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ORIGINAL RESEARCH

Cumulative effects of offshore wind farms on common guillemots (*Uria aalge*) in the southern North Sea - climate versus biodiversity?

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Abstract
Governments are under increasing pressure to reduce greenhouse gas emissions, and large-scale wind farms are being developed in marine environments worldwide. However, top predators are strongly affected by environmental change and anthropogenic activities. Common guillemots (*Uria aalge*, hereafter guillemots), as one of the world's most numerous seabird species, are prone to interference with offshore wind farms (OWFs). This study assessed the cumulative impacts of all operating OWFs on guillemots in the German North Sea. These estimates were applied to quantify the possible conflicts between guillemot occurrence and current German government plans to implement large-scale OWFs. If OWFs were implemented according to the current maritime spatial plan for the German Exclusive Economic zone, they would cover 13% of the German North Sea. Guillemot numbers peak during autumn, with German North Sea offshore waters hosting approximately 90,000 individuals. Guillemot density in autumn was significantly reduced within a radius of 19.5 km around operating OWFs. Applying this disturbance distance to current installation plans, about 70% of the German North Sea would be affected, and an estimated 68% of guillemots in the German North Sea would experience habitat loss. This highlights the possible threat to guillemots in the southern North Sea if the current German government plans are implemented. The current estimates are highly relevant to decisions regarding marine spatial planning and management recommendations. Such evaluations are essential for developing sustainable scenarios including reducing the human CO_2 footprint, whilst also conserving biodiversity.

Keywords Offshore wind farm · Marine spatial planning · Environmental impact · Habitat loss · Cumulative impact · *Uria aalge*

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Extended author information available on the last page of the article

Introduction

Rapid progress in climate change (IPCC 2018, 2021) has increased the commitment of governments to reduce greenhouse gas emissions (UNFCCC 2015a, b; European Commission 2019, 2021). In addition, the current international political situation has highlighted the need for western countries to become independent of foreign mineral oil and gas supplies (The Federal German Government 2023). Renewable energy resources are thus of increasing importance to allow for a change in energy supply on a global scale. Large-scale offshore wind farms (OWFs) are thus being planned and constructed worldwide (4COffshoreWind 2023; WindEurope 2022). To cover the expected electricity demands, the EU strategy on offshore renewable energy targets an installed capacity of 300 GW of offshore wind by 2050 (European Commission 2020). A report commissioned by the wind energy industry expects 85% of the OWF capacity to be developed in northern Europe (i.e., 380 GW), with 212 GW potentially implemented in the North Sea (WindEurope 2019). In the recently signed Esbjerg Declaration, Denmark, Belgium, The Netherlands, and Germany agreed to develop the North Sea as a European Green Power Plant, with the objective of delivering > 50% of the energy needed for the EU to achieve climate neutrality. Installed offshore wind capacities of ≥ 65 GW by 2030 and at least 150 GW by 2050 are needed to reach this target (The Federal German Government 2022). Under increasing pressure to address the climate crisis, the German target for OWFs in its Exclusive Economic Zone (EEZ) was also increased from 15 GW by 2030 (BSH 2017) to ≥ 30 GW by 2030, ≥ 40 GW by 2035, and ≥ 70 GW by 2045 (The Federal German Government 2021; Deutscher Bundestag 2022).

However, offshore waters provide essential habitats for top predators, such as seabirds and marine mammals (Schreiber and Burger 2001; Wilson and Mittermeier 2014), resulting in potential conflicts with the planned large-scale development of offshore renewable energy. Top predators are already strongly affected by environmental changes, e.g., through climate change and changes at lower trophic levels (Croxall et al. 1999; Descamps et al. 2017; Dias et al. 2019), as well as by anthropogenic activities (Frederiksen et al. 2004; Dias et al. 2019). Top predators are thus important indicators of the state of our ecosystems (Parsons et al. 2008; Sergio et al. 2006; Velarde et al. 2019), and play a central role in the health of the marine environment (Duffy 2003; Estes et al. 2011; Wilmers et al. 2012). On a global scale, climate change is currently one of the greatest threats to seabirds (Dias et al. 2019); however, the expansion of renewable energy production has strong impacts on seabirds and adds to existing threats (Dias et al. 2019; Garthe et al. 2023). The implementation of OWFs fundamentally changes the ecological characteristics of the construction areas (e.g., de Mesel et al. 2015; Vandendriessche et al. 2015; Daewel et al. 2022), leading to substantial decreases in habitat availability for various species (Dierschke et al. 2016; Garthe et al. 2023). Reactions to OWFs vary between avoidance and attraction (Perrow 2019; Dierschke et al. 2016), depending on the species, area, and season, potentially leading to increased energy expenditure (Masden et al. 2010) and/or mortality of individuals (Drewitt and Langston 2006).

Anthropogenic activities in the marine habitat have increased greatly, both on a global scale (Halpern et al. 2015, 2019) and in the North Sea (Emeis et al. 2015). The North Sea is already among the most intensively utilised sea areas worldwide, with impacts from activities such as fishing, transport, oil and gas exploitation, and gravel extraction (Halpern et al. 2008, 2019; Emeis et al. 2015). Many top predators, including seabirds, marine mammals, and fish, are affected by the various human activities in the southern North Sea,

e.g., through reduced availability of foraging habitats (Garthe et al. 2023; Peschko et al. 2020a), noise emissions during OWF construction (Dähne et al. 2013; Hastie et al. 2015; Russel et al. 2016), shipping activities (Jones et al. 2017; Fliessbach et al. 2019), or habitat changes after OWF installation (de Mesel et al. 2015; Vandendriessche et al. 2015).

Common guillemots (*Uria aalge*, hereafter guillemot) are distributed widely in the northern Hemisphere (BirdLife International 2021) and is among the most abundant seabird species in the world, and in the North Sea (Skov et al. 1995). Its high abundance means that guillemots are a key seabird species in the southern North Sea. However, the species has previously been shown to have strong reactions to OWFs (see overview by Dierschke et al. 2016; Vanermen et al. 2015; Peschko et al. 2020a, b; Mercker et al. 2021a). Guillemots are listed as being of least concern in the IUCN Red List for the EU member states and for European waters (regional level) (BirdLife International 2021). However, the number of individuals overwintering in German waters decreased by > 75%, representing the strongest decline of all wintering waterbird species in Germany over the past 12 years (Gerlach et al. 2019). The offshore waters of the German North Sea are highly important for guillemots breeding in Europe (Camphuysen and Leopold 1994; Harris et al. 2015; Buckingham et al. 2023). Their abundance and widespread occurrence in the North Sea, their strong but not complete avoidance of OWFs, as well as the existing broad and detailed knowledge of their biology and ecology (e.g., Dunn et al 2020) mean that guillemots are an ideal model species for studying the effects of OWFs on the marine ecosystem.

Using a comprehensive long-term dataset of the distribution and abundance of guillemots, this study aimed to quantify the cumulative effects of all OWFs currently operating in the German North Sea on guillemot occurrence during two sensitive seasons, including autumn, when the highest number of guillemots occurs in the study area. The study also aimed to quantify the conflict between guillemot occurrence in German offshore areas and the German government's current plans to implement large-scale OWFs, and to provide data to inform relevant national and international management plans and decisions regarding the consequences of large-scale construction plans on an important indicator species for the marine ecosystem. Finally, the study aimed to provide an example of the application of knowledge about species distribution, abundance, and species-specific OWF avoidance to provide essential information for future planning of offshore renewable energy installations.

Methods

Study area

The study focused on the German EEZ in the North Sea (Fig. 1), where 22 wind farms with a power of approximately 7 GW were operating as of December 2022 (Fig. 1, BSH 2022a). The German government plans to construct offshore wind farms in the German EEZ with capacities of ≥ 30 GW by 2030, ≥ 40 GW by 2035, and ≥ 70 GW by 2045 (The Federal German Government 2021; Deutscher Bundestag 2022). The maritime spatial plan for the German EEZ defined priority areas for wind energy to ensure the implementation of this increased expansion target of the federal government for 2030 (BSH 2021b, priority areas, Fig. 1), with additional areas reserved to secure sites for further expansion (BSH 2021b, reservation areas, Fig. 1). Plans for OWF implementation in the areas defined by the maritime spatial plan are currently under development but have not been finalised. The current

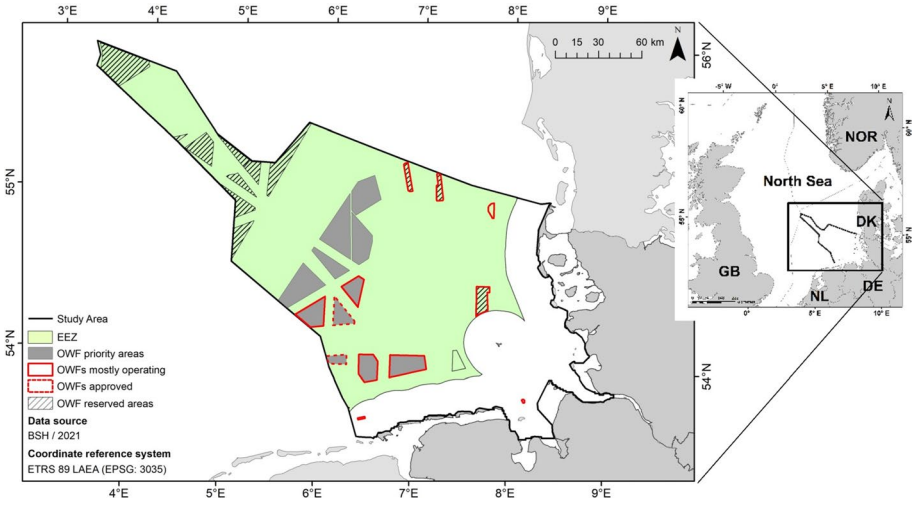

Fig. 1 Location of the study area in the southern North Sea (inserted map) and in the German Bight, indicating locations of the planned OWF areas in the German EEZ based on the maritime spatial plan (dark grey areas = priority areas for OWF implementation by 2030, shaded areas = reserved for OWF implementation by 2035/2040 (BSH 2021a, b); planned OWF areas are visualised according to BSH (2021b)). Red lines = areas with OWFs operating or under construction, dashed red lines = areas with approved OWFs

preliminary draft site-development plan indicates that an area greater than the combined priority and reserved areas included in the maritime spatial plan is needed to implement 70 GW of offshore wind power in the German EEZ (BSH 2023b). This study refers to the priority and reserved areas defined by the maritime spatial plan (BSH 2021b), as shown in Fig. 1, but does not focus on the OWF capacity or the year of the planned implementation, which is subject to change.

Datasets used for analysis of effects of operating OWFs

Data on guillemot occurrence were obtained from aerial and ship-based surveys between 2003 and 2020. The records originate from several seabird monitoring and research projects conducted by the University of Kiel (e.g., the German Marine Biodiversity Monitoring for seabirds on behalf of the Federal Agency for Nature Conservation, Borkenhagen et al. 2019), from monitoring during the construction and operation of offshore wind farms in the German EEZ and from environmental impact studies. The data were collected using ship-based surveys, observer-based aerial surveys, or digital aerial surveys. Details of the field methods are given in Supplementary file 1. The datasets of the different sources were reviewed, harmonised and stored in a combined database (for details of the database, data sources, field methods, and sea states selected for analysis, see Garthe et al. 2015, 2023; Peschko et al. 2020a). Because the effects of OWFs on guillemots during spring and the breeding season are well known (Peschko et al. 2020a, b), the current study was restricted to periods for which there is currently no information on the effects of OWFs on guillemots: autumn (the time between the breeding season and winter; 16. July–30. September, species-specific classification slightly modified from Garthe et al. 2007) and winter (01. October–29. February, Garthe et al. 2007). Autumn is also the season with peak guillemot

numbers in the German North Sea. The final data set comprised a total of 26,307 observations of guillemots and 90,264 km^2 of survey effort. Following the method recently presented by Garthe et al. (2023), the data were assigned to five wind farm clusters based on the minimum distance to the next OWF (after construction) (see also Supplementary file 2 and below). Further information on the data-collection method for this database can be found in Supplementary file 1.

Quantification of wind farm avoidance by guillemots

A 'before–after control impact' (BACI) analysis approach was used to estimate the relative change in guillemot density in the area influenced by OWFs and the response range to the OWFs. An impacted area and a control area were defined (areas or rings depending on the nearest distance to the OWF) and relative comparisons of spatial and temporal differences before and after OWF construction were subsequently used to extract the unbiased OWF impact (Smith 2002; Schwarz 2014; Mendel et al. 2019). We quantified the potential effects of currently operating wind farms using a similar approach to Garthe et al. (2023). We describe the main aspects of the modelling approach below. For further details, please see Garthe et al. (2023).

BACI model covariates

BACI analysis was carried out using generalised additive models, as described in several studies investigating the effects of OWFs on seabirds (e.g., Peschko et al. 2020a; Garthe et al. 2023). To evaluate potential OWF effects on the distribution and abundance of guillemots, the binary variable *period* was introduced and defined for each wind farm cluster separately. The *before* period encompassed the period before any construction work in the wind farm cluster (see Supplementary file 2), and the *after* period started after completion of any construction work at the turbines, for each OWF separately. This approach was chosen because operation started independently for each wind farm in a cluster and an increasing number of OWFs started operating successively during the study period. To minimize the effect of possible long-term changes in guillemot abundance and distribution, the maximum duration of the *before* period was restricted to 6 years (see Supplementary file 2), while the *after* period included all data available until 2020. The length of the *after* period and the time between the *before* and the *after* periods ranged from < 1 year to several years (data used per cluster and OWF is shown in Supplementary file 2), and changes in overall distribution could thus have occurred in the meantime. However, the BACI approach is relatively robust against such changes, by comparing densities outside vs. inside the OWF between the *before* and *after* periods. Hence, the outcome depends on relative changes in OWF-related distributions, and is not influenced by changes in absolute abundance between different periods. The continuous distance to the nearest OWF was described by the variable *dist_owf*, which measured the distance to an OWF that did not exist in the *before* period, to evaluate changes in response to this variable in the *before* vs. *after* periods. All data for ≤ 35 km from any wind farm were used (see Supplementary file 2), while larger distances were not expected to affect the birds (Mendel et al. 2019; Peschko et al. 2020a; Garthe et al. 2023).

The change in density between 'inside affected area' vs. 'outside affected area' was analysed by defining the binary variable *B_dist_owf* (based on *dist_owf*, Garthe et al. 2023), as the OWF area plus various radii of *R* km around the OWFs as 'inside OWF', and all

distances further from the OWF as 'outside OWF'. Different radii ($R = 1$, 5, or 10 km) were applied.

The spatial range of disturbance was investigated by defining an impact area in the shape of a 'belt' around the OWFs, with an inner distance radius x and outer distance radius y to the nearest OWF (see "Habitat loss due to operating OWFs", Supplementary file 2 and Garthe et al. 2023). The area outside the belt was defined as the control area (from outer radius y up to a distance of 35 km), and the area within the belt was not included in the regression. A width of 3 km was chosen for the belt to allow for good spatial resolution of the measured effects, while maintaining a sufficiently large database for each belt. This analysis was increased in a stepwise manner from x = 0 km (comprising the area occupied by the OWFs) to x = 30 km, to determine the distance up to which the BACI effect within the belt was still significant, corresponding to an estimate of the disturbance distance (Garthe et al. 2023).

The spatial distribution patterns in the *before* vs. *after* periods were investigated using the above regression methods but excluding *dist_owf*-related variables from the predictors, to allow for a maximally objective prediction of patterns related to OWF sites. In particular, the dependency on the variables *depth*, *dist_coast*, and the 2D spline depending on spatial coordinates were independently estimated for each period and no information about OWF locations was used (Garthe et al. 2023). For distribution maps, the predict-function of the fitted regression model was used by prescribing detection-related covariate values (sea state, method) to provide optimal detectability (approximating the real number without detectability-dependent loss). Notably however, these patterns do not represent temporally homogeneous situations, given that time frames for the *before* periods differ between OWF clusters and for the *after* periods between OWFs.

Details of the environmental covariates included in the models, BACI regression model structure, model-validation strategy, and calculation of the distribution maps can be found in Garthe et al. (2023).

All statistical analyses, validation procedures, and visualizations were carried out using R software (R Core Team 2023), with the following packages: *ggplot2* (Wickham 2009) for visualizations and plots, *MASS* (Venables and Ripley 2002), *pscl* (Zeileis and Kleiber 2008), and *mgcv* (Wood 2006) for regression analyses, and *Distance* (Thomas et al. 2010) for distance-sampling-related procedures.

Dataset used for analysis of bird patterns in relation to OWFs scenarios

This dataset included Seabirds at Sea data collected during observer-based ship and aerial surveys in the German North Sea from 1990 to 2016, as part of several seabird monitoring and research projects conducted by the University of Kiel (e.g., the German Marine Biodiversity Monitoring on behalf of the Federal Agency for Nature Conservation). Population estimates (Gerlach et al. 2019) and distribution maps for guillemots in the German North Sea in autumn were based on predictions of guillemot abundance generated by an integrative statistical approach (Mercker et al. 2021b). Details of the field methods and methods used to determine abundance estimates and patterns are provided in Supplementary file 1.

Estimation of potential habitat loss due to OWF scenarios

This analysis focused on the distribution and abundance of guillemots in autumn, when guillemot numbers in the German North Sea are highest. The avoidance reaction quantified

for autumn (see "Quantification of wind farm avoidance by guillemots") was applied to their modelled distribution in the German North Sea (see "Dataset used for analysis of bird patterns in relation to OWFs scenarios"), as detailed below.

To estimate the effect of the OWF installation on guillemot abundance, the geographical extents of three different OWF scenarios in the German EEZ were visualised, based on the maritime spatial plan (Fig. 1, BSH 2021b): (a) present situation = currently operating OWFs (approximately 7 GW); (b) priority areas = priority areas for OWF implementation up to 2030 (approximately 30 GW, BSH 2023a) including the present situation; and (c) priority areas + reserved areas = priority + reserved areas for implementation of offshore wind power up to 2035/2040 (roughly 50 GW, BSH 2021a, b, 2022b). These three scenarios were applied to illustrate the changing magnitudes of effects depending on different OWF development scenarios. The area that would be covered by OWFs was calculated for each scenario (see "Possible habitat loss due to OWF scenarios"). The area affected by the OWFs ('affected area') was estimated based on the spatial extent of significant avoidance in autumn (see "Habitat loss due to operating OWFs" and "Possible habitat loss due to OWF scenarios"). The number of guillemots present in the affected area during species-specific autumn (16 July–30 September; Garthe et al. 2007) was extracted, based on their modelled distribution, and this value was set in relation to the total population size of guillemots in the German EEZ and the whole German North Sea, respectively, to estimate the proportion affected (see "Possible habitat loss due to OWF scenarios"). The value of the reduction in guillemot density inside the affected area (obtained from the above BACI analysis) was then applied to assess the number of guillemots actually encountering habitat loss as a consequence of the different OWF installation scenarios.

Results

Distribution patterns before and after OWF installation

High densities of guillemots were found in autumn, in both the *before* and *after* periods, in the submerged portion of the glacial Elbe River valley in the south-east of the study region, as well as in the western and north-western parts of the study region (Fig. 2). In winter, guillemots were concentrated in the south before OWF construction, and additionally concentrated in the north-west after OWF construction (Fig. 3). Some areas of future OWF clusters did not include areas with high densities in the *before* period for either season, but some areas showed medium-to-high densities before construction and very low densities after OWF construction (e.g., autumn & winter: BARD-Cluster, see also Supplementary file 2). After OWF construction, guillemot densities were very low in autumn. Densities after construction were also low in winter in most clusters, except in the southernmost OWF cluster, where medium-to-high guillemot densities were present.

Habitat loss due to operating OWFs

Guillemot abundance declined strongly and significantly after, compared with before construction of OWFs, with a reduction of 91% within the OWFs + 1 km radius (95% confidence interval (CI) = 84%–94% reduction) and 76% within the OWFs + 10 km radius (95% CI = 71%–81%) in autumn, and by 67% within the OWFs + 1 km radius (95% CI = 53%–77%) and 50% within the OWFs + 10 km radius (95% CI = 41%–57%) in winter

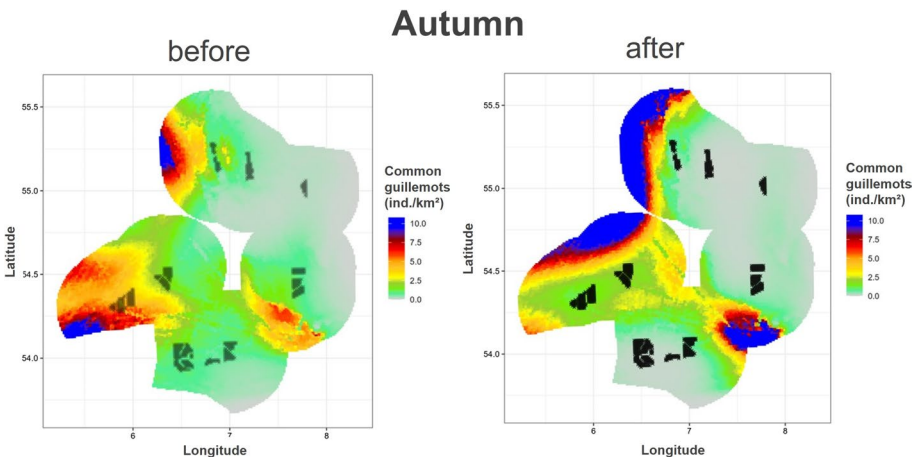

Fig. 2 Predicted density of guillemots in all wind farm clusters in autumn (individuals per km^2) before (left) and after construction of OWFs (right). Future wind farms are indicated in grey (left) and operating wind farms are indicated in black (right). Time periods (before vs. after) for the different OWF clusters differ such that depicted patterns represent an artificial mosaic of spatially varying time frames

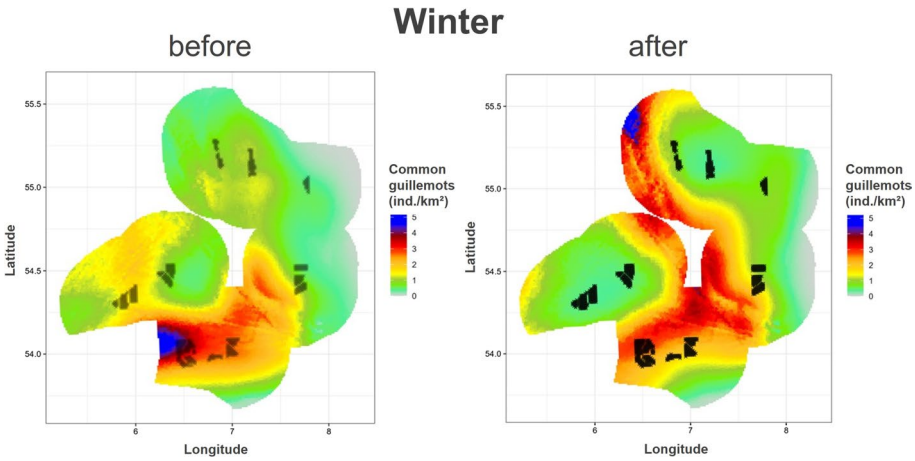

Fig. 3 Predicted density of guillemots in all wind farm clusters in winter (individuals per km^2) before (left) and after construction of OWFs (right). Future wind farms are indicated in grey (left) and operating wind farms are indicated in black (right). Time periods (before vs. after) for the different OWF clusters differ such that depicted patterns represent an artificial mosaic of spatially varying time frames

(Table 1; here statistically significant refers to p-values of $p < 0.05$, which is equivalent to 95% CIs not intersecting with the value zero).

Guillemot density in autumn was significantly affected up to a distance of 18–21 km (mean = 19.5 km) from the border of the OWFs (Fig. 4, mean and 95% CI were below the expected abundance levels based on the ratio during the *before* period, i.e., blue line in Fig. 4), and guillemot density inside this affected area (OWF + 19.5 km radius) was reduced by 79% (95% CI = 74%–83%; Table 1). In winter, the density was significantly

Table 1 Changes in guillemot abundances in autumn and winter and response radius determined by BACI analysis across all OWF clusters

Season	% Abundance change in OWF area (+1 km)		% Abundance change in OWF area (+5 km)		% Abundance change in OWF area (+10 km)		Response radius (km)		% Abundance change in OWF area + response radius	
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Range	Mean	Mean	95% CI
Autumn	−91	−94, −84	−80	−84, −74	−76	−81, −71	18–21	19.5	−79	−83, −74
Winter	−67	−77, −53	−54	−62, −45	−50	−57, −41	15–18	16.5	−51	−58, −42

CI confidence interval

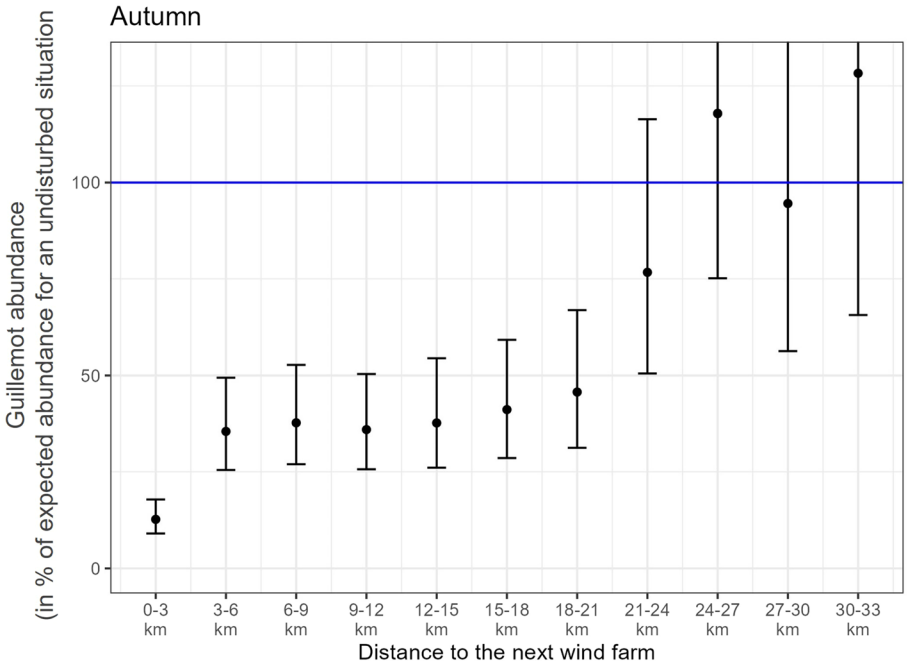

Fig. 4 Relative guillemot abundance after OWF construction in autumn in % of expected abundance without disturbance (100%, blue line). Values shown for stepwise analysis of 3-km-wide belts around the OWFs (x-axis). Mean values = black dots; 95% CIs = length of bars

affected up to a distance of 15–18 km (mean = 16.5 km) from the border of the OWFs (Fig. 5), and guillemot density inside this area (OWF + 16.5 km radius) was reduced by 51% (95% CI = 42%–58%; Table 1).

Possible habitat loss due to OWF scenarios

If offshore wind power was realised within all the currently planned areas (priority + reserved areas + operating OWFs), OWFs would cover 13% of the German North Sea (German North

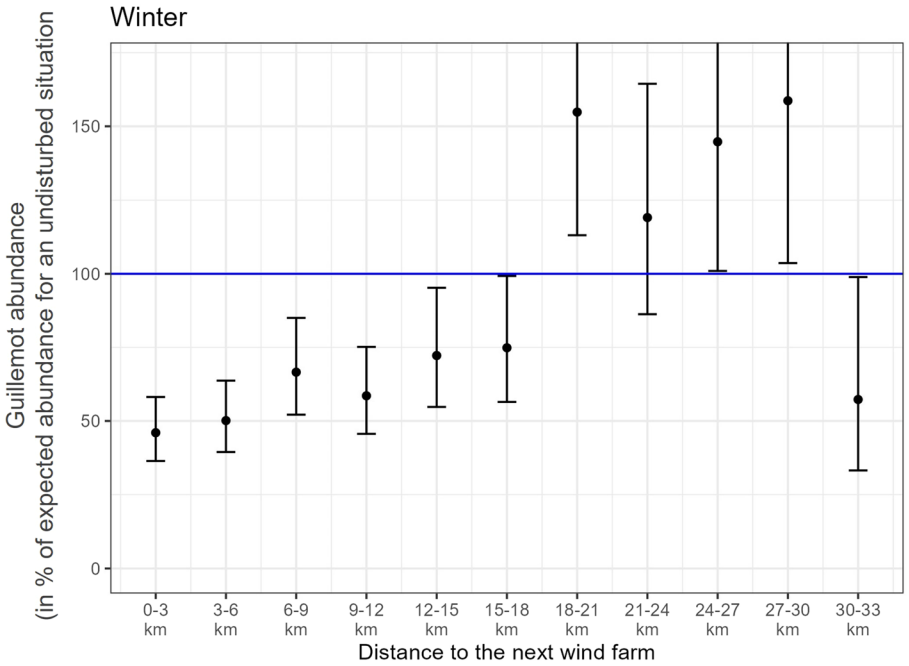

Fig. 5 Relative guillemot abundance after OWF construction in winter in % of expected abundance without disturbance (100%, blue line). Values shown for stepwise analysis of 3-km-wide belts around the OWFs (x-axis). Mean values = black dots; 95% CIs = length of bars

Sea = German EEZ and territorial sea areas combined) and 18% of the German EEZ (Fig. 6, Table 2). The planned OWF areas show substantial overlap with abundance hotspots for guillemots in the German North Sea in autumn (Fig. 6), when the offshore waters host approximately 90,000 guillemots (Table 3).

Applying the response radius of 19.5 km to the OWF areas indicates that 70% of the German North Sea and 82% of the German EEZ would be affected by the planned wind farms (Table 2), including a major part of the core areas used by guillemots in autumn in the German North Sea (Fig. 7). In the present scenario, approximately 26,000 (i.e., 28%) guillemots occurring in the German North Sea use the affected area (Table 3), of which approximately 20,000 individuals experience habitat loss, because the density is reduced by 79% up to a radius of 19.5 km around the OWFs. Thus, in the present scenario, approximately 22% of the German guillemot population in the North Sea in autumn experience habitat loss (Table 3). In the scenario including both priority and reserved areas, approximately 77,000 (i.e., 86%) guillemots in the German North Sea use the potentially affected area (Table 3), of which 61,000 individuals would experience habitat loss due to a reduction in density of 79% up to a radius of 19.5 km around the OWFs. Thus, about 68% of the German guillemot population in the North Sea in autumn would experience habitat loss (Table 3).

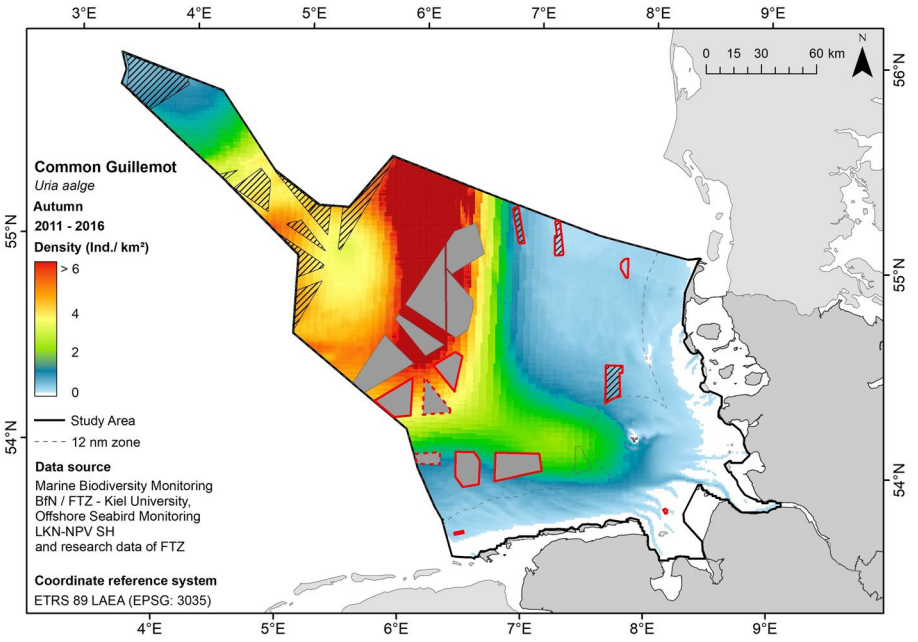

Fig. 6 Modelled distribution of guillemots in the German North Sea (German EEZ and territorial sea areas combined) in autumn. Priority areas for OWF implementation up to 2030 are shown in grey (including OWFs already in use or under construction), shaded areas are reserved for OWF implementation up to 2035/2040 (BSH 2021a, b); solid red lines = operating OWFs, dashed red lines = approved OWFs

Table 2 Areas of German North Sea and German EEZ covered by OWFs in the present situation (including approved OWFs), for OWF priority areas (plus the present scenario), and if all planned OWFs in the priority and reserved areas were constructed

	Area (km^2) German North Sea	% of German North Sea	Area (km^2) German EEZ	% of German EEZ
Present scenario	1,502	4	1,493	5
Present scenario + 19.5 km response radius	15,156	40	12,174	43
Present scenario + priority areas	3,366	9	3,357	12
Present scenario + priority areas + 19.5 km response radius	19,819	53	16,840	59
Present scenario + priority + reserved areas	5,042	13	5,033	18
Present scenario + priority + reserved areas + 19.5 km response radius	26,296	70	23,324	82

Area covered by OWFs and area affected by applying mean 19.5 km response radius is shown. Total area of German North Sea = 37,583 km^2, total area of German EEZ = 28,604 km^2. The German EEZ is listed in addition to the German North Sea, because it is the relevant unit for political decisions

Discussion

Based on extensive data regarding the occurrence of guillemots in the German North Sea, this study examined the impact of currently operating OWFs on guillemot

Table 3 Number of individuals present in the OWF areas for the different OWF scenarios, and percentages of guillemots in the German EEZ and the German North Sea affected by the different scenarios

Autumn	Individuals affected		% Individuals affected		% Habitat loss	
	German North Sea	German EEZ	German North Sea	German EEZ	German North Sea	German EEZ
Present scenario + 19.5 km response radius	26,000	24,000	28	28	22	22
Present scenario + priority areas + 19.5 km response radius	53,000	52,000	59	60	47	48
Present scenario + priority + reserved areas + 19.5 km response radius	77,000	76,000	86	88	68	69

Percentage of guillemot population experiencing habitat loss is also shown. Number of guillemots present in the German EEZ in autumn = 87,000 and in the German North Sea = 90,000. Habitat loss based on the recently estimated density reduction of 79% for guillemots in OWFs plus 19.5 km response radius. The German EEZ is listed additionally to the German North Sea, because it is the relevant unit for political decisions

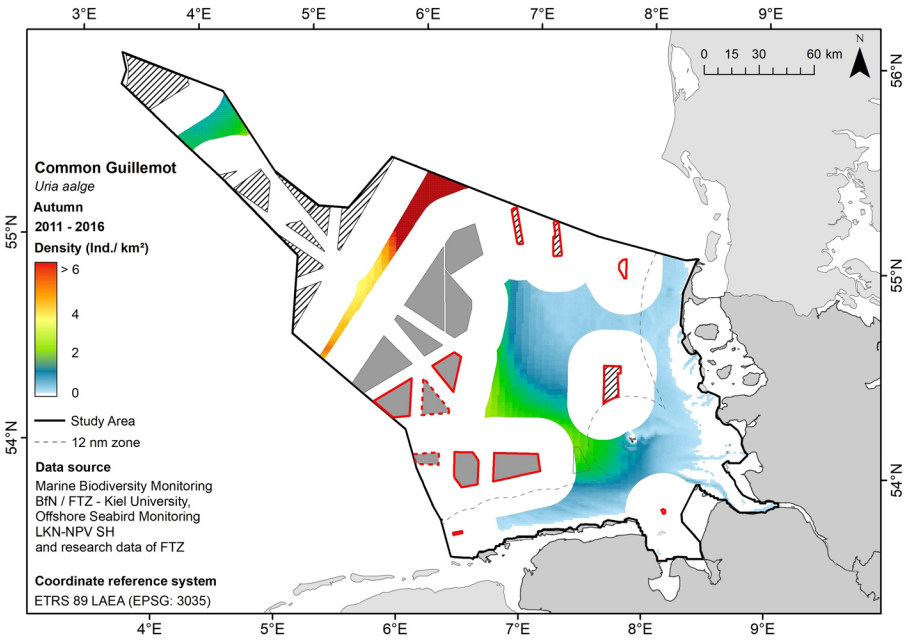

Fig. 7 Modelled distribution of guillemots in the German North Sea during autumn. Priority areas for OWFs up to 2030 are shown in grey (including OWFs already in use or under construction), shaded areas reserved for OWF implementation up to 2035/2040 (BSH 2021a, b); solid red lines = operating OWFs, dashed red lines = approved OWFs. The response radius of 19.5 km around the OWFs is shown in white

abundance in the German North Sea, as well as the possible impact of German plans for further large-scale OWFs in a guillemot hotspot in the southern North Sea in autumn. Large numbers of guillemots are present in the area where OWFs are to be built, making this part of the North Sea an important area for the European guillemot population in autumn (c.f. BirdLife International 2015).

The current results suggest that operating OWFs have a much larger impact on guillemot densities in the German North Sea in autumn and winter than previously reported for other seasons or for the entire yearly cycle (Leopold et al. 2013; Vanermen et al. 2015; Vallejo et al. 2017; Peschko et al. 2020a). Especially in autumn, areas formerly used by guillemots in medium to high numbers were no longer used or were used by fewer guillemots after OWF construction. Although birds tend to be more flexible in their choice of habitat outside the breeding season, the seasons investigated in this study are considered to be especially sensitive for guillemots, encompassing the moulting period in autumn and winter (July to October, Mendel et al. 2008), as well as the period with cold water temperatures and increased energy demand and mortality in winter (Gaston and Jones 1998; Sonntag 2001; Fort et al. 2009, detailed discussion see below).

The following discussion emphasizes the results for autumn, when guillemot numbers in the German North Sea are at their highest; however, the effect in winter is also strong and needs consideration, especially in areas with high numbers of wintering guillemots.

Current plans for future OWFs would affect 70% of the German North Sea for guillemots, leaving limited undisturbed space and alternative foraging areas in German

waters. The only breeding colony of guillemots in German waters is very small (mean of 2,685 breeding pairs on Helgoland between 2000–2019; Dierschke et al. 2011, 2020), and most of the 77,000 individuals that use the affected area of the German North Sea in autumn originate from other colonies, e.g., along the North Sea coast (Camphuysen 2002; Harris et al. 2015; Dunn et al. 2020; Buckingham et al. 2023). The current extent of the planned anthropogenic activities would therefore affect guillemots from different parts of the North Sea.

Applying estimates of guillemot OWF avoidance to data on their abundance and distribution in the German North Sea revealed that 68% of guillemots occurring in this area in autumn are likely to experience habitat loss if offshore wind power is implemented in all the currently designated areas.

Substantial habitat loss can have several consequences for guillemots. The area planned to be covered by OWFs not only serves as a foraging area for guillemots in autumn, but is also important as an area where they moult and rear their chicks in autumn. This has implications for their physical condition and behaviour, given that guillemots are flightless while moulting, which restricts their ability to move (Harris and Wanless 1990; Dunn et al. 2020). A high proportion of adult guillemots have to forage for themselves and their offspring (Harris et al. 1991; Gaston and Jones 1998; Camphuysen 2002; Burke et al. 2015), making them especially dependent on productive foraging areas (Dunn et al. 2020) and vulnerable to changes in habitat conditions. Displacement by large-scale OWFs may prevent access to profitable foraging areas in their usual habitat in autumn. The negative effect in autumn could be further exacerbated, given the high energy demand and auk mortality in winter (Sonntag 2001; Fort et al. 2009; Burke and Montevecchi 2018); if guillemots already experience suboptimal foraging conditions in autumn and start the winter season in poor body condition, their winter mortality is likely to increase. In addition, carry-over effects of poor body condition of guillemot chicks (possibly related to high summer temperatures in 2018) were recently found to be the main cause of a mass mortality event in the southern North Sea in winter 2019 (Leopold et al. 2019). Furthermore, an increased number of individuals sharing a substantially reduced area of foraging habitat will lead to higher intraspecific competition.

It can be speculated that the reef effect (Lindeboom et al. 2011) might increase the abundance of possible prey species in the OWF areas, making them more valuable foraging areas for guillemots in the future. However, most studies have found that guillemots avoided OWFs (Vanermen et al. 2015; Welcker and Nehls 2016; Peschko et al. 2020a, b), despite the increased abundance of some prey species in OWFs in general (Van Deurs et al. 2012; Reubens et al. 2013; Stenberg et al. 2015). Even in the breeding season when guillemots are strongly restricted in their foraging range, GPS tracking showed that individuals strictly avoided OWFs located close to their colony on Helgoland (Peschko et al. 2020b). In contrast, no effect of OWFs on guillemots was detected in the Solway Firth (UK, Vallejo et al. 2017). Estimates for the winter season analysed in the current study revealed that guillemots avoided some OWF areas in the south-western part of the German North Sea less than they avoided other areas further north and east; however, the overall effect for all clusters combined still revealed a strong negative reaction. We assume that the current findings represent the reaction of guillemots in the German North Sea well. When interpreting the current findings however, it is important to consider that the reactions of guillemots towards OWFs in areas of future wind farm developments might differ from the presented effects. Further studies are needed to determine if habituation to OWFs might occur over time, and how guillemots will be affected by future OWF developments, especially as larger areas become occupied by OWFs.

When interpreting the current findings, it is necessary to note that the study only considered direct (e.g., visual) negative effects of OWFs on bird densities, while additional dynamic, large-scale rearrangements could also take place, e.g., displacement of birds into distant regions not covered by the present approach. Thus, future studies should also consider possible dynamic large-scale changes in guillemot distributions due to the presence of future OWFs, to generate a more comprehensive picture of the possible future effects on the guillemot population.

Guillemots are also sensitive to ship traffic (Mendel 2012; Fliessbach et al. 2019), which strongly increases in and around OWFs because of maintenance activities at the turbines and transport to and from the OWFs (Burger et al. 2019; Mendel et al. 2019). The negative effects of OWFs thus extend to areas not directly affected by the turbines. In addition to OWF-related ship traffic, an intensively used ship-traffic lane crossing the southern North Sea from north-east to south-west (Alessandrini et al. 2017; BSH 2020) occupies a large part of the remaining area between the planned OWFs. General ship traffic is expected to increase (OSPAR 2010) and will exacerbate this situation. Furthermore, other anthropogenic activities, e.g., fisheries, will also become concentrated in the space between the OWFs and other available areas, increasing disturbance in these areas and further reducing the space available for guillemots. Alternative foraging areas with similar conditions that might compensate for this lost habitat and are located within an appropriate range will be restricted in German waters and in neighbouring countries which also use their offshore areas intensively and also plan to implement even larger scale OWFs (4COffshoreWind 2023).

Considering the various negative impacts, guillemots occurring in this area could be affected at a population level. If wind farms in Germany are realised as currently planned, 2.5%–3% of the European guillemot population would be affected by habitat loss (based on the European population estimate of 2,350,000–3,060,000 mature individuals; BirdLife International 2015). Moreover, the potential effects presented here do not include plans by other countries neighbouring the German EEZ, which also intend to cover large parts of their offshore areas with OWFs to meet the European goal to implement 300 GW of offshore wind power by 2050 (European Commission 2020; 4COffshoreWind 2023).

This study used a key top predator species in the southern North Sea as an example to assess the possible effects of large scale OWF implementation on the marine ecosystem. The strong disturbance responses exhibited by guillemots, combined with the large-scale implementation of OWFs, need to be considered when evaluating the conservation status of guillemots in the EU, especially in light of strong regional population declines (BirdLife International 2015; Gerlach et al. 2019). It is currently unknown how habitat loss will ultimately impact individual guillemots and whether it will affect the species at the population level. However, there are strong indications that displacement from preferred foraging habitats decreases the body condition, survival, and reproductive success of seabirds (Masden et al. 2010; Langton et al. 2014; Laursen et al. 2016), suggesting that large-scale OWFs have the potential to affect species at a population level (Busch and Garthe 2016).

Climate change is progressing rapidly and all possible efforts are needed to reduce human greenhouse gas emissions (Steffen et al. 2015a; IPCC 2018, 2021). However, the world is simultaneously facing one of the largest biodiversity losses in its history (Butchard et al. 2010; Hill et al. 2018; EEA 2019). Biodiversity is critically important for the stability of ecosystems (Hooper et al. 2012; Hautier et al. 2015; Steffen et al. 2015b) and stopping biodiversity loss is as fundamental for human societies as stopping climate change (Rockström et al. 2009; Cardinale et al. 2012; Steffen et al. 2015b). A sustainable scenario to reduce the human CO_2 footprint is therefore needed (Fuso Nerini et al. 2019) that can

balance these two major challenges (Steffen et al. 2015b): i.e., it is necessary to address climate change and simultaneously preserve biodiversity. This could be achieved by gradually increasing the area reserved for OWF implementation while allowing for the thorough monitoring of their effects on the marine environment, and including the lessons learned during the planning process. Planning also needs to consider research on and implementation of mitigation of OWF effects on wildlife, e.g., by adapting OWF locations, size and design, turbine height and spacing, as well as reducing OWF-associated ship traffic, light emissions, and noise emitted during construction.

Conclusion

The current findings clearly demonstrate the effect of currently operating OWFs, as well as the potential future threat to guillemots in the southern North Sea if the German government's plans to implement large-scale OWFs are realised. The combination of species-specific OWF avoidance values with data on seabird distribution and abundance provides essential information on the magnitude of possible effects of large-scale OWF implementation on seabird abundance. Similar approaches are important to allow the development of sustainable planning scenarios for renewable energy developments in offshore areas, while preserving marine biodiversity and ecosystem functioning. Similar estimates should thus be made for other seabird species and regions. Against the background of the recently signed Esbjerg and Ostend Declarations (The Federal German Government 2022, 2023), estimates such as those provided here are urgently needed to support planning and management decisions. Such evaluations are essential to allow the development of a sustainable scenario for reducing the human CO_2 footprint, whilst balancing the demands of climate change and biodiversity.

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Data availability Data are stored at the German Federal Maritime and Hydrographic Agency (BSH, Hamburg, Germany, https://www.geoseaportal.de), and German Federal Agency for Nature Conservation (BfN, Bonn, Germany, https://geodienste.bfn.de), and available on request.

Declarations

Competing interests The authors have no competing interests to declare.

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