% of trips passing through an OWF and 0%, 0.01–1%, $>$ 1–2% and $>$ 2% of positions inside the OWFs.

2.3. Behavioural classification

Behavioural states were identified by expectation-maximization binary clustering (EMbC, Garriga et al. 2016), as a robust non-supervised multivariate clustering algorithm that minimises prior assumptions and favours a semantic interpretation of the final clustering by splitting the input features into low and high values of speed and turning angle (Garriga et al. 2016). This offers a new approach to the classification of behavioural states and has already been successfully applied in several studies (Mendez et al. 2017; Jones et al. 2018). The algorithm assigns each location to one of the following four clusters (see Supporting Information S1, Table S1): high velocity/low turn (HL), high velocity/high turn (HH), low velocity/low turn (LL), and low velocity/high turn (LH). HL was interpreted as 'travelling/commuting' behaviour, the two states with low speeds (LL, LH) were merged into one and interpreted as 'resting', and HH was identified as 'foraging' behaviour (see Supporting Information S1, Table S1). EMbC analysis was conducted using the R package EMbC v2.0.1 (Garriga et al. 2018), and a smoother function was applied to account for temporal association in behavioural states.

The areas in which the different behavioural states were shown were visualized by assigning kernel densities of the positions to each category in ArcGIS using the ArcMET tool (version 10.2.2v3; Wall 2014). We furthermore investigated how close the gannets approached the single wind turbines during the different behavioural states, and we additionally used the 1-s intervals of the GPS bursts (c.f. below) to investigate which distances to the single turbines the gannets preferred while being in the OWF. For further details on both approaches, see Supporting Information S3.

2.4. *Flight heights*

Altitude estimates are improved by increasing the satellite-connection time (e.g. Corman and Garthe 2014). The e-obs devices were thus programmed to record GPS positions every second during bursts of 15 s duration (if the tag battery allowed), in addition to the normal GPS schedule. Variability of altitude measurements was quantified by conducting tests at two locations of known height, a rooftop (13.5 m) and nest (53 m), which showed mean values of 12.8 m ($\pm$2.3 m SD) and 53.4 m ($\pm$5.8 m SD), respectively. After inspection of the data, we decided to use bursts of $\geq$ 11 s duration for flight-height analysis. Appropriate data were available for eight gannets tagged in 2016. We analysed flight heights as described by Garthe et al. (2017b), with slight modifications. Briefly, if the last flight height measurement in a burst differed by $>$ 5 m from the preceding one, probably indicating a flight manoeuvre, we used the preceding measurement rather than the last one and assumed the best altitude estimate. We excluded the positions of resting birds using the EMbC method (see 'behavioural classification'). Using ArcGIS (version 10.3; Environmental Systems Research Institute (ESRI), 2016) we retrieved the information if a GPS-position with an associated flight height measurement was located inside the OWF (no buffer around OWF borders) or outside the OWF (= *owf_yn_height*). To find out if the gannets changed their flight heights inside compared to outside the OWF, we applied a generalised additive mixed model (GAMM) with the flight height as dependent variable and *owf_yn_height* as predictor. The appropriate probability distribution was chosen based on the AIC. We furthermore included the individual bird-ID as random factor to control for by-individual variability, and finally added the relevant autocorrelation terms. We additionally investigated the possible effect of the distance to single wind turbines on the flight height inside the OWFs (for further details, see Supporting Information S3).

2.5. *Statistical modelling*

2.5.1. *Preparation of covariates*

The means of the spatial covariates for a grid with a spatial resolution of 200 × 200 m were calculated using ArcGIS (version 10.3; Environmental Systems Research Institute (ESRI), 2016). The variables used for modelling included (1) *owf_yn* = a categorical variable indicating if the grid cell lies inside the OWF (no buffer around OWF borders) or outside the OWF, (2) *dist_Helgoland* = minimal distance of the grid cell to the island of Helgoland, (3) *depth* = mean water depth in the grid cell, and (4) *slope* = inclination of the seabed in the grid cell.

2.5.2. *PPMs*

We determined if the habitat use by gannets was affected by the presence of OWFs by applying a spatio-temporal-PPM (realized within the GAMM framework) to a dataset consisting of 49,185 raw data points collected in 2015 and 38,581 data points collected in 2016. We concentrated the analysis on an area of up to 15 km from the OWF border (Fig. 2a and b) as we aimed to understand the gannets reactions in close vicinity of the OWFs. Limiting the size of the study area to a 15 km buffer around the OWFs furthermore helped to minimize a possible bias by other factors (e.g. fishing vessels) which could not be included in the model, and moreover reduced possible influences of the natural high-density area very close to the colony (Fig. 2). Finally, we considered different covariates within the analysis (such as distance from the colony, depth, or slope), in order to distinguish between the OWF effect and the partial effect of these factors which could have influenced the spatial distribution within the chosen radius. Thus, the size of 15 km was the optimal compromise comprising enough data on the one hand and minimizing the possible influence of external factors on the other hand. We have furthermore chosen to concentrate our analysis on the OWF cluster close to Helgoland as we aimed to investigate how gannets react towards OWFs in close vicinity of their colony. For a sound analysis of the reactions to OWFs further apart from the colony, data were too sparse for the current analysis. Each year was analysed separately as the construction status of the OWFs was different in 2015 and 2016. Only the fully commissioned and operating OWFs were considered in the analysis.

Statistical analysis of telemetry data investigating resource selection is often challenging, and various modelling strategies have been developed, including (integrated) step selection functions (Thurfjell et al. 2014; Avgar et al. 2016) and point process approaches (Johnson et al. 2013; Renner et al. 2015). Both approaches use contrasting points (e.g., 'dummy points', 'pseudo-absences', or 'available steps') in addition to true tracking locations, making it possible to compare selected versus available resources. Methods using contrasting points tend to produce better results than techniques using presence points alone (Brotons et al. 2004; Elith et al. 2006; Barbet-Massin et al. 2012).

In the following analysis, we used and extended the spatio-temporal PPMs presented by Renner et al. (2015), which naturally and automatically resolve many of the questions and pitfalls associated with alternative approaches (Warton and Shepherd 2010; Warton and Aarts 2013; Renner et al. 2015). For example, the role and number of dummy points is not *ad hoc*, but can be deduced mathematically by the efficient estimation of an integral as a part of the PPM likelihood (Warton and Shepherd 2010; Warton and Aarts 2013). Additionally, PPMs represent a generalisation of many other frequently used methods (Johnson et al. 2008; Warton and Shepherd 2010; Aarts et al. 2012). Finally, the PPM likelihood can be approximated by a mathematical method using standard generalised linear or additive mixed modelling-regression software (Johnson et al. 2013; Renner et al. 2015), ensuring flexible and individual implementation. Details of the modifications of the PPMs compared with the spatio-temporal PPMs are presented by Johnson et al. (2013) (see Supporting Information S2).

2.5.3. *Model selection.*

When applying the GAMM-PPM to the tracking raw data, convergence of the log-likelihood was approached after two cycles of refinement of the dummy point mesh in 2015 and one cycle of refinement in 2016 leading to 357,252 respectively 43,607 dummy points.

The optimal model regarding the set of fixed-effect predictors was selected by comparing 12 different models for each year, based on the Akaike Information Criterion (AIC; Akaike 1973). Inspection of the results of the best models showed that all models revealed similar patterns in the data, indicating that our main results were robust across different models. We first inspected a basic model only including autocorrelation terms, random effects, and the variable *owf_yn*, which was the main focus of the analysis:

$$Z \sim \beta + te\left(log_{d_t}, log_{d_s}, angle,\ k = c(5,5,5)\right) + s(trip_{id}, bs = \text{'}re\text{'}) + s(bird_{id}, bs = \text{'}re\text{'}) + owf\_yn \quad (1)$$

where β is the intercept and *te()* a tensor-product regression spline considering temporal, spatial and directional autocorrelation, where the optimal number of knots (maximal 5 per variable to avoid over-smoothing) has been estimated via generalised cross-validation. $Trip_{id}$ and $bird_{id}$ where included as random effects, indicated by the term *s(…, bs = 're)*. In order to approximate the PPM likelihood based on standard

GAMM software, a weighted regression Poisson model has been fitted, using regression weights *W* and observations *Z*, where Z = 1/W has been defined for tracking points, and Z = 0 for dummy points. Especially, *W* are appropriate quadrature weights based on the 2D rectangle rule (for more technical details see for example Johnson et al. 2013).

We subsequently added other variables to the basic model to find the best model for our data. We restricted the number of variables added to the basic model to a maximum of three to keep the models interpretable. The best model was then selected via the AIC. For the data collected in 2015 the best model additionally included the covariates *dist_Helgoland* and *depth*:

$$Z \sim \beta + te\left(log_{d_t}, log_{d_s}, angle,\ k = c(5,5,5)\right) + s(trip_{id}, bs = \text{'}re\text{'}) \\ + s(bird_{id}, bs = \text{'}re\text{'}) + owf\_yn + dist\_Helgoland + deph \tag{2}$$

For the data collected in 2016 the best model additionally included the covariates *dist_Helgoland* and *slope:*

$$Z \sim \beta + te\left(log_{d_t}, log_{d_s}, angle,\ k = c(5,5,5)\right) + s(trip_{id}, bs = \text{'}re\text{'}) \\ + s(bird_{id}, bs = \text{'}re\text{'}) + owf\_yn + dist\_Helgoland + slope \tag{3}$$

2.5.4. Model validation, numerical realisation, and software

PPM model-validation plots for the final GAMM-PPM were generated based on PPM-Pearson residuals (Baddeley and Turner, 2005; Baddeley et al. 2005). All statistical analyses were performed using the free statistical software R (R Core Team 2017). Spatial statistics were performed using *spatstat* (Baddeley and Turner, 2005), dummy-point meshes and trapezoid rule-based quadrature weights were created using *mvQuad* (Weiser 2016), GAMM and GAM fits were performed using the package *mgcv* (Wood 2006). All the codes were programmed such that the main parts of the code could be run using parallel computing, using the *parallel* package and the *bam()* function from the *mgcv* package.

3. Results

3.1. Overview of foraging trips

We recorded a total of 1182 individual foraging trips by 28 gannets (12 females and 16 males) in 2015 and 2016 (Table 1). Only the mean duration was significantly higher in 2016 than in 2015 (Table 1). The same large-scale area was used for foraging in both years (Fig. 1).

3.2. Avoidance of and attraction by OWFs

3.2.1. Foraging trips

Most individuals mainly avoided the OWFs north of Helgoland ('predominantly avoiding individuals', n = 25, 89% of individuals; Fig. 2) and most foraging trips passed the OWFs at the south-west border (Fig. 2a and b). However, two individuals in 2015 and one in 2016 (all males) frequently entered the OWFs north of Helgoland ('attracted individuals', n = 3, 11% of individuals, Fig. 2c and d) and also visited other OWF areas further from the colony (Fig. 2e and f). Of all individuals tagged in 2015, eight (= 67%) did not enter the OWFs during their foraging trips (Table 2, considering trips with ≥ 3 positions in OWF), two (= 17%) entered the OWFs during 0.01%–10%, and two (= 17%) entered them during > 10% of their foraging trips (Table 2). In 2016, eight (= 50%) did not enter the OWFs, seven (= 44%) entered on 0.01%–10% and one (= 6%) on > 10% of their foraging trips. In 2015, five (= 42%) of the tagged individuals recorded no positions in the OWFs (two = 13% in 2016), four (= 33%) recorded 0.01%–1% (12 (= 75%) in 2016), two (= 17%) recorded > 1%–2% (one = 6% in 2016), and one (= 8%) recorded > 2% of their positions in the OWF (one = 6% in 2016) (Table 2). When comparing the individual amount of trips crossing and positions in the OWFs between the two years, no significant difference in either %-trips or %-positions in OWFs between 2015 and 2016 was found (Table 2).

3.2.2. Behaviour

Differentiating among the behavioural categories foraging, travelling, and resting, showed that individuals 'predominantly avoiding' the OWFs mainly used areas west and north-west of Helgoland (i.e. southwest or west of the OWFs) to commute to and from the colony (Fig. 3a). They seldom entered the OWFs when travelling between the colony and foraging areas. These individuals used many different areas for foraging, some north-west and some north-east of Helgoland, and some located south and north-east of the OWFs (Fig. 3b), but very few located in the OWFs. Additionally, they did not enter the OWFs while resting (Fig. 3c). In contrast, the gannet that was attracted to the OWFs mainly used an area between the island and the OWFs for commuting to and from the colony and frequently entered the OWFs when travelling (Fig. 3d). For this individual, most of its foraging area was located in the OWFs or nearby, north-west of the OWFs (Fig. 3e). In 2015 the individuals attracted to the OWF also used it intensely for foraging, however they additionally foraged outside the OWF (see Supporting Information S4). Only individuals attracted to the OWF in 2015 entered the wind farms while resting (see Supporting Information S4), in 2016 individuals only entered the OWFs rarely or not at all when resting (Fig. 3f). Only data for the 2016 breeding season are shown here, but similar patterns were detected in 2015 (see Supporting Information S4).

The kernel densities of the core foraging areas (25% foraging percentile) of the individuals attracted to the OWFs overlapped with the operating OWFs by 12.5% in 2015 and by 33% in 2016 with one more OWF operational (Table 3). Only 6.5% (7.1% in 2016) of the core travelling and 2.6% (0% in 2016) of the core resting areas of these individuals overlapped with the OWFs in 2015. For individuals predominantly avoiding the OWFs in both years, < 1% of the kernel densities of each behaviour overlapped with the OWFs.

In all three behavioural states and also when analysing the 1-s intervals of the GPS bursts, a preference for the area between 250 and 450 m distance from the turbines was revealed for the gannets when they were inside the OWF (Fig. 4, and Supporting Information S3, Fig. S3; distance between single wind turbines = 600–1200 m). The strongest avoidance was found between 0 and 250 m distance from the turbines (Fig. 4, and Supporting Information S3, Fig. S3). A slightly higher preference for closer distances to the turbines appears for the foraging behaviour, though it was not found to be significant (for further details see Supporting Information S3). The separate visualization of the distance to the turbines for 'attracted' and 'predominantly avoiding' individuals furthermore shows, that when being inside the OWFs, attracted individuals approached the turbines more than individuals avoiding the OWFs (Fig. 4b).

Table 1
Total number of foraging trips in 2015 and 2016, as well as mean values for: duration, maximum distance, and total distance.

	2015	2016	χ^2	*p*-value
Trips (n)	580	602	–	–
Duration (h)	7.83 (0.33–61.23)	10.93 (0.33–116.87)	6.7134	<0.01
Max. distance (km)	38.37 (1.10–388.36)	53.11 (1.10–392.67)	1.9879	0.16
Total distance (km)	110.28 (2.33–1021.17)	139.61 (2.77–1118.53)	0.312	0.58

$\chi^2$and *p*-values for LMMs. Values in brackets indicate the minimum and maximum.

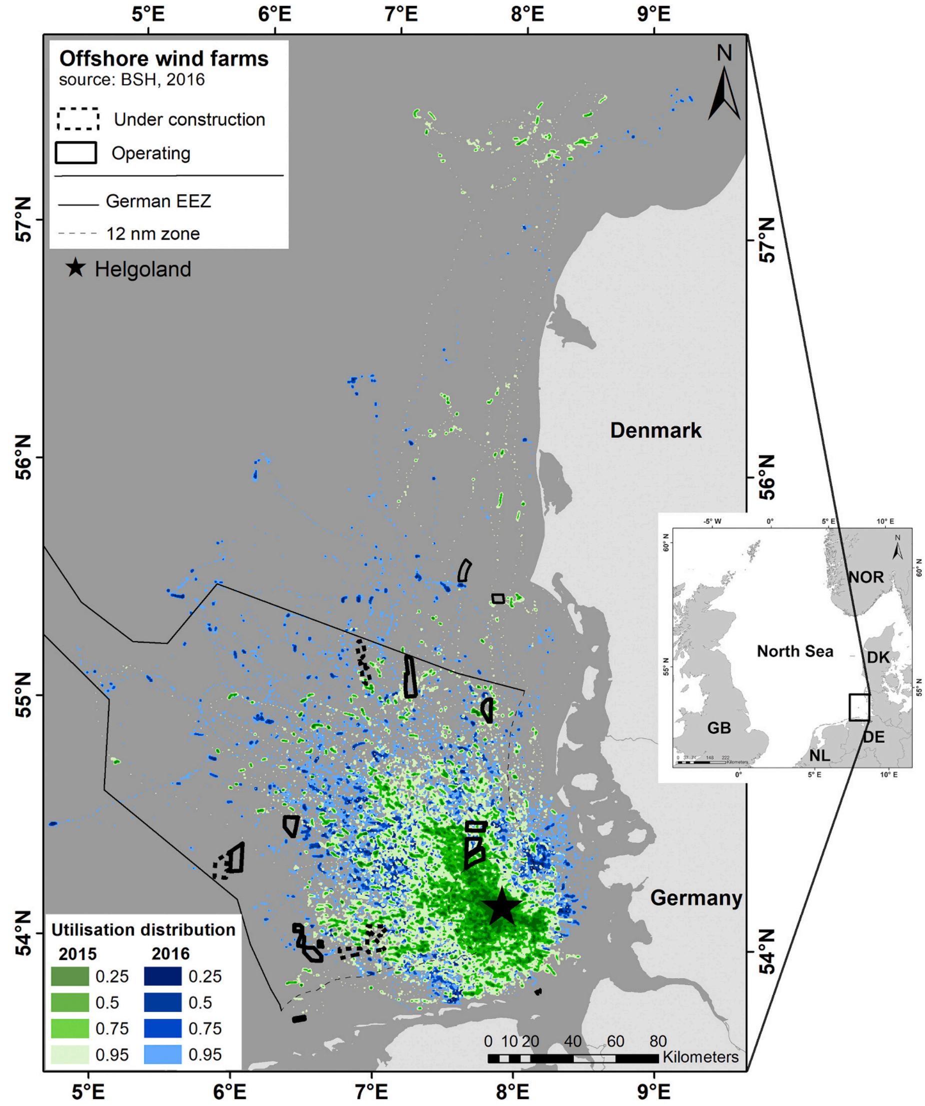

Fig. 1. Kernel densities of northern gannets tagged in 2015 (green) and 2016 (blue). OWF status in 2016: dashed black line = under construction, solid black line = operating. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2.3. *Flight heights*

Gannets flew at significantly higher altitudes inside compared with outside the OWFs (mean height 17.9 m (n = 209) vs 14.4 m (n = 2640), respectively, $p = 0.082$) (Table 4, Fig. 5). Flight heights were mostly below the rotor-blade zone (RBZ; 30–150 m) (Fig. 5). Individuals 'predominantly avoiding' the OWFs showed higher flight heights inside compared to outside the OWFs (mean height 27.3 m (n = 60) vs 14.7 m (n = 2200), respectively, with their mean altitude inside the OWFs just below the RBZ, however the GAMM did not detect a significant effect ($p = 0.287$). The individual 'attracted' to the OWFs flew at significantly higher altitudes inside than outside the OWFs ($p = 0.059$), but mainly used altitudes below the RBZ. Flight heights during travelling were not significantly higher inside than outside the OWFs (mean 17.9 m (n = 91) vs 12.8 m (n = 1645), respectively, $p = 0.157$). There was no significant difference in flight heights during foraging behaviour ($p = 0.413$). Altitudes were significantly higher during foraging compared with travelling (mean 17.8 m (n = 1113) vs 13.7 m (n = 1736), respectively, $p < 0.001$). In most distances to the turbines 'attracted individuals' tended to use lower flight heights than the 'predominantly avoiding' individuals, the latter tending to use increased flight heights with distance to the turbines (Fig. 6). However, no significant change of the flight height with distance to the turbines was revealed (all p-values > 0.1).

3.2.4. *Avoidance strength*

Both the basic and best models revealed a significantly reduced selection of the OWFs compared with the surrounding area in 2015 (basic model, Table 5; best model, Table 6, variable 'inside OWF', estimate = −0.240, p = < 0.001, response = exp(estimate) = 21% reduced selection inside the OWF compared with outside, lower confidence interval (CI) = 30% reduction, upper CI = 11% reduction). Both the basic and best models revealed a significantly reduced selection of the OWFs compared with the surrounding area in 2016 (basic model, Table 7; best model, Table 8; variable 'inside OWF', estimate = −0.461, $p = < 0.001$, response = exp(estimate) = 37% reduced selection inside the OWF compared with outside, lower confidence interval (CI) = 45% reduction, upper CI = 28% reduction).

4. Discussion

This study provides the first detailed characterisation of the reactions of gannets during the breeding season to OWFs, and is one of the first comprehensive studies of these effects based on telemetry data. Gannets' reactions indicated that they were susceptible to OWF effects such as habitat loss, increased flight distances, and collisions, with potential effects on their energy budget and mortality. These findings add to our

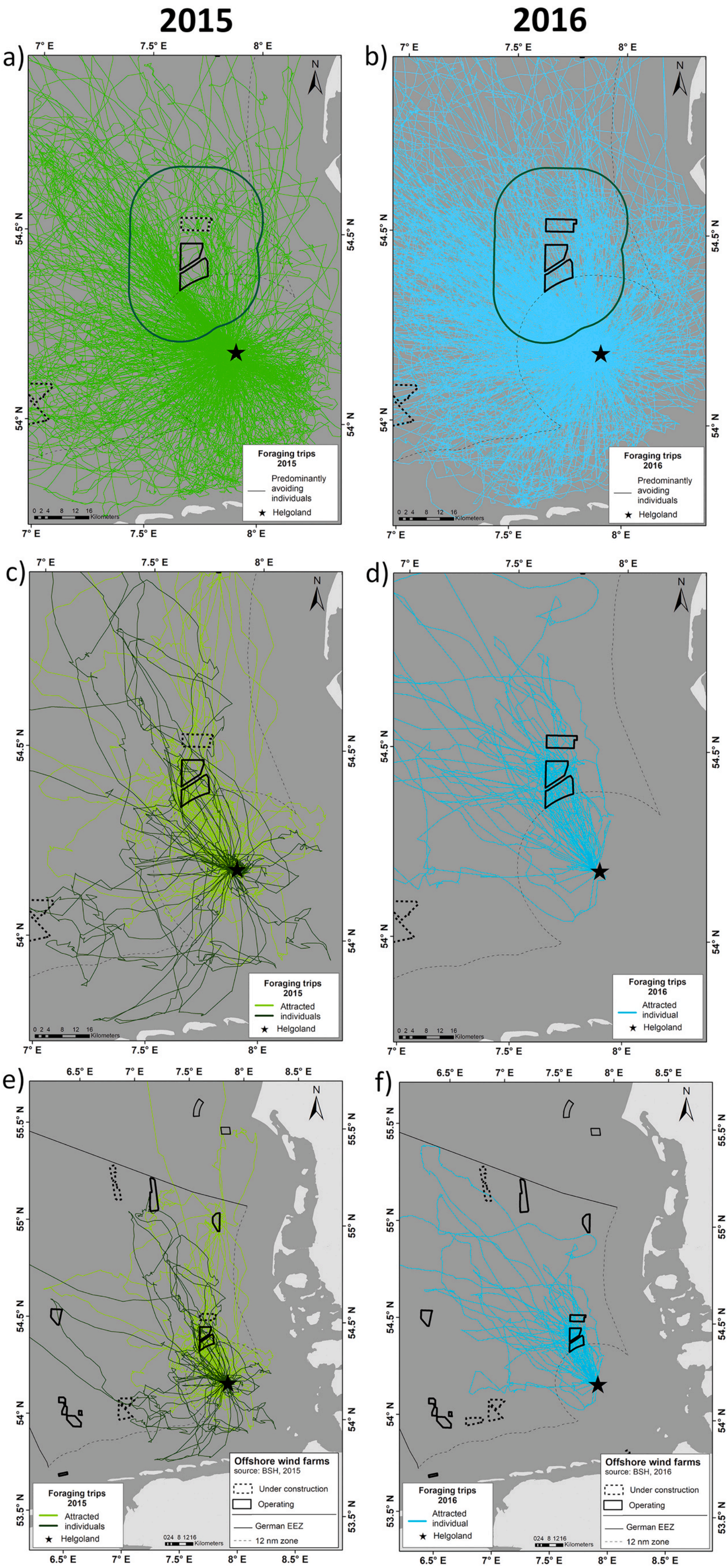

Fig. 2. Flight behaviours of gannets tagged in 2015 (n = 10) (a) and 2016 (n = 15) (b) that 'predominantly avoided' the OWFs (all individuals shown in the same colour). Gannets tagged in 2015 (n = 2) (c) and 2016 (n = 1) (d) that were classified as 'attracted individuals' (individuals shown in different colours). (e) & (f) Large-scale movements of individuals shown in (c) and (d). OWFs: dashed black = under construction, solid black = operating, dark green line = 15 km buffer applied for PPM analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 2
Percentages of individuals in relation to their use of OWFs.

		No. and (%) of individuals		Linear mixed model	
	%	*2015*	*2016*	χ^2	*p*
Trips with ≥ 3 positions in OWF	***0***	8 (67)	8 (50)	0.4069	0.524
	0.01–10	2 (17)	7 (44)		
	> 10	2 (17)	1 (6)		
Positions in OWF	***0***	5 (42)	2 (13)	0.0053	0.942
	0.01–1	4 (33)	12 (75)		
	> 1–2	2 (17)	1 (6)		
	> 2	1 (8)	1 (6)		

OWF = 0 m distance to border of the OWF.

current knowledge regarding the vulnerability of gannets to OWFs in close vicinity to their breeding colonies, and should thus be included in models of collision risks and population-level effects.

Using a PPM approach, we showed that the gannets resource selection of the OWF area was significantly reduced compared with the surroundings in both breeding seasons. The reduction was lower than that reported by line-transect surveys (Vanermen et al. 2015; Welcker and Nehls 2016); however, these studies were estimated for the entire yearly cycle rather than focussing on the breeding period. Gannets might be more flexible in their choice of habitat when they are not bound to their colony and do not need to feed their offspring. In contrast, gannets may accept passing through OWFs more during the breeding season if it reduces their travel time and costs considerably. However, avoidance estimated from survey data (investigating effects on density or abundance of species) cannot be compared directly with values estimated from tracking data (inferring resource selection), and the resulting

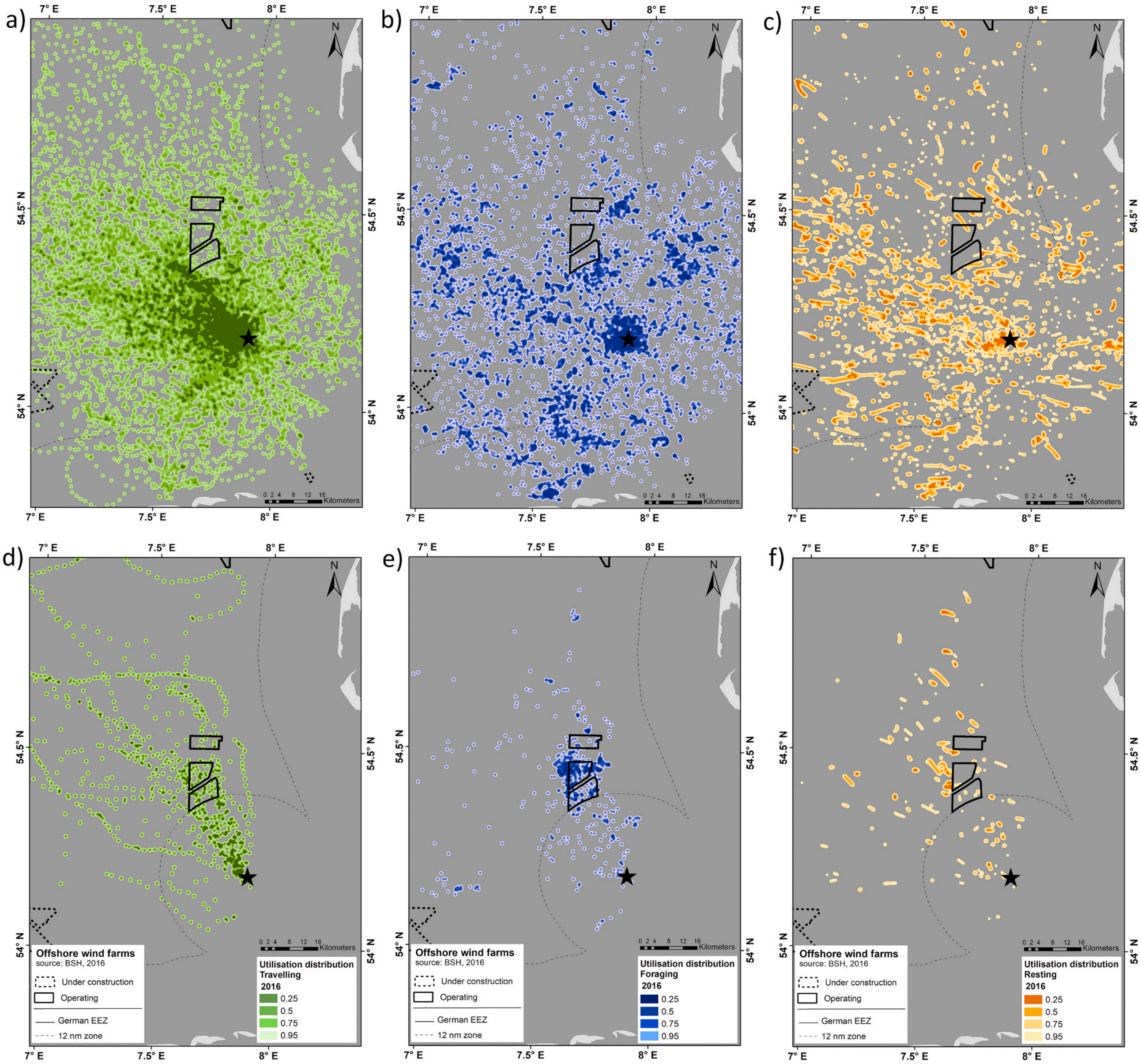

Fig. 3. Kernel densities of travelling (a, d), foraging (b, e), and resting (c, f) positions of gannets tagged in 2016 visualized as percentiles. Dark colour = 25% percentile, light colour = 95% percentile. (a, b, & c) Individuals 'predominantly avoiding' the OWFs, and (d, e, & f) individual 'attracted' to OWFs. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 3
Percent overlap with OWFs (no buffer around the OWFs) for each behaviour and individuals often using (= 'attracted') or predominantly not using (= 'predominantly avoiding') the OWFs in 2015 and 2016.

		Foraging		Travelling		Resting	
Year	Percentile	Ind. using OWFs	Ind. not using OWFs	Ind. using OWFs	Ind. not using OWFs	Ind. using OWFs	Ind. not using OWFs
2015	**25%**	12.47	0.00	6.50	0.00	2.61	0.00
	50%	8.32	0.00	4.76	0.00	2.39	0.00
	75%	5.61	0.05	3.71	0.15	2.77	0.01
	95%	4.16	0.13	2.71	0.33	2.80	0.03
	99%	3.44	0.19	2.17	0.38	2.70	0.06
2016	**25%**	33.39	0.05	7.10	0.05	0.00	0.06
	50%	27.59	0.21	5.86	0.13	0.03	0.20
	75%	18.76	0.36	5.42	0.46	1.09	0.20
	95%	13.32	0.49	4.67	0.60	2.57	0.24
	99%	10.88	0.55	4.12	0.64	2.86	0.26

reduction in resource selection is not readily comparable to the reduction in abundance.

Our study also showed that 89% of gannets predominantly avoided the OWFs, which thus created a barrier effect and/or habitat loss. Displacement could lead to an increase in foraging-trip length and energy expenditure, especially during the breeding season, with consequent effects on energy and time budgets (Masden et al. 2010; Searle et al. 2014). This could in turn reduce adult condition or survival (Masden et al. 2010) and lead to a decrease in chick growth rates and survival, ultimately reducing reproductive success (Langton et al. 2014). We can currently only speculate on how the strength of the reaction towards the OWFs affects the birds' energy budgets and reproductive success. However, if individuals in other colonies react similarly to OWFs in the vicinity, this could for example have a strong impact on the world's largest breeding colony on the Bass Rock in Scotland, UK (~75, 000 breeding pairs in 2014; Murray et al. 2015). Effects on (sub)populations thus need to be considered.

Behavioural analysis showed that birds avoiding OWFs predominantly used areas to the south-west of the OWFs for commuting between the colony and foraging areas. These areas were already intensely used before the OWF construction (Garthe et al. 2017a). However, the close proximity of the intensely used areas to the south-western tip of the OWFs strongly underlines the influence of the OWF on the gannets' flight directions.

Birds avoiding the OWFs are less prone to collide with turbines. However, they sometimes entered the OWFs, and although no significant difference was found between inside and outside the OWFs for gannets predominantly avoiding the OWFs, flight heights measured on these occasions showed that they flew at altitudes just below or inside the RBZ. Thus, gannets that predominantly avoid the OWFs appear to fly at altitudes inside the OWFs that could increase their collision risk. The reason why birds tended to fly higher inside compared with outside the OWFs remains unclear and should be investigated in future studies with larger sample sizes. However, when gannets were inside the OWFs flight heights of individuals predominantly avoiding the OWFs tended to increase with the distance to the turbine (though no significant change was found). Individuals predominantly avoiding the OWFs did not approach the turbines closely (shortest distance = 79 m), but preferred to stay between 250 and 450 m distance to the turbines (similar to the attracted individuals, spacing between turbines = 600–1200 m), which correlates with half the distance between neighbouring turbines. Gannets hence preferred to stay in areas which were as far as possible from the turbines, predominantly in the middle between the turbine rows. It can thus further be concluded, that gannets which predominantly avoided the OWFs used flight heights inside the OWFs which increased their risk to collide with the turbines, but also preferred distances to the turbines which would in turn reduce their collision risk. These findings hence suggest, that actual collision risk inside the OWFs is moderate, however, further studies with larger sample sizes of flight height and distance to turbines are needed to confirm the here presented findings. Moreover, bad weather conditions decrease manoeuvrability of flying birds, which can lead to higher collision risk during such periods.

In contrast to the avoidance behaviour shown by most gannets, three

Table 4
Flight heights of eight gannets tagged in 2016 inside and outside the OWFs.

			Altitude (m)			GAMM
Bird	Location	n	Mean	SD	Median	*p-value*
All	inside OWF	209	17.9	17.9	15.9	0.082
	outside OWF	2640	14.4	18.0	10.7	
Attracted	inside OWF	149	14.2	12.3	14.3	0.059
	outside OWF	440	12.7	15.4	9.6	
Avoiding	inside OWF	60	27.3	24.9	23.3	0.287
	outside OWF	2200	14.7	18.5	10.7	
Travelling	inside OWF	91	17.9	19.2	14.3	0.157
	outside OWF	1645	12.8	17.6	7.4	
Foraging	inside OWF	118	18.0	16.8	16.5	0.431
	outside OWF	995	16.9	18.4	14.9	

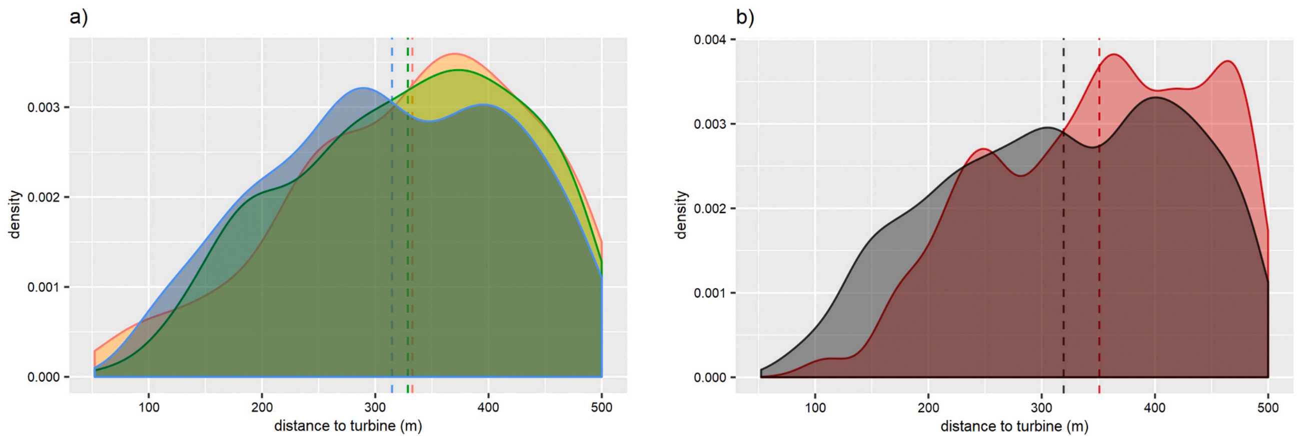

Fig. 4. Density plots of the distance to the single wind turbines when gannets were inside the OWFs for a) based on all positions in 2015 and 2016 for which behavioural states were detected (n = 959); Orange = resting, green = travelling, blue = foraging. b) Density plot based on 1-s interval GPS-positions collected in 2015 and 2016 (n = 5146) for individuals 'attracted' to the OWF (dark grey, no. positions = 2994) and individuals 'predominantly avoiding' the OWF (red, no. positions = 2152). Dashed lines indicate the mean values. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

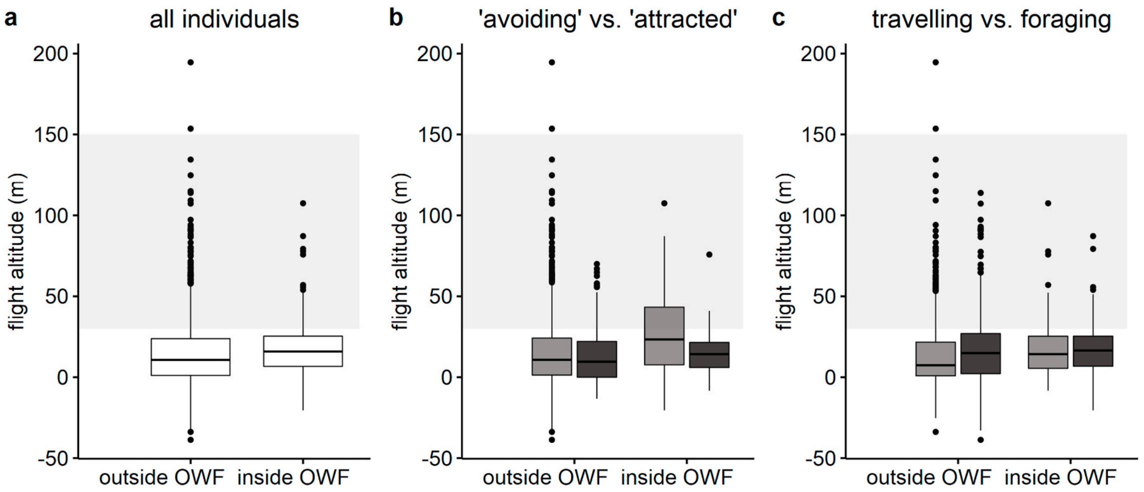

Fig. 5. Flight heights outside and inside OWF for (a) all birds, (b) 'predominantly avoiding' (light grey) and 'attracted' (dark grey) individuals, and (c) travelling (light grey) and foraging (dark grey). Grey background = rotor-blade zone.

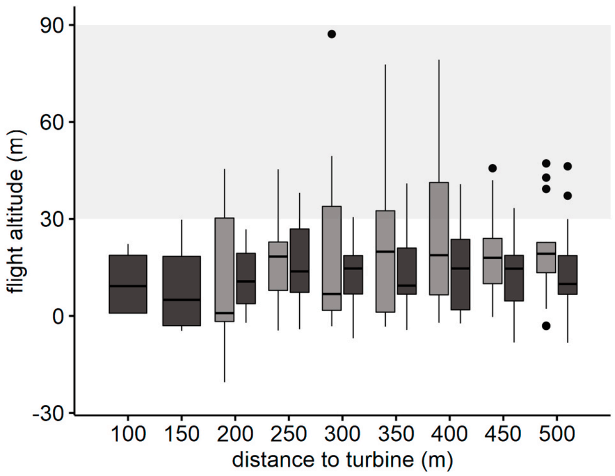

Fig. 6. Flight height with distance to the turbines for the individual 'attracted' to the OWF in 2016 (dark grey, n = 1) and individuals 'predominantly avoiding' the OWF in 2016 (light grey, n = 15). Grey background = rotor-blade zone.

Table 5
Results of basic point process model for 2015.

Parametric coefficients	Estimate	Standard Error	z value	Pr(>|z|)
(Intercept)	2.805	0.098	28.598	<2e-16
inside_OWF	**−0.231**	**0.062**	**−3.704**	**< 0.001**
Smooth term	edf	Ref.df	χ^2	*p*-value
te(log_ds,angle, log_dt)	73.893	83.840	35113	<2e-16
s(trip_id)	147.508	166.000	7393	<2e-16
s(bird_id)	1.769	11.000	1250	0.005

Parametric coefficients and smooth terms are shown. Terms relevant to the analysis of OWF effects indicated in bold.
edf = estimated degrees of freedom; Ref.df = reference degrees of freedom.

Table 6
Results of the best model for 2015.

Parametric coefficients	Estimate	Standard error	z value	Pr(>|z|)
(Intercept)	3.293	0.230	14.315	<2e-16
inside_OWF	**−0.240**	**0.063**	**−3.825**	**<0.001**
dist_Helgoland	0.017	0.002	6.837	<0.001
depth	0.036	0.007	5.039	<0.001
Smooth terms	edf	Ref.df	χ^2	*p*-value
te(log_ds,angle, log_dt)	73.944	83.900	35386	<2e-16
s(trip_id)	147.439	166.000	7276	<2e-16
s(bird_id)	1.737	11.000	1193	0.005

Parametric coefficients and smooth terms are shown. Terms relevant to the analysis of OWF effects indicated in bold.
edf = estimated degrees of freedom; Ref.df = reference degrees of freedom.

Table 7
Results of basic point process model for 2016.

Parametric coefficient	Estimate	Standard error	z value	Pr(>|z|)
(Intercept)	0.587	0.099	5.941	<0.001
inside_OWF	**−0.423**	**0.066**	**−6.392**	**<0.001**
Smooth term	edf	Ref.df	χ^2	*p*-value
te(log_ds,angle, log_dt)	72.061	83.220	13801.300	<2e-16
s(trip_id)	114.992	139.000	11642.400	<2e-16
s(bird_id)	0.916	15.000	124.600	0.141

Parametric coefficients and smooth terms are shown. Terms relevant to the analysis of OWF effects indicated in bold.
edf = estimated degrees of freedom; Ref.df = reference degrees of freedom.

individuals entered the OWFs frequently. These birds foraged intensely, and in 2016 even predominantly, in the OWFs. Foraging conditions close to or inside the OWFs might be good due to the so called 'reef effect' (Lindeboom et al. 2011), which leads to an increase in benthic structures and hence increased fish diversity and abundance at the turbines (e.g. Stenberg et al. 2015; Vandendriessche et al. 2015). However, we did not find a significant preference for closer distances to the turbines while foraging. Moreover, birds preferred to stay between 250 and 450 m distance to the turbines, and it is currently unknown if the food accessibility is comparable to undisturbed areas, or if foraging in these areas is beneficial and can sustain breeding success.

The individuals that were attracted to the OWFs were not prone to displacement, but their risk of colliding with the turbines was generally increased as they often entered the OWFs and stayed there for foraging. The flight height of the bird that frequently entered the OWFs in 2016 was higher inside compared to outside the OWFs but generally below the RBZ both while inside and outside the wind farm. This could indicate an individual preference for flying at this height, irrespective of the presence of the OWF, and a larger sample size is therefore needed to determine if birds attracted to and using OWFs might adapt their flight height to altitudes below the RBZ.

Gannet flight heights were measured as part of a recent study

Table 8
Results of the best model for 2016.

Parametric coefficients	Estimate	Standard error	z value	Pr(>|z|)
(Intercept)	1.207	0.110	10.997	<2e-16
inside_OWF	**−0.461**	**0.067**	**−6.874**	**<0.001**
dist_Helgoland	−0.017	0.001	−14.275	<2e-16
slope	−1.711	0.375	−4.567	<0.001
Smooth terms	edf	Ref.df	χ^2	*p*-value
te(log_ds,angle, log_dt)	73.297	84.420	13284	<2e-16
s(trip_id)	114.984	139.000	12033	<2e-16
s(bird_id)	0.932	15.000	132	0.124

Parametric coefficients and smooth terms are shown. Terms relevant to the analysis of OWF effects indicated in bold.
edf = estimated degrees of freedom; Ref.df = reference degrees of freedom.

modelling gannet collision risks with future OWFs located <50 km from breeding colonies in Scotland, UK (Cleasby et al. 2015). They revealed that predominantly foraging birds would be at risk of collisions because they flew at rotor-blade height, whereas commuting birds flew below the rotor blade height. We also found higher flight heights during foraging compared with travelling. However, although gannets breeding on Helgoland generally flew at higher altitudes inside OWFs compared with outside, they predominantly flew below the rotor blades. The turbines may exert wake effects that could potentially affect the birds' flight manoeuvrability (Stevens and Meneveau, 2017), which potentially causes them to avoid the area close to the rotor blades. The tendency to fly higher inside OWFs nevertheless increases their risk of colliding with the turbines. A larger sample of flight heights inside OWFs is needed to clarify the gannets' behaviours and draw conclusions about the actual collision risk. More data on other parameters, like the position of the birds with respect to the single turbines as well as their distance to the turbines during the different behavioural states, are furthermore needed to better understand the gannets risk to collide with the turbines.

During this study, individuals tagged in both years showed no distinctive patterns in their reaction towards OWFs to allow any conclusions to be drawn on a possible change with time. The resource selection of the OWF areas decreased from 2015 to 2016. This could indicate an increased avoidance of the OWFs and thus an increasing habitat loss with time. However, as the values did not differ significantly, future studies including more years are needed to demonstrate if and how the gannets' reactions towards OWFs change over time, at both the individual and sub-population (Helgoland) levels.

The effects documented in the current study are of considerable relevance to other gannet colonies, and should be considered during the planning of future wind farms, especially when located close to large seabird colonies (e.g. the Bass Rock, Scotland, UK), with the potential to affect large numbers of individuals. This study provides fundamental information that will improve models of collision risk and population-level effects in relation to seabirds and OWFs.

Credit author statement

VP, SG & BM developed the idea for the manuscript. VP, SG, JD conducted fieldwork in 2015 and 2016. MM and VP developed the statistical modelling approach. VP analysed the data. VP wrote the manuscript. SG, BM, JD and MM reviewed and approved the manuscript. BM, SG and VP acquired the financial support of the project.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2020.111509.

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