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**Ecology of top predators in the North Sea –
Baseline for and effects of offshore wind power
developments**

Dissertation

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Verena Maria Angela Peschko

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Referent: Prof. Dr. Stefan Garthe

Koreferentin: Prof. Dr. Karen Wiltshire

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SUMMARY

The North Sea is amongst the most intensively utilised sea areas worldwide and the marine habitat occupied by human uses substantially increased during the past years as numerous offshore wind farms (OWFs) were built. Further areas will be altered in the near future as the construction of already approved OWFs and the consenting of additional areas for OWFs is still in progress. Therefore, knowledge on possible effects of OWFs on marine wildlife is crucial to inform researchers and those involved in management and decision-making in politics and industry.

Due to the importance of apex predators for a healthy marine environment and their role as indicators for the state of the ecosystems it is of utmost importance to increase our knowledge on their occurrence, habitat use and behaviour and to understand if and how they are affected by anthropogenic activities.

In this thesis, fundamental knowledge on the ecology of several important top predator species is provided and applied as baseline information to investigate their reactions towards OWFs constructed in the southern North Sea. To provide a comprehensive view on the different aspects two main methods were applied: Observer-based and digital aerial and ship based surveys offer the opportunity to study the species abundance and distribution as well as changes of these on a large spatial and temporal scale. Telemetry of individual animals provides detailed information on their movements and behaviour during specific periods of their annual life cycle and enables to directly observe their reaction to changes in their environment.

Five top predator species (including one species group) which differ substantially in their ecological requirements and constraints, e.g. due to their foraging behaviour, were chosen: black-legged kittiwakes (*Rissa tridactyla*) are surface feeders, common guillemots (*Uria aalge*) and the species group of loons (*Gavia* spp.) are pursuit divers, northern gannets are plunge divers (*Morus bassanus*), and grey seals (*Halichoerus grypus*) predominantly feed on benthic organisms. As wide ranging and abundant species they are prone to experience interference with OWFs at various locations. Differing reactions to OWFs were reported in previous studies: Loons belong to the most sensitive species with respect to avoidance of OWFs, for common guillemots and black-legged kittiwakes avoidance but also attraction or indifference were reported, and gannets have been shown to strongly avoid OWFs. However, the reaction of seabirds towards large scale OWFs in the southern North Sea and towards OWFs located close to their breeding colonies, as well as their individual behaviour in response to OWFs were poorly studied so far. Furthermore, although grey seals have become an important part of the ecosystem in the southern North Sea over the last 50 years, information on their habitat use and their reaction towards OWFs was sparse and currently missing for the German North Sea.

Based on an extensive, long-term and large scale dataset collected by means of visual and digital surveys before (2000-2013) and after construction of the OWFs (2015-2017) an effect analysis was conducted for the species group of loons, as well as for common guillemots and black-legged kittiwakes. Loon abundance and distribution was strongly affected by the OWFs located close to one of their most important resting sites during spring migration. The abundance of loons decreased highly significantly by 94.5% inside the 3 km zone around the OWFs. The associated ship traffic also had a significant negative impact on loons, indicating that OWFs deterred them through the combined effect of ship traffic and the wind turbines themselves. Strong effects of the OWFs located 23-35 km north of Helgoland were furthermore detected for common guillemots in spring (63% reduced density in the OWF area plus 3 km buffer) and for common guillemots and black-legged kittiwakes in the breeding season (44% and 45% reduced density in the OWF area plus 3 km buffer).

Telemetry was moreover applied on breeding northern gannets and for the first time in German waters on breeding common guillemots and weaned grey seal pups to study their movements and behaviour and to gain detailed information on their individual reaction towards OWFs. Strong effects were revealed for both seabird species during two breeding seasons, with most individuals strongly avoiding the OWFs. Of the tagged common guillemots 16% shortly entered the OWFs during two to three occasions and 10% of the northern gannets frequently entered the wind farms when foraging or commuting between colony and foraging areas. A point process modelling (PPM) approach furthermore revealed a significantly reduced resource selection inside the OWFs compared to outside. For northern gannets resource selection was reduced by 37% and for common guillemots by 67%. An even stronger OWF avoidance (76% reduced resource selection) was shown for guillemots when turbine blades were rotating. For the grey seal pups a PPM approach revealed that they strongly increased their distance to Helgoland already in the first weeks and generally during the first 70 days at sea covered by the model. The frequency of the foraging behaviour increased from the beginning until week four, whereas the fast travelling behaviour increased throughout the whole study period. Furthermore, the pups' individual spatial overlap with OWFs under construction and in operation was revealed but no obvious behavioural response to OWFs was detected.

This thesis strongly enhances our knowledge on the ecology of important top predators in the southern North Sea and provides new and detailed information on the effects of OWFs on the studied species. Different reactions towards OWFs were detected and for the seabird species substantial habitat losses were revealed. The here presented findings will contribute fundamentally to future studies on anthropogenic impacts, to environmental monitoring or to conservation and management implications of the respective species and need to be considered during the planning process of future OWFs.

ZUSAMMENFASSUNG

Die Nordsee gehört zu den am intensivsten durch den Menschen genutzten Meeresgebieten. Durch den Bau zahlreicher Offshore-Windparks (OWP) ist die Fläche des durch menschliche Nutzung beanspruchten Habitats während der letzten Jahre stark angestiegen. Da der Bau bereits genehmigter OWPs andauert und zusätzliche Flächen für OWPs beantragt sind, wird die beanspruchte Fläche weiter zunehmen. Es ist daher entscheidend, mögliche Auswirkungen von OWPs auf die marine Tierwelt zu untersuchen, um die erzielten Erkenntnisse der Wissenschaft sowie Entscheidungsträgern in Politik und Industrie zur Verfügung stellen zu können.

Top-Prädatoren leisten einen wichtigen Beitrag zur Erhaltung eines gesunden marinen Ökosystems und dienen als Indikatoren für den Zustand dieser Ökosysteme. Es ist daher von besonderer Bedeutung, ihr Vorkommen, ihre Habitatnutzung sowie ihr Verhalten zu untersuchen und herauszufinden, ob und wie sie durch anthropogene Aktivitäten beeinträchtigt werden.

In der vorliegenden Arbeit wurden wichtige Kenntnisse über die Ökologie verschiedener wichtiger Top-Prädatoren-Arten erarbeitet und als Grundlage dafür genutzt, ihre Reaktionen auf OWPs zu untersuchen, die in der südlichen Nordsee errichtet wurden.

Um ein umfassendes Bild der verschiedenen Aspekte zu erlangen, wurden zwei Methoden angewendet: Observer-basierte und digitale flugzeug- und schiffsgestützte Erfassungen ermöglichen es, die Abundanz und Verteilung der Arten sowie Änderungen dieser über lange Zeiträume und für große Gebiete zu untersuchen. Telemetrische Methoden ermöglichen es, detaillierte Informationen über die räumlichen Bewegungen und das Verhalten von Individuen während bestimmter Phasen ihres jährlichen Lebenszyklus zu erlangen. Des Weiteren können mit Hilfe dieser Methode mögliche Reaktionen auf Veränderungen im Lebensraum der Tiere genau beobachtet werden.

Um die verschiedenen Aspekte zu untersuchen wurden fünf Top-Prädatoren-Arten (bzw. eine Artengruppe) ausgewählt, die unterschiedliche ökologische Ansprüche haben. Dies zeigt sich z.B. in ihrem Nahrungssuchverhalten: Dreizehenmöwen (*Rissa tridactyla*) erbeuten ihre Nahrung an der Wasseroberfläche, Trottellummen (*Uria aalge*) und die Artengruppe der Seetaucher (*Gavia* spp.) verfolgen ihre Nahrung unter Wasser, Basstölpel (*Morus bassanus*) erbeuten ihre Nahrung stoßtauchend und Kegelrobben (*Halichoerus grypus*) jagen überwiegend am Meeresgrund. Durch ihre weiträumige Verbreitung kann es in vielen Gebieten zu einer Überschneidung ihres Vorkommens mit OWPs kommen und in vorangegangenen Studien wurden unterschiedliche Reaktionen auf OWPs festgestellt: Seetaucher gehören zu den Arten die OWPs am stärksten meiden. Für Trottellummen und Dreizehenmöwen wurden neben starker Meidung auch neutrale Reaktionen und sogar Anlockung nachgewiesen. Für Basstölpel wurden überwiegend Meidereaktionen festgestellt. Einige Aspekte, wie z.B. die Reaktion von Seevögeln auf großräumige OWPs in der südlichen Nordsee, ihre Reaktion auf

OWPs nahe ihrer Brutkolonien, sowie individuellen Reaktionen auf OWPs wurden bisher kaum untersucht. Obwohl die Zahl der Kegelrobben in den letzten 50 Jahren stark zugenommen hat und sie somit zu einem wichtigen Teil des marinen Ökosystems der südlichen Nordsee geworden sind, waren bisher wenige - bzw. in der deutschen Nordsee keine - Informationen zu ihrer Habitatnutzung und möglichen Reaktionen auf OWPs verfügbar.

Basierend auf einem umfangreichen Datensatz, der mit Hilfe visueller und digitaler Surveys in einem großräumigen Gebiet und über einen langen Zeitraum vor (2000-2013) und nach Errichtung der OWPs (2015-2017) erhoben wurde, konnte eine Effektanalyse für die Artengruppe der Seetaucher, sowie für Trottellummen und Dreizehenmöwen durchgeführt werden. Die Abundanz und Verteilung der Seetaucher wurde stark durch OWPs beeinträchtigt, die sich nahe eines ihrer wichtigsten Frühjahrs-Rastgebiete befinden. Innerhalb der OWPs inklusive eines 3km Puffers um die OWP-Grenzen verringerte sich die Abundanz der Seetaucher hochsignifikant um 94.5%. Auch der zusätzliche durch die OWPs bedingte Schiffsverkehr hatte einen signifikant negativen Effekt auf die Seetaucher, was darauf hindeutet, dass der Effekt der OWPs auf eine Kombination des Schiffsverkehrs und der Turbinen zurückzuführen ist. Starke Effekte der OWPs, die sich 23-35 km nördlich der Insel Helgoland befinden, wurden für Trottellummen im Frühjahr (63% reduzierte Dichte innerhalb der OWPs plus 3 km Puffer) und für Trottellummen und Dreizehenmöwen während der Brutzeit festgestellt (44% bzw. 45% reduzierte Dichte).

Des Weiteren wurden telemetrische Methoden an brütenden Basstölpeln und zum ersten Mal in deutschen Gewässern an brütenden Trottellummen und an Kegelrobbenjungtieren angewendet um ihre räumlichen Bewegungen sowie ihr Verhalten zu untersuchen und um detaillierte Informationen über ihre individuellen Reaktionen auf OWPs zu erlangen. Für beide Seevogelarten wurde während zwei Brutsaisons festgestellt, dass die meisten Tiere die Parks deutlich mieden. Von den besenderten Trottellummen flogen 16% an zwei bis drei Gelegenheiten für kurze Zeiträume in die Parks hinein. Von den besenderten Basstölpeln hielten sich 10% häufig während der Nahrungssuche und auf der Flugstrecke zwischen Kolonie und Nahrungsgebieten in den Parks auf. Mit Hilfe eines Punktprozess Modellansatzes (PPM) konnte gezeigt werden, dass das OWP Gebiet im Vergleich zur Umgebung gemieden wurde. Basstölpel wählten das OWP-Gebiet um 37% weniger, Trottellummen um 67% weniger als die Umgebung. Eine noch stärkere Meidung (76%) zeigte sich für Trottellummen, wenn sich die Rotoren der Turbinen drehten. Für Kegelrobbenjungtiere konnte mit Hilfe des PPMs gezeigt werden, dass sie ihre Distanz zu Helgoland schon innerhalb der ersten Wochen und auch innerhalb der ersten 70 Tage, die untersucht wurden, stark erhöhten. Die Häufigkeit des Nahrungssuchverhaltens stieg innerhalb der ersten sieben Wochen an, die Häufigkeit des schnellen gerichteten Schwimmens stieg jedoch über den gesamten untersuchten Zeitraum. Es konnte keine eindeutige Reaktion auf OWPs festgestellt werden, jedoch zeigte sich eine individuell unterschiedliche räumliche Überlappung

des durch die Kegelrobbenjungtiere genutzten Habitats mit den in Betrieb oder im Bau befindlichen OWPs.

Diese Arbeit leistet einen wichtigen Beitrag zu unserem Wissen über die Ökologie wichtiger Top-Prädatoren der südlichen Nordsee, und liefert neue und umfassende Informationen über die Effekte von OWPs auf die untersuchten Arten. Es zeigten sich unterschiedliche Reaktionen auf die OWPs und für die untersuchten Seevogelarten wurden erhebliche Flächenverluste festgestellt. Die gewonnenen Erkenntnisse werden grundlegend zu zukünftigen Studien anthropogener Effekte, zum Umweltmonitoring und zu Schutz- und Managementimplikationen der jeweiligen Arten beitragen. Des Weiteren leisten die hier gewonnenen Erkenntnisse einen wichtigen Beitrag für den Planungsprozesses zukünftiger OWPs.

GENERAL INTRODUCTION

GENERAL INTRODUCTION

As top predators are located at the upper end of the food chain they are strongly affected by changes in the environment, in lower trophic levels (Croxall et al. 1999, Boyd & Murray 2001, Descamps et al. 2017) or through anthropogenic activities (Frederiksen et al. 2004), and are thus important indicators of the state of our ecosystems (Boyd & Murray 2001, Weimerskirch et al. 2003, Parsons et al. 2008, Sergio et al. 2006, 2008). Knowledge on their distribution, habitat use and behaviour is crucial to gain information on the current state of the marine ecosystems and to be able to detect and interpret possible changes through time (Weimerskirch et al. 2003, Paredes et al. 2014, Peschko et al. 2016). Such knowledge furthermore provides the basis to improve our understanding of the time frames and magnitudes in which changes can occur (Markones et al. 2008, Garthe et al. 2011, 2015). Moreover, it often allows to investigate which environmental or anthropogenic variables strongly influence the top predators' occurrence (Markones et al. 2007, Garthe et al. 2009, 2011, Scott et al. 2010). Due to the role of apex predators for a healthy marine environment (Duffy 2003, Estes et al. 2011, Wilmers et al. 2012) it is of utmost importance to identify these variables and to increase our understanding of their influence. Anthropogenic activities in the marine habitat strongly increased, both on a global scale (Halpern et al. 2015, 2019) and also in the North Sea (Emeis et al. 2015). The North Sea is amongst the most-intensively utilised sea areas worldwide for activities including fishing, transport, oil and gas drilling, and gravel extraction (Halpern et al. 2008, 2019, Emeis et al. 2015). We thus urgently need to assess possible effects of anthropogenic activities, as some of them have the potential to strongly affect marine top predators (Furness et al. 2013, Maxwell et al. 2013, Chen et al. 2016, Dierschke et al. 2016, Jones et al. 2017, Fliessbach et al. 2019) and consequently entire marine ecosystems (Jackson et al. 2001, Estes et al. 2011, Rocha et al. 2015).

In the past decade the marine habitat occupied by human uses substantially increased as additionally to the various existing anthropogenic uses (BSH 2019) numerous offshore wind farms (OWF) were built in Europe (Perveen et al. 2014, 4COffshoreWind 2019, BSH 2019). Further areas will be occupied in the near future as the construction of already approved OWFs and the consenting of additional areas for OWFs is still in progress (4COffshore 2019, BSH 2019). The German government plans to implement OWFs generating 6.5 GW power until 2020 and 15 GW until 2030 (BSH 2017) making Germany one of the countries with the most extensive plans for OWF installations (Beiersdorf & Radecke 2014). In the German North Sea currently 19 OWFs are in use, four are under construction and seven are approved.

A possible conflict with this development arises from the fact that top predators such as seabirds and marine mammals thoroughly depend on offshore areas for foraging, resting and migration (Schreiber & Burger 2001, Wilson & Mittermeier 2014). The possible effect of an offshore wind farm largely depends on the local environmental conditions, the species occurring in and depending on the

respective marine area (Drewitt & Langston 2006, Skeate et al. 2012, Vanermen & Stienen 2019) as well as on the species' annual life cycle stage e.g. with regards to breeding, migrating, and moulting (Masden et al. 2009, 2010, Furness et al. 2013, Busch & Garthe 2016, 2018, Russel et al. 2016). Depending on the species different behavioural reactions towards OWFs are known, ranging from complete avoidance to attraction (Garthe & Hüppop 2004, Drewitt & Langston 2006, Furness et al. 2013, Dierschke et al. 2016, Russel et al. 2016). When avoiding OWFs species can possibly lose a former valuable (foraging) habitat or have to extend their travel route to reach their foraging areas (Fox et al. 2006). Both could lead to an increased energy consumption if alternative foraging habitats are of poor quality or if individuals have to travel longer distances to arrive at their foraging areas (Fox et al. 2006). When attracted to OWFs seabirds are prone to collide with the rotors or turbines which leads to an increased mortality (Drewitt & Langton 2006, Fox et al. 2006). Marine mammals however might be attracted to operating OWFs due to the 'artificial reef' effect (Petersen & Malm 2006). An increased diversity and abundance of fish (e.g. Stenberg et al. 2015) make these areas potentially valuable feeding grounds, as shown for harbour seals (Russell et al. 2014). Possible long-term effects of the different reactions towards OWFs at the population level however are difficult to estimate (Fox et al. 2006; Goodale & Milman 2014; Searle et al. 2017).

Studying different top predator species thus allows to substantially increase our knowledge on their occurrence, movements, behaviour and habitat use in the southern North Sea. This will enable us to gain profound and important insights on the potential effects of OWFs on the different species. Such information substantially adds to the current knowledge to be included in planning, management and conservation recommendations provided to decision makers.

Species studied

As top predators, the species selected for this thesis represent an important part of the marine ecosystem in general (Frank et al. 2005, Trzcinski et al. 2006, Baum & Worm 2009, Estes et al. 2011) as well as of the North Sea ecosystem in particular (de la Vega 2016, 2018, Aarts et al. 2019, Horn et al. 2019). The species studied have different ecological requirements and constraints, e.g. due to their foraging behaviour: black-legged kittiwakes (*Rissa tridactyla*) are surface feeders, common guillemots (*Uria aalge*) and the species group of loons (*Gavia* spp.) are pursuit divers, northern gannets are plunge divers (*Morus bassanus*), and grey seals (*Halichoerus grypus*) are predominantly benthic feeders. Hence, they interact differently with their environment and their reactions towards possible changes vary consequently (Croxall & Prince 1980, Baird 1990, Parsons et al. 2008, Wanless et al. 2009). All of the selected species are wide ranging and abundant top predators which are thus prone to experience interference with OWFs at various locations. They showed differing reactions to OWFs in previous

studies (Dierschke et al. 2016, Edren et al. 2010, Skeate et al. 2012) and several aspects like their reactions towards large scale OWFs in the southern North Sea and towards OWFs located close to their breeding colonies, as well as their individual behaviour in response to OWFs were poorly studied so far.

Common guillemots

The common guillemot (hereafter guillemot) is one of the most numerous seabird species in the northern hemisphere and the most abundant seabird species in the North Sea, with a total of approx. 7.3 Mio breeding pairs worldwide and 5.6-5.8 Mio individuals in EU waters (Harris & Wanless 2004). In the IUCN Red List for the EU member states common guillemots are listed with least concern (BirdLife International 2018), for European waters (regional level) they are classified as near threatened (BirdLife International 2015a). They forage while diving from the sea surface and mainly prey on schooling pelagic fish species like sand eel (*Ammodytes* spp.), herring (*Clupea harengus*) or sprat (*Sprattus sprattus*, Sonntag & Hüppop 2005). In the German North Sea, the guillemot population is estimated to be highest in winter with approx. 34,500 individuals (Garthe et al. 2007a). In spring many individuals return to their breeding colonies mainly located in the UK, thus 18,500 individuals are found in German North Sea waters. During the breeding season the overall abundance in German waters is lowest with 7,000 individuals which mainly belong to the only breeding colony on Helgoland (Garthe et al. 2007a).

In several studies in Belgium and The Netherlands guillemots largely avoided OWF areas (Leopold et al. 2013, Vanermen et al. 2015, 2016), i.e. with a reduced abundance of 71% in the OWF area compared to the surrounding areas (Vanermen et al. 2015). Reduction of bird abundance was also found by Welcker & Nehls (2016; 75% reduced density in the OWF area, response radius 2.5 km) and Mendel et al. (2014) at the Alpha Ventus wind farm. In contrast, other studies, e.g. in the UK, found that guillemots were attracted by or indifferent to OWFs, with no changes in abundance (PMSS 2007, Vallejo et al. 2017).

Northern gannets

The northern gannet (hereafter gannet) is widely distributed in the North Atlantic, with 1.5 -1.8 Mio mature individuals (BirdLife International 2018a). In the IUCN Red List gannets are listed with least concern (BirdLife International 2018a). They mainly prey on schooling pelagic fish species like mackerel (*Scomber scombrus*), sand eel, herring, and sprat while plunge-diving mostly from 11-60 m height (Garthe et al. 2014). In the German North Sea gannets occur with highest numbers in summer and

autumn (1,400 and 2,700 individuals respectively) and with lowest numbers in winter and spring (230 and 800 individuals respectively, Garthe et al. 2007a).

Gannets have been ranked as one of the most vulnerable species to collide with OWF turbines (Furness et al. 2013, Bradbury et al. 2014). Furthermore, strong avoidance of OWFs was found for gannets in most studies on OWF effects (reviewed in Dierschke et al. 2016, Garthe et al. 2017a, b). At the OWF Blight Bank, the density in the OWF area was reduced by 85% (Vanermen et al. 2015). A study conducted at the Alpha Ventus wind farm in German waters detected a reduction of 75% inside the OWF area compared to the surrounding waters (Welcker & Nehls 2016).

Black-legged kittiwakes

The black-legged kittiwake (hereafter kittiwake) is the most numerous gull species in the world, with 14.6–15.7 Mio individuals, and circumpolar distributed (Coulson 2011, Wetlands International 2018). For European waters 3.5–4.4 Mio mature individuals are estimated (BirdLife International 2015) of which the largest part breed in colonies in the United Kingdom. In the IUCN red list kittiwakes were recently listed as vulnerable species (BirdLife International 2018b), and they are also listed in the OSPAR list of threatened or declining species (OSPAR Commission 2008). In contrast to diving seabird species, e.g. guillemots, kittiwakes are surface feeders mainly preying on energy-rich pelagic schooling fish, like sand eel and herring, but also on young whiting (*Merlangius merlangus*) or Nereidae (Markones et al. 2009). Therefore, they are especially vulnerable to a change in prey occurrence at the surface, e.g. due to climate change and overfishing (Frederiksen et al. 2004, 2008, Suryan et al. 2006). This probably is one of the reasons for the decline of kittiwake populations throughout their global range since the 1980s (Frederiksen 2004, 2008, Descamps et al. 2017). In German waters, kittiwakes are observed year round at between 13,000 and 20,000 individuals (Garthe et al. 2007a).

For kittiwakes some studies reported avoidance (Leopold et al. 2013, Vanermen et al. 2016), with an abundance reduction of 86% in the OWF area (Vanermen et al. 2016), others found no clear response behaviour (Krijgsveld et al. 2011, Percival 2013, Welcker & Nehls 2016), or even attraction (Canning et al. 2013, Vanermen et al. 2015). As kittiwakes are known to fly a considerable part of the time at turbine blade height (Krijgsveld et al. 2011, Johnston & Cook 2016, Borkenhagen et al. 2018), collision risk also needs to be considered for this species (Furness et al. 2013, Busch & Garthe 2018).

The only guillemot and gannet colonies and one of the few kittiwake colonies in the south-eastern North Sea are located on the island of Helgoland (54°11' N, 7°55' E), which is a small island 48 km from the German coastline in the south-eastern North Sea (Fig. 1). The breeding numbers are relatively small

and encompass 3,178 guillemot, 1,071 gannet, and 5,201 kittiwake breeding pairs (Dierschke et al. 2018). The number of breeding guillemots did not change considerably for many years now (Dierschke et al. 2011, Dierschke et al. 2018). Gannets started to breed on Helgoland in 1991 and numbers of breeding pairs increased rapidly (Dierschke et al. 2011, Dierschke et al. 2018). After being relatively stable for many years, the numbers of breeding kittiwakes slowly started to decline in 2004 (Markones et al. 2009, Dierschke et al. 2011). During the breeding season the area around Helgoland is thus of special importance for the guillemots, gannets and kittiwakes breeding in German waters.

Species group - Loons

In the North Sea the species group of loons mainly consists of red-throated loons (*Gavia stellata*; 90 %) and to a minor proportion of black-throated loons (*Gavia arctica*; 10 %, Garthe et al. 2007a, Dierschke et al. 2012). Both are listed with least concern in the IUCN Red List although numbers are declining (BirdLife International 2018c, d). One of the most important resting sites for loons is located in the German North Sea, where internationally important numbers (20,200 individuals, Garthe et al. 2015) use German waters mainly during spring migration (Skov et al. 1995; Mendel et al. 2008, Garthe et al. 2007a; 2015). Red throated loons are generalist opportunistic feeders which in the German North Sea mainly prey on benthic-pelagic schooling fish belonging to the groups of clupeids, mackerel, flatfish, gadoids and sand eels (Kleinschmidt et al. 2019).

Loons belong to the most sensitive species group with respect to avoidance of OWFs, which was shown by studies on single OWF sites in the North Sea (e.g. Petersen et al. 2006, Leopold et al. 2013, Dierschke et al. 2016, Mendel et al. 2014). Furthermore, red-throated loons are also very sensitive with respect to ship traffic: It has been shown that this species shows high flush distances in front of approaching vessels (Bellebaum et al. 2006, Fliessbach et al. 2019) and exhibits significantly lower densities in areas with permanently higher ship traffic (Hüppop et al. 1994, Mitschke et al. 2001, Schwemmer et al. 2011). Due to their sensitive nature and due to a significant proportion of the biogeographic population resting in European waters, loons are listed on the Annex I of the EU Birds Directive and are rated particularly threatened with respect to human activities (e.g. Garthe & Hüppop 2004, Furness et al. 2013).

Grey seals

The abundance of grey seals along European mainland coasts in the North Sea has increased since 1967, after being almost absent or very low for several hundred years (Scheibel & Weidel 1988, Reijnders et al. 1995, Härkönen et al. 2007, Brasseur et al. 2015). In 2018, 6,144 grey seals were

counted during the moulting season in the entire Wadden Sea area and 1,179 in the German North Sea (Brasseur et al. 2018a). The largest colony in German waters is located on Helgoland. Pup numbers on Helgoland increased by 38% between 2014/2015 and 2015/2016, and 12% between 2016/2017 and 2017/2018 (Brasseur et al. 2016, 2018a). A maximum number of 426 births was recorded on Helgoland and a total of 1,377 pups were counted in the entire Wadden Sea area in the breeding season 2017/2018 (Brasseur et al. 2018a). Grey seals are predominantly benthic and demersal feeders (Brown et al. 2012, Jessop et al. 2013) which prey on a diversity of species belonging to the groups of sand eels, gadids like cod (*Gadus morhua*), whiting and pollock (*Pollachius virens*), and flatfish like dab (*Limanda limanda*), flounder (*Platichthys flesus*) and sole (*Pleuronectes platessa*) as well as herring, *Sepia* spp., and redfish (*Sebastes* sp.) (Beck et al. 2007, Ridoux et al. 2007, Brown et al. 2012, Wilson & Hammond 2019).

So far, information on grey seals reaction towards OWFs is sparse (Brasseur et al. 2010, Edren et al. 2010, Skeate et al. 2012) and is currently missing for the German North Sea, despite being a sea area with increasing implementation of OWFs (BSH 2019). Pile-driving activities during the construction of OWFs might displace seals, mask communication signals, or cause temporary or permanent hearing loss (Kastak et al. 2008, Kastelein et al. 2012, Hastie et al. 2015, Russell et al. 2016). Grey seals might be attracted to OWF areas during their operation due to their 'artificial reef' effect (Petersen & Malm 2006). The diversity and abundance of fish in these areas increased (Stenberg et al. 2015) making them potentially valuable feeding grounds, as shown for harbour seals (Russell et al. 2014).

Study area

Despite efforts to study possible effects on the marine environment of the German North Sea in the test area Alpha Ventus (Beiersdorf & Radecke 2014) the possible effect of numerous large scale wind farms is difficult to predict from such small scale studies. Since October 2015, three wind farms with 208 turbines, covering an area of 105 km², and located only 23-35 km north of the island of Helgoland are in operation (Fig. 1). The construction of the OWFs in a) close vicinity of Helgoland where the only breeding colonies of several key seabird species and the largest grey seal colony in the German North Sea are located and b) in an area very close to one of the most important resting sites for loons during spring migration, called for an assessment of possible effects of these OWFs on the locally abundant top predator species.

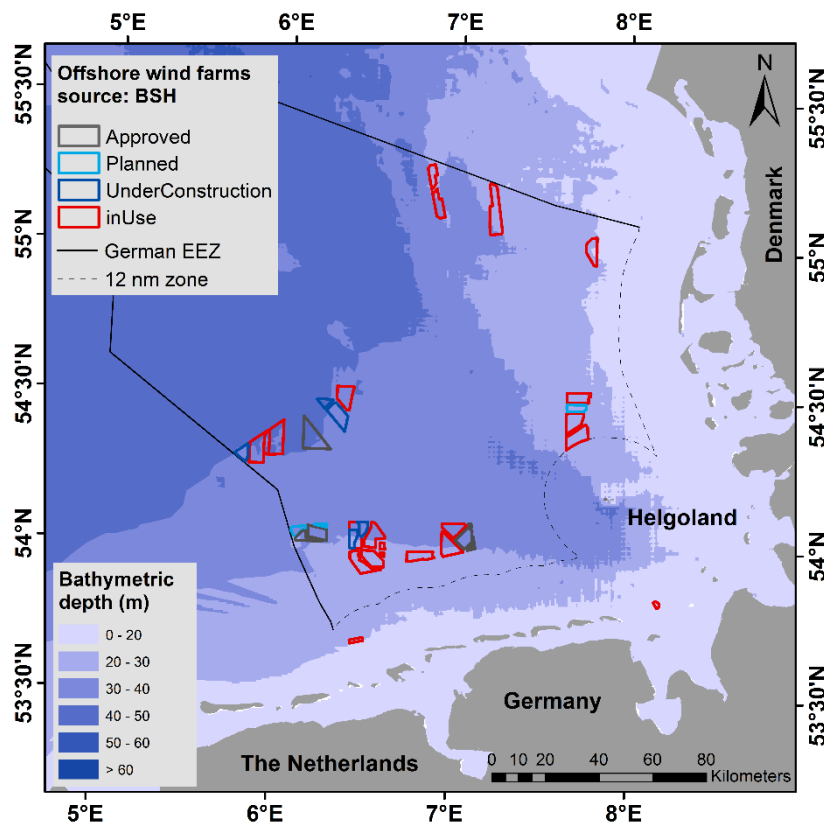


Fig. 1: Current status of OWFs in the German EEZ (North Sea). Modified from Federal Maritime and Hydrographic Agency 2019 (https://www.bsh.de/DE/THEMEN/Offshore/Nutzungskarten/_Anlagen/Downloads/Nordsee-OffshoreWindparks.pdf?__blob=publicationFile&v=4. Accessed at 22.08.2019).

Methods applied

Different methods are currently applied to study the effect of OWFs on top predators (Dierschke et al. 2016, Garthe et al. 2017a, Warwick-Evans et al. 2018, Perrow 2019). Visual or digital aerial and ship based surveys provide valuable information on the species abundance and distribution in a respective survey area and enable us to detect possible changes through time (Mendel et al. 2014, Garthe et al. 2015, Peschko et al. 2016). They are thus largely applied in environmental impact assessments (EIAs) for offshore wind farms (Mendel et al. 2014, reviewed in Dierschke et al. 2016, Welcker & Nehls et al. 2016, Perrow 2019). However, for less abundant species or species which are difficult to detect or identify at sea (i.e. seals) it can be difficult to gather enough data for a reliable impact assessment based on survey methods. Furthermore, the flight altitudes of seabirds, the behaviour in and around the OWFs as well as the individual reaction towards the OWFs and its changes through time cannot be studied in detail.

Telemetry methods generate valuable data on fine- and large-scale habitat use and behaviour (Garthe et al. 2007, Breed et al. 2009, Ponchon et al. 2017, Thaxter et al. 2018) as well as alterations of these with regard to changes in their life cycle (Carter et al. 2017, Brasseur et al. 2017b) or changing environmental conditions (Breed et al. 2011, Garthe et al. 2011, Paredes et al. 2014). Furthermore, animal movement data can provide detailed insights in individual behaviour (Patterson et al. 2008, Votier et al. 2010, Garriga et al. 2016). So far, only few studies applied telemetry devices to investigate OWF effects on top predators (Thaxter et al. 2015, 2018, Hastie et al. 2015, Russel et al. 2016, Garthe et al. 2017a, b).

Both methodological approaches were applied in this thesis to gain valuable knowledge on the ecology of the different species and to study if and how they are affected by the OWFs in the southern North Sea.

Objectives and thesis outline

Due to the different state of knowledge for each species and as not all questions could be answered with this thesis, I decided to focus on different aspects. Due to the urgency of the topic, for seabirds this thesis mainly investigated the possible effects of the OWFs in the southern North Sea. For grey seal pups, precedent to this thesis, little knowledge on their occurrence and habitat use in German waters was available. Therefore, providing basic data on their area use and behaviour and collecting first information on possible interactions with OWFs was most important. Aiming at providing as much valuable knowledge on the different top predator species as possible this thesis hence addressed the following questions:

Based on survey data (guillemots, kittiwakes, loons):

- How did the respective seabird species use the habitat before the construction?
- Did their density and distribution change in response to the OWF presence?
- Up to which distance did they respond to the OWFs?
- Did guillemots and kittiwakes show a different reaction depending on the season?
- Can we disentangle the effect of OWFs and associated ship traffic on loons? Can we quantify the effect of shipping on loons?

Based on telemetry data (gannets, guillemots, grey seals):

- Gannets & guillemots:
 - How far and for how long did they travel during their foraging trips? Where did they forage, commute and rest?
 - Can we detect and quantify their responses to OWFs using telemetry data?
 - Are they displaced by or attracted to the OWFs?
 - Are there individual differences in their reaction towards the OWFs?
 - How do they behave in the vicinity of or inside the OWFs? Do they forage there?
 - Do they behave similarly in consecutive years?
- Grey seals:
 - How did grey seal pups use the habitat of the southern North Sea after weaning?
 - How far did they disperse and which areas did they use for foraging?
 - How did these aspects change with increasing age of the pups?
 - Did their area use overlap with OWFs?

This thesis comprises five independent chapters to answer these questions.

On the basis of an extensive, large scale dataset collected via observer-based and digital aerial and ship based surveys before and after OWF construction **Chapter I** studied the possible effect of the recently constructed OWFs and associated ship traffic on the density and distribution of the species group of loons in one of its most important resting sites. **Chapter II** used a similar dataset to investigate the effects of the OWFs north of Helgoland on the density and distribution of common guillemots and black-legged kittiwakes in spring and during the breeding season. In **Chapter III** GPS-telemetry was applied to study the reactions of breeding northern gannets to the OWFs located close to their colony. **Chapter IV** applied GPS-telemetry as well to examine the effect of the OWFs north of Helgoland on breeding common guillemots. The dispersal, habitat use and behaviour of grey seal pups as well as their spatial overlap with OWFs in the German North Sea was studied by means of satellite-telemetry in **Chapter V**.

CHAPTER I:

Operational offshore wind farms and associated ship traffic cause profound changes in distribution patterns of loons (*Gavia* spp.)



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Operational offshore wind farms and associated ship traffic cause profound changes in distribution
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Operational offshore wind farms and associated ship traffic cause profound changes in distribution patterns of loons (*Gavia* spp.)

Bettina Mendel, Philipp Schwemmer, Verena Peschko, Sabine Müller, Henriette Schwemmer, Moritz Mercker, Stefan Garthe

Abstract

Seabirds select suitable habitats at sea, but these habitats may be strongly impacted by marine spatial planning, including the construction of offshore wind farms (OWFs) and the associated ship traffic. Loons (*Gavia* spp.) are particularly vulnerable to anthropogenic activities and are also of high conservation status, making them particularly relevant to marine planning processes. We investigated the effects of OWF construction and ship traffic on loon distributions in the German North Sea on a large spatial scale, using a ‘before–after’ control impact analysis approach and a long-term data set. Many OWFs were built in or close to core areas of loon distributions. Loons showed significant shifts in their distribution in the ‘after’ period and subsequently aggregated between two OWF clusters, indicating the remaining suitable habitat. The decrease in loon abundance became significant as far as about 16 km from the closest OWF. Ship traffic also had a significant negative impact on loons, indicating that OWFs deterred loons through the combined effect of ship traffic and the wind turbines themselves. This study provides the first analysis of the extensive effects of OWFs and ships on loons on a large spatial scale. The results provide an essential baseline for future marine spatial planning processes in the German North Sea and elsewhere.

Keywords: environmental impact, Marine Special Protection Area, habitat loss, management, Red-throated loon, avoidance behaviour

Introduction

Shallow-shelf sea areas have long been used by humans. The North Sea is amongst the most-intensively utilised sea areas worldwide for activities including fishing, transport, oil and gas drilling, and gravel extraction (Emeis et al. 2015, Halpern et al. 2008). The installation of offshore wind farms (OWFs) in many sea areas throughout Europe and elsewhere represents a relatively new human use requiring considerable attention in terms of the marine planning process. In order to meet their climate goals, many European governments have started to install and plan further OWFs within relatively large sea areas (e.g. Breton & Moe 2009, Langston 2010). Germany intends to extend its offshore power generation to 6,500 MW by 2020 and to 15,000 MW by 2030, leading to a large increase in the number of OWF sites, mainly in the German North Sea, making Germany one of the countries with the most extensive plans for OWF installations (Beiersdorf & Radecke 2014). Seventeen OWFs are currently (2018) in operation, with five further ones under construction and several more being approved in German sea areas (BSH 2017).

In terms of the process of marine spatial planning, these permanent installations at sea represent a major addition to other types of marine human activities, whilst competing with sea areas assigned for nature conservation (Emeis et al. 2015, Moksness et al. 2009, Nolte 2010) and potentially overlapping with areas used by resting and foraging seabirds. Previous studies have pointed out contrasting effects (negative or positive) of OWFs on seabirds that vary strongly among areas and species (Dierschke et al. 2016, Drewitt & Langston 2006, Fox & Petersen 2006, Furness et al. 2013, Garthe and Hüppop, 2004, Masden et al. 2009). In addition, the construction and maintenance of OWFs is further associated with a strong increase in shipping activities in and around OWFs (Exo et al. 2003).

OWFs may have direct effects on birds such as collision of individuals with the turbines, with subsequent impacts on the whole population (Fox et al. 2006, Goodale & Milman 2014, Masden et al. 2009). Furthermore, the energy budget and condition of individual birds may also be affected indirectly through the effects of OWFs on habitat loss and reduced food availability (Drewitt & Langston 2006, Fox et al. 2006, Stienen et al. 2007), though the long-term effects of these indirect effects at the population level are hard to estimate (Fox et al. 2006, Goodale & Milman 2014, Searle et al. 2017). However, birds have been shown to lose suitable resting and foraging habitats or to select less suitable sea areas (Stienen et al. 2007). Furthermore, they may need to increase their flight time by flying around OWFs on their way to suitable foraging sites (Drewitt & Langston 2006, Masden et al. 2009). This study aimed to quantify the indirect effects (i.e. habitat loss by OWFs and associated ship traffic) on loons (*Gavia* spp.) to provide baseline data for future studies that might address population consequences.

Loons belong to the most sensitive species group with respect to the avoidance of OWFs, as shown for single OWF sites in the North Sea (e.g. Dierschke et al. 2012, 2016, Leopold et al. 2010, Mendel et al. 2014, Petersen et al. 2006a, b, Welcker & Nehls 2016). Furthermore, Red-throated loons (*Gavia stellata*) are also very sensitive to ship traffic, demonstrating long flush distances in front of approaching vessels (Bellebaum et al. 2006) and significantly lower densities in areas with permanently higher ship traffic (Hüppop et al. 1994, Schwemmer et al. 2011). Their sensitive nature and the fact that a significant proportion of the biogeographic population occurs in European waters means that loons are listed in Annex I of the EU Birds Directive and are considered to be particularly threatened with respect to human activities (e.g. Furness et al. 2013, Garthe and Hüppop 2004). Negative effects on loons at both the individual and population levels as a result of avoidance of OWFs cannot be ruled out (Dierschke et al. 2016, 2017), and loons are therefore currently rated as a species group requiring particular consideration with respect to marine spatial planning in Germany and the UK (Busch et al. 2013).

Most loons in the North Sea are red-throated loons (90 %), with a minor proportion of black-throated loons (*G. arctica*; 10 %) (Dierschke et al. 2012, Garthe et al. 2007a). The German North Sea represents one of the most important resting sites for loons with internationally important numbers, especially during spring migration (Garthe et al. 2007a, 2015, Mendel et al. 2008, Skov et al. 1995), when around 20,200 loons use German waters (Garthe et al. 2015). The 'Eastern German Bight' Special Protection Area (SPA) has been established to acknowledge the importance of this resting site and the high sensitivity of loons with respect to human disturbances (Fig. 1). However, there is a potential conflict with the 'Butendiek' OWF, which was approved before but installed after the establishment of the SPA (Garthe et al. 2012), while further OWFs ('Helgoland Cluster') are located just south of the border of the SPA (Fig. 1).

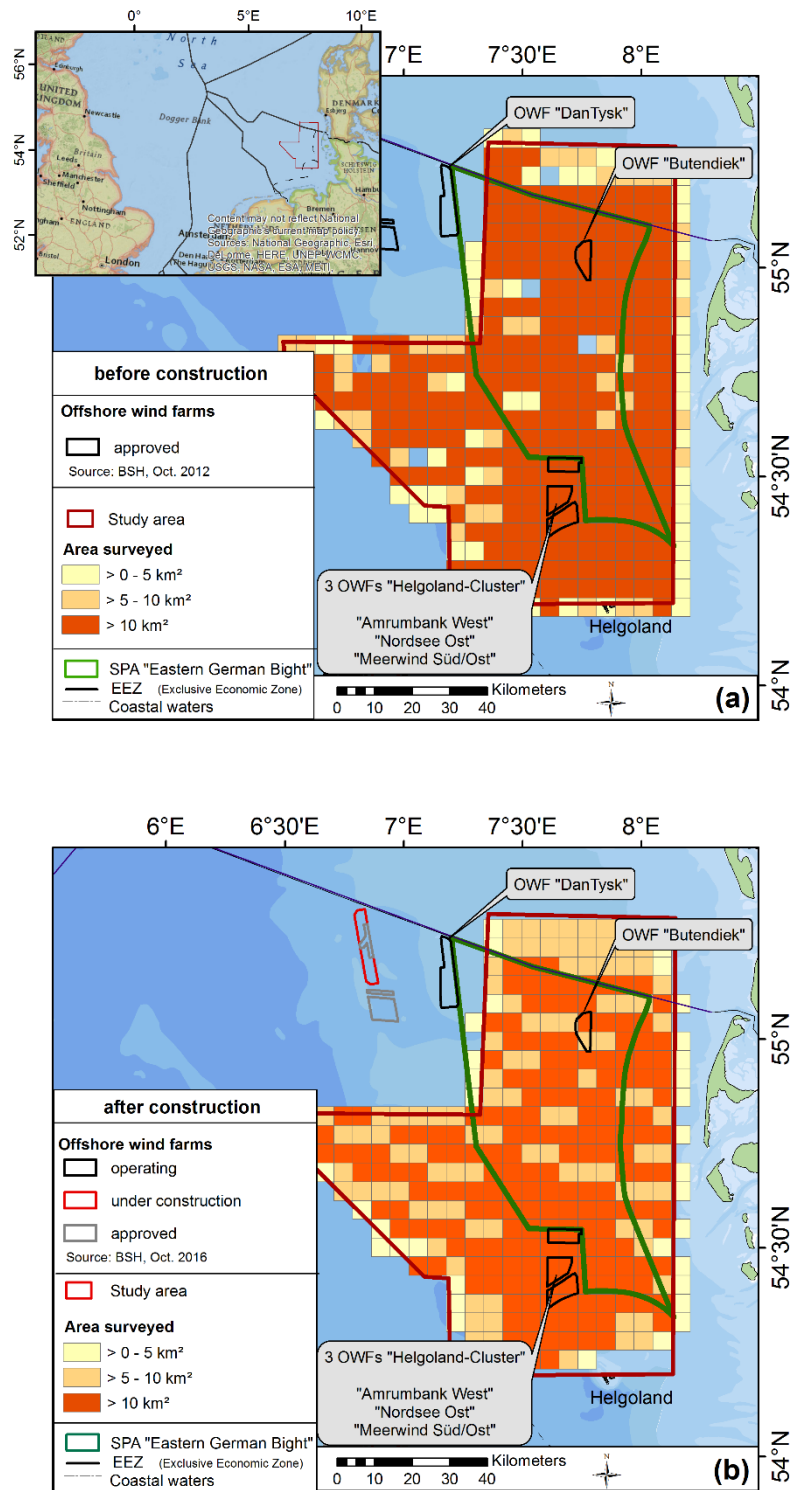


Fig. 1: Location of the study site within the south-eastern North Sea (inserted map in Fig. 1a) and in the eastern German Bight (North Sea) with locations of the different OWFs and the area surveyed for loon abundance (yellow to red squares) across the ‘Eastern German Bight’ Special Protection Area (SPA, bold green line) for the ‘before’ (a) and ‘after’ periods of the analysis (b). Start of construction: ‘Nordsee Ost’ OWF during summer 2012; end of all construction works: ‘Butendiek’ OWF during summer 2015.

Information on the long-term and large-scale effects of OWFs on loons is currently limited and there has been no long-term comparison of their distributions before and after the installation of OWFs. Furthermore, the effects of increasing construction- and maintenance-related ship traffic have rarely been considered (Boon et al. 2010, Christensen et al. 2003).

We therefore hypothesized that loons would avoid OWF areas and that their distribution patterns would differ before and after the installation of OWFs. We also hypothesized that the ship traffic associated with OWF sites would cause avoidance reactions among loons. Against this background, this study aimed to shed light on five specific topics. (1) We had access to a long-term dataset covering the 14-year period before the installation of the OWFs ('before'). We therefore aimed to compare this information directly with the distribution of loons after the installation of OWFs ('after'), using a long-term perspective not achievable in most previous studies. Mandatory operational monitoring of the four offshore windfarms in focus is still ongoing. (2) Most previous studies of the potential effects of OWFs on loons have focussed on the effects of single OWF sites and their direct vicinities (see Dierschke et al. 2016). These therefore only allowed the reactions of loons to be studied on a relatively small spatial scale, and could only show that loon numbers were impacted within the respective site but could not show where they had moved to (Rexstad & Buckland 2012). In contrast, the current study aimed to analyse the large-scale effects of multiple OWFs on loon distribution, considering potential shifts between the 'before' and 'after' periods. (3) There is currently a need to disentangle the potential effects of OWFs from the effects of natural habitat characteristics that determine the distribution of loons (Garthe 1997, Winiarski et al. 2014). We therefore developed a model including stable natural parameters such as water depth and distance to land, as well as anthropogenic predictors such as distance to closest OWF and shipping traffic. (4) Given that the installation and maintenance of OWFs is associated with large increases in ship traffic, the effects of shipping need to be quantified and separated from the effects of the OWFs themselves. To date, this only has been analysed based on general ship densities (e.g. APEM 2013, 2016, Leopold et al. 2014), while OWF ships present a dynamic source of disturbance for loons. This study therefore aimed to relate loon and ship distributions at very high spatial and temporal scales by relating ship distributions derived from the Automatic Identification System (AIS) with loon abundance assessed during aerial surveys. (5) Given a negative effect of OWFs on loons, we aimed to quantify the avoidance distance to OWFs to draw conclusions about the degree of resulting (permanent) habitat loss.

In this study, we adopted two different approaches to analyse different aspects of the effects of OWFs on loons: we used 'before' data to demonstrate the importance of the OWF areas before construction, and also focused on the simultaneous effects of OWFs and ships associated with OWFs after construction. The combined interpretation of these approaches allowed a comprehensive evaluation of the effects of OWFs on loons.

Materials and methods

Study area

The study was conducted within the eastern part of the Exclusive Economic Zone of the German North Sea, south of 55°17' N, north of 54°11', east of 6°30' E, and west of 8°9' E (Fig. 1a). The study site was located within an area 8–100 km off the Wadden Sea islands of northern Germany. The water depth ranged from 10–40 m. Loon distribution was recorded within the SPA 'Eastern German Bight' and beyond, and the study site therefore covered the core area of highest loon densities within German waters (Garthe et al., 2015). The 'Butendiek' OWF is located in the core area of the SPA, while the 'Helgoland Cluster' OWFs are located at the border of the SPA and south of the core loon distribution (Fig. 1a).

Recording loon distribution and data processing

Loon distribution was recorded, both, in the period prior to OWF construction and in the period after construction:

(1) Before construction: These data cover the months of spring migration (i.e. March to April) of the years 2000-2013 and are the similar database as used by Garthe et al. (2015). The records originated from environmental impact assessment studies required for licensing procedures of offshore wind farms in the German EEZ and from seabird monitoring and research programmes (for details see Garthe et al. 2015, Fig. 1a). The data were recorded using visual aerial and ship-based surveys. Briefly, loons were counted along transects of a known area, which allowed the densities to be computed (see Diederichs et al. 2002, Garthe et al. 2002 for a full description of both recording methods).

(2) After construction: These data also cover the months of spring migration (i.e. mainly March to April, but including the last week of February and the first week of May to enhance the sample size of surveys) of the years 2015-2017. Data originated from ongoing mandatory monitoring of the wind farms during operation, and from the 'Helbird' research project funded by the German Federal Ministry for Economic Affairs and Energy. Overall, data for the after period were based on 10 digital aerial surveys in 2015–2017 (Fig. 1b). Those data were obtained by video-based digital recordings instead of visual observations. Briefly, an aircraft sampled a transect of a known area using a video camera and all seabirds found were recorded and used to compute overall densities (for a detailed description of the method see Buckland et al. 2012, Thaxter & Burton 2009). A change from visual to digital survey methods was mandatory for safety reasons because the flight altitude needed to be higher during the construction and operational phases of the turbines (168 m, instead of 91 m for visual observations), which excluded visual recordings.

(3) During construction: No data were considered in this study, as disturbance during the construction of the OWF is temporary and mainly associated with construction ships, and its contribution to the overall effect of the OWF on the loon population was assumed to be of low importance in relation to the expected lifetime of the OWF (Christensen et al. 2003).

Visual observations of seabird distributions are known to underestimate birds in parts of the transect further from the observer (Buckland et al. 2001, 2015). We therefore applied a species-specific correction factor for aerial and ship-based observations, respectively (see Garthe et al. 2015 for details). However, no distance correction was necessary for the video-based digital surveys because the probability of detecting a bird was equal across the whole transect.

All three recording methods relied on the principle that transect sampling of birds could be used to compute densities. However, we did not compare absolute density values between the ‘before’ and ‘after’ periods, because the visual and digital methods have not been confirmed to produce the same absolute values (Buckland et al. 2012, Skov et al. 2016); this could only be tested by performing both methods at the same time, and no such dataset is currently available. Thus, both periods were compared by computing the relative deviance from the maximum density in each period in %, and using this to compare the distributions and locations of high-density areas of loons between the two periods.

Data were spatially pooled in a grid with cells of 2.5 x 2.5 km for the ‘before’ and ‘after’ periods, for each of the three methods (visual aerial and ship-based surveys, video-based digital recordings), respectively. Bird numbers and monitored areas were each summed per grid cell, and eventually used to compute mean densities for each period, while geographical coordinates were averaged for each cell.

Integrating covariates for the ‘before–after’ control impact (BACI) approach

We related the average distribution data for loons with environmental variables using ArcGIS (version 10.3; Environmental System Research Institute, 2016). The environmental variables included: (1) *dist_coast* = minimum distance to the mainland and larger islands (except Helgoland); (2) *dist_helgoland* = minimum distance to Helgoland; (3) *dist_owf* = minimum distance to the border of the OWF; and (4) *mean_depth* = mean water depth.

This first model, hereafter named the BACI approach, did not consider the effect of ships because ship data at a sufficiently high spatio-temporal resolution were only available for the ‘after’ period. To distinguish between the effect of the OWFs and the effect of ship traffic on loons, we therefore developed a second model (ship model) using only the data from the ‘after’ period.

To merge the environmental variables with the bird-count data in an optimal way, we first pooled the covariates to a spatial grid of 2.5 x 2.5 km, and then fitted each covariate with a generalized additive model (GAM) using the function `gam()` in the R-package `mgcv` (R Core Team 2017, R version 3.4.2; Wood 2006). We used only latitude and longitude as a smooth 2D-predictor based on cubic splines with the maximal degree of freedom, so that the result represents a cubing interpolation on the given (possibly irregular) grid. Thirdly, we used the `predict()` function to predict the values straight to the coordinates as given in the pooled bird-count data. Finally, the additional categorical variable `owf_zone` for 'inside OWF-affected area' vs. 'outside OWF-affected area' was defined for two different zones: 1) inside: ≤ 3 km vs. outside: > 3 km (measured from the nearest turbine), given that OWF-associated ships operate mainly within a 3 km radius around the OWF and this distance class has been used in previous studies of the impact of single OWFs (Vanermen et al. 2015, Welcker and Nehls, 2016); and 2) inside: ≤ 10 km vs. outside: > 10 km, because an initial analysis showed the greatest decrease in loon densities up to a distance of 10 km from the turbines.

Set up and validation of regression models for the BACI approach

The BACI approach is based on surveying a potentially impacted situation and a control situation before the impact (variable '*period*'), and relative comparisons of spatial and temporal differences can then be used to extract the unbiased impact (Schwarz 2014, Smith 2002). We formulated the BACI approach within the framework of generalised additive mixed models (GAMMs), which are known to describe biological count data appropriately (Zuur et al. 2007, 2009, 2012). We used a continuous linear or smooth predictor measuring the distance to the border of the next OWF. This allowed us to estimate how the abundance of loons changed in relation to the distance from the OWF and to estimate avoidance distances. Notably, we introduced a variable for the observation method ('visual ship-based surveys' vs. 'visual aerial surveys' vs. 'digital aerial surveys') as a random intercept to account for differences in detection among these methods. We were aware that this variable was partially collinear with the variable '*period*' because only digital aerial surveys were used 'after' and only visual surveys were performed 'before'. Importantly, the estimation of the interaction term '*period* x *wind_farm*' (see below) representing the BACI approach was not influenced by this, because only relative differences in loon densities were evaluated.

This approach produced the following full model for the BACI approach (not yet thinned regarding its predictors; see below):

$$\log(y_{ij}) = \beta_0 + u_i + f(\text{mean_depth}_j) + f(\text{dist_coast}_j) + f(\text{dist_helgoland}_j) + s(\text{latitude}, \text{longitude}) + [\text{wind_farm}_j] + \text{period}_j + [\text{wind_farm}_j] \times \text{period}_j + \text{offset}(\log(\text{area}_j)) + \varepsilon_{ij} \quad (1)$$

where $\varepsilon_{ij} \sim N(0, \sigma^2)$ and $u_i \sim N(0, \sigma^2_{u_i})$ were independent and identically distributed. Here, y_{ij} is the vector of bird numbers, where the index j refers to the observation number and i is related to the method-ID. $f()$ depicts either a linear term or a cubic regression spline $s()$ (tested during predictor selection), where, in the case of a spline, the optimal number of knots was estimated via cross-validation. The variable $[wind_farm_j]$ was either considered as a linear term, $dist_owf_j$ measuring the distance to the next wind turbine, as an additive smoother, $s(dist_owf_j)$, or as a bivariate variable, owf_zone_j , the latter distinguishing between 'inside OWF-affected area' and 'outside OWF-affected area'. For each model, an appropriate probability distribution was selected for y_{ij} via Akaike Information Criterion (AIC; Akaike 1973) analysis (see below).

We modified the common selection and validation strategies to validate the optimal GAMM model (Field et al. 2012, Korner-Nievergelt et al. 2015, Zuur, 2012 Zuur et al. 2009, 2010, 2012;) using the following steps: (1) Based on the entire model (1), we selected an appropriate probability distribution/stochastic part of the model using the AIC. Namely, we compared Poisson-, negative binomial-, Tweedie-, zero-inflated Poisson distribution, and observation-level random intercept Poisson models. All five probability distributions are known to describe the stochastic part in regression models of (overdispersed) count data reasonably well (Kokonendji et al. 2004, Korner-Nievergelt et al. 2015, Linden & Maentyniemi 2011, Zuur et al. 2012). (2) The optimal model regarding the set of fixed-effect predictors was selected from the full model by comparing 16 different models. (3) Model validation was carried out by visual inspection of the residual plots to assess all the required model assumptions (Zuur et al. 2010). Corresponding auto-correlation structures were added to the model if required.

AIC favoured a negative-binomial distribution, and subsequent predictor selection produced the following final model:

$$\log(y_{ij}) = \beta_0 + u_i + \beta_1 dist_coast_j + s(latitude, longitude) + [wind_farm_j] + period_j + [wind_farm_j] \times period_j + offset(\log(area_j)) + \varepsilon_{ij} \quad (2)$$

Residual analysis revealed no violation of linearity, homogeneity, independence, or normality of the random intercept.

Integrating covariates for the ship model

Ship traffic has been shown to have a significant effect on loon distribution (Bellebaum et al. 2006, Schwemmer et al. 2011), and ship traffic in the study area has increased greatly due to the construction and maintenance of OWFs. It is therefore important to disentangle the effects of these two sources of anthropogenic activities (OWFs and ship traffic) on loons. Ship traffic shows temporal inhomogeneity,

with more traffic in the morning and evening hours, and it was therefore necessary to consider the data spatio-temporally instead of purely spatially, as with the BACI approach. Data were only used for five digital-survey flights from the ‘after’ period because no real-time ship data were available for the ‘before’ period or for any other survey days during the ‘after’ period. Bird data were spatially assigned to an optimal grid of 2.5 x 2.5 km for each survey day separately and treated as described above. To consider the time, we also calculated the mean time at which the loon observations were recorded for each grid cell.

Data on ship distributions were recorded in parallel with the digital-survey flights to record loon distribution using an AIS spotter (www.aisspotter.com). Because the ship data consisted of irregular position data in terms of time and space, they were linearly interpolated to obtain positions at least every minute. To merge the ship data with the loon-distribution data, it was assumed that all ships within the time interval $[t - \delta_t, t]$ and within a circle around (x, y) with radius r may influence bird density, for each time point t and each pair of spatial coordinates (x, y) . Given that the optimal values δ_t and r are not known *a priori*, we tested all existing combinations between $\delta_t \in \{2, 60, 120, 180, 250, 300, 350, 400, 600, \infty\}$ sec and $r \in \{1, 2, 3, 4, 5, 6, 7, 8, 9, 10\}$ km, and created a separate variable counting all ships within the given time and space interval for each of the 100 combinations. Here, $\delta_t = \infty$ depicts a case where all available ship data have only been spatially correlated to bird-count data without considering temporal distance to the observations. We subsequently compared 100 resulting regression models (see below) to find the optimal values of δ_t and r . However, the AIC value was not appropriate for selecting the optimal model because the ship densities and OWF-related variables were collinear, and the model with only one of both variable types would be favoured due to the parsimony of the AIC-based selection. In contrast, we aimed to consider both (collinear) variables to distinguish explicitly between the unique effects of ships and wind turbines on loon abundance. An appropriate measure should thus relate the effect size of the ship-dependent variable with its reliability. Hence, we selected the model with the highest $|\beta|/SE_\beta$ value, where β is the ship-related regression coefficient and SE_β is its standard error.

Set up and validation of regression models for the ship model

The GAMMs were set-up as described above for the BACI approach. Notably, the ID of the digital-survey flight was introduced as a random intercept to account for different numbers of birds or different monitoring conditions between surveys.

This produced the following GAMM structure of the ship model (not yet thinned regarding its predictors):

$$\log(y_{ij}) = \theta_0 + u_i + f(\text{mean_depth}_j) + f(\text{dist_coast}_j) + f(\text{dist_helgoland}_j) + [\text{wind_farm}_j] + [\text{ship_number}_j] + \text{offset}(\log(\text{area}_j)) + \varepsilon_{ij} \quad (3)$$

where $\varepsilon_{ij} \sim N(0, \sigma^2)$ and $u_i \sim N(0, \sigma^2_u)$ were independent and identically distributed. Here, y_{ij} is the vector of bird numbers, where the index j refers to the observation number and i is related to the survey flight ID. $f()$ depicts a linear or smooth predictor (tested during AIC-based predictor selection). The variable $[\text{wind_farm}_j]$ was either considered as a binomial predictor ('inside' vs. 'outside'), a linear term (distance to the OWF border), or a cubic regression spline depending on the latter. The variable $[\text{ship_number}_j]$ was considered as the total number of temporally and spatially related ships, additionally depending on the *a priori* defined parameters δ_t and r (see above). In contrast to the BACI approach, we did not consider a spatial smooth because this predictor would interfere with the correct estimation of $[\text{wind_farm}_j]$. GAMM-model selection and validation strategies were performed as described for the BACI approach (see above), including integration of the appropriate autoregression structures (if required).

AIC-based selection of the probability distribution again favoured a negative-binomial distribution. The optimal values of δ_t and r required to blend the observation and ship data showed that the highest (β/SE) -values (indicating high precision of the ship-related regression coefficient) were $\delta_t = 5$ min and $r = 5$ km. Subsequent predictor selection revealed the following final model:

$$\log(y_{ij}) = \theta_0 + u_i + f(\text{mean_depth}_j) + \beta_1 \text{dist_coast}_j + s(\text{dist_helgoland}_j) + [\text{wind_farm}_j] + [\text{ship_number}_j] + \text{offset}(\log(\text{area}_j)) + \varepsilon_{ij} \quad (4)$$

where $s()$ depicts the cubic regression splines with optimal degrees of freedom estimated via cross-validation.

Analysis using different sizes of the underlying spatial grid for spatio-temporal pooling revealed an optimal grid size of 2.5 x 2.5 km, leading to a temporal autocorrelation of model residuals of order 2 (in contrast to the model based on raw data, where the autoregressive order (AR order) was > 30). Model-validation plots indicated no violation of linearity or homogeneity, spatial residual plots and a semivariogram indicated no violation of spatial independence, and a plot of the partial autocorrelation function (pACF-plot) revealed a temporal autocorrelation of approximately order 2, which was integrated as an AR(2)-structure into the model.

Results

Loon abundance before and after OWF installation

The spatial distribution patterns of loons changed profoundly between the ‘before’ and ‘after’ periods (Fig. 2). During the ‘before’ period, the core area with the highest loon densities clearly overlapped the area of the planned ‘Butendiek’ wind farm, while moderately high densities stretched out to the area of the planned ‘Helgoland Cluster’. In contrast, there was a clear shift to the area located between these two OWF sites during the ‘after’ period (Fig. 2). The areas of the OWFs themselves, as well as the immediate vicinities, showed extremely low abundances of loons during the ‘after’ period. The core area of loons during the ‘after’ period was thus still located in the centre of the SPA, but the birds were more aggregated within the still-undisturbed sea area.

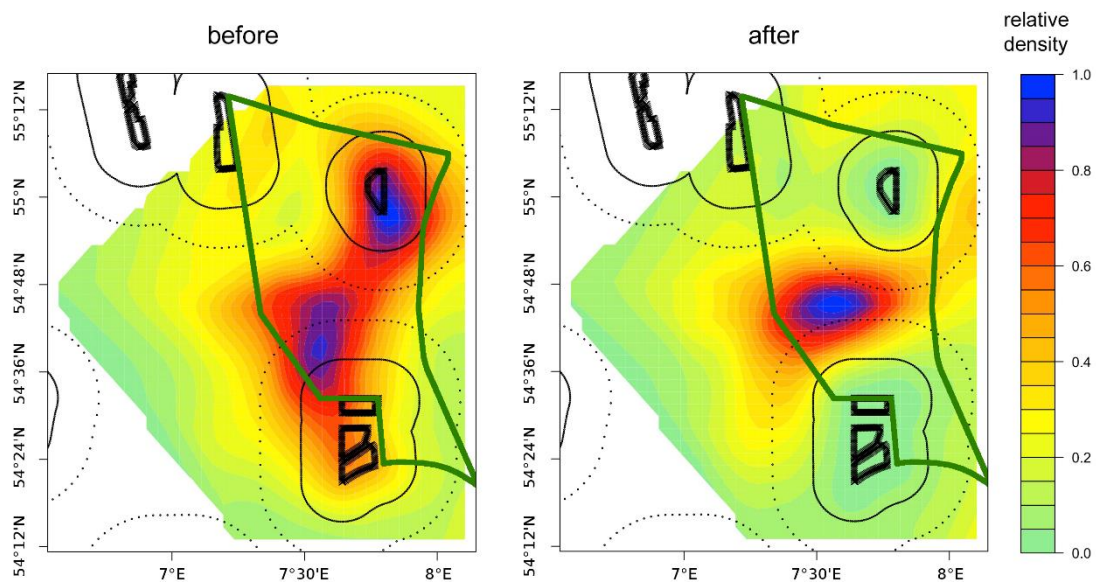


Fig. 2: Spatial density plots of predicted loon distributions ‘before’ vs. ‘after’ the construction of OWFs, based on the BACI-GAMM. Bold black lines: OWFs; thin black lines: 10 km distance buffer; dotted black lines: 20 km distance buffer; bold green line: Special Protection Area.

We also introduced the distance from the wind farm as a smooth term, estimated separately for each period. This revealed a striking difference between the two periods (Fig. 3): the ‘before’ plot suggested that the future wind farm areas were sites with naturally increased loon abundance, while the ‘after’ plot showed a strong decline in loon abundance due to the OWFs (Fig. 3). The start of this decline was already visible at > 20 km from the OWFs (see also dotted black lines in the ‘after’-plot in Fig. 2b). To determine the distance from the wind farm at which the decline in abundance was significant, we approximated the first derivative of the corresponding smooth (Fig. 3 ‘after’) by calculating its first finite difference.

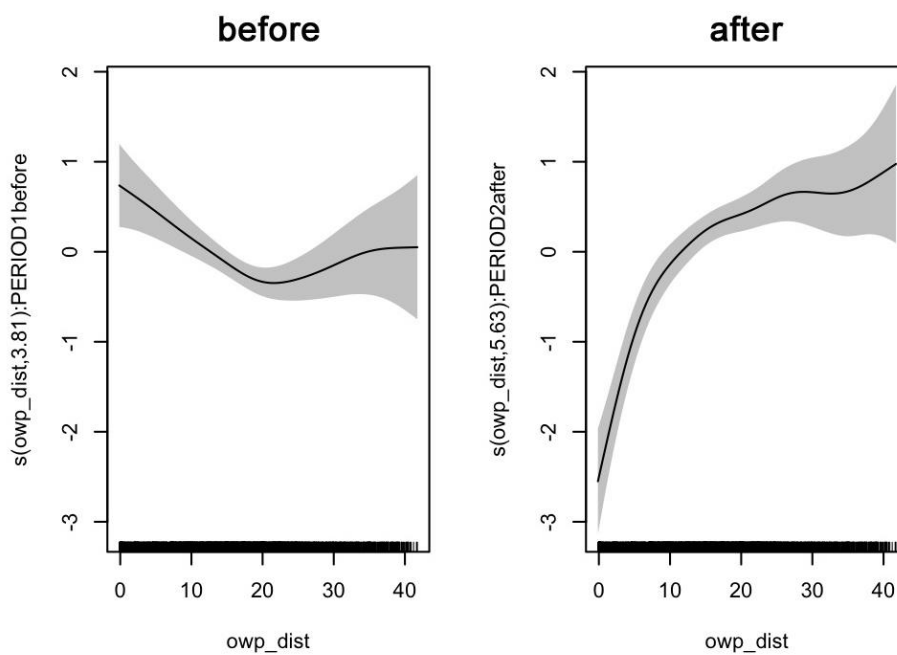


Fig. 3: Change in loon abundance in relation to distance from the closest OWF site ‘before’ (left) and ‘after’ construction of the OWFs. Smoothed curve: predicted number of loons at a given distance from the closest OWF; shaded area: 95 % confidence interval; small lines on the x-axis: observations of loons at a given distance from the OWF.

To determine the distance at which the change in loon density became significant, we calculated confidence intervals for the first derivatives via bootstrap analysis and subsequently evaluated where the lower confidence interval intersected with zero. This occurred at around 16.5 km from the OWFs (Fig. 4). However, the greatest decline in density was at distances within 10 km from the OWF (Figs. 3, 4). Avoidance of wind farms within 10 km was also clearly visible in the distribution maps (solid black lines in Fig. 2b).

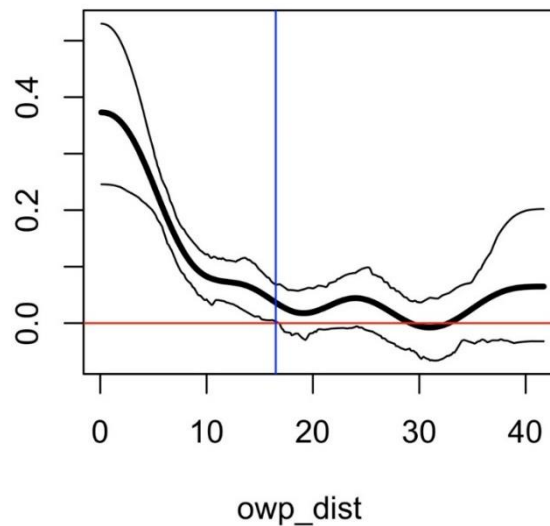


Fig. 4: First finite difference of the smooth depending on the distance from the closest OWF, partially evaluated for the ‘after’ period. Red line indicates a derivative of zero, blue line indicates distance at which the derivative was significant. Thick black line corresponds to the first derivative; thin black lines depict 95 % confidence intervals.

Additionally, the binomial wind farm-related variable *owf_zone* was highly significant for both radii (3 or 10 km, respectively). The abundance of loons decreased highly significantly by 94.5 % inside the 3 km zone around the OWFs within the study site (interaction term in Table 1; $\beta = -2.9$, $p < 0.0001$), while the abundance was still decreased by 83.7 % inside the 10 km zone (Table 2, $\beta = -1.8$, $p < 0.001$). The distance to land (*dist_coast*) had no significant effect on loon densities (Table 1; Table 2).

Table 1: Regression results of the BACI approach–GAMM using the binomial variable ‘inside wind farm’ vs. ‘outside wind farm’ (*owf_zone*) for a radius of 3 km.

	Estimate	Standard Error	z value	Pr(> z)
(Intercept)	-1.05	1.17	-0.90	0.37
period[after]	0.40	0.85	0.47	0.64
owf_zone ¹ [inside]	0.70	0.13	5.07	≤ 0.001
dist_coast ²	0.02	0.02	0.70	0.43
period[after]xowf_zone[inside]	-2.90	0.22	-13.16	≤ 0.001

¹Offshore wind farm zone.

²Distance to coast.

Table 2: Regression results of the BACI approach–GAMM using the binomial variable ‘inside wind farm’ vs. ‘outside wind farm’ (*owf_zone*) for a radius of 3 km.

	Estimate	Standard Error	z value	Pr(> z)
(Intercept)	-1.41	1.17	-1.21	0.23
period[after]	0.73	0.95	0.76	0.45
owf_zone ¹ [inside]	0.66	0.12	5.59	≤ 0.001
dist_coast ²	0.02	0.02	1.01	0.31
period[after] xowf_zone[inside]	-1.81	0.12	-15.26	≤ 0.001

¹Offshore wind farm zone.

²Distance to coast.

Distinguishing between effects of ships and OWFs

Loon densities were still reduced if ships were included in the overall model as a predictor for the ‘after’ period, as was the case without considering the effect of ships, as shown above. Applying a 3 km radius around the wind farms, OWFs alone reduced the loon density by 70.8 % compared with the sea areas outside the OWFs ($p < 0.001$; Table 3). If the radius was extended to 10 km around the OWFs, the loon density was still reduced by 44.5 % ($p < 0.001$) by the OWFs alone.

Table 3: Regression results for the *ship-owf*-approach–GAMM distinguishing between the effect of ships and the effect of OWFs in the ‘after’ period for a radius of 3 km.

	Estimate	Standard Error	z value	Pr(> z)
(Intercept)	0.29	0.58	0.5	0.62
owf_zone¹[inside]	-1.23	0.31	-4.03	≤ 0.001
dist_coast²	-0.01	0.01	-0.55	0.58
n_ships³	-0.37	0.08	-4.82	≤ 0.001

¹Offshore wind farm zone.

²Distance to coast.

³Number of ships.

Table 4: Regression results for the *ship-owf*-approach–GAMM distinguishing between the effect of ships and the effect of OWFs in the ‘after’ period for a radius of 10 km.

	Estimate	Standard Error	z value	Pr(> z)
(Intercept)	0.73	0.58	1.26	0.20
owf_zone¹[inside]	-0.59	0.17	-3.51	< 0.001
dist_coast²	-0.01	0.01	-1.00	0.32
n_ships³	-0.48	0.07	-6.44	< 0.001

¹Offshore wind farm zone.

²Distance to coast.

³Number of ships.

When ships as single predictor were removed from the model, the estimated effect of OWFs (now combined with the effect of the ships) on loons was 84 % using a 3 km radius ($p < 0.001$). This suggested that ships also had a strong negative effect on loon abundance, accounting for at least 14 % of the joint OWF–ship effect.

Thus, in the ship model, the effect of OWFs alone was not as strong as estimated by the BACI approach (i.e. without considering ship traffic; > 94% and > 84%, respectively). There are two possible explanations for these different estimations. (1) the ship model was only fitted using data from the ‘after’ period because no ship data were available for the ‘before’ period. Hence, the estimated reduction in effect does not take account of the fact that bird densities within the OWFs showed the

highest loon abundances before the construction of the farms (see above), leading to a strong underestimation of the reduction effect. (2) Although the ship model considered the effect of ships, these were at least partially correlated with OWF location (Fig. 5). Thus the BACI approach actually estimated the joint reduction effect of OWFs and ships, whereas the ship model evaluated both impacts separately, which may have led to a reduction in the OWF effect compared with the BACI approach.

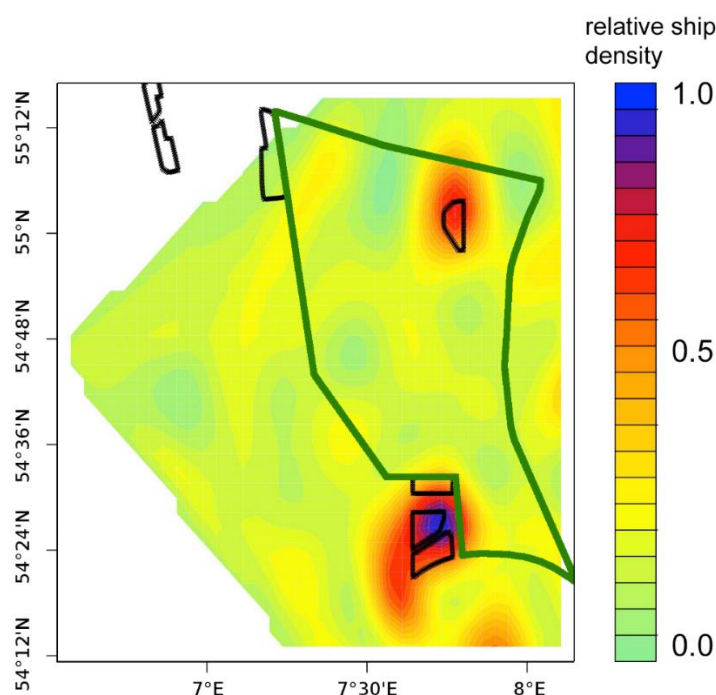


Fig. 5: Spatial density plot of ship distribution in the 'after' period based on AIS data.

Indeed, the ship model showed a significant negative impact of ships on loon abundance (Table 3-4), with a highly significant decline of 31 % in abundance for each additional ship in the spatio-temporal range of the loons (i.e. 5 min and 5 km from the loon sighting; see Methods) ($p < 0.001$). This suggests that one in three loons left the area as one ship approached. The spatial component of ship disturbance was much stronger than the temporal component; i.e. our regression models selecting for the optimal δ_t and r revealed that ships within 5 km had a strong impact on loon abundance, whereas the time lag between the loon sighting and the AIS signal of the ship was less relevant (with an optimum at approx. 5 min). This suggests that ships may affect loons most strongly at a distance of ≤ 5 km.

As seen with the BACI approach, the distance to land had no significant influence on loon abundance (Table 3-4).

Discussion*Distribution patterns before and after OWF installation*

Our results demonstrated that the distribution patterns of loons, which had remained stable over a period of many years (Garthe et al. 2015), were substantially altered at both small and large spatial scales by the installation of OWFs in the German North Sea. We developed our BACI approach on a solid database including 14 years of large-scale surveys in the period ‘before’ OWF installation. To the best of our knowledge, all previous reports have been based on a maximum of 1–3 years of data prior to the construction of OWFs, and have mostly focused on the effect of a single OWF (e.g. Leopold et al. 2013, Petersen et al. 2014). Although we were unable to compute absolute differences in loon populations between the two periods due to a change in survey methods, our results demonstrated profound large-scale shifts in distribution patterns, as well as significant avoidance of the OWF areas.

We observed a shift in the loon-abundance hotspot to the western–central area of the SPA that remained undisturbed by OWFs in the ‘after’ period. This hotspot is located about 20 km distant from all surrounding OWFs. Several previous studies have highlighted the environmental parameters that are most important for determining loon distribution patterns. Frontal systems are expected to increase prey availability for loons (Skov & Prins 2001), while nearshore and shallow sandy sea areas also play a major role (O’Brien et al. 2008, Skov & Prins 2001, Skov et al. 2016). Our results suggest that the area of the ‘Butendiek’ OWF, which was installed in the northern part of the SPA, was of particular importance for loons before the construction of this OWF, given that this was the area of maximum loon abundance during the ‘before’ period. The ‘Helgoland-Cluster’ OWFs are located south-west of the border of the SPA, and our results showed that, in contrast to the ‘Butendiek’ area, loon abundances in the ‘before’ period were significantly lower compared with abundances within the SPA. However, loons are known to occur here regularly (Garthe et al. 2015).

One aim of this study was to disentangle the importance of natural habitat structures and anthropogenic pressures on loons. Our modelling approach showed that natural habitat predictors, such as distance to the coast/Helgoland and water depth did not play major roles compared with the effects of OWFs and shipping (see below). This suggests that anthropogenic pressures are the most important factors driving the distribution patterns of loons within their natural hot spots.

Still, we cannot completely rule out that undetected changes in ecological conditions might have additionally led to the shift in distribution patterns. For instance, it could be assumed that loons might have followed shifts in their prey community. However, given that loons are known to feed on a variety of fish species (Guse et al. 2009), a shift in fish distribution that could account for the change in loon distribution seems highly unlikely. The reef effect is even known to likely increase benthic and fish

communities inside OWFs (e.g. Vandendriessche et al. 2015, Vanermen et al. 2015) which in turn may enhance the quality of these sites for piscivorous seabirds. However, given that these sites were avoided by loons, despite of a likely higher fish availability and as loon distribution patterns had been stable over a period of many years in the 'before' period (Garthe et al. 2015), it seems to be convincing that OWFs and associated ship traffic are the main factors explaining the shifts in distribution patterns.

Incorporating distance from the nearest OWF as a smoothed term in the model allowed us to highlight the fact that loons reacted as far as 20 km from OWFs, with significant changes in densities at a distance of 16.5 km and the greatest changes in abundance within 10 km. These values were higher than those reported in previous studies (summarized in Dierschke et al. 2016, Welcker and Nehls 2016). However, most previous studies only investigated local avoidance effects (often only up to 4 km distance; Leopold et al. 2013, Petersen & Fox 2007, Petersen et al. 2006, Welcker & Nehls 2016) and were therefore unable to detect any larger-scale avoidance reactions. This highlights the importance of a sufficiently large-scale approach and the inclusion of multiple OWF sites (Rexstad & Buckland 2012), as in the current study. To emphasize the importance of scale, we quantified the effects of OWFs on loons by defining the affected sea areas by both 3 km and 10 km radii.

The 3 km distance class was chosen based on previous studies that showed avoidance distances for single OWFs up to this value (Vanermen et al. 2015, Welcker and Nehls 2016). However, our results suggest that this distance was too short, based on the effects of multiple OWFs on a larger spatial scale.

The reason for the relatively large-scale effect of OWFs on loons detected in the current study is not completely clear. It is possible that visual cues are not the only reason for the large disturbance distance. Previous studies showed that OWFs not only affected seabirds and other marine wildlife directly (Bergström et al. 2014, Goodale & Milman 2014, Lindeboom et al. 2011), but may additionally cause changes in the abiotic environment, such as sediment properties and water stratification due to turbulence caused by the piles (Carpenter et al. 2016, Nagel et al. 2018). Carpenter et al. (2016) pointed out that an individual OWF may enhance mixing of the water column, with a cascade of effects on the whole ecosystem in an area of 10–20 km from the OWF, though the physical–biological interactions remain unclear. This was in accordance with the disturbance distance of loons found in the current study. Petersen et al. (2014) also showed significantly lower loon abundances up to 13 km from OWFs, which also matched the results of the current larger-scale approach.

Finally, it is important to critically explore the question of the power of the data used in this study. For the type of data used, previous investigations have shown that high survey intensities are required to safely trace declines in seabird populations, mainly as a result of high variability in distribution patterns (e.g. MacLean et al. 2013, Vanermen et al. 2015a). However, compared to our study that was conducted over a large sea area, both studies mentioned above focussed on rather small study sites,

likely enhancing small-scale variability in counting data. According to Vanermen et al. (2015a) the statistical power after 10 years of survey was sufficiently high to detect reliable changes. For the 'before' period, 13 years of data were available for our BACI approach, indicating a valid data base. In contrast, the 'after' period only consists of 10 aerial surveys over a period of three years, suggesting that the data base for the 'after' period may still be too weak. However, the significant negative and consistent effects of OWFs and associated ship traffic on loon distribution during all surveys of the 'after' period indicates that the data base is sufficient to yield valid results. Nevertheless, it will be necessary to enhance the data base for the 'after' period by future surveys to confirm the results and to enhance the statistical power.

Distinguishing between the effect of ships and OWFs

The installation of OWFs causes a substantial increase in ship traffic in the surrounding area due to maintenance and service activities (Exo et al. 2003). Although ship traffic is known to affect the distribution patterns of seabirds and particularly of loons (Bellebaum et al. 2006, Schwemmer et al. 2011), the combined effect of OWFs and their associated ship traffic has rarely been reported; however, the few available studies noted a significant impact of ship traffic on loon distribution (APEM 2013, 2016, Leopold et al. 2014, Skov et al. 2016). Loons have been shown to exhibit a behavioural response to approaching ships, and flight distances of up to 2 km have been documented (Bellebaum et al. 2006; Schwemmer et al. 2011). This corresponds to the current results, which suggested a significant reduction in loon densities within a radius of up to 5 km from the vicinity of ships, with the temporal aspect of ship distribution having little effect.

Inclusion of ship abundance in the model showed a reduced density of loons of up to 70 % based on the 3 km distance zone. This reduction could be considered to reflect the effect of the OWFs alone. In contrast, the joint effect of OWFs and ships led to a reduction of 84 %, indicating the additional negative impact of ships on loon densities. The exact reduction in densities due to ships alone could not be computed reliably because of the collinearity of ship traffic and OWFs. Importantly, their mobile nature means that ships are both spatially and temporally variable predictors, and a reliable estimation of their overall effects on birds will always be biased. This issue will remain difficult to address even in future studies, given that ships aggregate strongly in the vicinity of OWFs and present no fixed predictor.

The greater reduction in loon densities following inclusion of ship traffic in the model demonstrates the importance of reviewing the cumulative impact of multiple anthropogenic pressures in the marine environment. Previous studies have focussed on cumulative effects simply by investigating the

combined effects of multiple OWFs (Busch et al. 2013, Desholm 2009, Dierschke et al. 2003, 2006, Fox et al. 2006, King et al. 2009, Mendel & Garthe 2010). However, given the strong effect of ships on loon abundance, it seems necessary to include other anthropogenic pressures in estimates of cumulative effects on loon abundance in general.

Conclusions

The large-scale avoidance effects of OWFs (and ships) on loons suggest that loons are unlikely to suffer from enhanced direct mortality, e.g. because of collisions (Leopold et al. 2010, Petersen et al. 2006, this study). Furthermore, a low flight altitude of only up to 10 m above the sea surface (van Bemmelen et al. 2011) reduces the collision risk for loons. Indirect effects, such as habitat loss, are thus likely to be key factors affecting loons in relation to OWFs. However, the consequences of such indirect effects e.g. on population levels of seabirds, and density-dependent effects are hard to assess, and appropriate methodologies are largely lacking (Green et al. 2016, Horswill et al. 2017). When assessing the consequences of habitat loss due to the installation of OWFs and the associated enhancements in ship traffic, it is essential to consider which alternative sea areas could be used as resting and foraging grounds. In the current case, alternative sites seemed to be very limited because the SPA was virtually surrounded by OWFs. This might explain why loons tended to concentrate in the centre of the SPA rather than moving outside it.

Although it was not possible to compute absolute differences in abundance between the 'before' and 'after' periods in this study, it is hoped that this issue will be resolved when enough data become available from parallel digital and visual surveys of sea areas where visual observations are still allowed. However, the relative reduced densities of loons with respect to OWFs and ship traffic as well as the avoidance distances provided in the current study will serve as a baseline for further studies. A suitable approach for quantifying the overall habitat loss for loons would involve computing the relative proportion of habitat loss within a certain area (e.g. within the SPA). Dierschke et al. (2006) suggested summing the total OWF areas and adding an additional buffer zone to assess the overall habitat loss. Applying this approach to the current study allowed the minimum habitat loss due to the OWFs in the SPA to be computed, indicating that complete loss of the sea area within a 3 km radius around the OWFs for loons (as strongly supported by the current study) would equate to a loss of 8.8 % of the SPA (overall size 3,135 km²) for loons. This should be regarded as an absolute minimum, given that our results clearly showed that the density of loons was greatly reduced beyond 3 km from the nearest OWF.

Although we are not able to compare absolute density values between the 'before' and 'after' periods, our results indicated that loons aggregated in the centre of the SPA after OWF installation, representing an increase in loon density in a much smaller sea area. Given that loons tend to occur in

comparatively small flocks, only occasionally exceeding 5–10 individuals/km² (Garthe et al. 2015, O’Brien et al. 2012), this change in distribution might promote density-dependent effects (Blanc et al. 2006, Horswill et al. 2017, Lewis et al. 2001). A possible shift towards suboptimal habitats may lead to suboptimal body conditions prior to breeding, which could in turn reduce the reproductive success and enhance mortality in adult birds (Coulson et al. 1983, Hüppop 1995). Even a slight increase in the mortality of adult loons of only 0.3 % can have significant negative effects on population levels (Rebke 2005).

To assess the role of habitat loss on loons, it is crucial to know if habituation to OWFs will occur or if the habitat loss will be permanent. Although studies from the UK and The Netherlands have indicated slight (though insignificant) increases in loon abundances after 4–5 years since construction, studies from Denmark have shown no signs of habituation (Petersen & Fox 2007, Petersen et al. 2008). Similarly, the current study found no habituation 3 years after construction. However, the monitoring of the operating wind farms is still ongoing and thus results on habituation are preliminary. Given that the degree of habituation remains very unclear, we strongly recommend the need for long-term monitoring to assess any potential large-scale effects of cumulative anthropogenic drivers on loon distribution, particularly within the most relevant sea areas for loons (e.g. Vanermen et al. 2015, a).

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CHAPTER II:

Offshore windfarm effects on seabird abundance - strong effects revealed for spring and breeding season



Peschko V, Mendel B, Müller S, Markones N, Mercker M, Garthe S (in preparation for submission)
Offshore windfarm effects on seabird abundance - strong effects revealed for spring and breeding season

Offshore windfarm effects on seabird abundance - strong effects revealed for spring and breeding season

Verena Peschko, Bettina Mendel, Sabine Müller, Nele Markones, Moritz Mercker, Stefan Garthe

Abstract

With the increasing number of offshore wind farms (OWF) being built worldwide a possible conflict arises with the ecological requirements of top predators entirely depending on offshore areas for the largest part of their lives. We studied ecological effects of OWF on two seabird species breeding in the southern North Sea which have different habitat preferences and so far have been shown to differ in reactions towards OWFs. Based on an extensive, large scale dataset collected via observer-based and digital aerial and ship based surveys between 2000 and 2013 (before OWF construction) and 2015 - 2017 (after OWF construction) we revealed strong effects of OWF on both species for different seasons. The ratio between 'OWF area' (OWF + 3 km buffer) and surrounding area differed between the periods before and after OWF construction. Substantially lower relative densities were detected in the OWF area after OWF construction and significant reductions up to a certain detectable 'response radius' were found: Guillemot density in the OWF area decreased highly significantly by 63% ($p < 0.001$), and a response radius of about 9 km was detected for the spring season. In the breeding season guillemot density was reduced by 44% ($p < 0.05$, OWF + 3 km buffer vs. surrounding area, after OWF construction compared to before construction) without an estimable response radius. The kittiwakes' relative density in the OWF area significantly decreased in the breeding season by 45% ($p < 0.01$) with a response radius of about 20 km, in spring the density decreased by 10% ($p = 0.65$). This study investigated how OWFs affect the distribution of seabirds breeding in a nearby colony and if OWF effects vary with the season. Our findings underline the value of large scale and long-term assessments considering the seasonal variation in the species yearly cycle to quantify OWF effects on seabird populations. Such information substantially adds to the current knowledge and needs to be included in planning and management recommendations provided to decision makers.

Keywords: offshore wind farm, BACI, environmental impact, guillemots, kittiwakes, habitat loss, habitat model, management

Introduction

To saturate the increasing demand for renewable energy resources, offshore wind farms (OWFs) are numerous approved and constructed worldwide (Perveen et al. 2014). The German Government plans to implement OWFs generating 6.5 GW power until 2020 and 15 GW until 2030 (BSH 2017). Currently 19 OWFs are in use, four are under construction and several more are approved in German waters (BSH 2019).

A possible conflict with this development arises from the fact that top predators such as seabirds thoroughly depend on offshore areas for foraging but also for resting and moulting (Schreiber & Burger 2001). Depending on the species, different behavioural reactions towards OWFs are known, ranging from complete avoidance to attraction (Garthe & Hüppop 2004, Drewitt & Langston 2006, Furness et al. 2013, Dierschke et al. 2016). In this context the common guillemot (*Uria aalge*, hereafter guillemot) and the black-legged kittiwake (*Rissa tridactyla*, hereafter kittiwake) are especially important to study as both are key seabird species in the German North Sea, have different ecological requirements and showed locally differing reactions to OWF in previous studies (Dierschke et al. 2016).

The impact of an OWF strongly depends on the importance of the respective area for a species and on the species' annual life cycle stage e.g. with regards to breeding, migrating, moulting (Masden et al. 2009, 2010, Furness et al. 2013, Busch & Garthe 2016, 2018). In several studies in Belgium and The Netherlands guillemots largely avoided OWF areas (Leopold et al. 2013, Vanermen et al. 2015, 2016), i.a. with a reduced abundance of 71% in the OWF area compared to the surroundings (Vanermen et al. 2015). In other studies, e.g. in the UK, guillemots were attracted or did show indifferent reactions with no changes in abundance (PMSS 2007, Vallejo et al. 2017). For kittiwakes some studies reported avoidance (Leopold et al. 2013, Vanermen et al. 2016) with an abundance reduction of 86% in the OWF area (Vanermen et al. 2016), others found no clear response behaviour (Krijgsveld et al. 2011, Percival 2013, Welcker & Nehls 2016) or even attraction (Canning et al. 2013, Vanermen et al. 2015). As kittiwakes are known to fly a considerable part of the time at turbine blade height (Krijgsveld et al. 2011, Johnston & Cook 2016, Borkenhagen et al. 2018), collision risk also needs to be considered for this species (Furness et al. 2013, Busch & Garthe 2018). In Germany only two studies focusing on the effects of the relatively small OWF *alpha ventus*, north of the East Frisian Islands, are published so far (Mendel et al. 2014, Welcker & Nehls 2016).

Until now few studies explicitly investigated how seabirds react to an OWF in close vicinity to their colony during the breeding season (Masden et al. 2010, Langton 2013) and how their reaction towards OWFs changes with the season (Krijgsveld et al. 2011). However, this is considered important since reactions can change due to different seasonal requirements, e.g. during the breeding season. Furthermore, displacement or attraction may have very different consequences depending on the

season which needs to be considered when concluding on population level effects (Busch & Garthe 2016, 2018).

Guillemots and kittiwakes belong to the most numerous seabird species worldwide and are thus prone to experience interference with OWF at various locations. It is thus urgently needed to profoundly understand their reactions towards OWFs.

Seabirds underlie a row of other pressures, and populations of kittiwakes have declined substantially throughout the species global range presumably due to prey reductions by climate change and overfishing (Descamps et al. 2017). Today they are listed as vulnerable on the IUCN Red List (BirdLife 2018b). In the IUCN Red List common guillemots are listed with least concern, EU wide they are classified as near threatened (BirdLife International 2015a, 2016).

The only guillemot colony and one of the few kittiwake colonies in the south-eastern North Sea are located on the island of Helgoland, 48 km off the German coast (Fig. 1). The breeding numbers are relatively small and encompass 3,178 guillemot and 5,201 kittiwake breeding pairs (Dierschke et al. 2011, Dierschke et al. 2018). The number of breeding guillemots did not change considerably for many years now (Dierschke et al. 2011, Dierschke et al. 2018). After being relatively stable for many years, the numbers of breeding kittiwakes slowly started to decline in 2004 (Markones et al. 2009, Dierschke et al. 2011). During the breeding season the area around Helgoland is thus of special importance for the guillemots and kittiwakes breeding in German waters.

Since October 2015, three wind farms with 208 turbines in total covering an area of 105 km² located only 23-35 km north of Helgoland are in operation. Their construction in the vicinity of the breeding colony calls for an assessment of possible effects on the locally breeding seabird species.

In the scope of various research and monitoring projects as well as EIAs, systematic seabird surveys have been conducted in the study area since the year 2000, which allows for thorough analyses of guillemot and kittiwake distribution and abundance before the construction of the OWFs based on an extensive long term data base. In combination with surveys conducted during the operational phase of the OWFs between 2015 and 2017 this comprehensive data base offers the unique opportunity to (1) understand how the species react in different seasons (spring- and breeding season respectively) and due to the isolated location of the colony solely study the effects of OWFs on a local breeding birds, and thus to (2) provide conservation and management with detailed information on these species reaction towards OWFs.

Materials and methods

Study area

The study area is situated in the eastern part of the German North Sea between 55.28 and 54.18°N, 6.51 and 8.16°E (Fig. 1). Water depth ranges from 10 m to 40 m with largest depth mainly concentrated in the post-glacial river Elbe valley in the south-west of the study area (Fig. 1). The island of Helgoland is located close to the southern border of the study area. Four wind farms are located in the study area, the OWF “Butendiek” in the north and the OWFs of the “Helgoland-Cluster” (Amrumbank West, Nordsee Ost, Meerwind) in the south, minimum 23 km north of Helgoland.

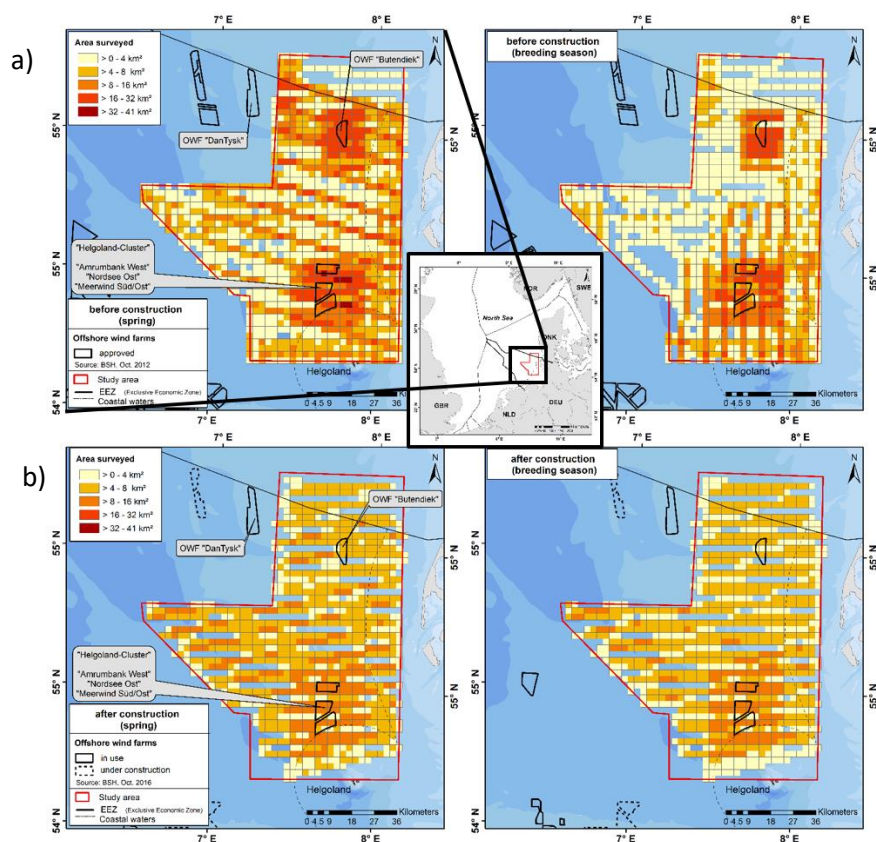


Fig. 1: Location of the study area in the North Sea, inserted map, as well as survey effort in spring and breeding season during a) before and b) after OWF construction. OWFs are delineated with black lines.

Data collection and processing

Data on guillemot and kittiwake distribution for the period before construction of the OWFs (in the following named “before”) were collected via observer-based aerial and ship based surveys between 2000 and 2013. The records originate from environmental impact assessment studies (EIA) required for licensing procedures of OWFs in the German EEZ (before impact studies of the OWF areas, Fig. 1) as well as from 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 (BfN); for details on the data basis see Garthe et al. 2015). Applying the distance-sampling method, seabirds were counted along transects in a predefined area in order to compute densities of the species (for a description of both methods see Diederichs et al. 2002, Garthe et al. 2002). In the period before the OWF installation a total of 9,574 km² were covered in spring and 6,235 km² in the breeding season.

Data on guillemot and kittiwake distribution for the period after construction of the wind farms (in the following named “after”) were collected via digital aerial surveys between 2015 and 2017 (for a detailed description of the method see Thaxter & Burton 2009, Buckland et al. 2012). The records originate from ongoing mandatory monitoring of the wind farms during operation of OWF as well as from the research project ‘Helbird’, funded by the German Federal Ministry for Economic Affairs and Energy. A change from observer-based to digital aerial survey methods was mandatory for safety reasons as during the construction and operational phase of the turbines the flight altitude needed to be much higher which did not allow for observer-based recordings. In the period after the OWF installation a total of 5,633 km² were covered in spring and 5,185 km² in the breeding season. The pooled survey effort conducted in the before and after period is shown in Fig. 1.

As disturbance during the construction of the OWFs is temporary compared to the expected OWF lifetime (Christensen et al. 2003), we only analysed the effect of the main operational phase where OWFs affect seabirds i.e. as a visual barrier or via disturbance by supply vessels working in the area (Exo et al. 2003, Drewitt & Langston 2006).

For the period before the OWF construction, species-specific distance correction factors were applied for observer-based aerial (guillemots: 3.3, kittiwakes: 2.3, Markones & Garthe 2012) and ship-based observations (guillemots: 2.1, kittiwakes: 1.9, Garthe et al. 2009), respectively. Otherwise seabird densities in transect bands which are further away from the observer would be underestimated (Buckland et al. 2001; 2015). For the video-based digital surveys no distance correction was necessary as the detection probability is equally high across the whole transect.

As it is not known whether the aerial observer-based and digital methods lead to comparable results (Buckland et al. 2012, Skov et al. 2016), we did not compare absolute densities between the “before”

and “after” period. Instead, we used relative deviance from the maximum density in each period in percent to compare the distribution and the position of high density areas of guillemots and kittiwakes between the two periods.

For each species and method, data were spatially pooled in a grid with cells of 2.5 x 2.5 km size for the “before” and “after” period respectively and separately for the “spring-season” (21.02. - 06.05.) and the “breeding season” (07.05.-15.07.). For each grid cell per period and season, bird numbers and survey effort were summed up to calculate mean densities, whereas geographical coordinates were averaged. Preliminary data analysis revealed an unusually high number of kittiwake sightings apparently associated with fishing vessels during one survey day in spring (26.02.2016). Occurrence of fishing vessels and kittiwakes overlapped strongly with OWF areas, especially the 3 km buffer around the OWFs and a corridor between two wind farms. To eliminate fishing vessel effects from the OWF effect analysis, this day was excluded from the analysis of the kittiwake data.

Integrating covariates

ArcGIS (version 10.3; Environmental System Research Institute 2016) was used to calculate means of the environmental covariates for a grid with a spatial resolution of 0.2 x 0.2 km. Environmental variables included (1) *dist_coast* = minimal distance to the mainland and large islands (without Helgoland), (2) *dist_helgoland* = minimal distance to the island of Helgoland, (3) *dist_owf* = minimal distance to the border of the wind farms, (4) *mean_depth* = mean water depth and (5) *slope* = inclination of the seabed.

To merge the environmental variables in an optimal way with the seabird distribution data, we pooled the covariates to a spatial grid of 2.5 x 2.5 km, and fitted each covariate with a GAM using the function `gam()` from the R-package `mgcv` (Wood 2006, R Core Team 2017; R version 3.4.2). Here, we used only latitude and longitude as a smooth 2D-predictor based on cubic splines with the maximal degree of freedom, so that the result represents a cubing interpolation on the given grid. We then used the `predict()` function to predict the values to the coordinates of the seabird distribution grid. The categorical variable *owf_zone*, which enables us to compare “inside affected area” vs. “outside affected area” was defined in two categories: a) for guillemots and kittiwakes “inside OWF” was defined as the OWF plus a 3 km buffer around the turbines (version one of *owf_zone*, Table 1), as OWF associated ships mainly operated in a radius of up to 3 km around the OWF; b) “inside OWF” was defined as the OWF plus 9 km (guillemots) or 20 km buffer (kittiwakes) around the turbines (version two of *owf_zone*, Table 1), as a first analysis showed the strongest reductions in densities to a distance of 9 km and 20 km for the respective species (see section 3.3. & 3.4.):

Table 1: Categories defined for the variable *owf_zone* for the respective season.

Species	Season	Version of <i>owf_zone</i>	Inside OWF (dist_owf in km)	Outside OWF (dist_owf in km)
Guillemots	spring + breeding	1	< 3	> 3
	spring + breeding	2	< 9	> 9
Kittiwakes	spring + breeding	1	< 3	> 3
	breeding	2	< 20	> 20

Set up and validation of regression models for the BACI-approach

Based on surveys of a potentially impacted and a control area before and after the OWF construction (variable *period*), with the BACI (“before” – “after” control impact analysis) approach, relative comparisons of spatial and temporal differences can be used to extract the unbiased OWF impact (Smith 2002, Schwarz 2014). We formulated the BACI approach within the framework of generalised additive mixed models (GAMMs) which are well known to appropriately describe biological count data (Zuur et al. 2007, 2009, 2012, Korner-Nievergelt et al. 2015). To estimate how abundance of guillemots and kittiwakes changed depending on the distance to OWFs and to estimate avoidance distances we used a continuous linear or smooth predictor measuring the distance to the border of the closest OWF. A variable for the observation method (“ship based surveys” vs. “observer-based aerial surveys” vs. “digital aerial surveys”) has been introduced as a random intercept to especially account for differences in seabird detection between these methods. We are aware that this variable is partially collinear with the variable *period*, since in the “after” period only digital aerial surveys have been used and in the “before” period only observer-based aerial surveys have been performed. Thus, we could not distinguish between natural abundance fluctuations from “before” to “after” and detection differences of the differing methods. Importantly, the estimation of the interaction term ‘wind_farm x period’ (see below) representing the BACI approach was not influenced by this, since here, only relative differences in seabird densities were evaluated. Also changes in seabird distribution can nevertheless be revealed.

This resulted in the following full model for the BACI approach (not yet thinned regarding its predictors; see below and hence equal for both guillemots and kittiwakes):

$$\begin{aligned}
 \log(y_{ij}) = & \beta_0 + u_i + p(\text{mean_depth}_j) + p(\text{dist_coast}_j) + p(\text{dist_helgoland}_j) + \\
 & p(\text{slope}_j) + s(\text{latitude}_j, \text{longitude}_j) + [\text{wind_farm}_j] + \text{period}_j + \\
 & [\text{wind_farm}_j] \times \text{period}_j + \text{offset}(\log(\text{area}_j)) + \varepsilon_{ij}
 \end{aligned} \tag{1}$$

with $\varepsilon_{ij} \sim N(0, \sigma^2)$ and $u_i \sim N(0, \sigma^2_u)$ independent and identically distributed. Here, y_{ij} is the vector of seabird numbers, where the index j refers to the individual observation and i is related to the observation method. $s()$ delineates a cubic regression spline where the optimal number of knots has been estimated via cross-validation. $p()$ depicts polynomial terms up to order five (which have been separately selected during predictor selection, c.f. following subsection). The variable [*wind_farm_j*] was either considered as a linear term *dist_owf_j* measuring the distance to the border of the next OWF, or as an additive smoother, $s(\text{dist_owf}_j)$, or as a bivariate variable, *owf_zone_j*, the latter distinguishing between "inside affected area" and "outside affected area". For each model, an appropriate probability distribution has been selected for y_{ij} via AIC analysis (see below).

To obtain and validate the optimal GAMM-model, we modified the selection and validation strategies (Field et al. 2012, Zuur 2012, Zuur et al. 2009, 2010, 2012, Korner-Nievergelt et al. 2015) by the following steps:

- (1) Based on the full model (1) we selected an appropriate probability distribution of the model using the Akaike Information Criterion (AIC; Akaike 1973). We compared a Poisson-, negative binomial-, Tweedie-, zero-inflated Poisson-distribution as well as an "observation-level random intercept poisson model". All five probability distributions are known to describe the stochastic part in regression models of (overdispersed) count data reasonably well (Kokonendji et al. 2004, Linden & Maentyniemi 2011, Zuur et al. 2012, Korner-Nievergelt et al. 2015).
- (2) Predictor selection was based on LASSO (Tibshirani 1996, 1997, Korner-Nievergelt et al. 2015) testing > 50 different linear and polynomial terms of the above mentioned possible predictors;
- (3) Model validation was performed by a visual inspection of the residual plots to assess all required model assumptions (Zuur et al. 2010). Corresponding auto-correlation structures were added to the model.

According to AIC, the negative-binomial distribution was slightly favoured to the tweedie-distribution in the *guillemot-model* for the breeding season and both *kittiwake-models* (spring- and breeding season), whereas in the *guillemot-model* for the spring season it was the other way round. In both *guillemot-models* and the *kittiwake-model* for the breeding season, the variables *mean_depth* and *dist_coast* appear only linearly, whereas the variables *dist_helgoland* and *slope* have been selected with several nonlinear terms. In the *kittiwake-model* for the spring season, the variable *mean_depth* also appears only linearly, *dist_coast* was not selected and the variables *dist_helgoland* and *slope* have been selected with several nonlinear terms. The residual analysis revealed no violation of linearity, homogeneity, independence or normality of the random intercept. The final model formulas and tables are shown in Supplement 1.

In the final models, for each species separately, the distance to the closest wind farm was introduced as a smooth term and separately estimated for each period (before and after) and each season (spring and breeding season). We additionally calculated the difference between the after-smooth versus the before-smooth (for each season separately). This difference-smooth depicts changes in bird density depending on the distance to the OWFs in the after-period compared to the before-period. We furthermore evaluated at which distance to the OWFs the abundance decline was significant (Supplement 2). We therefor approximated the first derivative of the "difference-smooth" between the "after-" and the "before-smooth" with respect to the distance. This derivative represents population increase or declines depending on the distance to the OWFs (details see Supplement 2).

Results

Distribution before and after the installation of the OWFs

The overall distribution of guillemots and kittiwakes in the different seasons was similar in the before- and the after-period (Fig. 2a, b). In spring high guillemot densities were found in the west to south-west of the study area. During the breeding-season guillemots concentrated more in the area close to the colony in the south of the study area but also often used some smaller areas in the south-west and east. In both seasons the area of the Helgoland-Cluster OWFs did not belong to the areas with the highest densities. Still, a comparison of distribution patterns clearly shows that, especially in spring, densities in these OWF areas were reduced compared to the surrounding waters in the after-period. In spring high kittiwake densities were found in the western to southern half of the study area and density in the OWF area was relatively low compared to the surrounding areas. During the breeding-season before the OWF construction kittiwakes concentrated in the south of the study area, in the area close to the colony as well as in the later OWF area. After the OWF construction high densities of kittiwakes stretched out further offshore to more westerly areas along the Elbe river valley. Density in the OWF area was low.

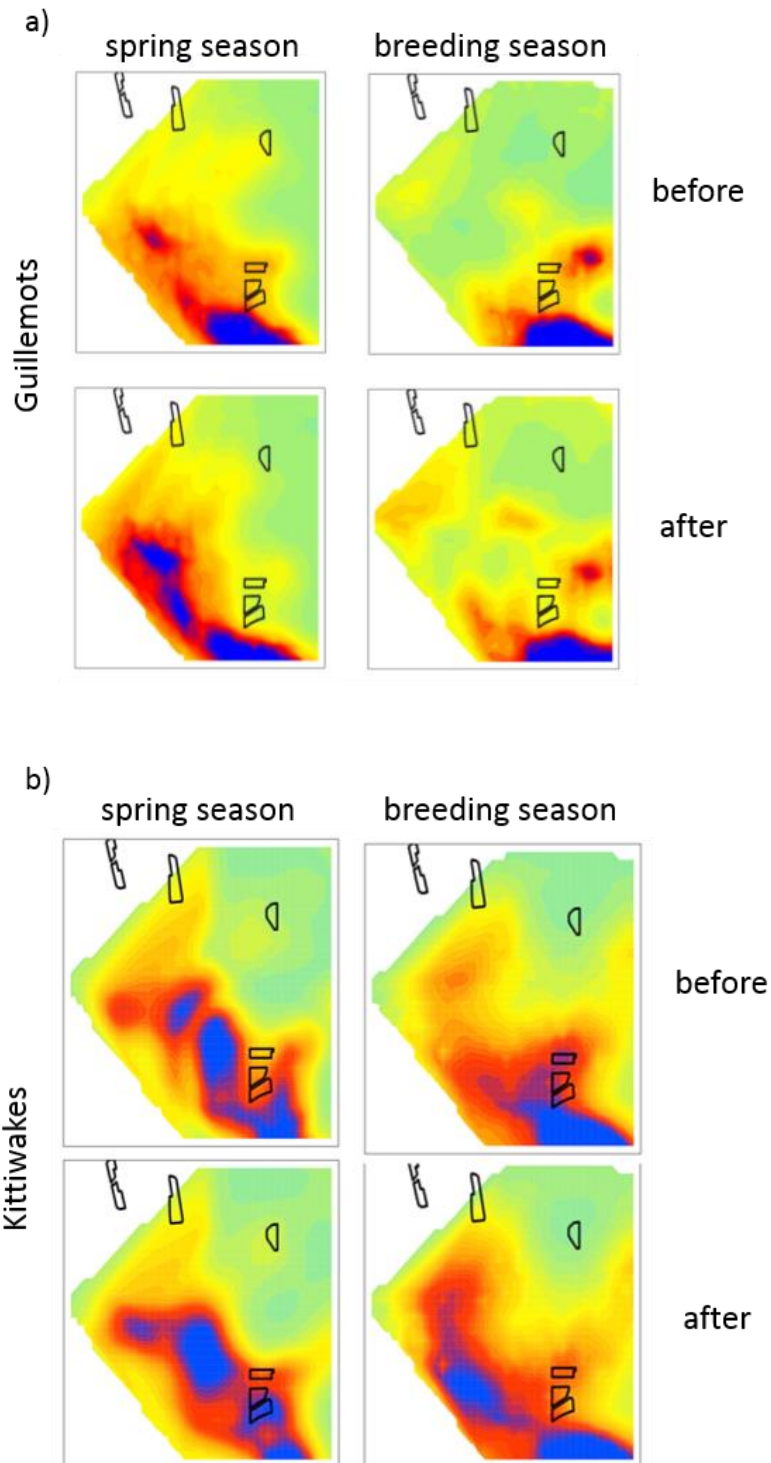


Fig. 2: Predicted density plots showing a) the guillemot densities and b) kittiwake densities on a relative scale for each species, season and period (rescaled for each plot) separately evaluated for before- and after-period as well as for spring- and breeding season. Green colour indicate low, blue colour high relative densities; black lines represent boundaries of offshore wind farms.

Guillemot density with distance to the OWFs

The distance to the OWFs as a smooth term is shown in Fig. 3a (first two rows), separately estimated for each period (before and after) and each season (spring and breeding season). The difference between the after-smooth versus the before-smooth of the distance to the closest wind farm (Fig. 3a, last row) shows that in spring, the guillemot numbers were significantly lower up to a distance of 9 km. During the breeding season, however, this reduction was much less pronounced.

For the spring season, the significant response distance was detected at ≈ 9 km (Table 2 & Supplement 2). For the breeding season, confidence bands were too wide to perform these calculations, hence no significant response distance could be detected.

Introducing the distance to the OWFs as the bivariate variable *owf_zone* (inside vs. outside OWFs, applying the 3 km radius around the OWFs), the interaction term between *owf_zone* and *period* revealed that the relative guillemot density was highly significantly reduced by 63% in spring ($p < 0.001$, Table 2) and by 44% in the breeding season ($p < 0.05$, Table 2) within the OWFs (+3 km buffer). Note that the confidence intervals (CIs) of the density reduction in spring and breeding season overlap (Table 2), hence the difference between the seasons is not statistically significant.

As we found in the preceding analysis that the response of guillemots to the OWFs was significant up to 9 km distance, we furthermore defined the binomial variable *owf_zone* (inside OWFs vs. outside OWFs) by setting the critical distance threshold to 9 km for both seasons. Corresponding regression results revealed that in spring, the population density was still highly significantly reduced by 49% ($p < 0.001$, Table 2) and also during the breeding season density was reduced within that radius (by 30%, $p < 0.05$, Table 2) although guillemots did not show a significant response distance as detected in spring (Fig. 3a & Supplement 2).

Kittiwake density with distance to the OWFs

The distance to the OWFs as a smooth term is shown in Fig. 3b (first two rows), separately estimated for each period (before and after) and each season (spring and breeding season). The difference between the after-smooth versus the before-smooth of the distance to the closest wind farm (Fig. 3b, last row) shows that in spring the abundance did not change strongly with distance to the OWFs. In contrast, during the breeding season, there was a strong, almost linear increase with increasing distance to the wind farm.

As expected, for the spring season no significant response distance could be detected (Table 2 & Supplement 2). For the breeding season a significant reduction in kittiwake density up to a distance of ≈ 20 km was revealed (Table 2 & Supplement 2).

Introducing the distance to the OWFs as the bivariate variable *owf_zone* (inside vs. outside OWFs, applying the 3 km radius around the OWFs), the interaction term between *owf_zone* and *period* revealed that for the spring season no significant difference could be detected (Table 2). However, kittiwake density was reduced by a non-significant 10% ($p = 0.65$) in the OWF area. In the breeding season kittiwake density was highly significantly reduced by 45% ($p < 0.01$). Note that the CIs of the density reduction in spring and breeding season overlap, hence the difference between the seasons is not statistically significant.

As we found in the preceding analysis that the response of kittiwakes to the OWFs in the breeding season was significant up to 20 km distance, we furthermore defined the binomial variable *owf_zone* setting the critical distance threshold to 20 km distance. Corresponding regression results revealed that the density was still significantly reduced by 29% ($p < 0.05$) in the breeding season for that area.

Table 2: Density reduction in the OWF area (+3 km radius), lower and upper confidence intervals (CIs) of density reduction, response radius, and density reduction inside the response radius for guillemots and kittiwakes in spring and breeding season.

species	season	% density reduction OWF area (+3km)	lower CI	upper CI	p-value	response radius (km)	% density reduction up to response radius	p-value
guillemots	spring	63%	94% reduction	280% increase	< 0.001	9	49%	< 0.001
	breeding	44%	90% reduction	190% increase	< 0.05	NA	30% ¹	< 0.05
kittiwakes	spring	10%	45% reduction	46 % increase	n.s.	NA	NA	NA
	breeding	45%	64.5% reduction	14.5% reduction	< 0.01	20	29%	< 0.05

¹9 km radius, which was detected for the spring season was applied.

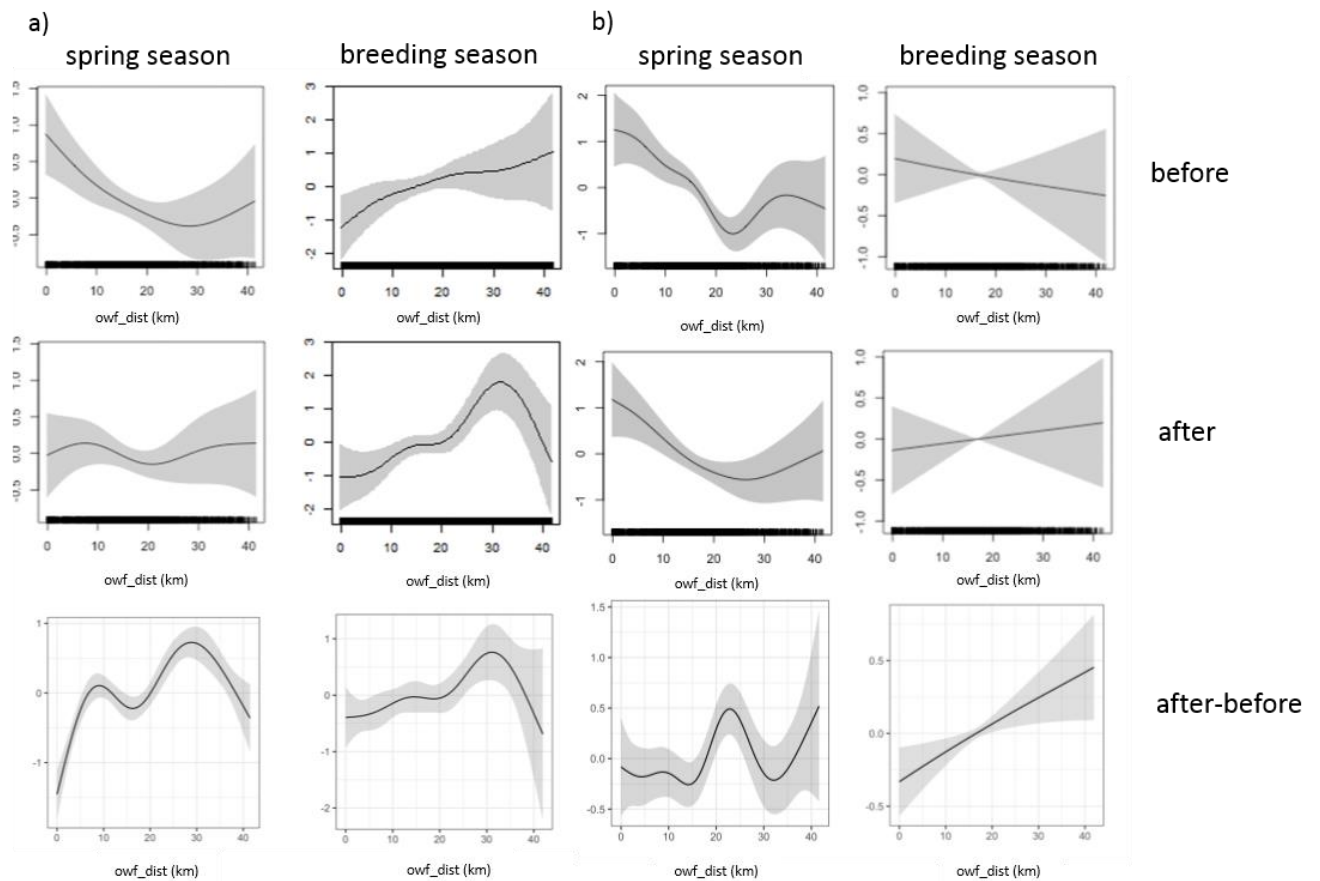


Fig. 3: a) Guillemot and b) kittiwake abundance changing with the distance to the wind farms (in km) before (above) and after (middle) the construction of the OWFs, separately evaluated for spring (left-hand side) vs. breeding season (right-hand side). The last row shows the difference between the “after-smooth” and the “before-smooth”, representing the change due to the construction of the OWFs.

Discussion

Based on an extensive dataset this study profoundly examined the impact of OWFs situated in close proximity to a seabird breeding colony and investigated seasonal differences in OWF effects.

OWF effects in spring (pre-breeding)

In spring seabirds are probably more flexible in habitat choice than during the breeding season as they do not have to feed any offspring and are thus less bound to their colony.

a. Guillemots

Guillemots were more dispersed in spring than during the breeding season. It is possible that the higher flexibility connected to the current stage in their yearly life cycle allowed them to avoid the OWF area even up to distances of 9 km.

As the guillemots belonging to the Helgoland colony already stay close to the colony from March on (Grunsky 1994, Dierschke et al. 2011) we can assume that part of the birds sighted in the study area during spring belong to the local breeding population. Even if guillemots only have to forage for themselves in that season there might be an effect on the individual fitness as birds are displaced by the OWFs and might enter the breeding season with a lower energy budget.

b. Kittiwakes

Kittiwakes were distributed widely in the study area in spring. As they feed at the water surface they are especially dependent on prey resources to be available (Coulson 2011, Paredes et al. 2014). Kittiwakes' prey species in the south-eastern North Sea (young whiting (*Merlangius merlangus*), Clupeids (Clupeidae) and sandeels (Ammodytidae); Markones et al. 2009) are known to be at low levels since many years now although recently some fish stocks are increasing again (ICES 2017a, 2018). It could be that the OWF areas were not significantly avoided in spring due to temporarily available prey resources. Some authors discuss if the turbines increase turbulences in the OWF area (Carpenter et al. 2016, Nagel et al. 2018) and thus increase prey availability for seabirds feeding at the surface (Mendel et al. 2014, Vanermen et al. 2015). This might happen temporarily as such processes depend on the local currents and winds (Carpenter et al. 2016), and the prey occurrence in the area (Jensen et al. 2003, Engelhard et al. 2008, van Deurs et al. 2012). At neighbouring wind farms in Belgium, flocks of foraging kittiwakes were observed inside the OWF and the percentage of kittiwakes observed during active foraging inside the OWF was significantly higher than in the control areas.

Our findings indicate that kittiwakes did not avoid the OWFs in spring. Although their distribution in spring might be driven strongly by other important habitat parameters, the absence of a significant avoidance of the wind farms interpreted in combination with the kittiwakes flight height (Krijgsveld et al. 2011, Johnston & Cook 2016, Borkenhagen et al. 2018) indicates a risk of colliding with the rotating turbine blades (Furness et al. 2013, Busch & Garthe 2018).

OWF effects in the breeding season

As central place foragers, during the breeding season seabirds are strongly bound to their colony and need to find enough food for themselves and their offspring (Orians & Pearson 1979). Breeding seabirds generally have to balance between energy intake and trip distance (Chaurand & Weimerskirch 1994, Suryan et al. 2000, Bertrand et al. 2012).

a. Guillemots

Tracking data revealed that guillemots medium foraging range during breeding season is 37.8 km (Thaxter et al. 2012), which was found to be lower for guillemots breeding on Helgoland (Peschko et al., unpubl.). Thus they forage relatively close to the colony and the OWFs are located inside this already quite restricted foraging range, which might have caused them to avoid the OWFs less than in spring. This is further underlined by the lack of a statistically significant response radius around the OWFs, which suggests that guillemots approached the OWFs more during breeding time.

At the OWF Bligh Bank in Belgium, Vanermen et al. (2015) found that guillemot density decreased by 71% in the OWF and by 61% in the OWF plus 3 km distance. Similar density reduction was found by Welcker & Nehls (2016) at the alpha ventus wind farm (75% reduced density in the OWF, response radius 2.5 km). However, in these studies no information on the reactions of breeding birds to the OWFs is available, as they are situated in areas without nearby colonies. Density reduction found in these studies is comparable with the reduction we found for the spring season. The smaller decrease in density compared to spring and no evident response radius for the breeding season might indicate that no alternative foraging areas were available for guillemots close to their colony, hence they avoided the OWFs less during the breeding season than during spring.

During the breeding period, displacement could cause a change in seabirds' energy and time-budget due to possibly increased foraging trip length and energy expenditure (Masden et al. 2010, Langton et al. 2014, Searle et al. 2014). This might lead to a reduction in adult provisioning rates and a reduced chick growth rate and survival ultimately resulting in a decreased reproductive success (Langton et al. 2014). Longer foraging trips, partially due to detours induced by OWFs, could moreover increase the risk of nest predation (Ashbrook et al. 2008, 2010) and lower adult condition or survival (Masden et al.

2010). Altogether this illustrates that displacement by OWFs can have substantial effects on offspring and adult survival.

For the breeding season we can assume that the largest part of the guillemots sighted in the study area belong to the colony on Helgoland, thus the OWF response can mainly be accounted to the breeding birds of Helgoland. Although it was not the most frequented habitat before construction the density reduction in the OWFs during the operational period leads to the conclusion that guillemots have to compensate for the loss of a formerly suitable habitat close to the colony. Moreover, the lack of response radius shows that they also used the habitat close to the OWFs. This indicates that, if possible, guillemots avoid OWFs up to large distances, as we found for the spring season. But during the breeding season they have to use habitat close to their colony even if OWFs are present. If and how this affects them in terms of energy intake and breeding success is unknown at present.

Busch & Garthe (2016) assessed effects of potential displacement due to the OWFs north of Helgoland on the local colony on the base of potential biological removal rates (PBR). The PBR indicates the number of losses additional to the natural mortality, which can be sustained each year by a certain population (Dillingham & Fletcher 2008). Transferring the findings of Busch & Garthe (2016) to our study results in 13% of the PBR estimated for the German guillemot population in the non-breeding and approximately 20% of the PBR in the breeding season on account of the OWFs north of Helgoland only. This is quite a substantial part if we keep in mind that the PBR part on account of other human activities (like shipping, fisheries, etc.) is not included in these calculations. Especially in the non-breeding season, when guillemots are distributed differently, a larger part of the PBR would be used up if all OWF areas in the German North Sea would be included (Busch & Garthe 2016).

Thus, although the guillemot colony on Helgoland is currently quite stable (Dierschke et al. 2018), the OWF presence has to be considered when interpreting future trends of abundance and breeding success.

b. Kittiwakes

It was shown by several studies that kittiwakes react very sensible to changes in their foraging environment and prey distribution in the breeding season (Frederiksen et al. 2004, Suryan et al. 2006, Descamps et al. 2017). During this season kittiwakes are even more dependent on valuable feeding areas than during non-breeding phases of the year. Such valuable feeding areas have been available in the later OWF areas before the construction (Fig. 2b). We found a significant reduction in kittiwakes' density in the OWFs (up to the response distance of 20 km) which indicates that due to the OWFs they lost habitat relatively close to the colony. Due to their ability to cover large distances in relatively short

time they are generally able to widely avoid OWFs during the breeding season. It could be that kittiwakes increased their foraging trip length compared to the period before the construction.

We can assume that most or even all of the kittiwakes sighted in the area during the breeding season belong to the Helgoland colony. The breeding success of this colony between 2015 and 2017 was below the value which would lead to a stable population (0.79-0.85 instead of 1.5 chicks per AON, Dierschke 2017). The decline started in 2004 (Markones et al. 2009), and important prey species like whiting and sandeel (Markones et al. 2009) were at very low levels for many years (ICES 2017a, 2018). The decrease in breeding success thus cannot directly be linked to the OWF presence but the loss of habitat due to the OWFs puts further pressure on the current situation. However, while avoiding the OWFs in the breeding season the adults face less risk of colliding with the turbines.

Recently published estimations by Busch & Garthe (2018) revealed that the Helgoland population of kittiwakes would face losses of about 294 individuals in the non-breeding season (annual PBR = 103 individuals, assumed turbine avoidance of 98.9 %) if all planned OWFs for the entire North Sea would be realised (OWF status: April 2016). For the breeding season it was estimated that 58 individuals breeding at the Helgoland colony would collide with turbines of the Helgoland-Cluster. The estimated number of collisions would strongly exceed the PBR even if estimated with less precautionary recovery factors than considered sustainable from the conservation perspective (Busch & Garthe 2018). As the kittiwake population is under considerable pressure already (Descamps et al. 2017, IUCN Red List 2018), additional losses due to OWFs can most probably not be buffered easily.

Potential OWF effects in other seasons

It needs to be considered that there are more OWFs present in the German North Sea which were not included in our study but which are located in important areas for both species outside the seasons studied here. For example in the area north of the East-Frisian Islands, where numerous wind farms are in operation, under construction and approved, high guillemot densities are found outside the breeding season (Mendel et al. 2008, Van Bemmelen et al. 2015, Guse et al. 2018). If similar disturbance effects as the ones found in our study apply to the wintering population in the southern German North Sea this would result in a large part of the usual habitat being (partly) lost for guillemots already now and even more so in the future. It is unknown whether areas with similar foraging conditions are available which could compensate for the lost habitat. Furthermore energy demand and mortality of auks is particularly high during the winter (Sonntag 2001, Gaston & Jones 1998, Gaston 2004, Fort et al. 2009) which raises further concern on their ability to cope with reduced foraging habitat.

Conclusion

On the basis of an extensive seabird survey dataset covering 13 years before and 3 years after OWF construction we were able to thoroughly investigate the effects of the OWFs north of the only breeding colony of guillemots and kittiwakes in the German North Sea. The isolated location of the breeding colony allowed to clearly observe the effects of OWFs on the local breeding birds without having to apportion the effect to different colonies with varying colony sizes and conditions. We could show that both species strongly avoided the OWFs north of Helgoland. The differing reaction depending on the season most probably is related to different seasonal requirements and constraints (Schreiber & Burger 2001).

The OWFs substantially add to the human induced impact on the guillemot population present in the German North Sea during different seasons. The share of the OWF effect in the PBR of the species has to be considered when interpreting future population trends. Our findings of the kittiwakes reaction towards OWFs together with the high collision estimates by Busch & Garthe (2016) and the currently reduced breeding success clearly indicates that the kittiwake population in the North Sea faces an additional impact which puts even more pressure on this already declining species. Both habitat loss and collisions have the potential to affect the population. Our considerations do not yet include other anthropogenic activities possibly further affecting the populations.

Our findings underline how important large scale and long-term assessments are that consider the different aspects of the species yearly cycle. As reactions vary depending on the season, a different impact on the population level can be assumed than would be expected from studies only analysing the overall yearly effect, both due to different functionalities of seasons for the birds' biology as well as different distributions of individuals and populations. E.g. for kittiwakes it could be that smaller or ambiguous effects are found when not differentiating between the seasons. However, it is important to relate the effects to the species respective stage in the yearly cycle as their vulnerability to anthropogenic impacts differs throughout the year and changing magnitudes of reactions might have different effects on the individuals and on local populations. Considering this is essential to profoundly understand if and how seabird populations will be affected by OWF presence. Such information substantially adds to the current knowledge and needs to be included in reliable estimations, future planning and management recommendations provided to decision makers.

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Supplement 1**Modell formulas and tables**

Regression results of the BACI approach–GAMM using the binomial variable ‘inside wind farm’ vs. ‘outside wind farm’ (owf_zone) for a radius of 3 km for guillemots and kittiwakes in spring and breeding season.

Guillemots spring:

Family: Tweedie(p=1.277)

Link function: log

Formula:

numberbird ~ s(METHOD2, bs = "re") + period + owf_zone + period: owf_zone + s(lat.km, lon.km) + offset(log_area) + dist_coast + mean_depth + dist_helgoland + slope + dist_helgoland_2 + dist_helgoland_3 + dist_helgoland_4 + dist_helgoland_5 + slope_2 + slope_3 + slope_4 + slope_5

Table S1: Results of the model for guillemots in spring.

Parametric coefficient	Estimate	Standard Error	t value	Pr(> t)
(Intercept)	-3.6534627	4.1650299	-0.877	0.380455
period[after]	0.5648360	0.0549476	10.280	< 2e-16
owf_zone[inside]	0.4933490	0.1268234	3.89	0.000102
dist_coast	0.0226344	0.0267958	0.845	0.398338
mean_depth	0.0524316	0.0194303	2.698	0.007002
dist_helgoland	-0.0026940	0.0587584	-0.046	0.963433
slope	6.4993724	1.8379888	3.536	0.000412
dist_helgoland_2	-0.2160995	0.5978150	-0.361	0.717762
dist_helgoland_3	0.0795399	0.3901454	0.204	0.838466
dist_helgoland_4	0.1062688	0.0999715	1.063	0.287864
dist_helgoland_5	-0.0529774	0.0647736	-0.818	0.413481
slope_2	-0.0129886	0.0448915	-0.289	0.772345
slope_3	-0.1069111	0.0365490	-2.925	0.003466
slope_4	0.0304261	0.0102078	2.981	0.002897
slope_5	-0.0022089	0.0008382	-2.635	0.008447
period[after]: owf_zone[inside]	-0.9830109	0.1785098	-5.507	3.93E-08
Smooth term	edf	Ref.df	F	p-value
s(METHOD2)	0.01251	1	0.008	0.425
s(lat.km,lon.km)	20.21963	23.92	5.243	2.11e-15

Guillemots breeding season:

Family: Negative Binomial(0.425)

Link function: log

Formula:

numberbird ~ s(METHOD2, bs = "re") + period + owf_zone + period: owf_zone + s(lat.km, lon.km) +
 offset(log_area) + dist_coast + mean_depth + dist_helgoland + slope + dist_helgoland_2 +
 dist_helgoland_3 + dist_helgoland_4 + dist_helgoland_5 + slope_2 + slope_4 + slope_5

Table S2: Results of the model for guillemots in the breeding season.

Parametric coefficient	Estimate	Standard Error	z value	Pr(> z)
(Intercept)	-2.397e+00	4.874e+00	-0.492	0.623
period[after]	-5.334e-02	4.074e-01	-0.131	0.896
owf_zone[inside]	2.311e-01	2.007e-01	1.152	0.250
dist_coast	6.753e-03	3.592e-02	0.188	0.851
mean_depth	1.303e-03	3.216e-02	0.041	0.968
dist_helgoland	2.156e-03	6.846e-02	0.031	0.975
slope	4.489e+00	2.081e+00	2.157	0.031
dist_helgoland_2	1.284e-02	7.445e-01	0.017	0.986
dist_helgoland_3	1.610e-01	5.053e-01	0.319	0.750
dist_helgoland_4	1.151e-01	1.347e-01	0.854	0.393
dist_helgoland_5	-4.537e-02	8.875e-02	-0.511	0.609
slope_2	-1.501e-02	5.323e-02	-0.282	0.778
slope_4	-1.592e-04	2.398e-03	-0.066	0.947
slope_5	-8.567e-06	2.049e-04	-0.042	0.967
period[after]: owf_zone[inside]	-5.767e-01	2.519e-01	-2.290	0.022
Smooth term	edf	Ref.df	χ^2	p-value
s(METHOD2)	0.9479	1.0	17.95	1.27E-05
s(lat.km,lon.km)	18.9466	23.1	72.09	6.00E-07

Kittiwakes spring:

Family: Negative Binomial(0.39)

Link function: log

Formula:

numberbird ~ s(METHOD2, bs = "re") + period + owf_zone + period: owf_zone + s(lat.km, lon.km) + offset(log_area) + mean_depth + dist_helgoland + slope + dist_helgoland_2 + dist_helgoland_4 + slope_4

Table S3: Results of the model for kittiwakes in spring.

Parametric coefficient	Estimate	Standard Error	z value	Pr(> z)
(Intercept)	6.8051907	5.3123034	1.281	0.20019
period[after]	-0.7507668	0.5769785	-1.301	0.19319
owf_zone[inside]	-0.2985414	0.1932583	-1.545	0.1224
mean_depth	-0.0474185	0.0303859	-1.561	0.11863
dist_helgoland	-0.1157104	0.0769656	-1.503	0.13273
slope	4.8831691	1.6545746	2.951	0.00316
dist_helgoland_2	1.1386934	0.971138	1.173	0.24098
dist_helgoland_4	-0.2362679	0.137711	-1.716	0.08622
slope_4	-0.0005414	0.0004301	-1.259	0.20806
period[after]: owf_zone[inside]	-0.1131613	0.251367	-0.45	0.65258
Smooth term	edf	Ref.df	χ^2	p-value
s(METHOD2)	0.982	1.00	53.35	1.60E-13
s(lat.km,lon.km)	24.652	27.08	370.77	<2e-16

Kittiwakes breeding season:

Family: Negative Binomial(0.571)

Link function: log

Formula:

numberbird ~ s(METHOD2, bs = "re") + period + owf_zone + period: owf_zone + s(lat.km, lon.km) +
 offset(log_area) + dist_coast + mean_depth + dist_helgoland + slope + dist_helgoland_2 +
 dist_helgoland_3 + dist_helgoland_4 + dist_helgoland_5 + slope_2 + slope_3 + slope_4 + slope_5

Table S4: Results of the model for kittiwakes in the breeding season.

Parametric coefficient	Estimate	Standard Error	z value	Pr(> z)
(Intercept)	0.5777243	4.0826453	0.142	0.88747
period[after]	-0.5918009	0.7038552	-0.841	0.40046
owf_zone[inside]	0.3508172	0.1766436	1.986	0.04703
dist_coast	0.0147461	0.0307226	0.480	0.63125
mean_depth	-0.0142126	0.0277419	-0.512	0.60843
dist_helgoland	-0.0268864	0.0560558	-0.480	0.63149
slope	1.5323262	2.1143806	0.725	0.46863
dist_helgoland_2	-0.5479248	0.6224477	-0.880	0.37871
dist_helgoland_3	-0.0209902	0.4349453	-0.048	0.96151
dist_helgoland_4	0.1412570	0.1173166	1.204	0.22856
dist_helgoland_5	-0.0600375	0.0809183	-0.742	0.45812
slope_2	-0.0649025	0.0634914	-1.022	0.30668
slope_3	0.0442367	0.0396614	1.115	0.26470
slope_4	-0.0081611	0.0078200	-1.044	0.29666
slope_5	0.0004486	0.0004485	1.000	0.31721
period[after]: owf_zone[inside]	-0.5954871	0.2244300	-2.653	0.00797
Smooth term	edf	Ref.df	χ^2	p-value
s(METHOD2)	0.9871	1.00	75.99	< 2e-16
s(lat.km,lon.km)	18.2072	22.46	87.33	1.34E-09

Supplement 2

Determination of response radius - Methods and Figures

To evaluate at which distance to the OWFs the abundance decline is significant (which depends not only on the shape of the smooth but also on the width of the confidence bands), we considered the smooths describing the nonlinear dependency of the population density on the distance to the OWFs (Fig. 3a,b, first two rows). In a first step, for each season separately, we calculated the difference between the "after-smooth" and the "before-smooth", which reveals the changed abundance due to the construction of the OWFs (Fig. 3a,b, last row). In a second step, we approximated the first derivative of the "difference-smooth" with respect to the distance. This derivative represents population increase or declines depending on the distance to the OWFs. Especially, we approximated $\partial [s(\cdot)]/\partial [\text{dist_owf}]$ by calculating the corresponding first finite difference. To answer the question at which distance the response of the guillemots to the OWFs becomes statistically significant (which is equivalent to a significant positive derivative), we additionally calculated confidence bands of the first derivative via bootstrap. Subsequently, we evaluated where the lower positive confidence limit intersects with zero, since here, the positive sign of the derivative which represents a density increase with increasing distance to the OWFs loses its significance (Fig. S1).

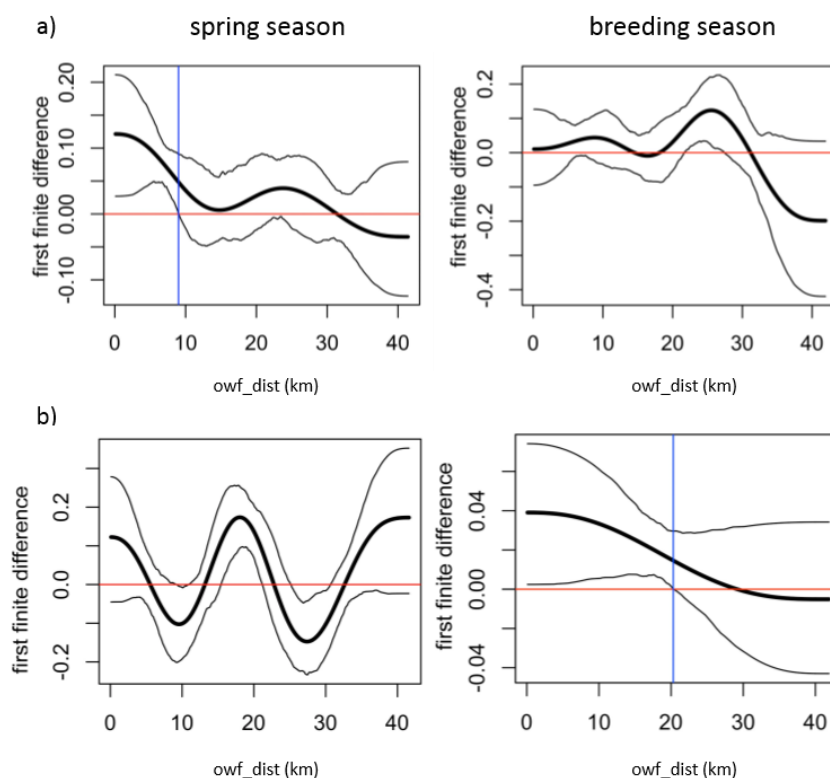
Results:

Fig. S1: First finite difference of the smooth depending on the distance to the OWFs (in km), based on the difference between the corresponding smooth in the after vs. the before period, a) for guillemots, b) for kittiwakes. Red line indicates a derivative of zero, blue line indicates at which owf_dist-value the derivative becomes statistically significant. Thick black lines correspond to the first derivative, thin black lines depict 95%-confidence bands.

CHAPTER III:

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



Peschko V, Mendel B, Mercker M, Dierschke J, Garthe S (in preparation for submission) Northern gannets (*Morus bassanus*) are strongly affected by operating offshore wind farms during the breeding season

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

Verena Peschko, Bettina Mendel, Moritz Mercker, Jochen Dierschke, Stefan Garthe

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 30 adult gannets breeding on Helgoland for several weeks over 2 years.

Most gannets predominantly avoided the OWFs in both years, but a few frequently entered them when foraging or commuting between the colony and foraging areas. Flight altitudes inside the OWFs were close to the rotor-blade zone, especially for individuals predominantly avoiding the OWFs and during commuting. A point process modelling approach for the 2016 breeding season revealed that resource selection inside the OWFs was reduced by 37% compared with the surroundings (outside OWF = up to 15 km from the OWF border).

This study provides the first detailed characterisation of gannets' reactions to OWFs during the breeding season and one of the first comprehensive studies of OWF effects on this species based on telemetry data. However, we can only speculate if their reactions might change over a longer time span and how many birds might actually collide with the turbines. Nevertheless, these documented effects need to be considered during the planning processes for future OWFs, especially those located close to large seabird breeding colonies.

Keywords: offshore wind farm, *Morus bassanus*, wildlife telemetry, point process modelling, flight height, individual behaviour

Introduction

Seabirds have increasingly encountered offshore wind farms (OWFs) in European waters over the past 10 years (Perveen et al. 2014). Seabirds such as northern gannets (*Morus bassanus*, hereafter gannet), depend on offshore areas for foraging, and also for resting and moulting (Schreiber & 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 & 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).

Different behavioural reactions towards OWFs range from complete avoidance to attraction (Drewitt & Langston 2006, Furness et al. 2013, Dierschke et al. 2016). Avoiding OWFs may cause species to lose former valuable habitats or to extend their travel routes, both leading to potentially increased energy consumption (Fox et al. 2006). In addition, seabirds attracted to OWFs are prone to collide with the rotors or turbines, leading to increased mortality (Fox et al. 2006).

As a wide-ranging seabird species, gannets can encounter OWFs during different stages of their annual life cycle, and with increasing frequency in range of their largest breeding colonies along the European coasts (Grecian et al. 2012, Bradbury et al. 2014, 4COffshoreWind 2019). Their flight height and manoeuvrability make gannets one of the most vulnerable species in terms of collision with turbines (Garthe & 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 investigating displacement by or attraction to OWFs (reviewed in Dierschke et al. 2016, Garthe et al. 2017a, b). At the Blight Bank OWF, 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 compared with the surrounding area (Welcker & Nehls 2016). In a recent pilot study, Garthe et al. (2017a) showed that three gannets equipped with GPS tags largely avoided the OWFs north of Helgoland. Displacement and collision effects of OWFs may thus have different consequence for gannets in terms of habitat loss and direct mortality.

The effects of OWFs on seabirds have mainly been studied by visual or digital surveys (reviewed in Dierschke et al. 2016, Mendel et al. 2019) or radar assessments (reviewed in Dierschke et al. 2016, Fijn et al. 2015). However, it can be difficult to gather enough data for a reliable impact assessment for less-abundant species from survey methods alone. Furthermore, flight altitudes, behaviours in and around OWFs, and individual reactions towards the OWFs, as well as changes over time, cannot be studied in detail by these methods.

GPS tracking can generate valuable data on fine- and large-scale habitat use and behaviours (Garthe et al. 2007, Ponchon et al. 2017, 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 OWF effects on seabirds (Thaxter et al. 2015, 2018, Garthe et al. 2017a, 2017b).

Three wind farms, comprising 208 turbines and covering an area of 105 km², are currently operating only 23–35 km north of Helgoland. However, the only gannet colony in the southern North Sea is located on Helgoland, and little is known about the effect of OWFs on breeding gannets, 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 compare resource selection inside and outside the OWFs.

Materials and methods

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 1,071 breeding pairs in 2017 (Dierschke *et al.* 2018). Using a noose pole, we caught 30 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). Eighteen 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 3,286 g (Wanless and Okill 1994), which was well below

the recommended threshold of 3% (Phillips *et al.* 2003, Vandenabeele *et al.* 2012). 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, with no visible effects on bird behaviour. 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 numbers V 242-7224.121-37 (80-6/13), V 242-26934/2016 (80-6/13)).

Data analysis

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 analysis of flight altitudes.

All trips with a duration of > 20 min and ≥ 1 km from the nest were classified as foraging trips, using an R code provided by Lascelles *et al.* (2015). Trip statistics, i.e. duration (h) and total and maximum distance (km) were calculated for each individual foraging trip using the R-package 'trip' (version 1.5.0, Summer 2016).

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 four clusters (see Supplement 1, 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 Supplement 1, 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).

Flight heights

Altitude estimates are improved by increasing the satellite-connection time (e.g. Corman & 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 (± 2.3 m SD) and 53.4 m (± 5.8 m SD), respectively. After inspection of the data, we decided to use bursts of ≥ 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’).

Statistical modelling

1. Preparation of covariables

The means of the spatial covariables for a grid with a spatial resolution of 200 x 200 m were calculated using ArcGIS (version 10.3; Environmental System Research Institute 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_coast* = minimal distance to the mainland

and large islands (except Helgoland), (3) *dist_Helgoland* = minimal distance to the island of Helgoland, (4) *depth* = mean water depth, and (5) *slope* = inclination of the seabed.

2. PPMs

Statistical analysis of telemetry data investigating resource selection is often challenging, and various modelling strategies have been developed (Hooten et al. 2017), 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 a number of 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, Barbet-Massin et al. 2012, Elith et al. 2006).

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 & Shepherd 2010, Warton & Aarts 2013, Renner et al. 2015, Hooten et al. 2017). 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 & Shepherd 2010, Warton & Aarts 2013). Additionally, PPMs represent a generalisation of many other frequently used methods (Johnson et al. 2008, Warton & Shepherd 2010, Aarts et al. 2012). Finally, the PPM likelihood can be approximated by a mathematical trick using standard generalised linear 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 Supplement 2).

3. Model selection

We determined if habitat use by gannets was affected by the presence of OWFs by applying a generalised additive mixed model (GAMM)-PPM to a dataset consisting of 7,181 raw data points collected in 2016. Only the year 2016 was chosen for this analysis because one OWF was still under construction in 2015. To concentrate the analysis on the area in and around the OWFs and avoid possible influences of the high-density area close to the colony, the data were restricted to an area covering the OWFs plus 15 km radius around the OWFs (Fig. 1). When applying the GAMM-PPM to the tracking raw data, convergence of the log-likelihood was approached after one cycle of refinement and 36,426 dummy points were created.

The optimal model regarding the set of fixed-effect predictors was selected by comparing 25 different models, 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 *OWFyn*, which was the main focus of the analysis:

$$Z \sim \beta + te(\log_{d_t}, \log_{d_s}, \text{angle}, k = c(5,5,5)) + s(\text{trip}_{id}, bs = 're') + s(\text{bird}_{id}, bs = 're') + OWFyn \quad (1)$$

where β is the intercept and $te()$ a tensor-product regression spline considering temporal, spatial and directional autocorrelation, where the optimal number of knots has been estimated via generalised cross-validation. *Trip_{id}* and *bird_{id}* were included as random effects, indicated by the term $s(\dots, bs = re)$. A Poisson distribution was chosen as the probability distribution.

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.

$$Z \sim \beta + te(\log_{d_t}, \log_{d_s}, \text{angle}, k = c(5,5,5)) + s(\text{trip}_{id}, bs = 're') + s(\text{bird}_{id}, bs = 're') + OWFyn + \text{dist}_{Helgoland} + \text{slope} \quad (2)$$

Notably, a classical Poisson-GAMM was not fitted, but the response-variable Z interplays with appropriate regression weights such that a PPM-likelihood is approximated. More details can be found in Johnson et al. (2013).

4. Model validation, numerical realisation, and software

PPM model-validation plots for the final GAMM-PPM were generated based on PPM-Pearson residuals (Baddeley et al. 2005a, Baddeley et al. 2005b). All statistical analyses were performed using the free statistical software R (Core Team 2016). Spatial statistics were performed using *spatstat* (Baddeley et al. 2005a), dummy-point meshes and trapezoid rule-based quadrature weights were created using *mvQuad* (Weiser 2016), GAMM and GAM fits were performed using *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.

Results

Overview of foraging trips

We recorded a total of 1182 individual foraging trips by 30 gannets in 2015 and 2016 (Table 1). The mean duration was significantly higher in 2016 than in 2015, but maximum and total distances were

not significantly different between the 2 years (Table 1). The same large-scale area was used for foraging in both years (Fig. 1).

Avoidance of and attraction by OWFs

a. Foraging trips

Most individuals tagged in 2015 and 2016 mainly avoided the OWFs north of Helgoland (90% of individuals; Fig. 2) and most foraging trips passed the OWFs at the south-west border (Fig. 2a, d). However, a few individuals (two in 2015 and one in 2016, all males) frequently entered the OWFs north of Helgoland (Fig. 2b, e) and also visited other OWF areas further from the colony (Fig. 2c, f).

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

	2015	2016	χ^2	<i>p</i>-value
No of trips	580	602	-	-
Duration (h)	7.83 (0.33–61.23)	10.93 (0.33–116.87)	6.7134	9.57E-03
Max. distance (km)	38.37 (1.10–388.36)	53.11 (1.10–392.67)	1.9879	1.59E-01
Total distance (km)	110.28 (2.33–1021.17)	139.61 (2.77–1118.53)	0.312	5.77E-01

χ^2 and *p*-values for mixed effect models. Values in brackets indicate the minimum and maximum values of the dataset.

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

	%	% of individuals		Linear mixed model	
		2015	2016	χ^2	<i>p</i>-value
All trips with positions in OWF	0	42	13	0.0636	0.801
	0.01–10	25	63		
	> 10	33	25		
Trips with ≥ 3 positions in OWF	0	67	50	0.4069	0.5236
	0.01–10	17	44		
	> 10	17	6		
Positions in OWF	0	42	13	0.0053	0.9418
	0.01–1	33	75		
	1–2	17	6		
	> 2	8	6		

OWF = 0 m distance to border of the OWF. χ^2 and *p*-values for mixed effect models.

Of the individuals tagged in 2015, 67% did not enter the OWFs during their foraging trips (Table 2, only considering trips with ≥ 3 positions in OWF), 17% entered the OWFs during 0.01%–10% of foraging trips, and 17% entered them during $> 10\%$ of foraging trips (Table 2). In 2016, 50% did not enter the OWFs, 44% entered on 0.01%–10% and 6% on $> 10\%$ of their foraging trips (Table 2). In 2015, 42% of the tagged individuals recorded no positions in the OWFs (13% in 2016), 33% recorded 0.01%–1% (75% in 2016), 17% recorded 1%–2% (6% in 2016), and 8% recorded $> 2\%$ of their positions in the OWF (6% in 2016) (Table 2). There was no significant difference in either %-trips or %-positions in OWFs between 2015 and 2016 (Table 2).

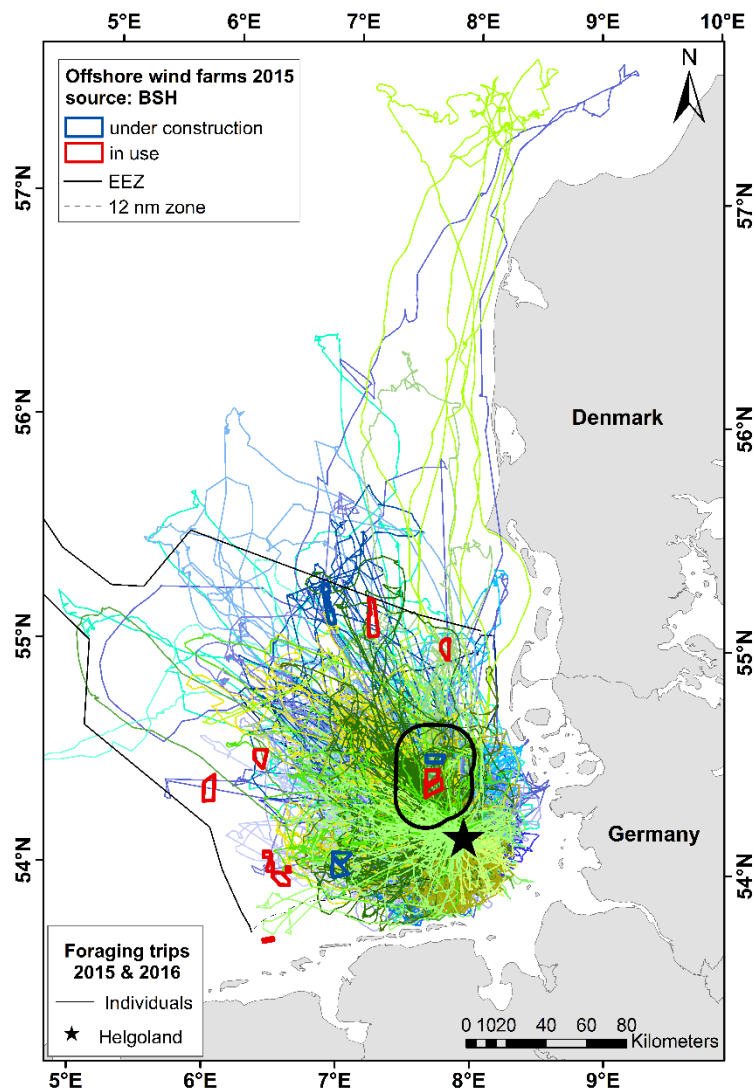


Fig. 1: Foraging trips of northern gannets tagged in 2015 (green) and 2016 (blue). OWF status in 2015: blue = under construction, red = in use, black line = 15 km buffer applied for PPM analysis.

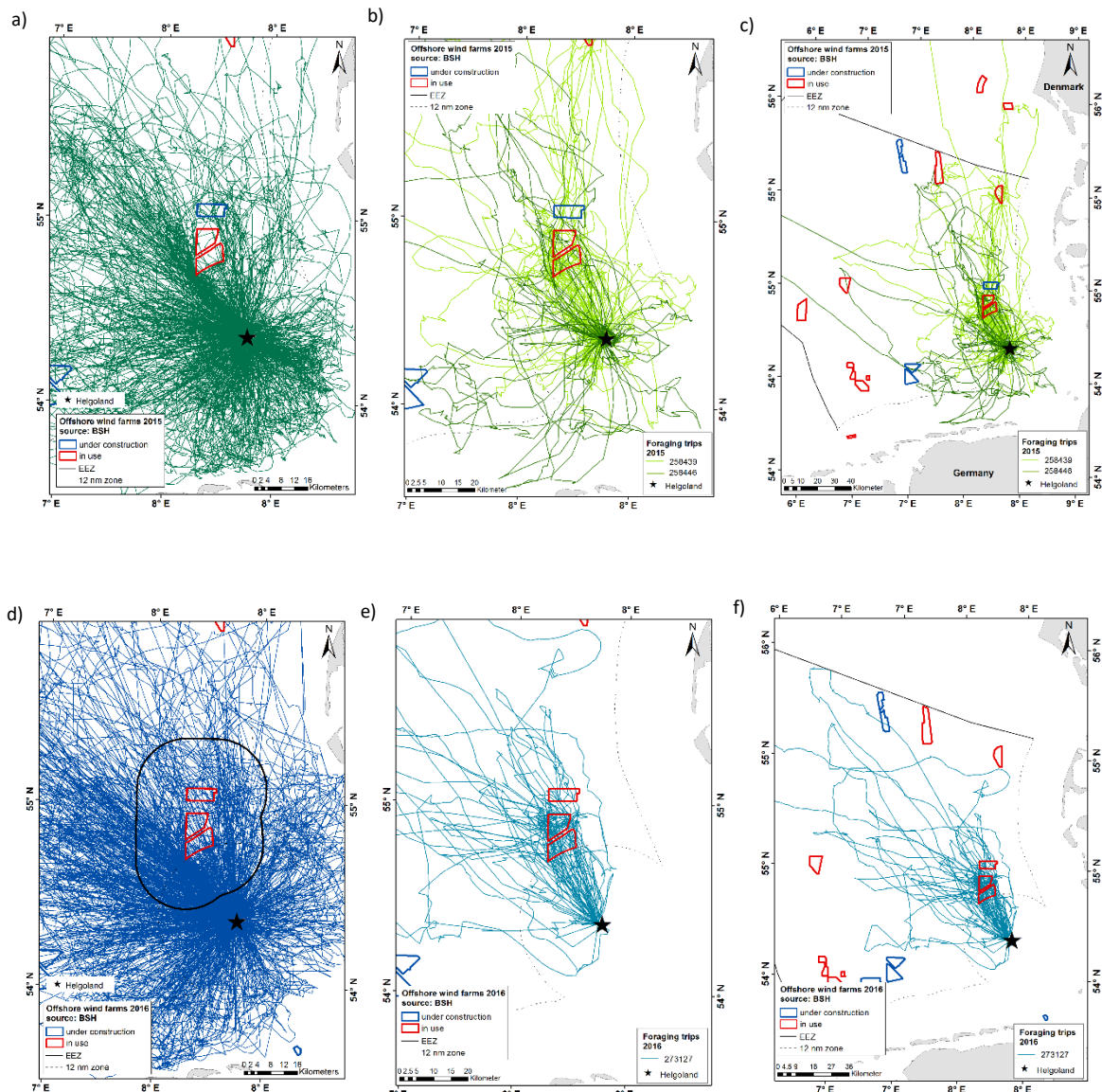


Fig. 2: Flight behaviours of gannets tagged in 2015 ($n = 12$) (a) and 2016 ($n = 15$) (d) that predominantly avoided the OWFs (all individuals shown in the same colour). Gannets tagged in 2015 ($n = 2$) (b) and 2016 ($n = 1$) (e) that often entered the OWFs (individuals shown in different colours). (c) & (f) Large-scale movements of individuals shown in (b) and (d). OWFs: blue = under construction, red = in operation, black line = 15 km buffer applied for PPM analysis.

b. Behaviour

Differentiating among the behavioural categories foraging, travelling, and resting, showed that individuals avoiding the OWFs mainly used areas west and north-west of Helgoland (i.e. south-west 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 (Fig. 3a). In contrast, the gannet that was attracted to the OWFs mainly used an area north-west of Helgoland, between the island and the OWFs, for commuting to and from the colony and frequently entered the OWFs when travelling (Fig. 3b). Individuals that mainly avoided the OWFs 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. 3c), but very few located in the OWFs. For the individual attracted to the OWFs however, most of its foraging area was located in the OWFs or nearby, north-west of the OWFs (Fig. 3d). In contrast, all individuals entered the OWFs rarely or not at all while resting (Fig. 3e, f). Only data for the 2016 breeding season are shown here, but similar patterns were detected in 2015 (data not shown).

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 (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 mainly avoiding the OWFs in both years, < 1% of the kernel densities of each behaviour overlapped with the OWFs.

Table 3: Overlap with OWFs (no buffer around the OWFs) calculated for foraging, travelling, and resting individuals often using or predominantly not using the OWFs in 2015 and 2016.

Year	Percentile	Foraging		Travelling		Resting	
		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

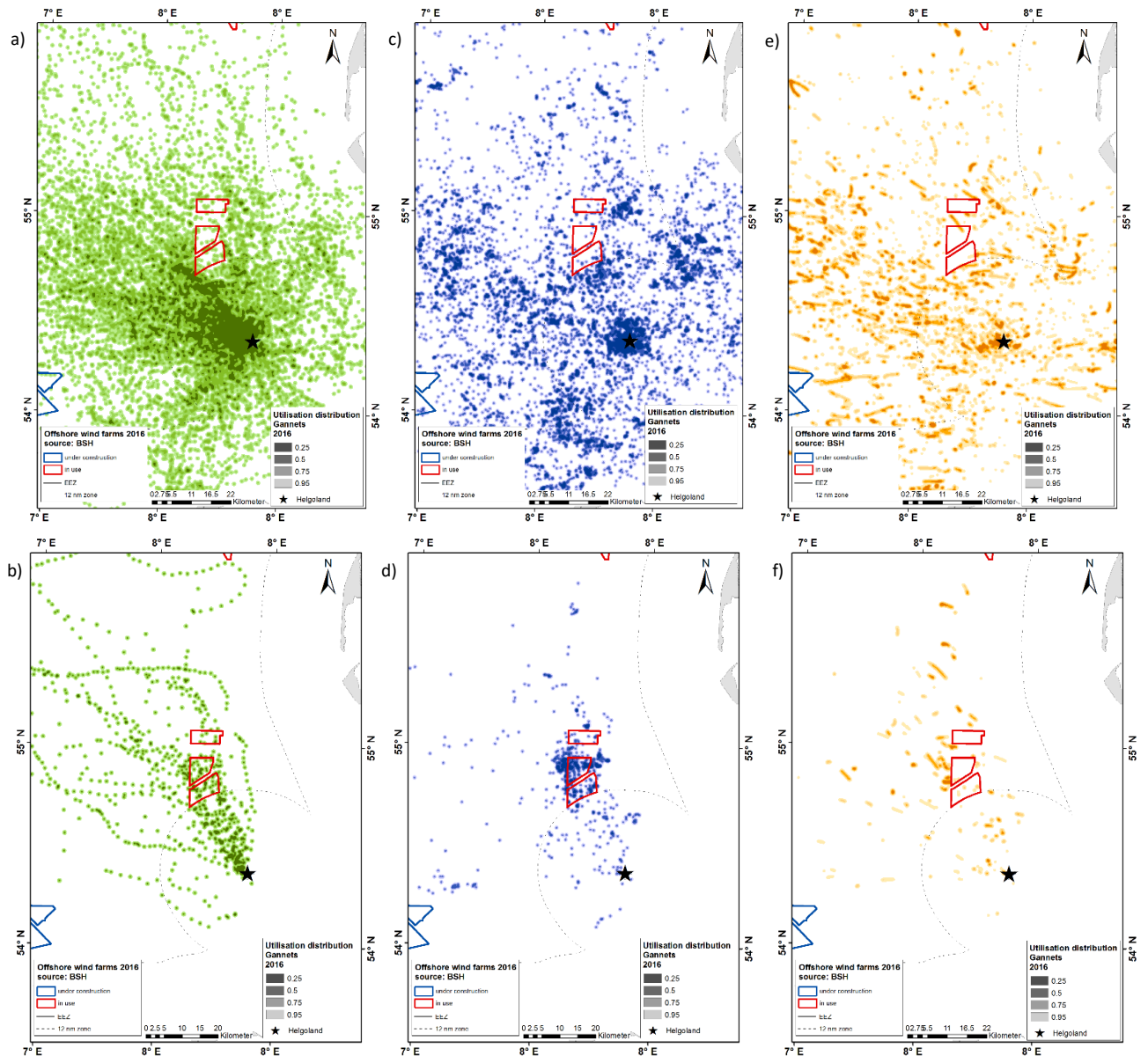


Fig. 3: Kernel densities of travelling (a, b), foraging (c, d), and resting (e, f) positions of gannets tagged in 2016 visualised as percentiles. Dark colour = 25% percentile, light colour = 95% percentile. (a, c, & e) Individuals predominantly avoiding the OWFs, and (b, d, & f) individual attracted to OWFs.

c. 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, $p = 0.002$) (Table 4, Fig. 4). Flight heights were mostly below the rotor-blade zone (RBZ; 30–150 m) (Fig. 4). Individuals predominantly avoiding the OWFs flew at significantly higher altitudes inside than outside the OWFs (mean height 27.3 m ($n = 60$) vs 14.7 m ($n = 2200$), respectively, $p < 0.001$) with their mean altitude just below the RBZ. The individual attracted to the OWFs showed similar flight heights inside and outside the OWFs ($p = 0.301$), mainly below the RBZ. Flight heights during traveling were significantly higher inside than outside the OWFs

(mean 17.9 m ($n = 91$) vs 12.9 m ($n = 1645$), respectively, $p = 0.001$). There was no significant difference in flight heights during foraging behaviour ($p = 0.640$). Altitudes were significantly higher during foraging compared with travelling ($\chi^2 = 14.807$, $p < 0.001$).

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

Bird	Location	n	Altitude (m)			Linear mixed model	
			Mean	SD	Median	χ^2	p-value
All	inside OWF	209	17.9	17.9	15.9	6.510	0.011
	outside OWF	2640	14.4	18.0	10.7		
Attracted	inside OWF	149	14.2	12.3	14.3	0.2305*	0.631
	outside OWF	440	12.7	15.4	9.6		
Avoiding	inside OWF	60	27.3	24.9	23.3	13.636	<0.001
	outside OWF	2200	14.7	18.5	10.7		
Travelling	inside OWF	91	17.9	19.2	14.3	6.689	0.010
	outside OWF	1645	12.8	17.6	7.4		
Foraging	inside OWF	118	18.0	16.8	16.5	0.762	0.383
	outside OWF	995	16.9	18.4	14.9		

*Linear model instead of a linear mixed effects model because there was only one individual, giving an F-value instead of χ^2 .

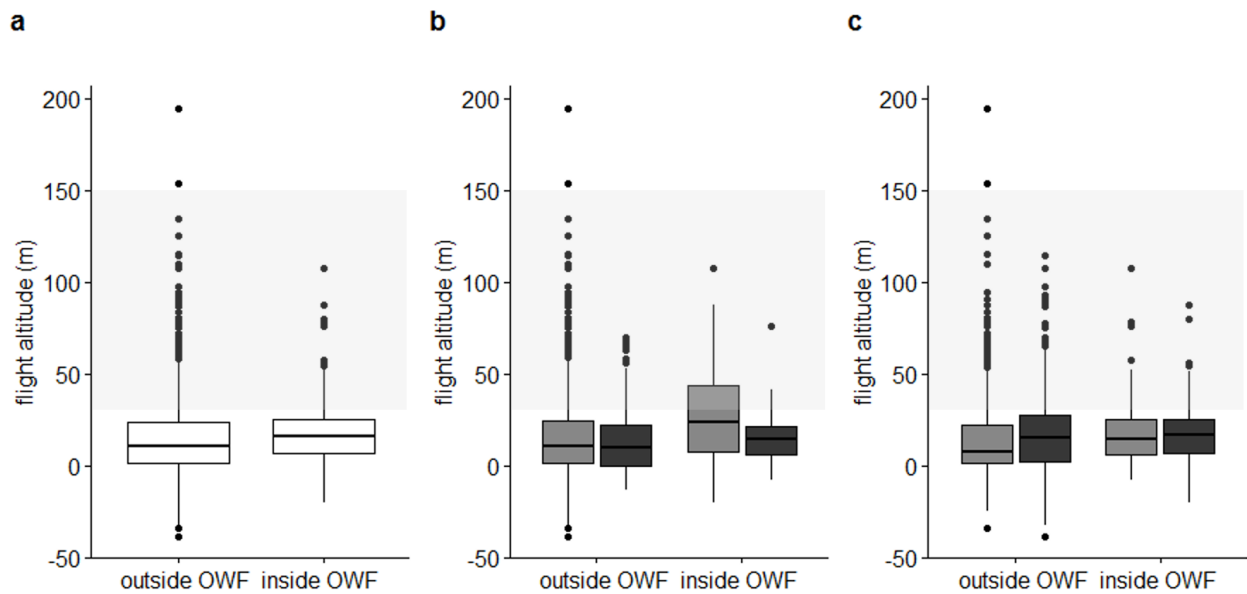


Fig. 4: Flight heights outside and inside OWF for (a) all birds, (b) avoiding (light grey) and attracted (dark grey) individuals, and (c) travelling (light grey) and foraging (dark grey) individuals. Grey background = rotor-blade zone.

d. Model results

Both the basic and best models revealed a significantly reduced selection of the OWFs compared with the surrounding area in 2016 (basic model, Table 5; best model, Table 6; variable 'inside OWF' estimate = -0.461 , $p = 6.26E-12$, response = $\exp(\text{estimate}) = 37\%$ reduced selection inside the OWF compared with outside, lower confidence interval (CI) = 45% reduction, upper CI = 28% reduction).

Table 5: Results of basic point process model.

Parametric coefficient	Estimate	Standard error	z value	Pr(> z)
(Intercept)	0.587	0.099	5.941	2.83E-09
inside_OWF	-0.423	0.066	-6.392	1.64E-10
Smooth term	edf	Ref.df	χ^2	p-value
te(log_ds,angle,log_dt)	72.061	83.220	13,801.300	<2e-16
s(trip_id)	114.992	139.000	11,642.400	<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

Table 6: Results of the best model.

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	6.26E-12
dist_Helgoland	-0.017	0.001	-14.275	< 2e-16
slope	-1.711	0.375	-4.567	0.000
Smooth terms	edf	Ref.df	χ^2	p-value
te(log_ds,angle,log_dt)	73.297	84.420	13284.000	<2e-16
s(trip_id)	114.984	139.000	12033.000	<2e-16
s(bird_id)	0.932	15.000	132.000	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

In summary, our data showed that most gannets avoided the OWFs in both years, but a few individuals used the OWF areas intensively when foraging or commuting between the colony and foraging areas. Slightly more trips and positions overlapped with the OWFs in 2016 than in 2015, but there was no significant difference between the years. Flight altitudes inside the OWFs were closer to the RBZ, especially for individuals that avoided the OWFs and during commuting behaviour. The modelling approach revealed a 37% reduction in the selection of the OWF area in 2016 compared with the surroundings.

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 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.

Strong avoidance of the OWF areas by gannets was also documented in other studies, though most of these focussed on effects throughout the yearly cycle (Vanermen et al. 2015, Welcker & Nehls 2016). Using a PPM approach, we showed that resource selection inside the OWF area was reduced by 37% in the breeding season in 2016. This was lower than that reported by line-transect surveys (Vanermen et al. 2015, Welcker & 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 chicks. 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 (using spatial occurrence of individuals and investigating effects on density or abundance of species) cannot be compared directly with values estimated from tracking data (using spatial and temporal information on individual occurrences to infer resource selection), and the resulting reduction in resource selection is not readily comparable to the reduction in abundance.

Our study also showed that 90% 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, Langton et al. 2014, 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 predominantly avoiding the OWFs are less prone to collide with turbines. However, they sometimes entered the OWFs, and flight heights measured on these occasions showed that they flew at altitudes just below or inside the RBZ (wind turbine models in OWF north of Helgoland: SWT-3.6-120 (Siemens), hub height 89 m, rotor diameter 120 m; 6.2M126 (Senvion), hub height 92 m, rotor diameter 126 m). Thus although they do not enter the OWFs frequently, gannets that predominantly avoid the OWFs appear to fly at altitudes inside the OWFs that would strongly increase their collision risk. The reason why birds fly higher inside compared with outside the OWFs remains unclear and should be investigated in future studies with larger sample sizes.

In contrast to the avoidance behaviour shown by most gannets, a few individuals entered the OWFs frequently while commuting and foraging. Behavioural analysis revealed that 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, Leopold et al. 2013, Vanermen et al. 2015), which leads to an increase in benthic structures and hence increased fish diversity and abundance at the turbines (e.g. de Mesel et al. 2015, Stenberg et al. 2015, Vandendriessche et al. 2015). The exclusion of fisheries from the OWF areas might also be important, because the soft seabed between the OWFs is not impacted by beam trawling (Vandendriessche et al. 2015, Schulze 2018). However, it is currently unknown if the food accessibility is comparable to undisturbed areas, and 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 strongly increased. The flight altitude of the bird that frequently entered the OWFs in 2016 was predominantly below the RBZ both while inside and outside the OWFs. 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 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 blades. We also found higher flight altitudes 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 tendency to fly higher inside OWFs nevertheless increases their risk of colliding with the turbines. Furthermore, the turbines may exert wake effects that could potentially affect the birds' flight manoeuvrability, even when flying below the rotor blades (Wang et al. 2016, Stevens & Meneveau 2017, Wu et al. 2019). A larger sample of flight altitudes inside OWFs is needed to clarify the gannets' behaviours and draw conclusions about the actual collision risk.

Although there was no significant difference between the data for the two study years, more individuals that predominantly avoided the OWFs appeared to enter them at times in 2016. Although it is impossible to draw conclusions based on 2 years' data, it suggests that the use of OWFs by birds predominantly avoiding them would increase over a longer time period, resulting in less habitat loss but increased collision risk, because gannets with less experience of flying inside OWFs would enter them more often. During this study, individuals tagged in both years showed no distinctive patterns to allow any conclusions to be drawn. Future studies 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.

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Supplement 1

Behavioural classification

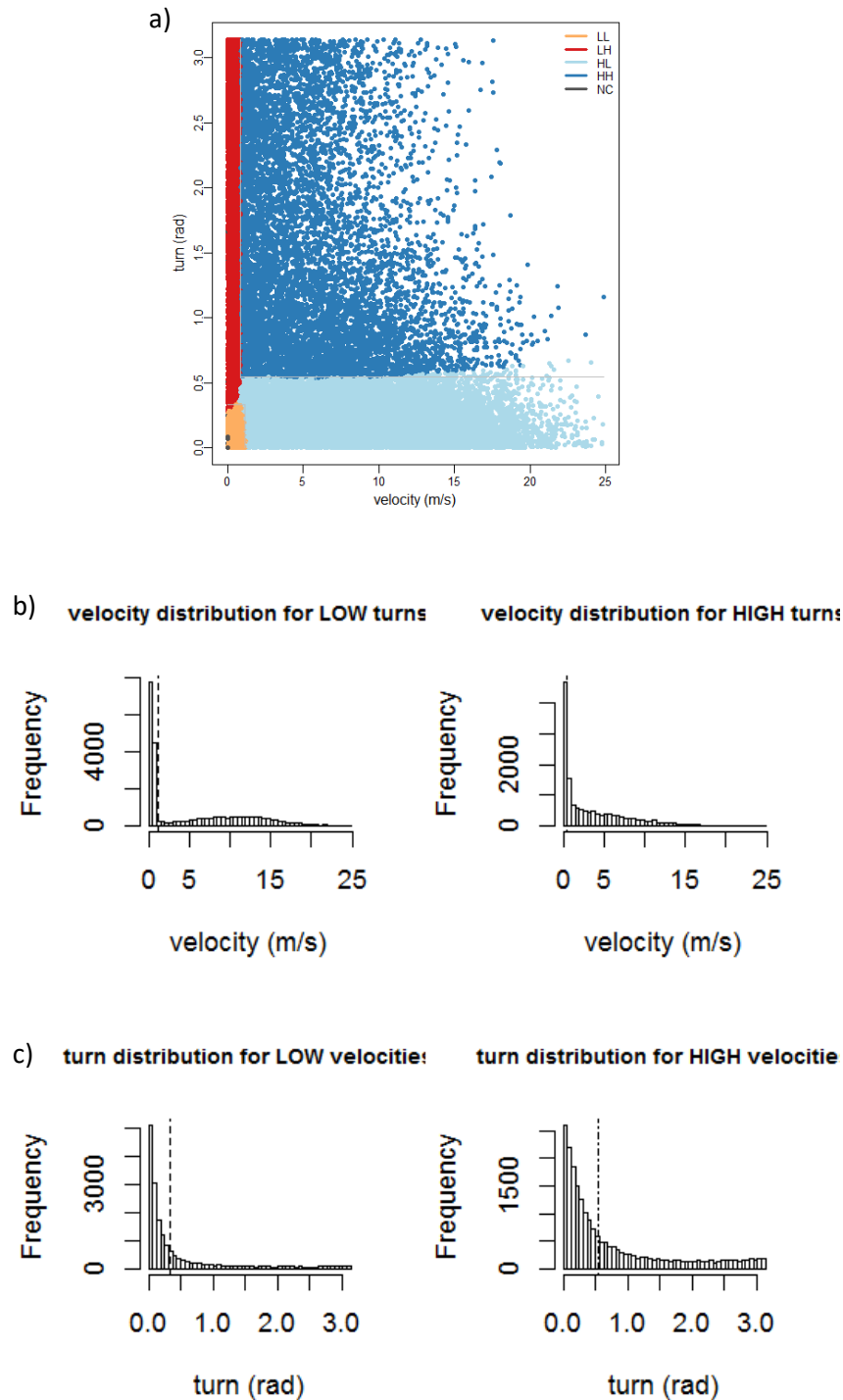


Fig. S1: (a) Velocity/turn scatter plot (clustering colour code: LL: orange, LH: red, HL: cyan, HH: blue). (b) Velocity (m/s) and (c) turning angle (rad) frequency distributions. Distributions for low/high values are shown separately. Black dashed and dot-dashed lines indicate the delimiters.

Table S1: Minimum and maximum speeds and turning angles for each behavioural state classification using EMbC for data recorded in 2015 & 2016. Two states with low speeds were merged into one behavioural state ‘resting’.

	Behaviour	Speed min (km/h)	Speed max (km/h)	Turn min (rad)	Turn max (rad)
2015	resting	0.0	4.1	0.0	11.3
	travelling	4.1	89.4	0.0	2.0
	foraging	3.3	89.4	2.0	11.3
2016	resting	0.0	4.2	0.0	11.3
	travelling	4.2	89.5	0.0	2.0
	foraging	3.2	89.5	2.0	11.3

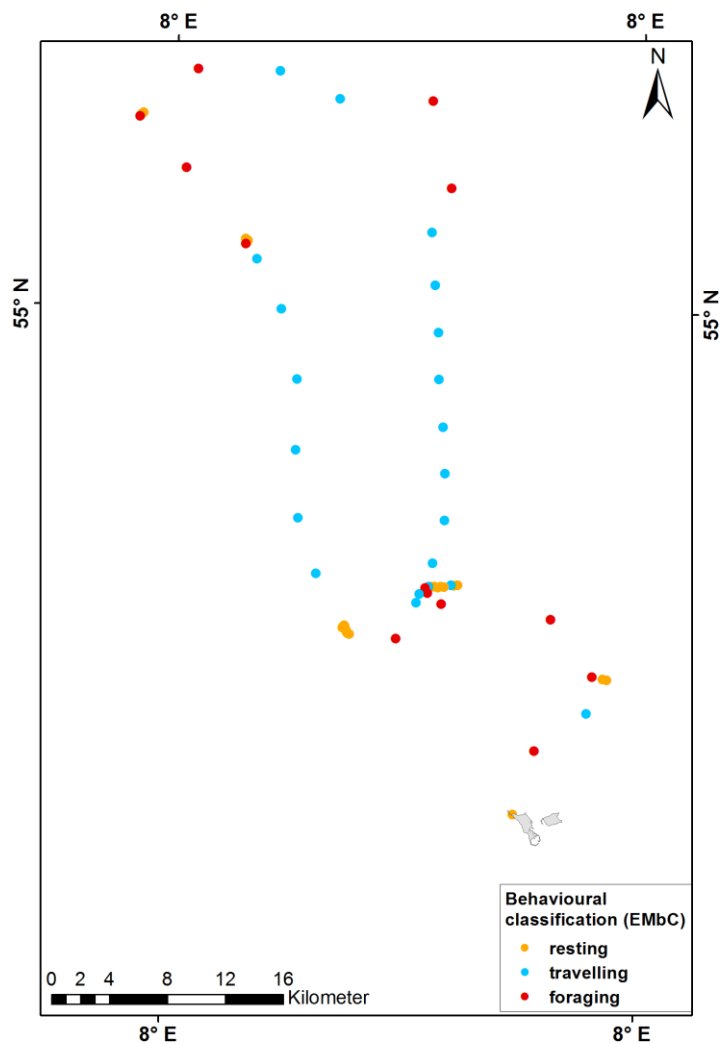


Fig. S2: Foraging trajectory with behavioural labelling: yellow = resting, red= foraging, blue= travelling.

Supplement 2

Point process modelling

The following is a short summary of the key extensions/modifications of the applied approach compared with the spatio-temporal point process models (PPMs) presented by Johnson et al. (2013):

1. Autocorrelation: Johnson et al. (2013) considered spatio-temporal autocorrelation using parametric terms. However, on one hand, data may also be correlated with respect to the turning angle (due to directed movement): the smaller the time steps between subsequent observations (relative to the velocity of the animal), the smaller the turning angles on average. On the other hand, temporal and spatial distances to the foregoing tracking point (d_t and d_s respectively) as well as the turning angle (α) may correlate in a complex manner. We therefore included these autocorrelations and their possible interactions as a tensor product smooth $te(d_t, d_s, \alpha)$ within the framework of generalised additive modelling (GAMM) (as described in Wood (2006)).
2. Mixed modelling: The assumption of independence is often violated, especially if the tracking data originate from different animal trips and/or individuals (Hurlbert 1984), and even if autocorrelation is considered correctly. Here, generalised linear mixed models probably provide the most natural and powerful approach to account for nested data, provided that the correlation structures are specified correctly (Fieberg et al. 2010). Additionally, mixed models use maximum likelihood estimation, which is the key to linking the mixed regression technique to the PPM approach (see later). Furthermore, this approach is also appropriate for drawing population-level inferences (Hooten et al. 2017), which is an important issue when several individuals have been tracked. We therefore extended the models of Johnson et al. (2013) by allowing for the consideration of $bird_{id}$ and $trip_{id}$ as random factors, thus finally using GAMMs.
3. Quadrature-weights: The aim of the dummy points in PPMs is to efficiently approximate an integral term of the model-likelihood, which is realized based on the use of appropriate quadrature weights. Based on extensive simulation studies, we tested different types of quadrature weights as provided by the R-package mvQuad (Weiser 2016) with respect to type I and type II error rates (Mercker 2019). Here, the best results were obtained using open Newton-Cote Formulas of degree 2, which were thus used throughout this study.
4. Over- and under-dispersion: In principle, PPM data can show over- or underdispersion. We tested for both using the function `dispersiontest()` from the R-package AER (Kleiber & Zeileis 2008). Based on the results of this test, we inflated or deflated the corresponding standard errors accordingly and re-calculated the p -values. Finally, we carried out extensive simulation

studies to confirm that this approach led to reasonable type I and type II error rates for various types of animal-tracking data (Mercker 2019).

CHAPTER IV:

Telemetry reveals strong effects of offshore wind farms on behaviour and habitat use of common guillemots (*Uria aalge*) during the breeding season



Peschko V, Mercker M, Garthe S (submitted) Telemetry reveals strong effects of offshore wind farms on behaviour and habitat use of common guillemots (*Uria aalge*) during the breeding season

Telemetry reveals strong effects of offshore wind farms on behaviour and habitat use of common guillemots (*Uria aalge*) during the breeding season

Verena Peschko, Moritz Mercker, Stefan Garthe

Abstract

Seabirds have increasingly encountered offshore wind farms (OWFs) in European waters in the past 10 years, resulting in potential conflicts with offshore foraging areas. During the breeding season, seabirds are restricted in their choice of foraging habitat and are under increased pressure to find enough prey to raise their offspring. However, information on the individual reactions of seabirds towards OWFs during the breeding season is lacking. Three OWFs located 23–35 km north of the island of Helgoland have operated since October 2015. We studied their possible effects on locally breeding common guillemots (*Uria aalge*) using GPS tracking. GPS tags were deployed on 12 breeding guillemots from Helgoland for 1.2–3.8 weeks during 2016–2017. Most individuals avoided the OWFs, but one individual in each year briefly entered the OWFs on two or three occasions. Using a point process model, we revealed a 67% reduction in the resource selection in the OWF areas compared with the surroundings. Furthermore, OWF avoidance was increased to 76% when the turbine blades were rotating. Guillemots mainly approached the OWFs from their eastern edge when resting or diving, and rarely approached the areas when commuting. These results provide a detailed description of guillemot reactions to OWFs during the breeding season, and the first comprehensive analysis of OWF effects on this species based on telemetry data. The strong avoidance effect for guillemots during the breeding season indicates the need to consider the presence of OWFs when interpreting future trends in the abundance and breeding success of this species.

Keywords: offshore wind farm, *Uria aalge*, wildlife telemetry, point process modelling, individual behaviour

Introduction

Seabirds increasingly encounter offshore wind farms (OWFs) in European waters (Perveen et al. 2014). Common guillemots (*Uria aalge*) are the most abundant seabird species in the North Sea, and show varying responses to OWFs (overview Dierschke et al. 2016). Guillemots in Belgium and The Netherlands largely avoided OWF areas (Leopold et al. 2013, Vanermen et al. 2015, 2016), with a reduced abundance of 71% in OWF areas compared with the surrounding areas (Vanermen et al. 2015), while Welcker & Nehls (2016) found a similar density reduction at the Alpha Ventus wind farm (75% reduced density in the OWF area, response radius 2.5 km). In contrast, other studies, e.g. in the UK, found that guillemots were attracted by or indifferent to OWFs, with no changes in abundance (PMSS 2007, Vallejo et al. 2017). However, few studies have explicitly investigated the reaction of seabirds towards OWFs during the breeding season (Masden et al. 2010, Thaxter et al. 2015, 2018), when they are restricted in their choice of foraging habitat and under increased pressure to find enough prey to raise their offspring (Orians & Pearson 1979).

GPS-tracking methods are increasingly applied to investigate the behaviour of seabird species (Garthe et al. 2007, Ponchon et al. 2017, Thaxter et al. 2018). These methods allow researchers to follow individual birds for weeks or months, thus providing powerful tools for studying both fine- and large-scale habitat use and the behaviour of marine top predators (Garthe et al. 2007, Ponchon et al. 2017, Thaxter et al. 2018), and for monitoring alterations in these factors in relation to environmental change or anthropogenic activities (Garthe et al. 2011, Paredes et al. 2014, Garthe et al. 2017a). Few studies to date have used GPS tags to investigate the effects of OWF on seabirds (Thaxter et al. 2015, 2018, Garthe et al. 2017a, b).

The only guillemot colony in the south-eastern North Sea is located on the island of Helgoland, 48 km off the German coast (Fig. 1). The breeding numbers are relatively small, comprising 3,178 breeding pairs in 2017 (Dierschke et al. 2011, Dierschke et al. 2018), and the number of breeding guillemots has remained relatively constant for the last several years (Dierschke et al. 2011, Dierschke et al. 2018).

However, three wind farms, including a total of 208 turbines and covering an area of 105 km², are currently operating only 23–35 km north of Helgoland, making it necessary to assess their possible effects on breeding guillemots.

In this study, we used GPS-tracking methods to investigate how guillemots breeding on Helgoland react to the presence of OWFs close to their colony; i.e. are they displaced or attracted by the OWFs? We also investigated individual differences in the reactions of the birds towards the OWFs, and examined how they behaved in the vicinity of the OWFs, e.g. in terms of foraging behaviour.

Materials and methods

Fieldwork and data collection

Guillemots were caught on the island of Helgoland (54°11' N, 7°55' E) in the south-eastern North Sea during the breeding seasons in 2016 and 2017, using a noose pole. Thirteen breeding guillemots were equipped with GPS devices, attached to the lower back using TESA® tape (Beiersdorf AG GmbH, Hamburg, Germany), of which 12 successfully transmitted data (seven in 2016, five in 2017). Each bird received a 'Uria' GPS-logger (13 g, Ecotone Telemetry, Poland) and six birds in 2016 also received a G5 temperature-depth recorder (TDR, 2.7 g, Cefas Technology, Suffolk, UK) attached either to the lower part of the tail feathers or to a ring mounted on the bird's leg. Three of the TDR loggers were retrieved. The attached devices represented 1.8% (mean value) of the guillemot's body mass (mean: 902 g), which was below the recommended threshold of 3% (Phillips et al. 2003, Vandenabeele et al. 2012). The mean handling time was 14 min, and the birds were then released in the close vicinity of the nest. The bird's eggs were observed during the handling period to prevent nest predation. Individuals were then either re-caught after 2–3 weeks and the devices removed, or the devices fell off when the birds moulted. All the GPS devices recorded the date, time, and position (latitude, longitude) with a scheduled sampling interval of 10 min, and recorded if the logger was submerged or not (wet/dry sensor) every second. Depending on the battery voltage and whether the bird was submerged during a scheduled GPS recording, the GPS interval could be extended to 11–20 min (19% of the dataset) or 21–30 min (3%). The devices transmitted the data via a UHF connection to a base station. The TDR devices recorded temperature at an interval of 20 s, and depth every 1 s. The TDR devices had to be retrieved for data download.

Data analysis

All trips with a duration > 12 min and \geq 500 m distance from the nest were classified as foraging trips, using an R code provided by Lascelles et al. (2015). Thirty-two trips were excluded from the subsequent analysis because the trip start or end time were unknown. Trip statistics, i.e. trip duration (h), trip maximum distance to Helgoland, and total distance (km) were calculated for each individual foraging trip using the R-package 'trip' (Summer 2016, version 1.5.0).

Behavioural classification

Based on the information from the wet/dry sensors, it was possible to determine when and for how long the birds were submerged. The locations of potential dives were retrieved via interpolation of the

corresponding GPS data to an interval of 1 s. Data on 6,145 dives were available from the TDR data for three individuals, and detailed dive characteristics were then analysed to define the threshold duration to classify a dive as foraging dive. Dives lasting ≥ 10 s were classified as foraging dives. Furthermore, based on inspection of the speed distribution the GPS data, birds moving at ≤ 4 m/s were classified as resting and birds travelling at > 4 m/s were classified as travelling, in accordance with a bimodal distribution. To visualise the areas in which the different behavioural states were shown, kernel densities of the positions assigned to each category were created in ArcGIS using the ArcMET tool (version 10.2.2v3; Wall 2014).

Statistical modelling

1. Preparation of covariables

ArcGIS (version 10.3; Environmental System Research Institute, 2016) was used to calculate the means of the spatial covariates for a grid with a spatial resolution of 200 x 200 m. 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_coast* = minimal distance to the mainland and large islands (except Helgoland); (3) *dist_Helgoland* = minimal distance to the island of Helgoland; (4) *depth* = mean water depth; (5) *slope* = inclination of the seabed; and (6) a temporal variable indicating turbine activity derived from the wind speed measured on Helgoland (https://werdis.dwd.de/werdis/start_js_JSP.do) *owf_onoff* = hourly status of turbines (rotating, ≥ 5.5 m/s wind speed; not rotating, < 5.5 m/s wind speed).

2. PPM

Statistical analysis of telemetry data investigating resource selection is often challenging, and various modelling strategies have previously been developed and discussed (Hooten et al. 2017). Popular approaches include (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 a number of 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 point process models (PPMs) presented by Renner et al. (2015), which naturally and automatically resolve many of the questions and pitfalls associated with alternative approaches (Warton & Shepherd 2010, Warton & Aarts 2013, Renner et al. 2015, Hooten et al. 2017). 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 & Shepherd 2010, Warton & Aarts 2013). Additionally, PPMs represent a generalisation of many other frequently used methods (Johnson et al., 2008, Warton & Shepherd 2010, Aarts et al. 2012). Finally, the PPM likelihood can be approximated by a mathematical trick using standard generalised linear mixed modelling-regression software (Johnson et al. 2013, Renner et al. 2015), ensuring flexible and individual implementation. Details of the modifications of the PPM compared with the spatio-temporal PPMs are presented by Johnson et al. (2013) (see Supplement 2 in chapter III).

3. Model selection

We determined if habitat use by guillemots was affected by the presence of OWFs by applying a generalised additive mixed model (GAMM)-PPM to a dataset consisting of 9,235 raw data points collected in 2016 and 2017. When applying the GAMM-PPM to the raw tracking data 54,715 dummy points were created.

The optimal model regarding the set of fixed-effect predictors was selected by comparing 19 different models 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 including only autocorrelation terms, random effects, and the variable *OWFyn*, which was the main focus of the analysis:

$$Z \sim \beta + te(\log_{d_s}, angle, k = c(5,5)) + s(trip_id, bs = 're') + s(bird_id, bs = 're') + OWFyn \quad (1)$$

where β is the intercept and *te()* a tensor-product regression spline considering temporal, spatial and directional autocorrelation, where the optimal number of knots has been estimated via generalised cross-validation. *Trip_{id}* and *bird_{id}* were included as random effects, indicated by the term *s(...,bs = re)*. A Poisson distribution was chosen as the probability distribution.

We subsequently added other variables to the basic model to identify the best model for our data. We restricted the maximum number of variables added to the basic model to three, to keep the models interpretable.

The best model was then selected via the AIC. This model enabled us to detect any reduction in resource selection inside compared with outside the OWF if the turbine blades were rotating (i.e. *OWFyn* = inside and *OWF_onoff* = rotating, see equation (2); interaction term shown in bold). Notably,

when interactions are included in a model, the variables included in the interaction term cannot be interpreted singularly (Field et al. 2012), but they were nevertheless included to improve the model:

$$Z \sim \beta + te(\log_{d_s}, angle, k = c(5,5)) + s(trip_{id}, bs = 're') + s(bird_{id}, bs = 're') + OWF_{yn} + dist_{Helgoland} + slope + OWF_{onoff} + \mathbf{OWF_{yn}: OWF_{onoff}} \quad (2)$$

The second-best model was also selected because it allowed us to determine if habitat selection inside the OWF was different from that outside the OWF, without analysing the combined effect of rotating turbines and OWF presence:

$$Z \sim \beta + te(\log_{d_s}, angle, k = c(5,5)) + s(trip_{id}, bs = 're') + s(bird_{id}, bs = 're') + OWF_{yn} + dist_{Helgoland} + slope \quad 3)$$

Notably, a classical Poisson-GAMM was not fitted, but the response-variable Z interplays with appropriate regression weights such that a PPM likelihood is approximated (for details see Johnson et al. 2013).

4. Model validation, numerical realisation, and software

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

Results

Overview of foraging trips

We recorded a total of 204 individual foraging trips by 12 guillemots in 2016 and 2017 (Table 1, Supplement 2 Table S1). The mean values of the duration, and the maximum and total distances of the foraging trips did not differ between the two years (Table 1, Supplement 2 Fig. S1). While the same area was generally used in both years (Fig. 1), individuals in 2017 used areas located more to the west of the colony.

Avoidance of and attraction by OWFs

1. Foraging trips

Most individuals completely avoided the OWFs north of Helgoland (Fig. 1). However, some individuals approached them closely, especially in the east or south. One out of seven tagged individuals in 2016 and one out of five tagged individuals in 2017 entered the OWFs on two to three occasions at night or in the evening, and stayed inside the OWFs for between 20 min and 2 h 11 min (mean = 1 h 1 min; Table 2, Fig. 1). For both these individuals, diving activity in the OWF area was recorded on one of the occasions (Table 2), but no dives were recorded or the positions of the dives were unavailable for the remaining occasions due to gaps in the GPS data. Only one individual entering the OWFs is shown in Fig. 1 because some parts of the data for the second bird did not allow trip classification. The positions of the latter individual are shown in Supplement 2, Fig. S2.

Table 1: Total number of foraging trips per year, as well as mean values for: duration, maximum distance, and total distance for all foraging trips in 2016 and 2017.

	2016	2017	χ^2	<i>p</i> -value
Individuals (n)	7	5		
Trips (n)	102	102	-	-
Mean duration (h)	10.77 (0.83–83.78)	12.97 (0.33–105.82)	0.004	0.950
Max. distance (km)	16.72 (0.79–65.38)	18.84 (0.46–67.19)	0.079	0.779
Total distance	47.69 (1.65–174.62)	53.04 (0.92–210.46)	0.081	0.776

Table 2: Start, duration, and number of positions in OWFs for the two guillemots entering the OWFs.

	Start in OWF	Time in OWF (hh:mm)	Positions in OWF (n)	Comment
L002015	16.05.2016 02:26	00:20	2	Commuting briefly through OWF Nordsee Ost
	17.05.2016 01:19	00:41	2	Some dives indicate foraging activity between the two GPS positions
	17.05.2016 22:44	01:50	2	
L002432	18.05.2017 19:07	02:11	9	
	19.05.2017 01:01	01:01	5	Some dives indicate foraging activity between the GPS positions
Mean		01:01		

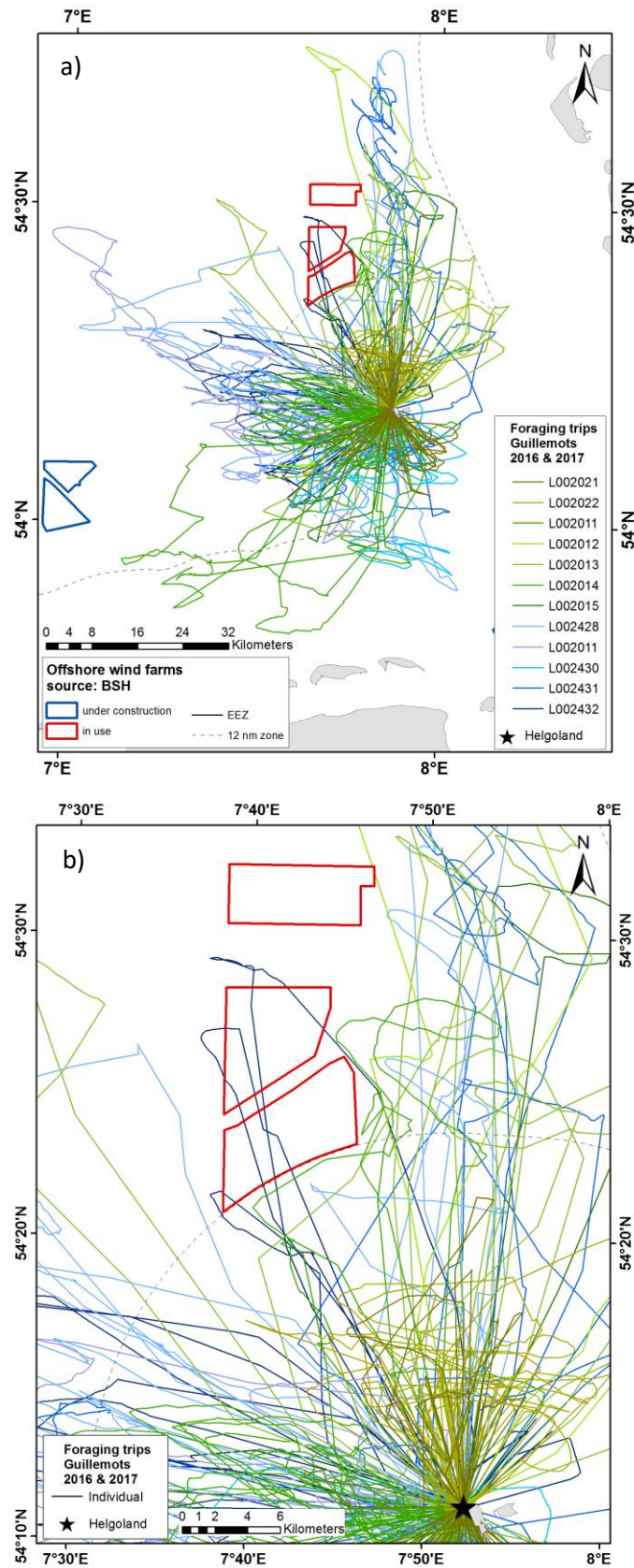


Fig. 1: Foraging trips of guillemots tagged in 2016 (green) and 2017 (blue). a) Overview, b) zoom on OWFs. OWF status 2016: blue = under construction, red = operating. OWFs on the left of a) were in use in 2017.

2. *Behaviour*

Differentiating among resting, foraging, and travelling behaviours showed, that the individuals mainly used areas north and north-west of Helgoland (i.e. south-west or east of the OWFs) to commute to and from the colony (Fig. 2a), and areas to the west, south-west, and north of Helgoland for resting and diving (Fig.2b & c). Guillemots rarely approached the OWFs when flying (Fig. 2d), and mainly approached from the east while resting, and also when diving (Fig. 2e & f).

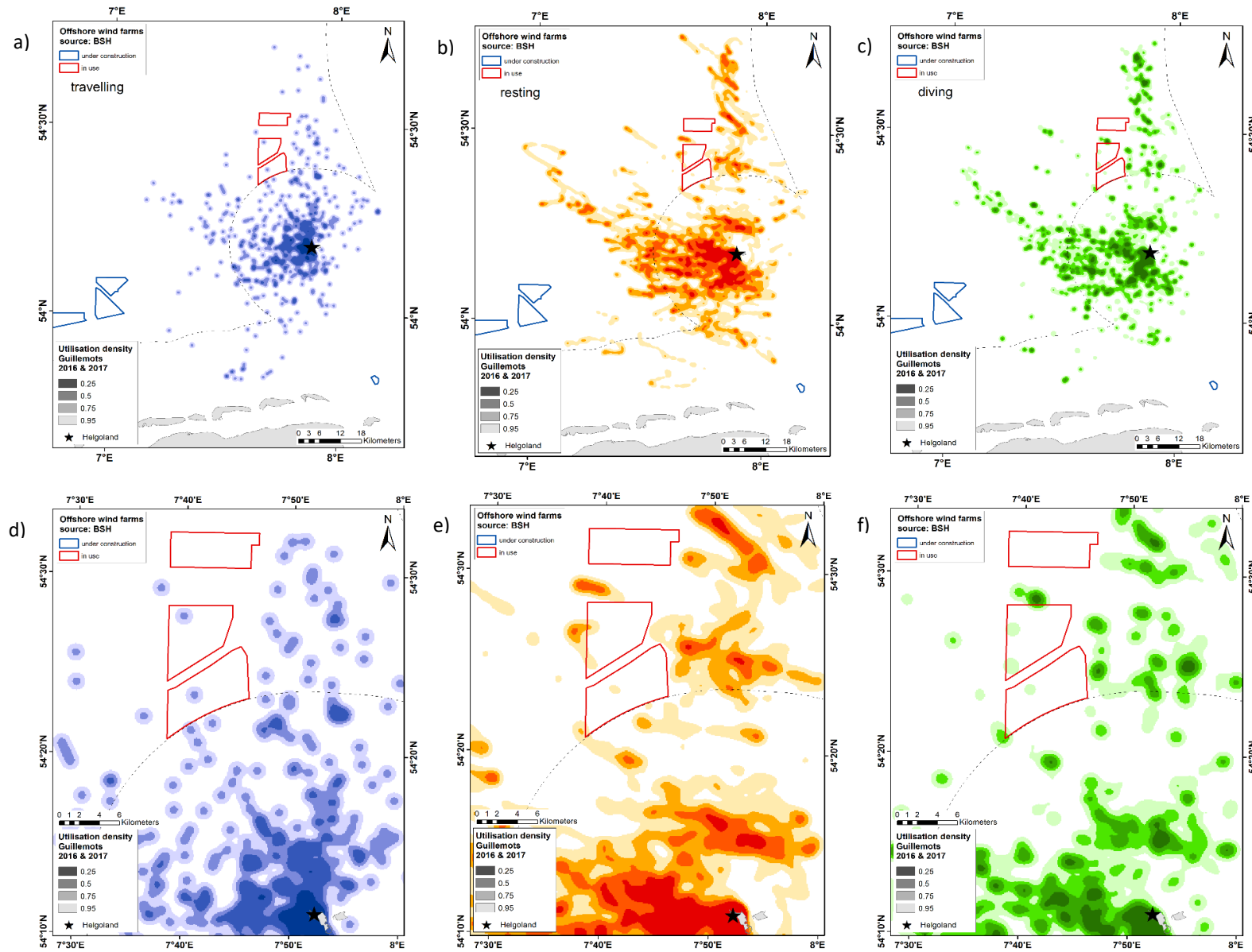


Fig. 2: Kernel densities of a) travelling, b) resting, and c) diving positions of guillemots tagged in 2016 & 2017 and (d, e, f) zoomed to OWF area. Positions visualised as percentiles: dark colour = 25% percentile, light colour = 95% percentile.

3. Model results

All the models revealed significantly reduced habitat selection in the OWF area compared with the surrounding areas (Tables 3-5). The second-best model revealed a by 67% reduced selection of the OWF area when rotation of the turbine blades was not considered (Table 4; variable 'owfyn_inside', estimate = -1.113, $p < 0.001$, response = $\exp(\text{estimate})$ = 67% reduced selection inside the OWF compared to outside, lower confidence interval (CI) = 81% reduction, upper CI= 43% reduction). The best model revealed a by 76% reduced selection of the OWF area compared with outside if the blades were rotating (Table 5; variable 'owfyn_inside:owf_onoff_rotating', estimate = -1.424, $p = 0.031$, response = $\exp(\text{estimate})$ = 76% reduced selection inside the OWF compared to outside, lower CI = 93% reduction, upper CI= 12% reduction).

Table 3: Results of basic point process model.

Parametric coefficient	Estimate	Standard Error	z value	Pr(> z)	
(Intercept)	-0.466	0.127	-3.670	0.000	***
OWFyn_inside	-1.435	0.278	-5.158	0.000	***
Smooth term	edf ^{a)}	Ref.df ^{b)}	χ^2	p-value	
te(log_ds,angle)	23.097	23.830	18,941.000	< 2e-16	***
s(trip_id)	180.912	202.000	19,256.000	0.002	**
s(bird_id)	7.185	11.000	26,258.000	0.056	.

Parametric coefficients and smooth terms are shown. Terms relevant for the analysis of OWF effects are indicated in bold.

a) edf = estimated degrees of freedom

b) Ref.df = reference degrees of freedom

Table 4: Results for the second-best model.

Parametric coefficient	Estimate	Standard Error	z value	Pr(> z)
(Intercept)	0.692	0.131	5.273	0.000
owfyn_inside	-1.113	0.278	-3.999	0.000
dist_Helgoland	-0.046	0.001	-48.546	< 2e-16
slope	-0.201	0.082	-2.448	0.014
Smooth term	edf ^{a)}	Ref.df ^{b)}	χ^2	p-value
te(log_ds,angle)	23.029	23.800	12,352.000	< 2e-16
s(trip_id)	179.745	202.000	17,273.000	0.001
s(bird_id)	7.506	11.000	17,917.000	0.125

Parametric coefficients and smooth terms are shown. Terms relevant for the analysis of OWF effects are indicated in bold.

a) edf = estimated degrees of freedom

b) Ref.df = reference degrees of freedom

Table 5: Results for the best model.

Parametric coefficient	Estimate	Standard Error	z value	Pr(> z)
(Intercept)	0.710	0.132	5.382	0.000
owfyn_inside	-0.567	0.318	-1.784	0.074
owf_onoff_rotating	-0.031	0.030	-1.048	0.295
dist_Helgoland	-0.046	0.001	-48.472	< 2e-16
slope	-0.201	0.082	-2.454	0.014
owfyn_inside:owf_onoff_rotating	-1.424	0.659	-2.159	0.031
Smooth term	edf ^{a)}	Ref.df ^{b)}	χ^2	p-value
te(log_ds,angle)	23.031	23.800	12,342.000	< 2e-16
s(trip_id)	179.684	202.000	16,426.000	0.001
s(bird_id)	7.494	11.000	16,666.000	0.140

Parametric coefficients and smooth terms are shown. The interaction term that can be interpreted is indicated in bold.

a) edf = estimated degrees of freedom

b) Ref.df = reference degrees of freedom

GPS tracking combined with PPM analysis showed that guillemots almost completely avoided the OWFs north of their breeding colony, with a 67% reduction in selection of the OWF areas compared with the surrounding areas. Furthermore, OWF avoidance was increased (76% reduction) when the turbine blades were rotating. Guillemots mainly approached the OWFs at their eastern edge when resting or diving, and rarely approached them when commuting. However, one individual in each study year briefly entered the OWF on two to three occasions.

Discussion

To the best of our knowledge, this study provides the first evidence for the impact of OWFs situated in close proximity to a guillemot breeding colony based on GPS-tracking data.

As central-place foragers, breeding seabirds have to balance their energy intake and trip distance (Chaurand & Weimerskirch 1994, Suryan et al. 2006, Bertrand et al. 2012). Displacement during the breeding season could thus increase foraging trip length and energy expenditure, thereby affecting adult condition or survival (Masden et al. 2010) and reproductive success (Langton et al. 2014).

The strong OWF avoidance detected for guillemots breeding on Helgoland, together with their comparatively small foraging distance, shows that the available foraging habitat close to the colony was greatly reduced by the OWFs. Guillemots breeding on Helgoland thus have to compensate for this lost habitat within their accessible distance. A recent study showed that the OWF area was not among the most intensively used areas by guillemots before its construction, but moderately high densities were still found during the breeding season (Mendel et al. 2018). In the same study, the density in the OWF (plus a 3 km buffer around the OWF) was reduced by 44% after the construction compared with the surroundings and with the period before construction. However, the effect in the breeding season was smaller than that in spring, and the authors discussed if the birds needed to approach the OWFs more during the breeding season, due to a lack of available foraging habitat close to the colony (Mendel et al. 2018). These previous results are supported by the present tracking study, which showed that the birds approached the OWFs closely, but generally did not enter them.

Other studies have revealed similar OWF avoidance behaviours in guillemots, but most focused on the entire yearly cycle and did not provide detailed information exclusively on the behaviour of breeding birds (Vanermen et al. 2015, Welcker & Nehls et al. 2016, Vallejo et al. 2017).

The use of areas close to the OWFs for resting and diving indicates that the guillemots foraged close to the turbines on some occasions. This could be related to the so called 'reef effect' (Lindeboom et al. 2011, Leopold et al. 2013, Vanermen et al. 2015), which reflects the increased fish diversity and abundance associated with the additional benthic structures of the turbines (e.g. de Mesel et al. 2015, Stenberg et al. 2015, Vandendriessche et al. 2015). However, guillemots did not use the areas close to the OWFs very intensively, but rather concentrated their foraging efforts in the west of the study area at distances of 12–18 km from the OWFs.

The increased avoidance of the OWFs when the rotor blades were turning indicated a stronger reaction to moving objects, which was suggested as a possible reason for OWF avoidance by birds (Dierschke et al. 2016). However, we found strong OWF avoidance across the entire dataset, irrespective of blade rotation, suggesting that the rotating blades were not the main cause of the avoidance reaction.

Nonetheless, it could be speculated that if measures were needed to reduce the effect, deactivation of the turbines could slightly reduce the disturbance.

Busch & Garthe (2016) assessed the effects of potential displacement due to the OWFs north of Helgoland on the local guillemot colony on the basis of potential biological removal rates (PBR). The PBR indicates the number of losses in addition to the natural mortality, which can be sustained each year by a certain population (Dillingham & Fletcher 2008). Transferring the findings of Busch & Garthe (2016) to our study indicated that the OWFs north of Helgoland accounted for 35% of the PBR estimated for the German guillemot population in the breeding season. This represents a substantial proportion of the PBR, bearing in mind that the effects of other human activities (e.g. shipping, fisheries, etc.) were not included in these calculations. However, it has to be kept in mind, that Busch & Garthe (2016) applied displacement values derived from changes in the species abundance in OWF areas for estimating the number of affected individuals. Thus, the changes in resource selection estimated from tracking data in our study potentially cannot directly be applied to their approach.

When interpreting the here presented findings, the duration of the study has to be considered. Studies conducted over several consecutive years will reveal if the observed pattern is consistent over time.

However, the strong avoidance effect found in this study during the breeding season shows that, although the size of the guillemot population on Helgoland is currently quite stable (Dierschke et al. 2018), the presence of the OWFs needs to be considered when evaluating the conservation and health statuses of common guillemots at their sole breeding site in German North Sea waters, and likely also at other sites within their distribution area.

Ethical approval: Guillemot catching and tagging was 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 - 26934/2016 (80-6/13)).

*Supplement 2***Table S1:** Overview of tagged guillemot individuals in 2016 and 2017.

Year	Individual	GPS start	GPS end	GPS (days)	GPS (weeks)	tag type
2016	L002011	10.05.2016 05:51	24.05.2016 09:02	14	2	Uria, TDR
2016	L002012	10.05.2016 06:31	18.05.2016 10:19	8	1	Uria, TDR
2016	L002013	10.05.2016 06:57	26.05.2016 09:43	16	2	Uria
2016	L002014	11.05.2016 05:50	06.06.2016 15:06	26	4	Uria
2016	L002015	11.05.2016 06:16	25.05.2016 06:05	14	2	Uria, TDR
2016	L002021	07.06.2016 05:25	24.06.2016 08:06	17	2	Uria
2016	L002022	08.06.2016 06:48	22.06.2016 17:49	14	2	Uria
2017	L002428	11.05.2017 04:03	26.05.2017 21:54	16	2	Uria
2017	L002011	11.05.2017 04:35	31.05.2017 04:26	20	3	Uria
2017	L002430	11.05.2017 05:04	01.06.2017 14:57	21	3	Uria
2017	L002431	11.05.2017 05:17	28.05.2017 04:11	17	2	Uria
2017	L002432	11.05.2017 05:33	25.05.2017 18:27	15	2	Uria
Total	12			199	28	

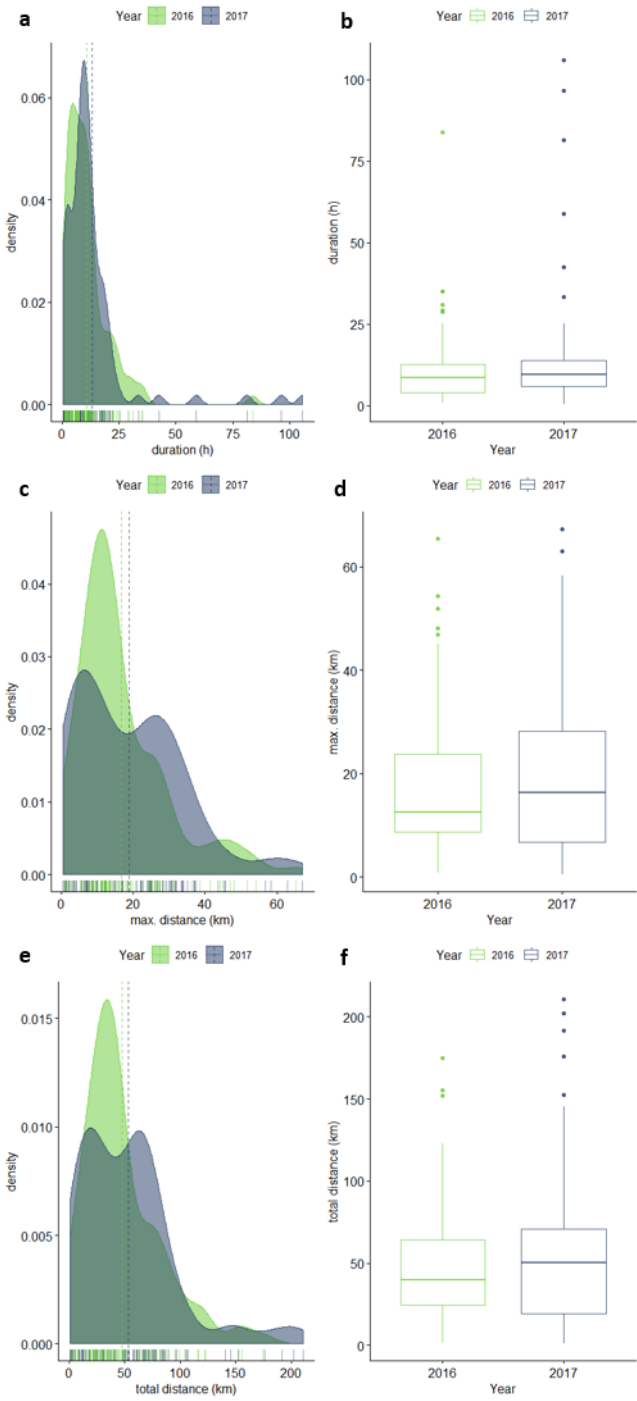


Fig. S1: Density plots (left) and box plots (right) of trip duration (h, a & b), max. distance (km, c & d), and total distance (km, e & f) for trips in 2016 and 2017.

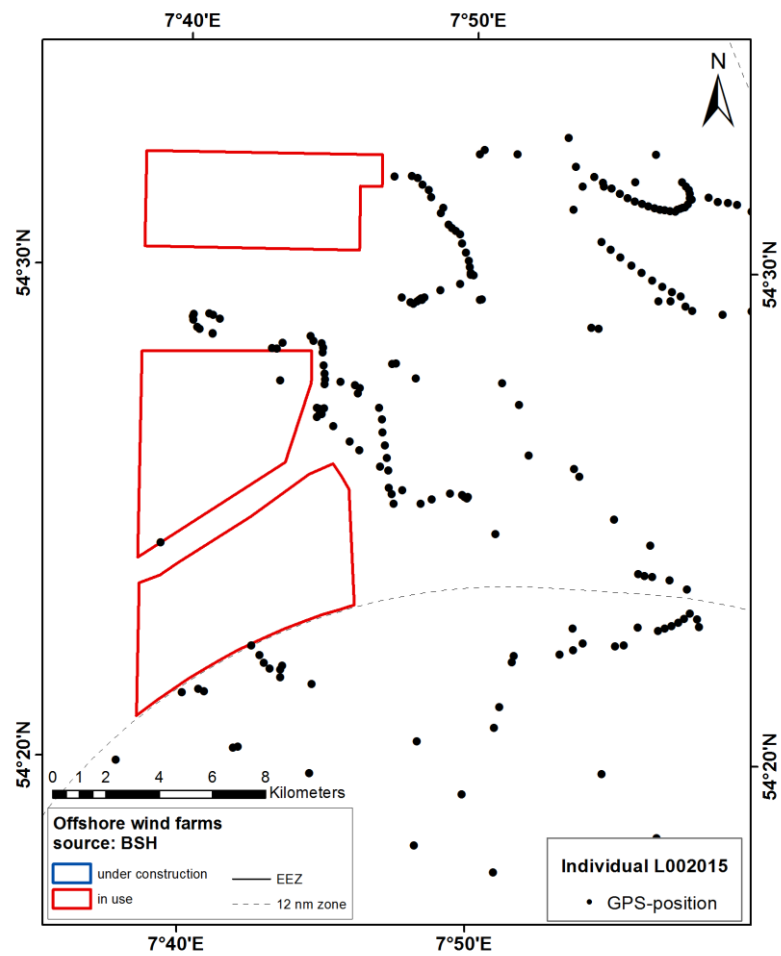


Fig. S2: GPS positions of guillemot (ring number L002015) close to OWF. These positions are not shown in Fig. 1 in the main part of the paper because of data gaps.

CHAPTER V:

Should I stay or should I go? Wide dispersal of grey seal pups in the southern North Sea



Photo: F. Christoffers

Peschko V, Müller S, Schwemmer P, Mercker M, Lienau P, Rosenberger T, Sundermeyer J, Garthe S (submitted) Should I stay or should I go? Grey seal pups disperse widely in the southern North Sea

Should I stay or should I go? Wide dispersal of grey seal pups in the southern North Sea

Verena Peschko, Sabine Müller, Philipp Schwemmer, Moritz Mercker, Peter Lienau, Tanja Rosenberger, Janne Sundermeyer, Stefan Garthe

Abstract

Grey seals have become an important part of the ecosystem in the southern North Sea over the last 50 years. However, little is known about their spatial utilisation of the German North Sea, especially in relation to the dispersal and behaviour of grey seal pups after weaning. We investigated these little-known aspects by recording the movements of 11 grey seal pups born at the largest German colony (Helgoland) for 1–9 months after leaving the colony between 2015 and 2017. The individuals moved widely throughout the southern North Sea, including some individuals that moved long distances along the Danish coast or to Dutch and UK waters. Using a point process modelling approach, we showed that pups moved further from Helgoland even within the first weeks and generally during the first 70 days at sea throughout the study period. Furthermore, the frequency of foraging behaviour increased from the beginning until week seven, whereas fast travelling behaviour increased throughout the whole study period. These findings reflect the transition from naïve to more experienced pups, with gradual increases in foraging effort and range to account for their increasing energy demands for survival and growth. This study extends our knowledge of the behaviour and spatial utilisation of the southern North Sea by grey seals as an increasingly important top predator, as well as highlighting changes of these aspects in relation to increasing age of the pups.

Keywords: behaviour, dispersal after weaning, grey seals, individual movements, point process modelling, spatial utilisation, telemetry

Introduction

The abundance of grey seals (*Halicoerus grypus*) along European mainland coasts in the North Sea has increased since 1967, after being almost absent or very low for several hundred years (Scheibel & Weidel 1988, Reijnders et al. 1995, Härkönen et al. 2007, Brasseur et al. 2015). In 2018, 6,144 grey seals were counted during the moulting season in the entire Wadden Sea area and 1,179 in the German North Sea (Brasseur et al. 2018a). The largest colony in German waters is located on Helgoland (54°11' N, 7°55' E), which is a small island 48 km from the German coastline in the south-eastern North Sea (Fig. 1). Pup numbers on Helgoland increased by 38% between 2014/2015 and 2015/2016, and by 12% between 2016/2017 and 2017/2018 (Brasseur et al. 2016, 2018a). A maximum of 426 births was recorded on Helgoland and a total of 1,377 pups were counted in the entire Wadden Sea area in the breeding season 2017/2018 (Brasseur et al. 2018a). Grey seal pups are weaned within 15–18 days (Kovacs 1987, Haller et al. 1996) and then left by their mother. Following a post-weaning fast during which they lose up to 25% of their body mass (Noren et al. 2008), the pups start to forage for themselves (Noren et al. 2008, Bennett et al. 2010). After leaving their colony, pups have an average of 36 days in which to develop successful foraging tactics before their protein reserves will become depleted and they face the risk of starvation (Bennett et al. 2007). This is therefore a crucial phase of their life cycle, when they need to develop successful foraging strategies to account for the high energy demands for survival and growth. An individual's first-year survival, recruitment into the breeding population and reproductive success are all strongly affected by their body condition during their early development (Beauplet et al. 2005, Bowen et al. 2015). Knowledge of their behaviour and habitat use, and changes in these in relation to the pup's age is therefore essential to understanding the important processes influencing the population and its adaptability in times of major environmental changes and increasing anthropogenic pressures. However, little is currently known about the spatial utilisation of the German North Sea by seals, especially in terms of grey seal pup dispersal and behaviour after weaning.

Weaned grey seal pups tagged at colonies along the UK east coast increased their foraging trip length and duration, as well as their dive duration and depth, during their first weeks at sea (Bennett et al. 2010, Carter et al. 2017). After an explorative phase, pups changed to a more local trip behaviour, commuting between haul-out areas and foraging locations, similar to adults (Carter et al. 2017). About 1.3% of pups born in colonies located along the east coast of the UK emigrate to the Netherlands, accounting for 35% of the annual growth of the Netherlands breeding population (Brasseur et al. 2015). This illustrates an intense exchange between colonies located along the North Sea coast, and further underlines the mobility of grey seal pups, which may settle far from their colony of birth. Some former studies have shown that grey seal pups in the North Sea can travel long distances (Hall et al.

2001, McConnell et al. 2004, Carter et al. 2017), but to the best of our knowledge, no study has reported on the dispersal of pups born in the southern North Sea.

Previous studies implied the existence of resident and transient components in the grey seal population of the North Sea (Brasseur et al. 2017), possibly associated with reduced intra-specific competition (Brasseur et al. 2017).

Given the increasing importance of grey seals as top predators in the southern North Sea, information on the habitat use and behaviour of pups born in colonies located in the southern North Sea is crucial to understanding their potential influence on the population dynamics and to interpret future changes.

Furthermore, offshore wind farm (OWF) development has evolved rapidly in recent years, both worldwide (Perveen et al. 2014) and in the German North Sea, which currently has 19 OWFs in operation, four under construction, and several more being approved (BSH 2019). A clear understanding of the possible interactions with and effects of OWFs on marine top predators is therefore important (Dähne et al. 2013, Hastie et al. 2015, Russell et al. 2016, BSH 2019). However, information for grey seals in this respect is generally sparse (Brasseur et al. 2010, Edren et al. 2010, Skeate et al. 2012) and is currently missing for the German North Sea, despite being a sea area with increasing implementation of OWFs (BSH 2019). Since October 2015, three OWFs including 208 turbines and covering an area of 105 km² have been in operation only 23–35 km north of the local grey seal colony on Helgoland.

Recording the movements of grey seal pups born on Helgoland and analysing the data using point process models (PPMs; Renner et al. 2015) will thus help to shed light on the dispersal of grey seal pups and their spatial utilisation and behaviour, as well as changes in these aspects in line with increasing age of the pups. This information will also provide some initial insights into their spatial overlap with OWFs in the German North Sea. This study aimed to provide some basic information on the changes in spatial utilisation and behaviour of grey seal pups during their first weeks of life. These results will eventually support decision-making with respect to grey seal conservation.

Materials and methods

Eleven grey seal pups, aged approximately 6–8 weeks, were equipped with satellite tags on the island of Helgoland between 2015 and 2017. Individuals were caught using a hand-held net, weighed, and measured. No sedation was used for device fixation. The fur was cleaned and the tag was attached to the fur on the upper back of the individual using epoxy glue (Devcon; Shannon, County Clare, Ireland), and the individuals were released once the glue had hardened. Tags were attached to a rectangular neoprene base with seven €2-sized small feet at its edges (Supplement 1, Fig. S1). Only these feet were

glued to the fur to break up the glue patch. The tags would thus fall off during the next moult, if not before. This method was successfully tested and monitored for about 1 year on a harbour seal (*Phoca vitulina*) in a seal rehabilitation centre. Seal 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). Two tag types were used (Supplement 2, Table S1, Fig. S2), both manufactured by Wildlife Computers (Redmond, King County, Washington, USA): SPLASH (in 2015; 215 g) and SPOT tags (in 2016 & 2017; 119 g). Both were programmed to generate an Argos position when the animal surfaced, with a maximum of 400 uplinks per day (SPLASH), or 38/h with a maximum of 800 uplinks per day (SPOT), and to pause when the animal hauled out on land. No difference in tag performance was observed.

Trip identification

Foraging trips for each individual were defined as a set of sequential locations at sea between two haul-out events. A location was identified as a haul-out location if it was within ≤ 1 km distance from the coast and/or located in areas of the Wadden Sea that may become dry at low tide. All other locations (> 1 km distance from the coast or in tidal channels) were assumed to be part of foraging trips. A trip was defined to start at the first recorded position > 1 km from the coast and to end at the last position > 1 km from the coast. Trips with less than three positions were excluded from the following analysis. Trip statistics, i.e. trip duration (h), total distance (km), and trip maximum and mean distances to Helgoland and to shore (km) were calculated for each individual foraging trip using the R-package “trip” (Summer 2016, version 1.5.0).

Utilisation distribution was estimated for each individual by applying a dynamic Brownian bridge movement model (Kranstauber et al. 2012) in the R-package move (Kranstauber et al. 2017, R Core Team 2017; R version 3.4.2), and summed for all individuals per year. ArcGIS (version 10.3; Environmental System Research Institute 2016) was used to visualize the utilisation distribution.

Data interpolation and behavioural classification

Before applying the PPM, Argos positions were filtered using the Douglas Argos-Filter option in Movebank (movebank.org, Douglas et al. 2012). Furthermore, state-space modelling (Jonsen et al. 2005, Patterson et al. 2008, and see Supplement 3) was applied to regularise the data set to 1-h intervals, with 720 min being the largest data gap that was allowed to be interpolated.

We identified behavioural states using expectation-maximization binary clustering (EMbC; Garriga et al. 2016), as a robust, non-supervised, multivariate clustering algorithm that minimises prior assumptions and favours the semantic interpretation of the final clustering by splitting the input features in low and high values of speed and turning angle (Garriga et al. 2016). The EMbC approach differs from other state-space approaches for behavioural classification (Jonsen et al. 2005) by classifying behavioural states on a fine scale, and the classification does not depend on temporal or contextual correlations of behavioural states (Garriga et al. 2016). EMbC thus offers a new approach for the classification of behavioural states, and has already been applied successfully in several studies (Mendez et al. 2017, Jones et al. 2018). The algorithm assigns each location to one of four clusters (Supplement 4, Table S2, Fig. S3, and Fig. S4): high velocity/low turn (HL), high velocity/high turn (HH), low velocity/low turn (LL), and low velocity/high turn (LH). HL was identified as fast directional movement and was interpreted as ‘fast travelling’ behaviour, the two states with high turning angles (LH, HH) were merged and interpreted as ‘foraging’ and LL was identified as slow directional movement and was interpreted as ‘slow travelling/resting’ behaviour. EMbC analysis was conducted using the R package EMbC v2.0.1 (Garriga et al. 2018), and a smoother function was applied to take account of temporal associations of behavioural states. More details of the method are provided in Supplement 4.

Statistical modelling

1. Preparation of covariables

ArcGIS (version 10.3; Environmental System Research Institute 2016) was used to calculate the means of the spatial environmental covariates for a grid with a spatial resolution of 5 x 5 km. Environmental variables included: (1) *dist_coast* = minimal distance to the mainland and large islands (except Helgoland); (2) *dist_Helgoland* = minimal distance to the island of Helgoland; (3) *mean_depth* = mean water depth; and (4) *slope* = inclination of the seabed. Temporal variables drawn directly from the tracking dataset included: (5) *year*; (6) *week_tag* = week after tagging date; (7) *trip_{id}* = the number of each foraging trip; and (8) *seal_{id}* = the individual seal. Furthermore, (9) *behaviour* identified by the EMbC method was used as a covariate in the modelling process.

2. PPMs

The statistical analysis of telemetry data investigating resource selection is often challenging, and various modelling strategies have previously been developed and discussed (Hooten et al. 2017). Popular approaches include (integrated) step selection functions (Thurfjell et al. 2014, Avgar et al. 2016) or point process approaches (Johnson et al. 2013, Renner et al. 2015). In addition to the true

tracking locations, both these approaches use a number of contrasting points ('dummy points', 'pseudo-absences' or 'available steps') making the comparison of selected versus available resources possible. 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), because this approach naturally and automatically resolves many of the questions and pitfalls arising from the alternative approaches (Warton & Shepherd 2010, Warton & Aarts 2013, Renner et al. 2015, Hooten et al. 2017). For example, the role and number of dummy points were not chosen *ad hoc* but were deduced purely mathematically by the efficient estimation of an integral as a part of the PPM likelihood (Warton & Shepherd 2010, Warton & Aarts 2013). Additionally, PPMs represent a generalisation of many other frequently used methods (Johnson et al. 2008, Warton & Shepherd 2010, Aarts et al. 2012). Finally, the PPM likelihood can be approximated by a mathematical trick using standard generalised linear mixed modelling (GLMM)-regression software (Johnson et al. 2013, Renner et al. 2015), ensuring a flexible and individual implementation. More details of the modifications of the PPMs compared with the spatio-temporal PPMs as presented by Johnson et al. (2013) are shown in Supplement 3.

3. Model selection

To ensure that the modelling approach was based on a robust dataset, and covering a period of profound changes in the pups behaviour (Carter et al. 2017), we only used data for the first 70 days of the tagging period. Continuous data were available for seven individuals during this period, while four individuals stopped transmitting data after 24–50 days (Supplement 2, Fig. S2).

We analysed habitat use by grey seal pups and changes in this use throughout the tracking period using a GAMM-PPM on a dataset consisting of 9,751 raw data points. Seal HG9 was removed because its dataset contained too few data points. When applying the GAMM-PPM to the tracking raw data 78,008 dummy points were created.

The optimal model regarding the set of fixed-effect predictors was selected by comparing 52 different models, based on the Akaike Information Criterion (AIC; Akaike 1973). Models including the variables *dist_coast*, *mean_depth* and *slope* were not selected through AIC analysis. Inspection of the results of the best models showed that all models had similar patterns of data, indicating that our main results were robust across different models. The best model selected based on the AIC included a second-order interaction term. Notably, the inclusion of interactions in a model means that lower order terms cannot be interpreted (Field et al. 2012); however, they are included to improve the model. The model enabled us to analyse if the pups showed increases or decreases in different behavioural categories in

relation to (a) week after tagging (i.e. age of the pups) and (b) distance to Helgoland, and if the distance to Helgoland generally changed with the week after tagging (see (1); interpretable interaction terms shown in bold).

$$Z \sim \beta + te(\log_ds, angle, \log_dt, k = c(5, 5, 5)) + s(trip_{id}, bs = re) + s(seal_{id}, bs = re) + s(year, bs = re) + \textit{behaviour} + s(week_tag) + s(dist_Helgoland) + \mathbf{ti(week_tag, by = \textit{behaviour})} + \mathbf{ti(week_tag, dist_Helgoland)} + \mathbf{ti(dist_Helgoland, by = \textit{behaviour})} \quad (1)$$

Here, β is the intercept, $ti()$ depicts a tensor product regression spline and the Poisson distribution was chosen as probability distribution. Tensor-smooth interactions were favoured during AIC-selection compared to models with cubic spline-interactions applied to rescaled variables. $Trip_{id}$, $seal_{id}$ and $year$ were all included as random effects, indicated by the term $bs = re$. The term $by = \textit{behaviour}$ indicates that the splines were estimated independently for each behavioural category. Notably, a classical Poisson-GAMM was not fitted, but the response-variable Z interplayed with appropriate regression weights such that a PPM-likelihood was approximated. For more details, see Johnson et al. (2013). Standard errors and p -values were estimated conservatively.

4. Model validation, numerical realisation and software

PPM model-validation plots for the final GAMM-PPM were generated based on PPM-Pearson residuals (Baddeley et al. 2005a, Baddeley et al. 2005b). All statistical analyses were performed using the free statistical software R (Core Team 2016). Fitting of the state-space models was straightforward using the R-package *bsam* (Jonsen et al. 2013). Spatial statistics were performed using *spatstat* (Baddeley et al. 2005a), dummy-point meshes and trapezoid rule-based quadrature weights were created using *mvQuad* (Weiser 2016), GAMM and GAM fits were performed using *mgcv* (Wood 2006), and visualisation was performed based on *itsadug* (van Rij et al. 2017). 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.

Results

Data for five female and six male grey seal pups were recorded from mid-January/beginning of February for periods of 24–267 days between 2015 and 2017 (Supplement 2, Table S1).

Individual grey seal pups from Helgoland moved widely throughout the southern North Sea, as visualized by their individual tracks (Fig. 1). The German part of the North Sea was used intensely in all years. Two individuals moved along the Danish coast up to the Skagerrak/Kattegat area and one moved

to Dutch and UK waters in 2015 and 2017, with individual HG12 settling at the UK coast after 9 weeks (Fig. 1). In contrast, individuals stayed closer to the colony in 2016 compared with the other 2 years (Fig. 1). Some individuals mainly stayed at the Helgoland colony (HG4 in 2016), but others frequently changed their haul-out locations (HG1, 2, 3, 8, and 11 in 2015 and 2017) or settled in areas along the coast, at least during the tracking period (HG6 & 7 in 2016).

During their first trips, grey seal pups predominantly stayed in waters around the island (Supplement 5, Fig. S5). However, from the second week on, several individuals appeared to follow similar patterns dispersing far along the mainland coasts of Germany, Denmark and the Netherlands, and even to offshore and coastal areas of the UK.

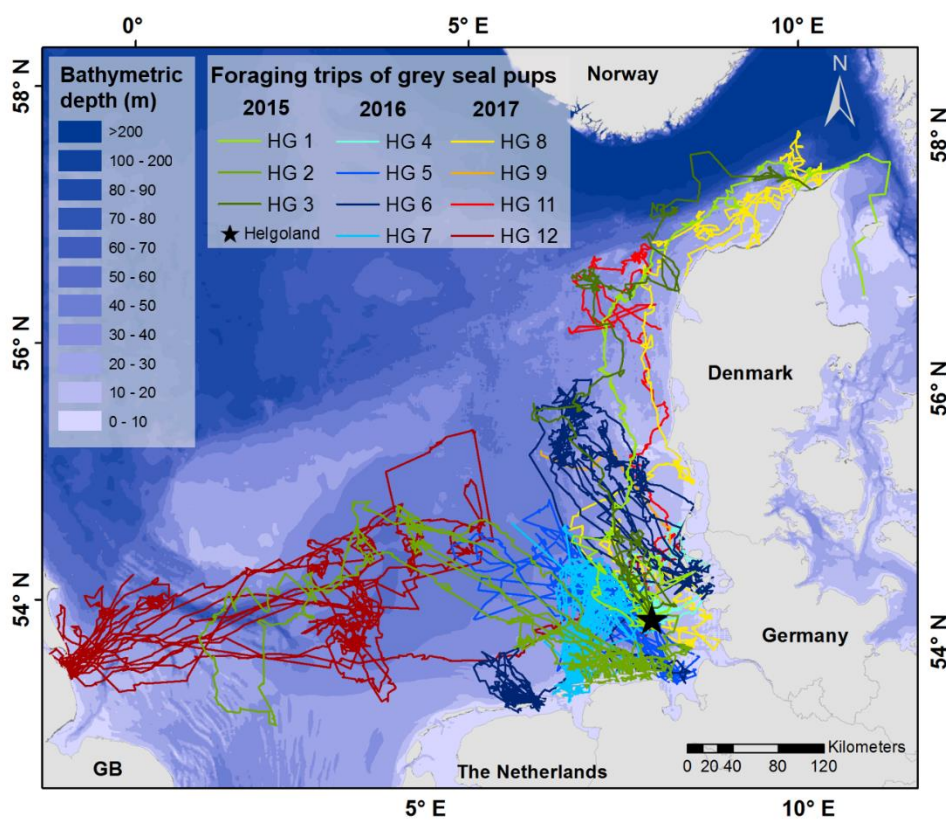


Fig. 1: Movement of individual juvenile grey seals in the North Sea. Helgoland is indicated by a black star.

Table 1: Numbers and characteristics of trips per individual seal.

Year	Individual	No of trips	Duration mean (d)	SD duration mean (d)	Total distance (km)	Max. distance to Helgoland (km)	Mean distance to Helgoland (km)	Max. distance to shore (km)	Mean distance to shore (km)
2015	HG1	9	4.39	5.38	386.34	157.84	123.55	50.57	36.73
	HG2	32	3.04	7.64	174.98	76.12	57.54	29.27	16.92
	HG3	4	10.60	6.53	604.32	223.64	171.27	73.48	48.03
	HG4	70	2.25	2.74	89.22	22.43	15.14	46.54	39.96
2016	HG5	32	5.40	6.74	193.39	77.43	48.37	62.02	37.84
	HG6	52	2.76	5.10	152.22	114.07	101.95	22.15	14.08
	HG7	33	4.48	4.97	205.63	93.64	72.62	49.64	29.01
	HG8	10	6.65	8.17	317.94	184.65	157.83	32.12	17.23
2017	HG9	1	23.74	na	274.63	176.97	61.38	110.44	40.59
	HG11	1	30.22	na	1634.84	331.59	230.89	93.26	39.25
	HG12	49	3.65	8.13	215.85	444.27	411.68	38.99	25.73
all seals	-	293	8.84	6.26	386.30	172.97	132.02	55.32	31.40

Mean values of: Trip duration (d), total distance travelled per trip (km), maximum and mean distances to Helgoland (km), maximum and mean distances to the coast (km).

A total of 293 foraging trips were recorded (Table 1), with between one (HG9 & 11) and 70 trips per individual. The mean trip duration varied from 2.25 (HG4, SD \pm 2.74 days) to 30.22 days (HG11) and covered a mean distance of 89–1634 km. The high values were mainly recorded from three individuals (HG3, 9, 11) for which we only recorded one to four foraging trips. The mean trip duration for all individuals was 8.84 days (SD \pm 6.26 days) and the mean total distance covered per trip was 386.3 km (Table 1). The mean maximum distance to the shore ranged from 22 (HG6) to 110 km (HG9). Bathymetric depth and distance from the coast were excluded from our model through the AIC (see below), but the data showed that the pups stayed in areas with a water depth of 0–40 m during the first weeks (Supplement 5, Fig. S6a). However, from week four onwards, some of the pups also explored areas with depths of > 40 m (Supplement 5, Fig. S6b), and the maximum bathymetric depth of the explored areas in the following weeks was 511 m. While exploring their habitat, pups stayed in areas within 200 km of the coast. The proportions of 60-min intervals (Table 2) classified for each of the three behavioural categories varied among individuals: between 29% and 54% of locations were classified as slow travelling/resting (mean of all individuals: 42%), between 42% and 67% as foraging (mean: 52%) and between 4% and 10% as fast travelling (mean: 6%).

Table 2: Proportion of 60-min intervals classified for each behaviour.

Individual	% Slow travel/rest	% Foraging	% Fast travel
HG1	29	67	4
HG2	39	55	6
HG3	49	45	6
HG4	38	57	5
HG5	42	48	10
HG6	35	59	6
HG7	46	49	5
HG8	46	49	5
HG11	54	42	4
HG12	40	50	10
mean all (\pm SD)	42 (\pm 7)	52 (\pm 7)	6 (\pm 2)

Model results

The model revealed that the distance of the pups to Helgoland increased throughout the weeks after tagging (Fig. 2, Table 3, interaction term '*ti(week_tag,dist_Helgoland)*', $p < 2e-16$). The model revealed a significant change in the frequency of foraging behaviour in relation to week after tagging (Table 3; interaction term '*ti(week_tag):foraging*', $p < 0.001$). The frequency of foraging increased approximately until week seven, and decreased thereafter (Fig. 3a). The interaction between the week after tagging and fast travelling behaviour revealed an increasing frequency for this behaviour with time (Table 3; interaction term '*ti(week_tag):fast travelling*', $p = 0.001$) (Fig. 3a). The model also revealed that slow travelling/resting (Table 3, interaction term '*ti(dist_helgoland):slow travel/rest*', $p = 0.013$) as well as foraging behaviour (Table 3, interaction term '*ti(dist_helgoland):foraging*', $p = 0.010$) both increased significantly with increasing distance to Helgoland (Fig. 3b).

Table 3: Results for the best model.

Parametric coefficient	Estimate	Std. Error	z value	Pr(> z)	
(Intercept)	-6.647	0.093	-71.857	<2e-16	***
behaviour2	-0.099	0.062	-1.615	0.106	
behaviour3	-0.160	0.123	-1.299	0.194	
Smooth terms	edf	Ref.df	Chi.sq	p-value	
te(log_ds,angle,log_dt)	54.043	61.404	23490.035	<2e-16	***
s(trip_id)	66.525	81.000	2817.805	<2e-16	***
s(seal_id)	2.852	9.000	237.610	0.088	
s(year)	0.486	2.000	29.768	0.237	
s(week_tag)	3.416	4.185	49.013	0.000	***
s(dist_Helgoland)	2.454	2.921	106.316	<2e-16	***
ti(week_tag):slow travel/rest	1.807	2.042	2.641	0.241	
ti(week_tag):foraging	2.689	2.902	63.065	0.000	***
ti(week_tag):fast travel	3.453	3.768	16.807	0.001	***
ti(week_tag,dist_Helgoland)	6.631	8.087	308.486	<2e-16	***
ti(dist_Helgoland):slow travel/rest	2.161	2.405	8.239	0.013	*
ti(dist_Helgoland):foraging	2.044	2.275	8.550	0.010	**
ti(dist_Helgoland):fast travel	1.528	1.834	2.233	0.209	

Parametric coefficients and smooth terms are shown. Interaction terms that can be interpreted are indicated in bold.

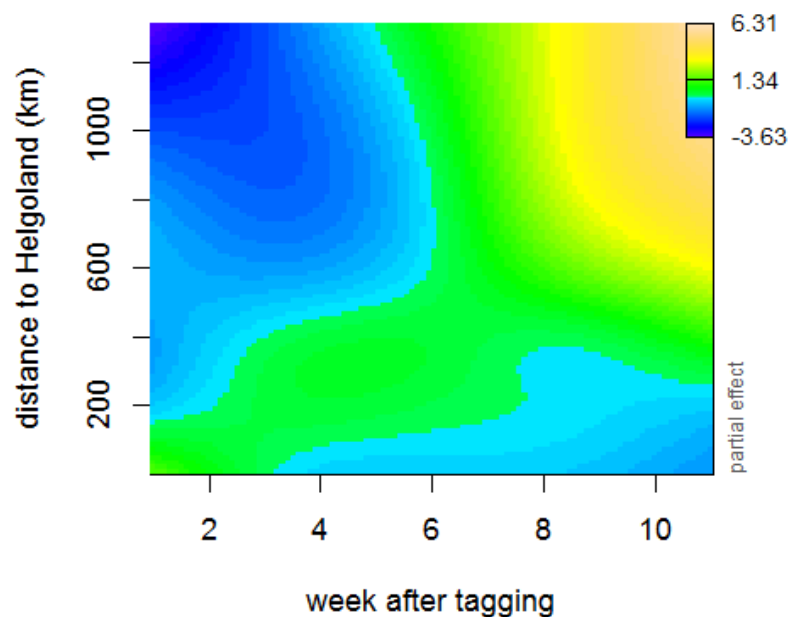


Fig. 2: Change in distance to Helgoland with week after tagging. Plot shows the partial (=isolated) effect of the interaction $ti(\text{week_tag}, \text{dist_Helgoland})$. The colour scale indicates relative differences in the smooth (blue = low preference, orange = high preference).

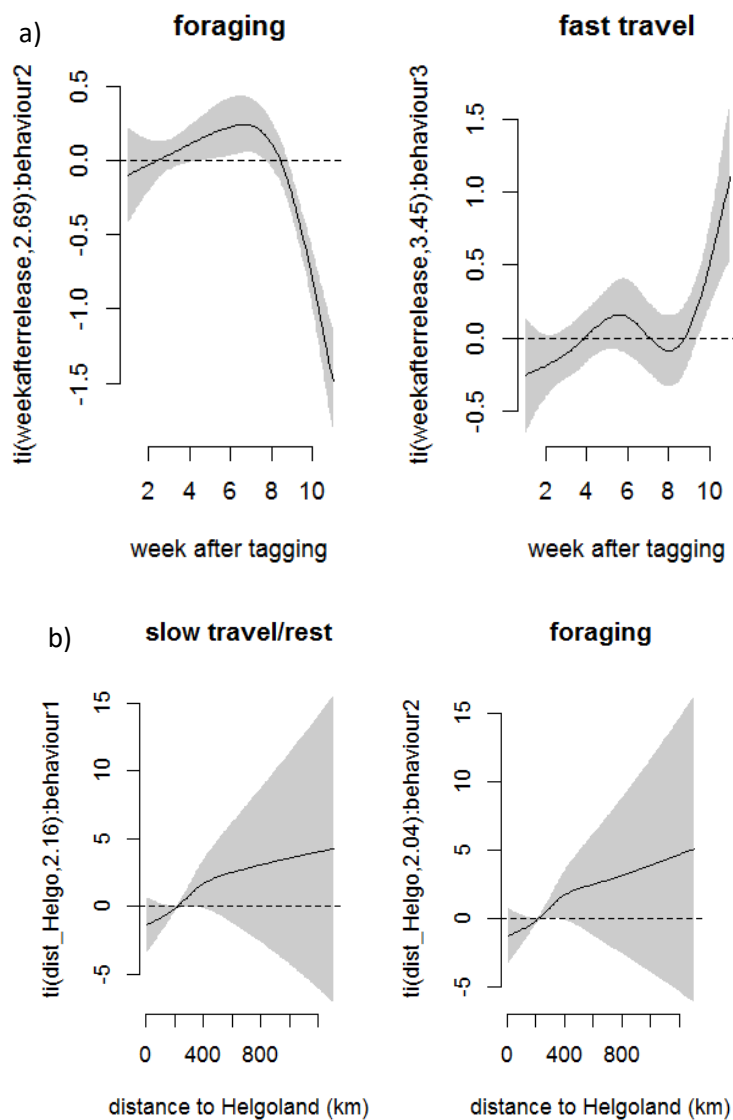


Fig. 3: Decrease/increase in behaviour with (a) week after tagging and (b) distance to Helgoland in km. The plot shows the partial (=isolated) effect of each interaction separately.

In summary, the model revealed that the frequency of foraging behaviour increased until the 7th week and then decreased, whereas fast travelling behaviour increased almost continuously. The model also showed a general increase in the distance to Helgoland with time, and a preference for distant areas from Helgoland for slow travelling and foraging behaviours.

Interaction with OWFs

There was no obvious behavioural response to OWFs (Fig. 4). Many individuals crossed OWFs under construction or in operation in the German North Sea while travelling to other areas, some individuals repeatedly stayed within the OWFs for longer time periods, and some individuals did not interact with OWFs at all. Notably, six individuals crossed OWF areas under construction or in operation in 2015 and 2016, within a few days of tagging (Fig. 4b & c; HG1, 3, 5, 6, 7, & 12). Some individuals repeatedly stayed within the OWFs for longer time periods (HG1, 4, & 7; Fig. 4b & c), with HG4 for example staying within an operating OWF during 10% of all deployment days for a mean of 4 h/day. HG7 repeatedly crossed an OWF under construction (3.5% of tracking days during the pile-driving period and 5% during general construction activities) on its way to its foraging grounds and stayed for a mean of 1 h. In contrast, two individuals tagged in 2017 (HG9 & 11) did not enter any OWF during the tracking period. Generally, some of the areas used most intensely by grey seals, especially in 2015 and 2016, overlapped with OWFs under construction or in use.

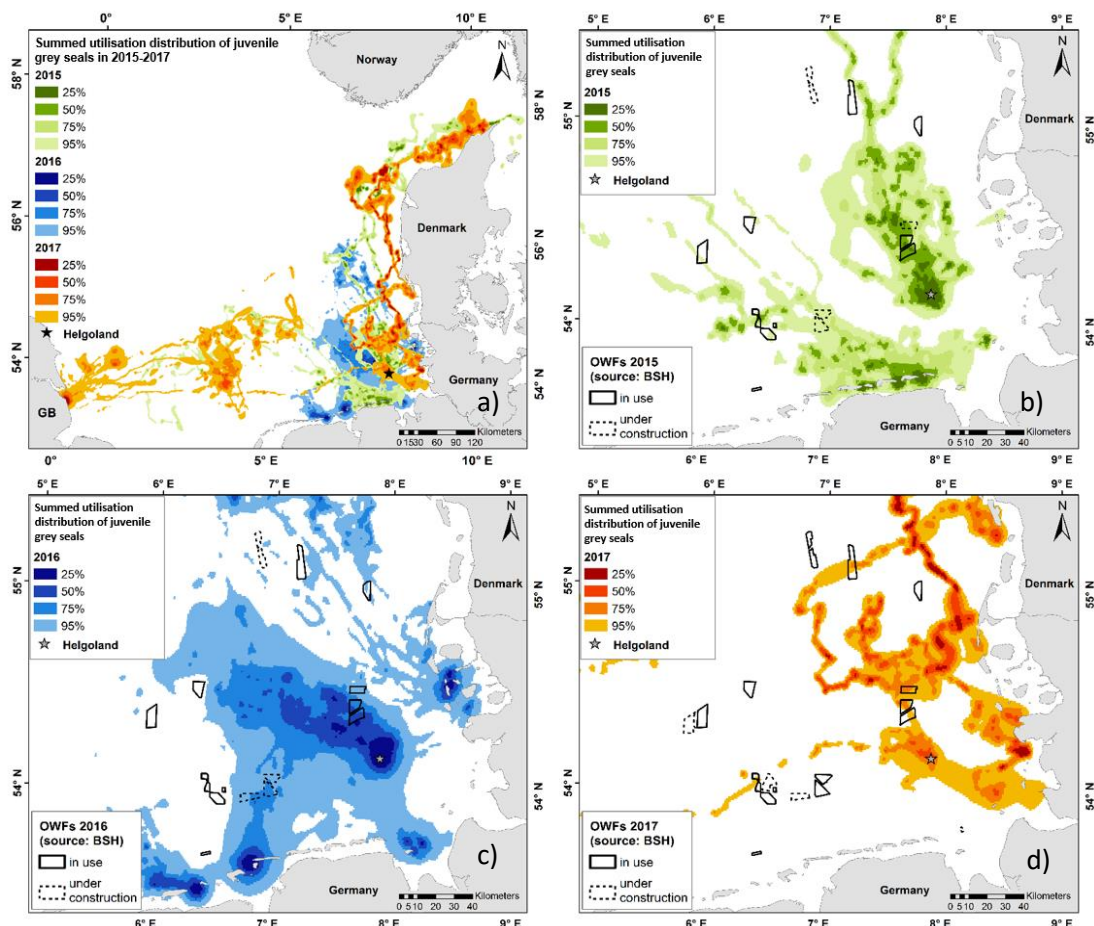


Fig. 4: Utilisation distribution (UD) of juvenile grey seals summed per year. (a) UD in whole North Sea and all years together, (b-d) zoomed to German North Sea, UD per year with offshore wind farm areas. UD: darkest colour indicates 25% percentile, lightest colour indicates 95% percentile. OWF areas in use are outlined with solid lines and OWFs under construction by dashed lines.

Discussion

The results of this study provide the first detailed characterisation of the dispersal and behaviour of recently weaned grey seal pups and their spatial utilisation of the German North Sea (Bennett 2010, Carter et al. 2017). Our modelling approach revealed how the behaviour of seal pups adapted during their first weeks at sea.

Tracking revealed that grey seal pups from Helgoland dispersed long distances in their first weeks after weaning and moved widely throughout the southern North Sea. The mean trip duration for most individuals was longer than that reported for adult grey seals in the North Sea (McConnell et al. 1999), and the mean duration for all individuals was comparable to that for young of the year (YOY, 5-month-old) individuals in the north-west Atlantic (Breed et al. 2011). The trip distances and durations demonstrated by the YOY (Breed et al. 2011) and by recently weaned grey seals in the north-western North Sea (Carter et al. 2017) were also longer than those recorded for adults. This has been discussed in the context of foraging inexperience, intra- and interspecific competition and exploration of their marine environment (Breed et al. 2011, Carter et al. 2017). For eight pups tagged on Helgoland, the amount of the time spent foraging was slightly higher than the time spent in slow travelling/resting, while fast travelling only occurred for a small amount of time. These findings resembled the findings for grey seal YOY in Canadian waters, where the individuals also spent more time foraging than travelling (59% and 32% respectively, Breed et al. 2011). Compared with adults and sub-adults, the foraging ratio of the YOY was much lower, which was set in the context of presumably less-efficient foraging trips. However, the YOY described by Breed et al. (2011) were already 5 months old when tagged, while the individuals tagged in the current study were much younger and thus less experienced.

Grey seal pups from Helgoland showed very different individual movement patterns, with some remaining more local than others. Most of the pups departed from the area around Helgoland during the first weeks of the tagging period and several pups dispersed far along the mainland coasts and towards the UK. This indicates intense exploration of other haul-out and foraging areas, possibly leading to later settlement in these areas (Brasseur et al. 2015).

Dispersal and behaviour

Based on the modelling approach, we were able to analyse different aspects of the grey seal pups' habitat use and behaviour and to reveal changes occurring throughout the tagging period as the pups grew older. The model showed that the pups increased their distance from Helgoland during the first

weeks and also generally throughout the whole period covered by the modelling approach. This pattern was especially evident for slow travelling and foraging behaviours.

Furthermore, the increasing frequency of foraging behaviour until week seven indicated that the pups gradually developed and applied this behaviour, and thus developed the ability to use their environment increasingly for foraging during these weeks after weaning. Our model also revealed that the pups increased their fast travelling behaviour with increasing age, again underlining their growing explorative behaviour with increasing age, but probably also indicating their ability to swim further and faster as they grow. This reflects the general transition from naïve to more experienced pups, which gradually increase their foraging effort and range to account for their increasing energy demands for survival and growth (Bennett et al. 2007). While exploring their habitat, the pups stayed within 200 km of the coast and successively used areas with deeper water. The diving ability of grey seal pups (i.e. dive depth and duration) has been shown to increase during the first months at sea (Noren et al. 2005, Bennett et al. 2010, Carter et al. 2017), and it can be expected that they might explore unknown and deeper areas as they grow older. Carter et al. (2017) showed that recently weaned grey seal pups born in colonies along the north-eastern coast of the UK stayed in areas of 55–80 m water depth during the first 40 days at sea, and that during this time, their dive depth increased from approximately 15 m at the start to 50 m at day 40.

The increase in distance to Helgoland could additionally be related to a change in habitat preference over time. Areas increasingly used were located either north of Helgoland, along the Danish North Sea coast, or to the south-west and west of Helgoland. Some of these areas were quite distant from the shore and thus deeper, and it is possible that the pups were able to increasingly use these marine areas as soon as they were able to dive deeper. In winter, prey density is higher in marine areas than in coastal waters, given that some fish species migrate towards deeper (warmer) waters (Woodhead 1964, de Veen 1978). This is also assumed to be potential reason for the increased foraging activity of harbour seals (Aarts et al. 2016) and grey seal YOY (Breed et al. 2011) in offshore waters during winter, as also shown for adult grey seals in the north-west Atlantic (Harvey et al. 2012). Furthermore, the preferences of juvenile and adult grey seals for shallow waters decreased during winter in the north-west Atlantic (Harvey et al. 2008). It is therefore likely that the pups encountered high prey densities in areas further offshore, which they were able to explore as soon as their diving ability increased.

Our findings underline that the pups used areas more distant from their colony of birth as they grew older. They explored their habitat, probably searched for profitable foraging areas and dispersed throughout the southern North Sea. They would be expected to become more experienced and successful foragers after the first weeks (Bennett et al. 2010, Carter et al. 2017), and to thus increasingly exploit the foraging areas that they discovered in the meantime. Depending on their

learning curve in the first weeks, but by 36 days after weaning at the latest, grey seal pups need to capture prey to replenish their protein reserves (Bennett et al. 2007) to survive and grow. This was reflected by the increasing foraging effort during the first few weeks, followed by a decrease as their foraging tactics presumably became more efficient.

Competition

Inter- and intra-specific competition could additionally influence the pups' preference for different habitats during different stages of their development. Adult grey seals in the north-west Atlantic used more coastal areas than juveniles (Harvey et al. 2008; Breed et al. 2011), while YOY were displaced from foraging habitats near the colony (Breed et al. 2013), and spatial segregation according to sex was demonstrated for both adult grey seals (Breed et al. 2006, 2009, Harvey et al. 2008) and for pups during their first weeks at sea (Carter et al. 2017). Weaned grey seal pups from the north-western North Sea, which includes many grey and harbour seal colonies (Jones et al. 2015), showed wide dispersal (Carter et al. 2017). Strong intra- and interspecific competition can affect pup behaviour in such areas (Breed et al. 2013), as discussed as a possible reason for the different behaviours of pups in the North Sea and Celtic Sea (Carter et al. 2017). However, our current findings showed that pups born in an area with less intraspecific competition also dispersed far from their breeding grounds and repeatedly explored areas with lower seal densities (i.e. the Danish North Sea coast, Brasseur et al. 2017a, 2018a). A recent study showed that adult and sub-adult grey seals tagged in the Netherlands never approached the North-Frisian coast of Germany and Denmark (Brasseur et al. 2017), which was frequently used by the pups tagged on Helgoland. Both the German and the whole Wadden Sea grey seal populations are small compared with the UK population (Lonergan et al. 2011, Brasseur et al. 2018a), suggesting that intraspecific competition is likely to be much lower than in UK waters. Nevertheless, the German harbour seal population is relatively large (16,145 individuals, 26,873 individuals in the entire Wadden Sea area; Galatius et al. 2017), and the behaviour of grey seal pups in the south-eastern North Sea may thus also be influenced by interspecific competition (Brasseur et al. 2018).

Behavioural classification

Slow travelling/resting and foraging behaviours showed similar dependencies on the distance to Helgoland, possibly due to different aspects of seal behaviour, or to the analytical methods applied.

Differentiation between resting and foraging behaviours based on movement data alone is known to be difficult because seals often rest between foraging bouts, and both behaviours occur on a small

spatial scale and at potentially slow speeds (McClintock et al. 2012, Ramasco et al. 2014, 2015, Russell et al. 2015). The EMbC approach aims to differentiate between the behavioural states using a robust clustering algorithm that minimises the prior assumptions and allocates the different states based on speed and turning angle (Garriga et al. 2016). Applied to our dataset, positions with small turning angles and low speed were grouped as one category, which we interpreted as slow travelling/resting behaviour. The characteristics of this behavioural class resembled the findings for resting at sea behaviour in other phocids (Ramasco et al. 2014, 2015). Given that the pups undergo behavioural changes over time (Carter et al. 2017, Bennett et al. 2010), prior information for adult behavioural parameters, such as values for speed and turning angle, cannot easily be applied to identify the behavioural states. However, EMbC analysis is not based on such prior information and thus provides an objective approach for classifying the pups' behavioural states. It is possible that not all foraging attempts during the first weeks were detected as such by the EMbC, because they may have been less distinguishable from other behaviours compared with fully developed foraging behaviour. However, distinct foraging behaviour would very likely be detected by the EMbC. Nevertheless, the analysis could be strengthened further by including information on diving behaviour to calibrate and improve the behavioural classification (Ramasco et al. 2015).

Interaction with OWFs

To the best of our knowledge, the current results provide some of the first evidence for the overlap in areas used by grey seals and OWFs worldwide (Aarts et al. 2017, Brasseur et al. 2018b). Our results indicated no obvious behavioural responses to the OWFs, but demonstrated that individual seals behaved differently in their vicinity.

Pile-driving activities during the construction of OWFs might displace seals, mask communication signals, or cause temporary or permanent hearing loss (Kastak et al. 2008, Kastelein et al. 2012, Hastie et al. 2015, Russell et al. 2016). Unfortunately, we do not know if the individuals in the current study passed through the OWFs during ongoing pile-driving activities, but our data demonstrated that seals did use or pass through OWF areas during construction. In a study conducted in The Wash in south-east England, harbour seals did not avoid OWFs during the construction phase as a whole, but their abundance was significantly reduced at up to 25 km distance during piling activity (Russell et al. 2016).

Grey seal pups might be attracted to OWF areas during their operation due to their 'artificial reef' effect (Petersen & Malm, 2006). The diversity and abundance of fish in these areas are increased (Stenberg et al. 2015), making them potentially valuable feeding grounds, as shown for harbour seals (Russell et al. 2014).

Given that most of the 11 individuals tracked in the current study used OWF areas either intensively and repeatedly, or entered them at least for short periods during different foraging trips, we speculated that a large proportion of the entire population was likely to interact with OWF areas in some way, especially if individual pups identified them as a valuable feeding habitat while developing their foraging tactics. However, whether foraging behaviour focussing on anthropogenic structures influences an individual's ability to forage in other areas or has other effects on its biological fitness remains unknown, but all the individuals tracked in the current study notably also foraged outside OWFs. This information on the interactions between grey seal pups and these newly introduced anthropogenic structures is of great interest. It provides an indication of their response to the presence of OWFs and shows that they use OWFs, and may consider them as a valuable feeding habitat, even during their first weeks at sea.

Conclusions

This study investigated the behaviour of grey seals during the potentially most vulnerable phase of their life cycle, when naïve individuals need to develop successful foraging strategies to cover their high energy demands. Knowledge of habitat preferences, behaviour and their changes in relation to age is crucial to our understanding of the important processes driving population dynamics, and to predict the populations' ability to cope with environmental changes and anthropogenic stressors. Our results showed that grey seal pups use large areas of the southern North Sea and disperse as far as 300 km from their colony of birth within 3 weeks. They explore different North Sea regions and colonies closely, leading to possible recruitment into breeding populations other than their colony of birth. The increase in foraging frequency with time suggests that the pups progressively use their environment for foraging during the first weeks after tagging, and reflects the transition from naïve to more experienced pups. They thus encounter various environmental conditions and face a multitude of anthropogenic activities, even during their first weeks and months at sea. Our findings underline the complexity of early development in grey seal pups and highlight the need to consider their habitat requirements during the marine spatial planning process, and to include them when investigating anthropogenic impacts. This study contributes to our knowledge of the spatial utilisation of the German North Sea by an increasingly important top predator, and thus provides important information for a broad audience, including researchers and those involved in management and decision-making in politics and industry.

Acknowledgements

We especially thank the team of the Seal Centre Friedrichskoog, Michael Janßen, Katharina Tilly, Rebecca Störmer, and the team of 'Verein Jordsand e.V.', the Alfred-Wegener-Institute Helgoland, the Institute of Avian Research 'Vogelwarte Helgoland', and the team of the Helgoland air field for supporting our work in the field. Parts of the analysis were conducted in the framework of the MONTRACK project (project no.: Z 1.2-532 02/AWZ/2017/2).

Supplement 1

Attachment method



Fig. S1: Tags were attached to a rectangular neoprene base with seven €2-sized small feet at its edges. Only these feet were glued to the fur to break up the glue patch. The tags would thus fall off during the next moult, if not before.

Supplement 2

*Details of tagged individuals and transmitting times of tags***Table S1:** Details of juvenile grey seals tagged between 2015 and 2017.

Year	Tag type	Individual	Start	End	Weeks	Months	Median no of pos. per day	Min. no of pos. per day	Max. no of pos. per day	Sex	Reduced length (cm)	Weight (kg)
2015	SPLASH	HG 1	16.01.2015	03.03.2015	6.6	1.6	29	2	58	f	71	39
		HG 2	16.01.2015	03.06.2015	19.7	4.9	15	1	33	m	83	57
		HG 3	16.01.2015	07.03.2015	7.1	1.8	15	0	25	m	65	41
2016	SPLASH	HG 4	05.02.2016	29.08.2016	29.4	7.4	12	0	32	f	61	35
		HG 5	05.02.2016	29.10.2016	38.1	9.5	5	0	28	m	62	32
		HG 6	05.02.2016	23.08.2016	28.6	7.1	17	1	34	f	65	33
		HG 7	05.02.2016	19.09.2016	32.4	8.1	9	0	26	m	68	34
2017	SPOT	HG 8	18.01.2017	29.03.2017	10.0	2.5	18	0	33	f	64	31
		HG 9	18.01.2017	11.02.2017	3.4	0.9	2	0	7	f	na	33
		HG 11	18.01.2017	17.02.2017	4.3	1.1	17	1	26	m	75	39
		HG 12	18.01.2017	16.09.2017	34.4	8.6	15	0	30	m	60	30

Reduced length: front flipper axle to tail end.

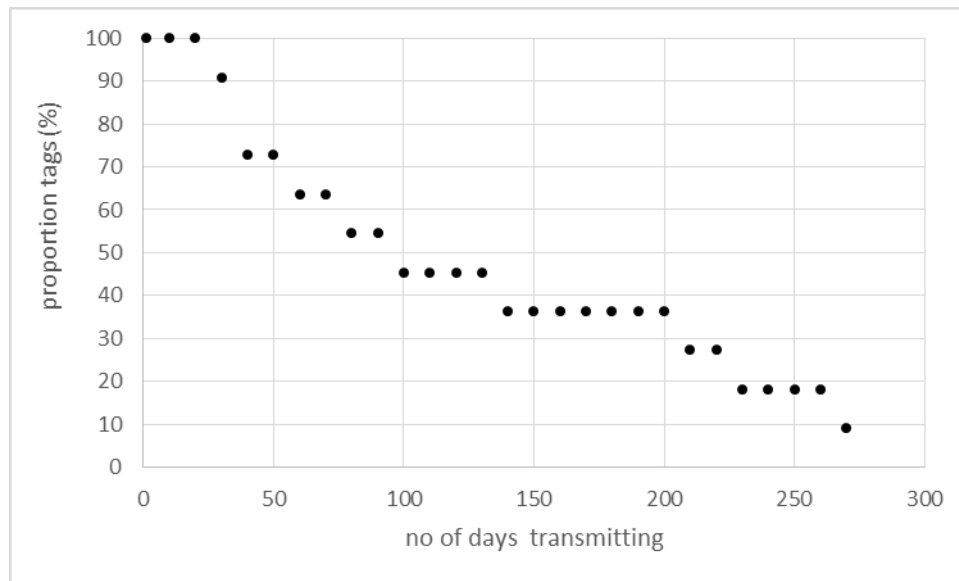


Fig. S2: Proportion of tags transmitting with increasing number of deployment days.

Supplement 3

Point process modelling

This provides a short summary of the key extensions/modifications of the applied approach compared with the spatio-temporal PPMs presented by Johnson et al. (2013):

1. Autocorrelation: Johnson et al. (2013) considered spatio-temporal autocorrelation using parametric terms. However, on one hand, data may also be correlated with respect to the turning angle (due to directed movement): smaller time steps between subsequent observations (relative to the velocity of the animal) would be associated with smaller turning angles on average. On the other hand, temporal and spatial distances to the previous tracking point (d_t respectively d_s) as well as the turning angle (α) may correlate in a complex manner. We therefore included these autocorrelations and their possible interactions as a tensor product smooth $te(d_t, d_s, \alpha)$ within the framework of generalised additive modelling (as described in Wood 2006).
2. Mixed modelling: The assumption of independence is often violated, especially if the tracking data originate from different animal trips and/or individuals (Hurlbert 1984), and even if autocorrelation is considered correctly. Here, GLMMs probably provide the most natural and powerful approach to account for nested data, provided that the correlation structures are specified correctly (Fieberg et al. 2010). Additionally, mixed models use maximum likelihood estimation, which is the key to linking the mixed regression technique to the PPM approach

(see below). Furthermore, this approach is also appropriate for drawing population-level inferences (Hooten et al. 2017), which is an important issue when several individuals have been tracked. We therefore extended the models of Johnson et al. (2013) by allowing for the consideration of $seal_{id}$ and $trip_{id}$ as random factors, thus finally using generalised additive mixed models (GAMMs).

3. Integration of state-space modelling: Although recent spatio-temporal PPM approaches do not assume regular sampling intervals per se (Johnson et al. 2013), it may be advantageous to regularise or densify the tracking data in some situations. Important habitats can be missed if the tracking data are irregular or sparse, leading to inflated standard errors of regression coefficients, making it difficult to obtain significant results. We addressed this problem by regularising the data prior to the PPM analysis using interpolation based on ‘state-space models’ (Jonsen et al. 2005, 2013, Patterson et al. 2008). These models explicitly distinguish between true stochasticity in the movement process (‘process error’) and spatial bias (‘location error’), and thus incorporate the latter while estimating the true path. This has the additional advantage that the degree of inherent imprecision/bias in the tracking data (especially in Argos-based tracking data) can be reduced (Patterson et al. 2008, Frair et al. 2010, Hebblewhite & Haydon 2010).
4. Quadrature-weights: In PPMs, the aim of the dummy points is to efficiently approximate an integral term of the model-likelihood, which is realized based on the use of appropriate quadrature weights. Based on extensive simulation studies, we tested different types of quadrature weights provided by the R-package *mvQuad* (Weiser 2016) with respect to type I and type II error rates (Mercker 2019). Here, the best results were obtained by open Newton-Cote formulas of degree 2, which have been used throughout this study.
5. Over- and underdispersion: In principle, PPM data can show over- or underdispersion. We tested for both using the function *dispersiontest()* from the R-package *AER* (Kleiber & Zeileis 2008). Based on the results of this test, we inflated or deflated the corresponding standard errors accordingly and re-calculated the p-values. Finally, we used extensive simulation studies to test that the approach led to reasonable type I and type II error rates for various types of animal tracking data (Mercker 2019).

Supplement 4***Behavioural classification***

We classified the behavioural states using expectation-maximization binary clustering (EMbC; Garriga et al. 2016), a robust, non-supervised, multivariate clustering algorithm that minimises prior assumptions and favours the semantic interpretation of the final clustering by splitting the input features by low and high values of speed and turning angle (Garriga et al. 2016). It offers a new approach for the classification of behavioural states, and has already been applied successfully in several studies (Mendez et al. 2017, Jones et al. 2018). Resting behaviour in pinnipeds was shown to be difficult to identify (McClintock et al., 2013) because it is often associated to foraging behaviour in both time and space (e.g. resting between foraging bouts; Ramasco et al. 2014, 2015). However, resting at sea was shown to represent a large part of the at-sea behaviour (Ramasco et al. 2014, 2015, Russell et al. 2015) and we therefore aimed to include it in our analysis. The EMbC approach differs from other state-space approaches for behavioural classification (Jonsen et al. 2005) because it classifies behavioural states on a fine scale, and the classification does not depend on temporal or contextual correlations of behavioural states (Garriga et al., 2016). It thus offers a valuable alternative, especially when identifying behavioural changes on a fine spatial or temporal scale. The algorithm assigns each location to one of four clusters (Table S2): high velocity/low turn (HL), high velocity/high turn (HH), low velocity/low turn (LL), and low velocity/high turn (LH). HL was identified as fast directional movement and was interpreted as ‘fast travelling’ behaviour, the two states with high turning angles (LH, HH) were merged and interpreted as ‘foraging’ and LL was identified as slow directional movement and was interpreted as ‘slow travelling/resting’ behaviour. EMbC analysis was conducted using the R package EMbC v2.0.1 (Garriga et al. 2016), and a smoother function was applied to take account of temporal associations of behavioural states. Although we filtered the dataset before the state-space interpolation, 2% of the interpolated data included positions with ≥ 3 m/s velocity, which were assumed to be beyond the realistic swimming speed of pinnipeds (Costa et al. 2010). We could exclude data with a velocity of > 6 m/s; however positions with speeds of 3–6 m/s (1.7 % of the dataset) were included in the analysis to allow stable clustering during the EMbC analysis. However, given that uncertainty of speed and turning values was considered during the clustering process (Garriga et al. 2016), 1.7 % represents only a small fraction of the dataset, and we only compared the behavioural classes relative to each other in the statistical modelling process, we believe that the results were negligibly affected by the data points with unrealistic swim speeds.

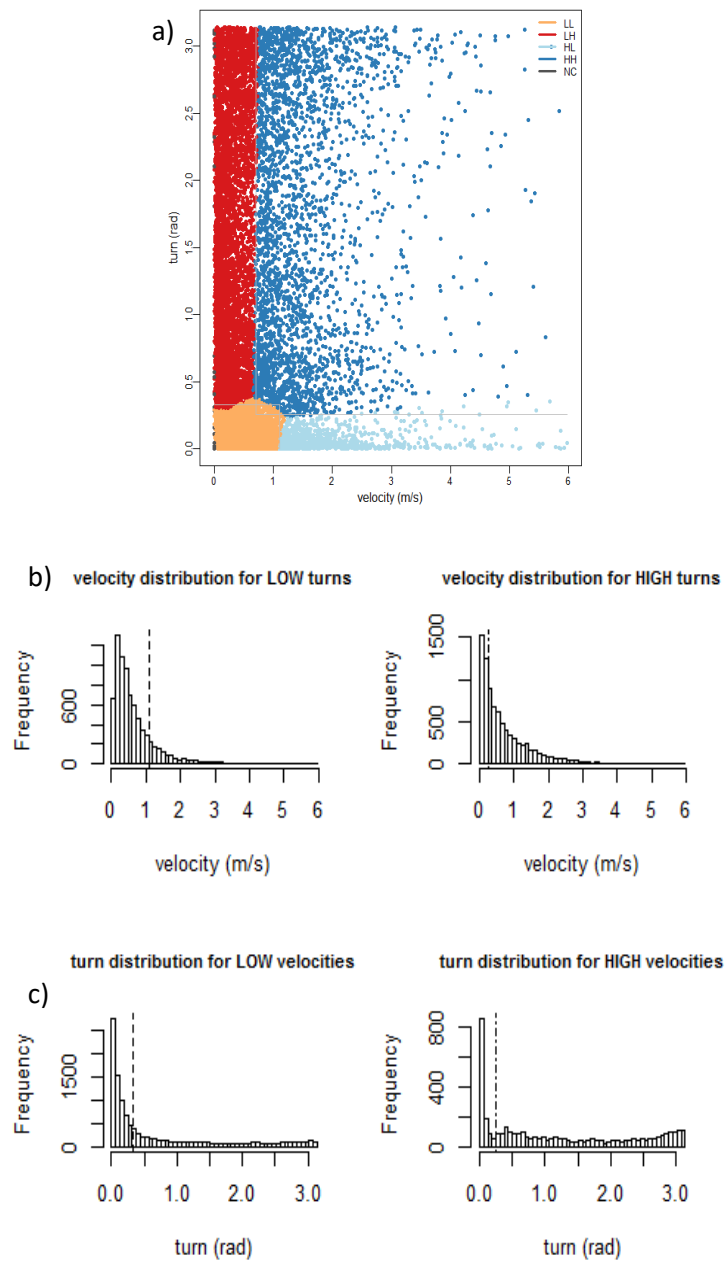
Results:

Fig. S3: (a) Velocity/turn scatter plot (clustering colour code: LL: orange, LH: red, HL: cyan, HH: blue); (b) velocity (m/s) and (c) turning angle (rad) frequency distributions. The distributions for low/high values are shown separately. Black dashed and dot-dashed lines show the delimiters.

Table S2: Minimum and maximum speeds and turning angles for each behavioural state classification using EMbC. Two states with turning angles > 0.32 rad were merged into one behavioural state ‘foraging’.

Behaviour	Speed min. (m/s)	Speed max. (m/s)	Turn min. (rad)	Turn max. (rad)
slow travelling/resting	0	1.11	0	0.33
foraging	0	5.97	0.33	3.14
fast travelling	1.58	5.97	0	0.45

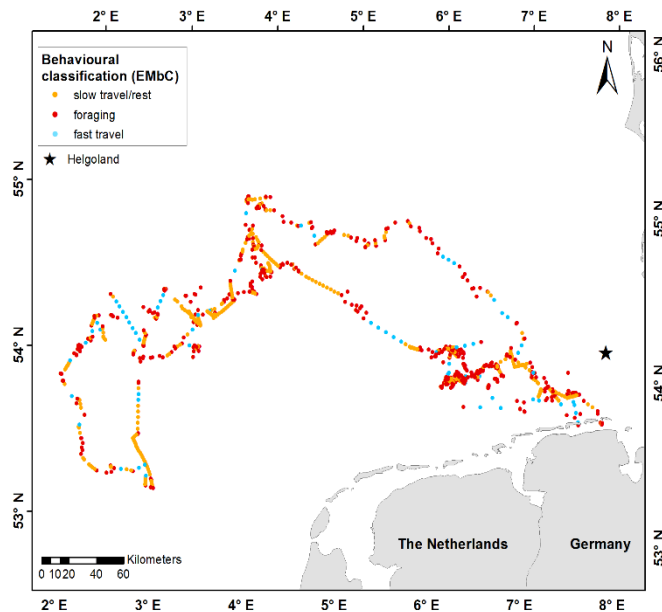


Fig. S4: Foraging trajectory with behavioural labelling: yellow = slow travelling/resting, red= foraging, blue= fast travelling.

Discussion

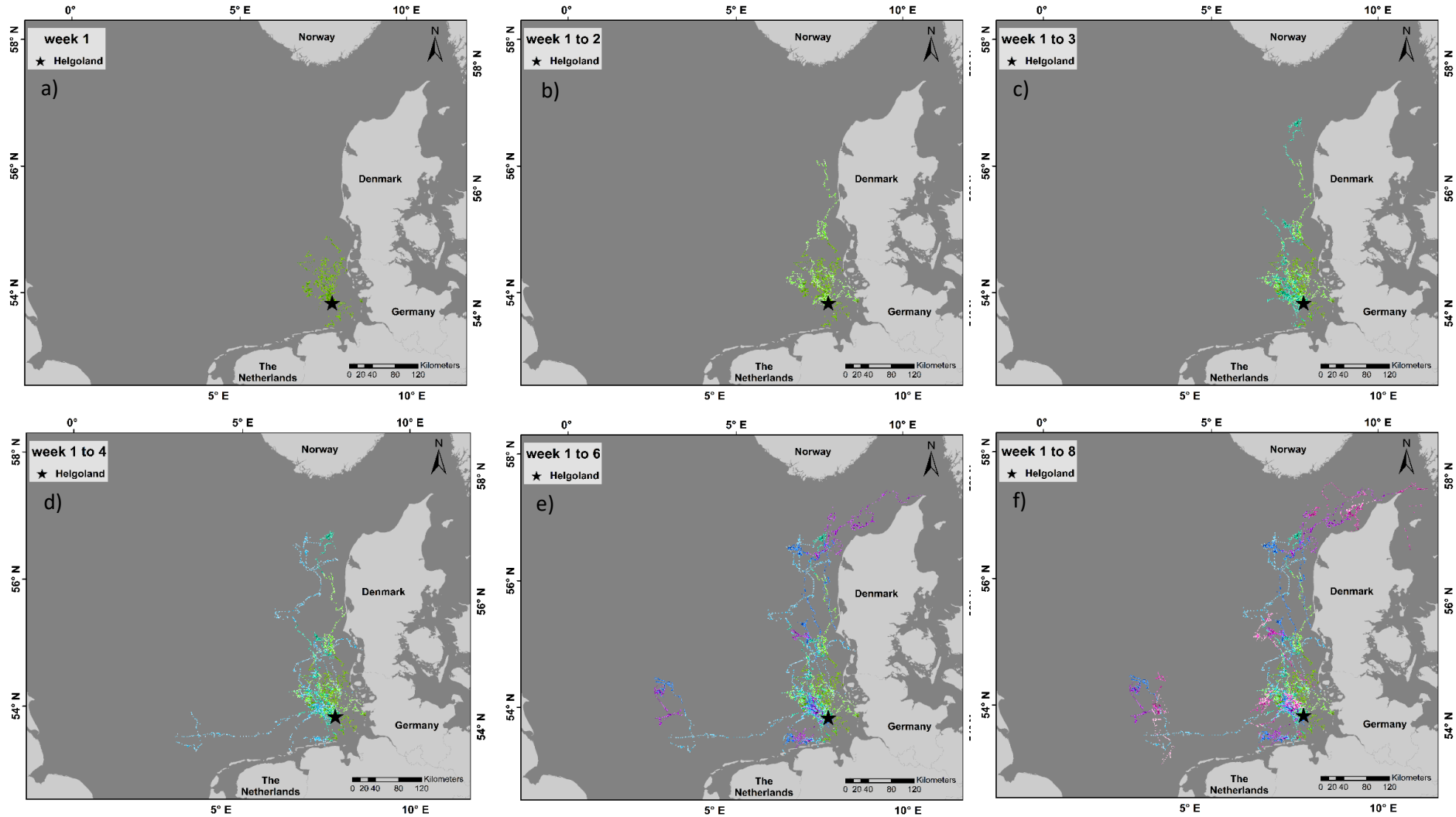
In terms of the seal pups’ behaviour in relation to their distance from Helgoland, slow travelling/resting and foraging behaviour both depended similarly on this variable. This could be due to different aspects in their behaviour or to the analytical methods applied.

It is known to be difficult to differentiate between resting and foraging behaviours based on movement data alone because seals often rest between foraging bouts, and both behaviours occur on a small spatial scale and at potentially slow speeds (McClintock et al. 2012, Ramasco et al. 2014, 2015, Russell et al. 2015). The EMbC approach aims to differentiate between these behavioural states using a robust clustering algorithm that minimises prior assumptions and allocates the different states based on speed and turning angle (Garriga et al. 2016). Applied to our dataset, positions with small turning angles and low speed were grouped as one category, which we interpreted as slow travelling/resting

behaviour (Table S2). The characteristics of this behavioural class resemble the findings for resting at sea behaviour in other phocids (Ramasco et al. 2014, 2015). Given that the pups undergo behavioural changes over time (Carter et al. 2017, Bennett et al. 2010), prior information for adult behavioural parameters, such as values for speed and turning angle, cannot easily be applied to identify the behavioural states. However, EMbC analysis is not based on such prior information and thus provides an objective approach for classifying the pups' behavioural states. It is possible that not all foraging attempts during the first weeks were detected as such by the EMbC, because they may have been less distinguishable from other behaviours compared with fully developed foraging behaviour. However, distinct foraging behaviour would very likely be detected by the EMbC. However, it is still possible that the behavioural classes detected by the EMbC did not fully represent the behavioural development of the pups. For example, the slow travelling/resting category included positions that probably represented resting behaviour, but also included positions representing slow travelling behaviour. This has to be considered when interpreting our results. The analysis could thus be strengthened further by including information on diving behaviour to calibrate and improve the behavioural classification (Ramasco et al. 2015).

Supplement 5

Weekly utilisation distribution of grey seal pups



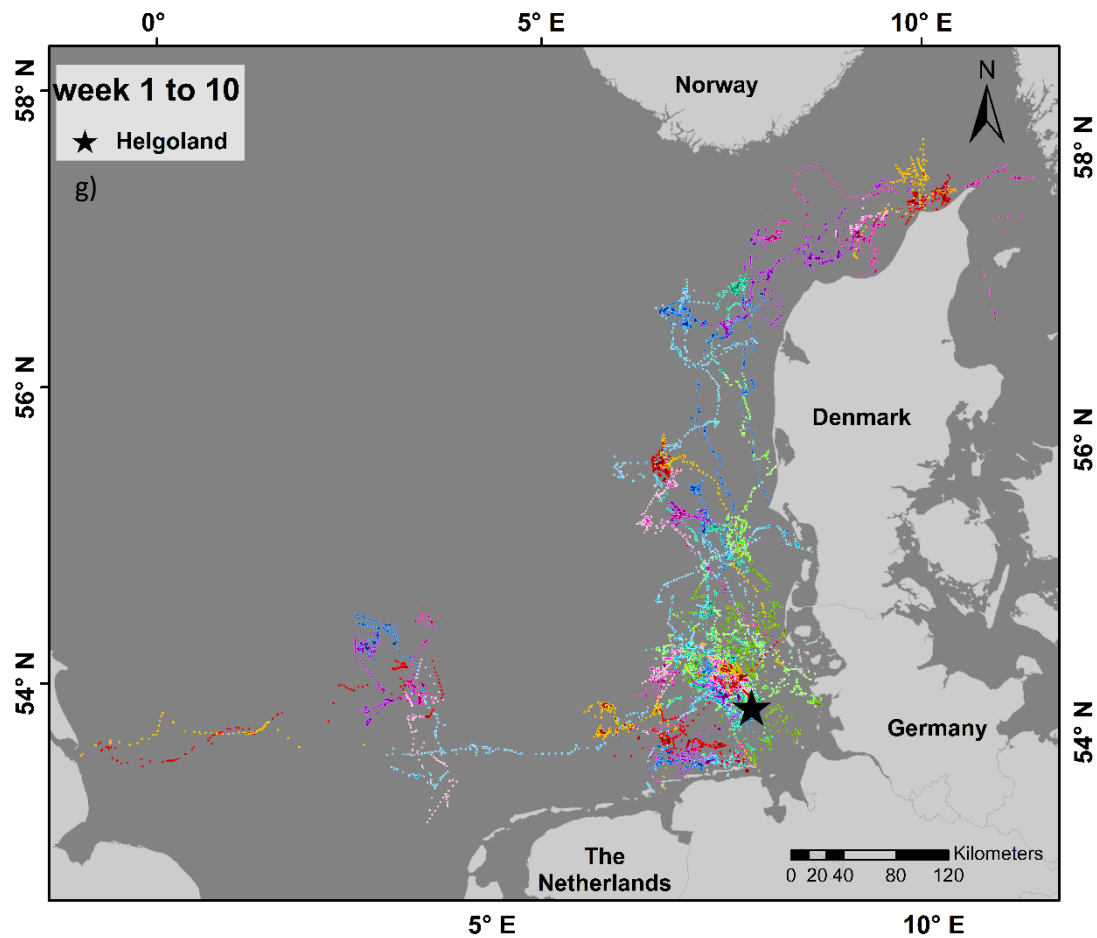


Fig. S5: Weekly utilization distribution (UD) of grey seal pups, visualised as percentiles: dark colours = 25% percentile, light colours = 95% percentile. Weeks 1–10 are shown: a) week 1, b) week 1–2, c), week 1–3, d) week 1–4, e) week 1–6, f) week 1–8, g) week 1–10. Colour scale: week 1 = dark green, week 2 = light green, week 3 = turquoise, week 4 = light blue, week 5 = blue, week 6 = violet, week 7 = pink, week 8 = pink, week 9 = red, week 10 = orange.

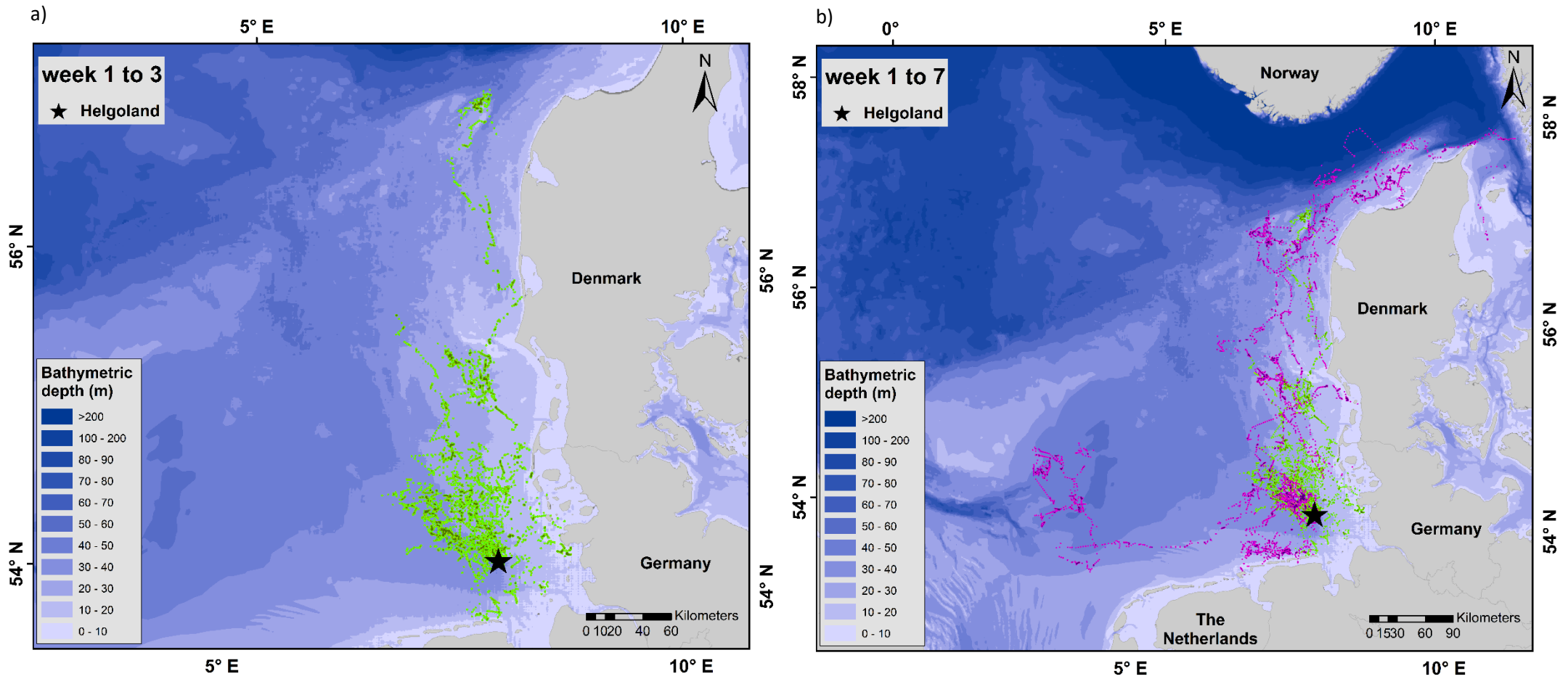


Fig. S6: Weekly utilization distribution (UD) of grey seal pups, visualised as percentiles: dark colours = 25% percentile, light colours = 95% percentile. a) Week 1–3 green and b) week 1–3 green and week 4–7 seven violet. Bathymetric depth in m is shown in blue.

GENERAL DISCUSSION

GENERAL DISCUSSION

Short summary

This thesis substantially adds to the current knowledge on the distribution and habitat use, movements and behaviour of several top predator species studied in the southern North Sea and provides detailed knowledge on their reactions towards offshore wind farms (OWF) constructed in this area. Different top predator species were studied, some of them during different stages of their annual life cycle, e.g. with regards to breeding, migrating, and moulting. Thus a comprehensive view on the ecology of several top predators and their vulnerability to OWFs is provided. It is shown that loon density and distribution was strongly affected by the OWFs located close to one of their most important resting sites during spring migration (Chapter I). Strong effects of the OWFs north of Helgoland were furthermore detected for spring (common guillemots) and for the breeding season (common guillemots, black-legged kittiwake and northern gannets, Chapter II - IV). Very far dispersal of grey seal pups during their first weeks after weaning as well as their individual spatial overlap with OWFs under construction and in operation was revealed.

Ecological aspects not highlighted in the chapters

In the frame of the thesis' subject many questions needed further investigation. However, we urgently have to increase our knowledge on possible effects of offshore wind farms on the marine wildlife to inform researchers and those involved in management and decision-making in politics and industry. To contribute to our current knowledge in this research field and as not all important aspects could be covered, this thesis mainly focused on the possible effects of OWFs on the different species. However, many aspects of their ecology were investigated to enable profound interpretation of the effects found. Some of the aspects fill relevant knowledge gaps on the species ecology but were not discussed in the chapters and thus will be discussed in the following.

An extensive, long-term and large scale dataset collected by means of visual and digital surveys before construction of the OWFs was used as basis for the OWF effect analysis on guillemots and kittiwakes and provided valuable knowledge on their use of the study area. In spring high guillemot densities were found in the west to north-west of Helgoland. During the breeding-season they concentrated more in the area close to the colony but also used some areas in the north-west and north-east of Helgoland. In spring high kittiwake densities were found in the north-west and north of Helgoland, during the breeding-season they concentrated closer to the colony. High densities were found in the area of the post-glacial Elbe river valley in spring (guillemots and kittiwakes) as well as in the breeding

season (kittiwakes). This area is characterized by a comparatively steep increase of the water depth which together with south- or north-easterly winds leads to the formation of an upwelling front (Krause 1986, Becker et al. 1992). Fronts are known to attract marine top predators (Skov & Prins 2001, Markones et al. 2008, Bost et al. 2009, Sabarros et al. 2013, Scales et al. 2014a, b, Cox et al. 2018) as they provide valuable foraging conditions for their prey species through accumulation of plankton (Franks 1992, Yoder et al. 1994, Genin et al. 2005). For kittiwakes a strong influence of frontal structures on their distribution in the southern North Sea during summer was already described (Markones et al. 2007, 2008).

Telemetry was applied on breeding seabirds and grey seal pups to study their movements, behaviour, and habitat use. For the first time in German waters telemetry was applied on adult guillemots and weaned grey seal pups and the sample size of gannets was substantially increased. The telemetry devices provided detailed information on the individuals' movements and behaviour during several weeks (seabirds) and up to several months (grey seals).

Fundamental knowledge on the gannets foraging behaviour during the breeding season in the southern North Sea was gained during two study years (Chapter III). The mean duration, mean total distance, and mean maximum distance of the gannets foraging trips were slightly smaller, but still comparable to a similar sized colony located in the Celtic Sea (Great Saltee Island, 2000 breeding pairs). In the Celtic Sea gannets travelled shorter distances and spend less time on a foraging trip than their conspecifics of a larger colony in the North Sea (Bass Rock, >40,000 breeding pairs, Hamer et al. 2001, 2006). Several studies showed that foraging ranges and trip duration of gannets increase with colony size (Lewis et al. 2001, Wakefield et al. 2013) which was set in context with density-dependent prey disturbance (Lewis et al. 2001). Although also depending on the general availability of prey in waters surrounding the colony, it can thus be assumed that in the small colony on Helgoland competition between individuals was relatively low and birds did not have to travel as far for finding valuable foraging areas. As part of the same study flight heights of gannets were collected by means of GPS-tracking for the first time in the southern North Sea. Significantly higher altitudes during foraging compared to travelling were found which is in line with findings for other areas (Cleasby et al. 2015). It is suggested that gannets increase their flight height when foraging to increase their range of view (Garthe et al. 2014). However, flight heights during foraging were generally lower than altitudes collected for this behaviour in other sea areas (Cleasby et al. 2015, Garthe et al. 2014). Additionally, dive depths of gannets tagged on Helgoland in 2015 were shallow (Garthe et al. 2017b) compared with previous studies in the North Sea (Lewis et al. 2002, Grémillet et al. 2006) and the north-west Atlantic (Garthe et al. 2000, 2007). It could thus be that gannets in the southern North Sea used lower altitudes while foraging than found for other sea areas as they did not have to locate prey from high altitudes or dive as deep for catching prey (Garthe et al. 2014).

Common guillemots were equipped with GPS-devices for the first time in German waters which provided novel insights into their individual movements and behaviour during the breeding season in the southern North Sea (Chapter IV). Guillemots mean foraging trip duration, mean total distance, and mean maximum distance were smaller than the mean values based on several studies provided by Thaxter et al. (2012, mean maximum distance = 37.8 km). As already stated afore this could be interpreted as indication of good foraging conditions and potentially lower density-dependent competition (Lewis et al. 2001, Ashmole 1963) than in other colonies.

Telemetry of gannets, guillemots and grey seals furthermore revealed an intense use of the area west and north-west of Helgoland (chapter III, IV & V). Many foraging areas were located close to the Elbe river valley as was also shown for kittiwakes and guillemots based on the survey methodology (chapter II). This suggests that the identified area is of special importance for several top predator species. A comprehensive investigation based on telemetry and oceanographic data thus would improve our understanding of processes influencing the top predators' choice of foraging areas in the southern North Sea.

Information on the preference for specific areas as well as the foraging trip characteristics and behaviour strongly enhances our knowledge on these top predator species in the southern North Sea and can be included in future studies on anthropogenic impacts (e.g. Cleasby et al 2015, Thaxter et al. 2015), in environmental monitoring (e.g. Hamer et al. 2006; Burger & Shaffer 2008) or in conservation and management implications of the respective species (Bograd et al. 2010, Camphuysen et al. 2012, Lascelles et al. 2012, Ronconi et al. 2012).

OWF effects –Relevance for other sea areas and possible cumulative effects

As OWF effects revealed in this thesis have strong implications for a broader audience, possible effects expected for other areas and potentially cumulative impacts in combination with other anthropogenic activities will be discussed in the following. However, while exploring these topics it always needs to be considered that caution is needed when transferring findings of one study area to another. Furthermore, the complexity of cumulative effects of several anthropogenic stressors needs careful consideration.

With regards to anthropogenic activities including fishing, transport, oil and gas drilling, and gravel extraction, the North Sea is one of the most intensively used sea areas worldwide (Halpern et al. 2008, Emeis et al. 2015). With the introduction of numerous offshore wind farms, the area occupied by human uses increased rapidly and substantially during the past decade (BSH 2019). Hence a considerable part of formerly undisturbed habitat is now additionally altered by human uses. Top

predators are thus prone to experience interference with different anthropogenic threats at various locations of their distribution range. Cumulative effects of one anthropogenic stressor present at different locations as well as cumulative effects of different stressors are difficult to quantify (Halpern et al. 2009, Maxwell et al. 2013, Foley et al. 2016). Especially for areas which are both, of special importance for top predators and characterised by a high density of (different) human activities, we have to increase our understanding of possible cumulative effects on the marine environment.

The sea area north of the East-Frisian islands in the southern North Sea can serve as an example: Here, high guillemot densities are found outside the breeding season (Mendel et al. 2008, Van Bemmelen et al. 2015, Guse et al. 2018) and also a hot spot of loons was present until 2009 (Mendel 2012, Garthe et al. 2018). However, in this part of the German North Sea nine wind farms are currently in operation, one is under construction and four more are approved (BSH 2019). Undisturbed habitat between the wind farms most probably is subject to intense OWF supply and maintaining vessel traffic as was observed i.e. at the Helgoland-Cluster (Chapter I). Moreover, an intensively used shipping lane is located south of the wind farm areas (Mendel et al. 2012, BSH 2019) which further reduces the natural habitat available in that area (Mendel et al. 2012).

If similar disturbance effects as the ones found in this thesis (Chapter II) apply to the wintering population of guillemots in the southern German North Sea this would result in a large part of the usual habitat being (partly) lost for guillemots already now and even more so in the future. Furthermore, this species, although not the most sensitive one (Fließbach et al. 2019), is sensitive to the disturbance by vessel traffic (Garthe et al. 2004, Mendel 2008, 2012) which further increases their anthropogenic induced stress level and reduces the habitat available in this area. It is unknown whether areas with similar foraging conditions are available which could compensate for the lost habitat. Furthermore, energy demand and mortality of auks is particularly high during the winter (Sonntag 2001, Gaston & Jones 1998, Gaston 2004, Fort et al. 2009) which raises further concern on their ability to cope with reduced foraging habitat.

Loons are one of the most sensitive seabird species to vessel traffic (Schwemmer et al. 2011, Fließbach et al. 2019) as well as OWF presence (Garthe et al. 2004, Furness et al. 2013, Dierschke et al. 2016, Chapter I). Before the OWF construction north of the East-Frisian islands they were thus already affected by the disturbance caused by the intensively used shipping lane (Schwemmer et al. 2011, Mendel 2012). After installation of the OWFs, the undisturbed habitat was even more reduced and both stressors simultaneously affected this especially sensitive group of species (Mendel 2012, Chapter I). Especially here a cumulative effect of both stressors can be assumed. As loons additionally to their high sensitivity to anthropogenic activities show high preference for nearshore and shallow sandy sea areas where frontal zones are located (Skov & Prins 2001, Skov et al. 2016), the availability of alternative valuable foraging grounds is limited. Although the exact reason for the decline is not

known, a recent study found that the formerly observed hot spot of loons in the southern German North Sea diminished during the years after installation of the OWFs (Garthe et al. 2018).

For grey seals it was predicted that noise emitted by shipping vessels can exceed levels known to induce temporary threshold shift (TTS, Jones et al. 2017). TTS is characterised as a temporary shift in hearing sensitivity where hearing recovers over a specified time (Southall et al. 2007). Vessel noise can furthermore mask important environmental sounds and communication signals from conspecifics (Southall et al. 2007, Bagočius 2015, Jones et al. 2017). To date little is known on the seals reaction towards and spatial overlap with shipping noise (Anderwald et al. 2013, Chen et al. 2016, Jones et al. 2017, Matthews 2017). Some studies report an avoidance of areas with intense shipping noise (Anderwald et al. 2013), abrupt behavioural changes when a vessel passes (Mikkelsen et al. 2019) or a change of duration and frequency of vocalisations (Matthews 2017). Furthermore, seasonal differences of sound exposure were detected for the Celtic Sea, with higher levels during winter when no oceanic fronts were present (Chen et al. 2016). Effects of anthropogenic noise might be of particular relevance for grey seal pups as they explore their habitat without parental guidance. Disruption of foraging behaviour could increase energetic costs and thus influence survival (Chen et al. 2016). Although this thesis did not find distinct negative reactions towards OWFs by grey seal pups, the potential cumulative effect of different anthropogenic stressors has to be considered (Jones et al. 2017) as also non-injurious effects can still accumulate to have population-level impacts (Williams et al. 2015). Especially when several operating OWFs and intense shipping activities are located in areas where grey seal pups frequently commute between haul out and foraging areas further offshore (i.e. the East Frisian coast, Chapter V & Peschko et al. unpublished data) cumulative effects need to be considered. Individuals, which might be attracted to the OWFs for foraging, could moreover experience intense vessel noise while staying inside the OWFs due to intense OWF supply and maintaining vessel traffic as was observed at the Helgoland-Cluster (Chapter I).

Along the coast of the UK, where much larger colonies of northern gannets are located than in German waters, the number of approved and operating OWFs increased drastically during the past years (4COffshore). Some of the consented OWF areas are located close (<50 km) to the world's largest gannet colony at Bass Rock in Scotland (75,000 breeding pairs; Murray, Harris & Wanless 2015) and will cover an area six times larger than the area covered by the OWFs north of Helgoland. Based on adults foraging ranges and flight heights during the breeding season predictions revealed that 1% of the individuals would be prone to collide with the turbines (Cleasby et al. 2015). These predictions were based on data collected before the OWF construction. This thesis, however, showed that although gannets breeding on Helgoland predominantly flew below the rotor blades, they used significantly higher flight heights inside the OWFs compared to outside (Chapter III). This suggests that the risk to collide with the turbines potentially is higher than data gained in areas without operating

OWFs would suppose. Furthermore, this thesis revealed that birds predominantly avoiding OWFs entered them more often in the second study year (second year of operating OWFs) than birds predominantly avoiding OWFs in the first study year. Although it is impossible to draw conclusions based on two years of data, this could indicate an increasing use of OWFs through time by birds predominantly avoiding OWFs. Habitat loss would likely be decreased but collision risk would increase as gannets, which have less experience inside the OWFs, would enter them more often. Additionally, these birds tended to use flight heights inside or close to the rotor blade zone which increased their vulnerability to collide even more. Transferring the findings of this thesis to the much larger colonies located in the UK thus indicates that an even larger part of the gannet colonies could be at risk of colliding. However for a more robust analysis more data on the flight heights of northern gannets needs to be collected. This thesis additionally showed that 90% of the tagged individuals mainly avoided the OWF area close to Helgoland. If 90% of the gannets breeding on Bass Rock would be displaced from important habitat close to their colony or have to increase their travel costs to reach appropriate foraging areas (Cleasby et al. 2015), this could have a strong impact on the world's largest breeding colony and thus a significant impact regarding the entire gannet population. Thus both OWF effects, displacement and collision, have the potential to adversely affect the wider gannet population and need careful consideration during future planning processes.

Kittiwakes and gannets are known to be attracted to fishing vessels as a potential source of prey (Garthe & Hüppop 1998, Votier et al. 2010, Bicknell et al. 2013, Bodey et al. 2014). In specific areas and times of fishing activities close to OWFs, fisheries could affect these species in combination with OWFs. A recent study showed that fishing occurs close to or in the corridors between several OWFs in the German North Sea (Schulze et al. 2018), which potentially also holds true for the waters of other European countries. Both species are vulnerable to collide with the turbines (Chapter III, Furness et al. 2013), gannets especially during foraging when they use higher altitudes (Chapter III, Cleasby et al. 2015). Hence, attraction to OWFs or areas very close to OWFs through fishing vessels could largely add to the risk of collision. A preliminary analysis for chapter II revealed, that during one survey day in spring very many kittiwake sightings occurred inside the OWF plus 3 km radius. AIS data (the same data as used in Chapter I) proved that fishing activities occurred in the 3 km radius and in the corridor between two OWFs during that day. It could thus be that the fishing activities have substantially increased the number of kittiwakes close to the OWFs. Within this thesis it was not possible to reveal the exact reason for the high number of sightings on that day. However, from Schulze et al. (2018) it is known that from 2016 on fishery took place in the surroundings of the OWFs north of Helgoland. It has to be noted here that this one survey day, which was excluded from the analysis in chapter II, underlines the need to study different anthropogenic activities cumulatively as they can strongly influence each other's effect on wildlife.

Future perspectives

This thesis answers many questions in the context of potential OWFs effects and regarding top predator ecology in the southern North Sea. However, several knowledge gaps still remain of which some will be discussed in the following.

Although part of this thesis already applied a large scale approach for some species (Chapter I & II), one of the aspects still rarely investigated is the potentially cumulative effect of several OWFs on a broader spatial scale (Chapter I & II, Garthe et al. 2018). Large scale approaches are important as species occurrence is not bound to artificial human borders and thus important patterns in distribution, abundance and behaviour possibly induced by the presence of several OWFs might be missed if only focussing on a restricted study area.

Cumulative assessments of the different anthropogenic stressors are mandatory to approach a better understanding of the human impact on the marine environment and to implement valuable management and conservation measures (Maxwell et al. 2013). However, cumulative assessments are especially difficult to implement as most studies only focus on one part of the entire system (one anthropogenic activity or one species, Maxwell et al. 2013), many of the single stressors are not fully understood yet and decision makers use different definitions for impact assessments (Foley et al. 2016). Approaches investigating the combined effect of different anthropogenic stressors on different species of top predators would greatly enhance our understanding of the anthropogenic impact on the marine ecosystem.

A long term telemetry study tracking different species and if possible some individuals in consecutive years, would greatly enhance our understanding of their ecology and reactions towards OWFs. It would allow to closely monitor their behaviour, movement and habitat use over a longer time span. Possible changes through time could thus be detected and interpreted which could substantially complement existing monitoring schemes. Additionally to the approaches presented in this thesis, other species or other aspects of the species ecology studied here could be included. As GPS-tracking only recently became a method applicable to smaller seabird species (such as kittiwakes) also lighter species can be tracked for several days up to weeks. As an example, while tracking of kittiwakes breeding at the colony on Helgoland would largely increase our knowledge on their foraging behaviour it could fundamentally add to our understanding of processes involved in the decline of breeding individuals (Markones et al. 2009, Dierschke et al. 2011). Furthermore, studying the grey seals diving behaviour in combination with high resolution GPS tracking would largely increase our knowledge on their foraging behaviour during possibly the most vulnerable phase of their life cycle. Finally, analysing the spatial utilisation of the different top predator species comprehensively and in combination with oceanographic variables would substantially increase our knowledge on areas of special importance for different top predator

species in the southern North Sea and could improve our understanding of processes influencing the top predators' choice of these foraging areas.

Based on a long-term telemetry study it could moreover be investigated if the studied species change their behaviour inside or close to the OWFs from year to year and potentially adapt to the presence of the OWFs or if their reaction stays unchanged through time. Detailed information on the individual behaviour close to or inside of OWFs would give insight if attracted individuals specialise on OWFs as foraging areas or if they change their foraging tactics between years. Furthermore, a long-term dataset would provide valuable insights on flight heights inside and close to the OWFs. Such data is urgently needed as it provides important knowledge on possible collision risk of vulnerable species (Furness et al. 2013).

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AUTHOR CONTRIBUTION

This thesis is based on five different manuscripts, which have already been published, are submitted to peer-reviewed scientific journals or in preparation for submission. In the following, I will describe my own contribution and that of all other authors to these manuscripts.

I Operational offshore wind farms and associated ship traffic cause profound changes in distribution patterns of Loons (*Gavia spp.*) (Chapter I)

Bettina Mendel¹, Philipp Schwemmer*¹, Verena Peschko¹, Sabine Müller¹, Henriette Schwemmer¹, Moritz Mercker², Stefan Garthe¹

¹Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany

²BIONUM - Büro für Biostatistik, Finkenwerder Norderdeich 15 A, 21129 Hamburg, Germany

*Corresponding author

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Author contribution: BM, VP and SG developed the idea for the manuscript. BM & VP conducted fieldwork between 2015 and 2017. BM, VP and MM analysed the data. BM, VP and PS wrote the manuscript. SG, SM, HS, MM reviewed and approved the manuscript.

II Offshore wind farm effects on seabird abundance - strong effects revealed for spring and breeding season (Chapter II)

Verena Peschko*¹, Bettina Mendel¹, Sabine Müller¹, Nele Markones¹, Moritz Mercker², Stefan Garthe¹

¹Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany

²BIONUM - Büro für Biostatistik, Finkenwerder Norderdeich 15 A, 21129 Hamburg, Germany

*Corresponding author

Current status: under review

Author contribution: VP, BM, SG developed the idea for the manuscript. VP & BM conducted fieldwork between 2015 and 2017. VP, BM and MM analysed the data. VP wrote the manuscript. BM, MM, SG, SM, reviewed and approved the manuscript.

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

Verena Peschko*¹, Bettina Mendel¹, Moritz Mercker², Jochen Dierschke³, Stefan Garthe¹

¹Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany

²BIONUM - Büro für Biostatistik, Finkenwerder Norderdeich 15 A, 21129 Hamburg, Germany

³Institute of Avian Research

*Corresponding author

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Author contribution: VP, SG developed the idea for the manuscript. VP, SG, JD conducted fieldwork in 2015 and 2016. MM and VP developed the statistical modelling approach (PPM). VP analysed the data. VP wrote the manuscript. SG, BM, JD and MM reviewed and approved the manuscript.

IV Telemetry reveals strong effects of offshore wind farms on behaviour and habitat use of common guillemots (*Uria aalge*) during the breeding season (Chapter IV)

Verena Peschko*¹, Moritz Mercker², Stefan Garthe¹

¹Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany

²BIONUM - Büro für Biostatistik, Finkenwerder Norderdeich 15 A, 21129 Hamburg, Germany

*Corresponding author

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Author contribution: VP and SG developed the idea for the manuscript. VP conducted fieldwork in 2016 and 2017. MM and VP developed the statistical modelling approach (PPM). VP analysed the data. VP wrote the manuscript. SG and MM reviewed and approved the manuscript.

V Should I stay or should I go? Grey seal pups disperse widely in the southern North Sea (Chapter V)

Verena Peschko*¹, Sabine Müller¹, Philipp Schwemmer¹, Moritz Mercker², Peter Lienau³, Tanja Rosenberger⁴, Janne Sundermeyer⁴, Stefan Garthe¹

¹Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany

²BIONUM - Büro für Biostatistik, Finkenwerder Norderdeich 15 A, 21129 Hamburg, Germany

³Seal Centre Nationalpark House, Norden Norddeich, Doerper Weg 24, 26506 Norden, Germany

⁴Seal Centre Friedrichskoog, An der Seeschleuse 4, 25718 Friedrichskoog, Germany

*Corresponding author

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ERKLÄRUNG

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig angefertigt habe und dass sie in Inhalt und Form meine eigene Arbeit ist. Abgesehen von der Beratung meines wissenschaftlichen Betreuers, wurden keine anderen als die angegebenen Hilfsmittel und Quellen genutzt. Die Arbeit wurde unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft erstellt.

Dies ist mein erster Promotionsversuch, mir wurde kein akademischer Grad entzogen. Diese Arbeit wurde weder ganz noch zum Teil an einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt, veröffentlicht oder zur Veröffentlichung eingereicht.

Für die mündliche Prüfung wird die Form der Disputation gewählt. Der Zulassung von Zuhörerinnen und Zuhörern bei der Disputation wird nicht widersprochen.

Büsum, den

Verena Maria Angela Peschko