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Risks to different populations and age classes of gannets from impacts of offshore wind farms in the southern North Sea

Christopher J. Pollock [a,*], Jude V. Lane [a], Lila Buckingham [b], Stefan Garthe [c], Ruth Jeavons [a], Robert W. Furness [d], Keith C. Hamer [a]

[a] School of Biology, University of Leeds, Leeds, UK
[b] UK Centre for Ecology & Hydrology, Bush Estate, Penicuik, UK
[c] Research and Technology Centre (FTZ), University of Kiel, Büsum, Germany
[d] MacArthur Green, Glasgow, UK

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ABSTRACT

The southern North Sea holds the world's highest concentration of offshore wind farms (OWFs). Northern gannets (*Morus bassanus*), a species considered at high risk from OWF impacts, show a strong seasonal peak there in November, but it is unclear which populations and age classes are most at risk of collision with wind turbines. We tagged adult and juvenile gannets at the world's largest colony (Bass Rock) and reviewed two sources of survey data for different age classes to study their movements through southern North Sea waters. Tracked birds showed peak numbers in the southern North Sea in mid-October, with much smaller numbers there during November. Adults were distributed throughout the area, including waters close to OWFs, whereas juveniles were confined to the coast. Survey data indicated high proportions of immature gannets in southern North Sea waters, suggesting higher collision risk than for adults. Gannets present in November may be predominantly from colonies further north than Bass Rock.

1. Introduction

Development of renewable energy resources is increasing apace in an attempt to reduce reliance on fossil fuels. Offshore wind farms (OWFs) harvest energy at sea, but their potential impacts on marine environments are a cause for concern. The UK is currently the largest offshore wind market, with 36% of global installed capacity (deCastro et al., 2019), calling particular attention to impacts of OWFs on marine life in UK waters.

Seabirds are declining globally due to multiple stressors including invasive species, bycatch and overfishing of prey (Croxall et al., 2012; Dias et al., 2019). In addition, potential adverse effects of OWFs on seabirds include risks of collision with turbine blades, barrier effects when energy is expended to avoid turbines, and displacement through exclusion from feeding grounds (Furness et al., 2013). The extent of these different effects depends upon birds' behaviour (e.g. home range size, flight height and speed) and varies seasonally (Lane et al., 2020).

Northern gannets (*Morus bassanus*) are long-lived seabirds breeding on coasts and islands of the North Atlantic Ocean. Often characterised by their resilience, recent reported declines in their most southerly breeding colony (Grémillet et al., 2020) indicate they are not impervious to changes in marine environments. Their flight heights, particularly when foraging (Garthe et al., 2014; Cleasby et al., 2015; Lane et al., 2019), place them at high risk of collision with wind turbines (Furness et al., 2013). Research also indicates strong avoidance of OWFs by gannets (Dierschke et al., 2016; Garthe et al., 2017; Peschko et al., 2021) which may result in habitat loss and increased competition for resources. At a relatively small colony on Helgoland, gannets during the breeding season show reduced selection of operational OWF sites, with 89% of tracked birds predominantly avoiding OWF sites, although 11% frequently entered them when foraging or commuting between the colony and foraging sites (Peschko et al., 2021). Most OWF impact studies on gannets, particularly those employing tracking data, have been conducted during the breeding season when most birds are central place foragers. Much less is understood about potential year-round effects, especially those during migration when many birds from European colonies may move through areas like the southern North Sea, which has the highest concentration of OWFs in the world (Fig. 1).

* Corresponding author. School of Biology, Faculty of Biological Sciences, University of Leeds, Irene Manton Building, Leeds, LS2 9JT, UK.
E-mail address: bscjp@leeds.ac.uk (C.J. Pollock).

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The coasts of Western Europe to West Africa represent a major flyway for the non-breeding season movements of gannets from colonies in the eastern Atlantic. At a metapopulation level they exhibit chain migration (Fort et al., 2012) wherein populations move approximately equal distances southward from each breeding colony through typical migration corridors, and rarely fly over land. Consequently, birds from more northerly colonies tend to winter further north than birds from more southerly colonies. However, migratory movements of individual gannets within a colony differ considerably, with some overwintering much nearer to the colony than others (Kubetzki et al., 2009; Grecian et al., 2019). In addition, many birds exhibit a clockwise loop migration around Britain and Ireland (Furness et al., 2018), travelling south through the Strait of Dover on their way to wintering grounds but returning via more westerly waters. This pattern is reflected in wind farm baseline survey data and impact assessments, which suggest a strong peak in risk in the southern North Sea during November each year (Furness et al., 2018). Using only aerial and boat-based survey data, however, it is not possible to determine which colonies birds are from, and thus colony-specific risk is hard to assess.

Gannets do not reach sexual maturity until age 4–5 years and in comparison to adults, little is known about the seasonal movements of younger birds. After fledging, gannets do not generally return to land until their third calendar year (Nelson, 2002) and so there is a large gap in our knowledge during this stage of their life cycle. Juveniles tracked during post-fledging migration from two European gannet colonies followed broadly the same path to West African waters as adults from the same colonies (Grémillet et al., 2015; Lane et al., 2021). Hence, it is important to assess the risks to these birds, especially for more northerly populations that are more likely to encounter OWFs during migration.

Neither is there abundant knowledge of the seasonal movements of immature birds aged 2–5 years. During the summer months, many immatures attend breeding colonies from where their foraging trips are much more expansive than those of adults (Votier et al., 2011; Grecian et al., 2018). Investigation of extensive aerial survey data shows strong seasonal segregation of immature and adult gannets in the English Channel and Bay of Biscay (Pettex et al., 2019). During the summer, central-place foraging breeding adults appeared to competitively exclude immature birds to more pelagic waters, whereas in the winter, their distributions overlapped. However, it was not known to what extent adults and immatures were segregated during migration.

Environmental impact assessments (EIA) must be conducted prior to consent of a new OWF development. EIAs tend to assume that all risk falls on adults from the nearest Special Protection Area (SPA) as a precautionary approach and that risk is divided equally across age classes in relation to age structure derived from demographic parameters and population modelling. These assumptions may not hold, however, and better ecologically informed EIAs would increase confidence in conclusions regarding risks to gannet populations. In this study, we use both

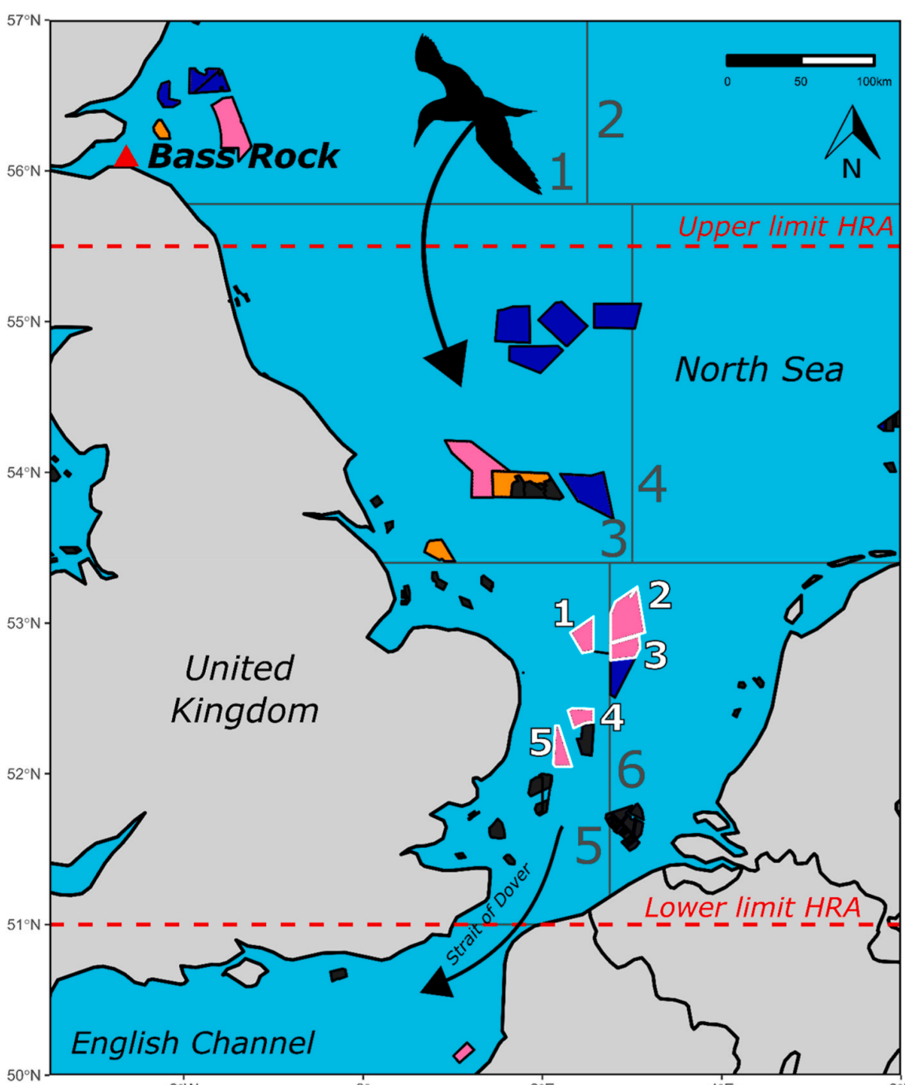

Fig. 1. OWF sites (polygons) in the southern North Sea with construction stage indicated by fill colour: pink = planned; blue = approved; orange = under construction; dark grey = operational. Polygons with white outlines are OWF sites which have aerial survey data (n = 5: 1 = Norfolk Vanguard West, 2 = Norfolk Boreas, 3 = Norfolk Vanguard East, 4 = East Anglia One North, 5 = East Anglia Two). Red dashed lines at 55.5°N and 51.0°N indicate upper and lower limits of the designated high-risk area (HRA; see Methods 2.2). Dark grey dividing lines and numbering indicate division of the North Sea into boxes for inspection of ESAS data. Bass Rock is indicated by a red triangle. Black arrows indicate the general direction of migrating gannets in autumn. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

tracking and survey data to obtain insights into which colonies and age classes of gannets are most at risk from OWF developments in the southern North Sea. We tagged adult and juvenile gannets on Bass Rock, the largest gannet colony in the world (Murray et al., 2015), to study their movement through southern North Sea waters during autumn migration. We then compared this with data on age classes of gannets recorded during aerial surveys of proposed OWF sites in UK southern North Sea waters and from selected areas of the North Sea reported in the European Seabirds at Sea (ESAS) database.

2. Methods

2.1. Tracking data - study site and sampling

Gannets were tracked from Bass Rock, Scotland (56°04′N, 2°38′W, see Fig. 1) between 2018 and 2020. Adults were caught at the nest site using a 6 m telescopic pole during the summers of 2018 and 2019. Each bird was weighed, fitted with a BTO ring or its existing ring number recorded, and fitted with a combined geolocation-immersion logger (MK 3006 British Antarctic Survey, Cambridge UK n = 58; Intigeo C65, Migrate Technology Ltd n = 4). The maximum combined mass of the ring and logger was ~8.5 g, approximately ~0.3% of the average adult body mass and therefore well within recommended guidelines (Phillips et al., 2003), and a previous study deploying similar geolocator tags on gannets reported no adverse effects on bird welfare (Kubetzki et al., 2009).

We recovered 37 of 62 deployed geolocators in April–August 2019 (22 of 26) and August 2020 (15 of 36), with all recovered devices deployed for one wintering period. We attached a new device to all 21 adults recaptured in 2019 to sample successive wintering periods, with seven individuals (33%) returning data from successive years.

We processed geolocator data following Lisovski et al. (2019). Twilights were annotated from light intensity data using the "twilightCalc" function in the "GeoLight" package (Lisovski and Hahn, 2012). The longest period of data from each individual, deduced by visually assessing the quality of light intensity data and cropped accordingly, was used going forwards. Locations were estimated using the "probGLS" package (Merkel et al., 2016), by running data for each individual through an iterative forward step selection framework in which weight is given to possible locations according to daily median sea surface temperature (SST) recorded by the logger and daily mean NOAA SST data at 0.25° resolution (Reynolds et al., 2007; Physical Sciences Division 2019). Further parameters chosen for this algorithm are provided in Table A.1 in the Appendix. The product is a "most probable track", comprising two refined locations per day. The estimated error of all locations reported in the results was 167 ± 724 km. This error is much greater than that associated with the tags used on juveniles (see following paragraph), but the two datasets are nonetheless broadly comparable owing to the large scale movements associated with gannet migration.

Juveniles (n = 42) were captured at the colony on October 5, 2018 (n = 21) and September 20, 2019 (n = 21). Each bird was weighed and fitted with a metal BTO ring. A solar powered Argos GPS-Platform Terminal Transmitter (GPS-PTT; Microwave Telemetry, Columbia, USA), programmed to record a GPS location once an hour between 0600 and 2000 and relayed to the Argos satellite system every 24 h, was then attached to the upper side of the three central tail feathers using Tesa © tape and cable ties. The total weight of the device plus tape and ties (~49 g in 2018, ~34 g in 2019) was <2% of body mass. Handling time of birds was no longer than 20 min after which birds were released on the colony. Argos locations were filtered by speed and location class (LC) to remove erroneous locations using the R package 'argosfilter' (Freitas, 2010; Langston et al., 2013); speeds >25 ms^{-1} and LC Z were removed. GPS data (precise to < 100 m, Argos, 2016) and Argos PTT location classes 3, 2, 1, A and B (precision <250 m to >1500 m) were then combined to reconstruct movements. All locations with duplicated dates and times were screened and only the duplicate with greater precision was retained. Data were received from 38 of the 42 juveniles, from which we selected only the data from birds that travelled south from the colony and passed through the Strait of Dover.

2.2. High-risk area

To compare adult and juvenile tracking data, we demarcated a "high-risk area" (HRA, Fig. 1) in the southern North Sea. The HRA was defined as between 55.5°N and 51.0°N since: (i) many gannets migrate south through the Strait of Dover on autumn migration (Furness et al., 2018); (ii) it encompasses most OWF sites in UK and adjacent North Sea waters; (iii) once birds have passed through the Strait of Dover (51°N) the number and density of OWFs further south is relatively low; (iv) the upper boundary is far enough south of the colony (~100 km) that birds that enter this are likely to have begun migration (i.e. not rafting around the colony), and; (v) the distance between the upper and lower limit (~500 km) is large compared to differences in the precision of the different sets of tracking data. This allowed us to inspect differences between the age classes in passage time (h) through the HRA, their migration phenology, and the distance of location estimates (km) from the shore.

Passage time southwards through the HRA (T_{HRA}) was calculated using the following equation:

$$T_{HRA}\ (\text{Time in high}-\text{risk area, hours}) = T_2 - T_1$$

Where T_1 is the last time a bird crossed the upper boundary while heading southwards (excluding other earlier incursions into the HRA) and T_2 is the first time the same bird crossed the lower boundary. For each track, location estimates on either side of both the upper and lower boundary of the HRA, were directly interpolated in order to obtain T_1 and T_2. This was done for both the adult (GLS) and juvenile (GPS-PTT) data using the "adehabitatLT" package (Calenge and Calenge, 2018). To ascertain migration phenology, allowing comparison with the survey data, the temporal midpoint between T_1 and T_2 was taken for each individual when travelling through the HRA. The shortest distance between each location estimate and the coast were calculated using the "sf" package (Pebesma, 2018).

2.3. Proposed OWF site surveys

Data derived from digital aerial surveys were supplied to us by APEM Limited, who carried out the surveys on five prospective OWF sites as part of baseline studies contributing to the required environmental impact assessment. Aerial surveys were undertaken by survey aircraft that obtained high-resolution still images with a reported resolution of 2 cm Ground Sampling Distance (APEM Ltd). For further details on the methods, see "Norfolk Vanguard Offshore Wind Farm Appendix 13.1 Offshore Ornithology Technical Appendix" (https://infrastructure.planninginspectorate.gov.uk/wp-content/ipc/uploads/projects/EN010079/EN010079-001547-Appendix%2013.01%20Ornithology%20Technical%20Appendix.pdf).

Surveys were conducted throughout the year, each lasting a minimum of two years in total, and all were completed within 2012–2018. We were provided data for all gannets observed in each survey, where age was also assigned where possible by APEM. These data were then processed to assess the relative abundance and seasonality of the different age classes across OWF sites in the southern North Sea. The five prospective OWF sites surveyed are all located in the southern North Sea (Fig. 1). OWF sites range in size from 209 km^2 to 725 km^2, with distance from the shore ranging from 40 to 92 km (Table A.2).

2.4. European Seabirds at sea data

The European Seabirds at Sea partnership (ESAS) has conducted extensive surveys of seabirds, predominantly from ships with strip-transect counts, with data going back as far as 1979 (Stone et al., 1995). We extracted data for gannets distributed in the southern North Sea (Fig. 1) from ESAS database version 5.0 (October 2011), covering the years 1980–2010, to compare seasonal and spatial variation from these surveys with our tracking data and with pre-construction digital aerial surveys of OWF sites.

3. Results

3.1. Tracking data

In 37 datasets recovered from adults, 27 birds travelled southwards at some point during 2018–2019, six of which did so on consecutive years, and entered the HRA (2018 n = 20, 2019 n = 13, HRA location estimates = 641, Fig. 2). 18 birds (10 in 2018, 8 in 2019) continued south through the Strait of Dover. Of 38 juveniles tracked, 11 flew south through the Strait of Dover (7 in 2018, 4 in 2019, HRA location estimates = 1105, Fig. 2). Within the HRA adults were apparently located over four times further from the coast than juveniles (mean ± SD; adult = 106 ± 61.5 km, juvenile = 21.5 ± 22.4 km, Figure A1). Consequently, 11% of adult location estimates inside the HRA (Fig. 2) appeared to fall inside OWF sites, compared to only 1% for juveniles.

Juveniles had a longer passage time through the HRA than adults appeared to, taking almost twice as long (mean ± SD; juveniles = 78.5 ± 27.3 h; adults = 47.5 ± 31.6 h, data from one juvenile removed as a clear outlier having spent 315 h in the HRA, Fig. 3). The midpoint of the HRA was reached by juveniles 3 days earlier than adults (median date, range; juveniles = 16th Oct, 29th Sep – 23rd Oct, adults = 19th Oct, 3rd Oct – 8th Nov, Fig. 4).

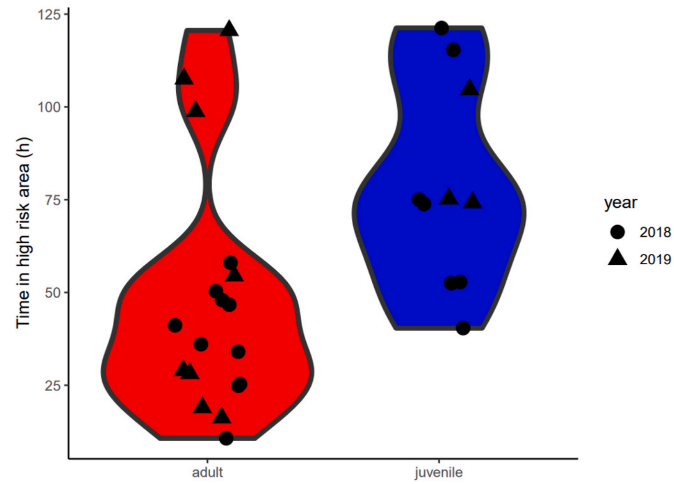

Fig. 3. Passage time (h) through the high-risk area for adults (n = 18, red) and juveniles (n = 10, blue) tracked from Bass Rock during autumn migration. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2. Digital aerial surveys

A total of 3901 gannets were detected during digital aerial surveys of prospective OWF sites in the southern North Sea of which 91% were

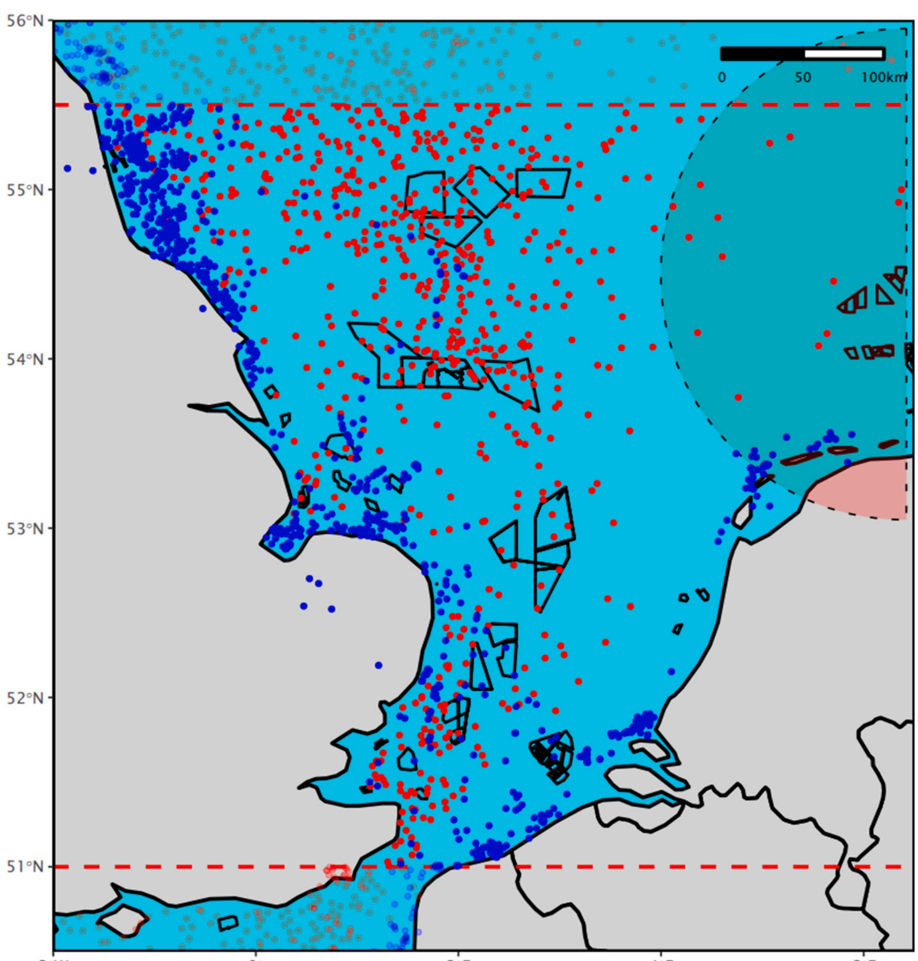

Fig. 2. Location estimates of adult (red, n individuals = 27), and juvenile (blue, n individuals = 11) during autumn migrations through the southern North Sea in 2018–2019. Red dashed lines indicate upper and lower limits of the designated high-risk area. OWF sites indicated by black polygons. Translucent semicircle with black dashed outline shows the mean estimated error (167 km) for adult GLS locations, whereas the error associated with GPS-PTT for juveniles (<1500 m) does not exceed the size of the plotted blue points. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

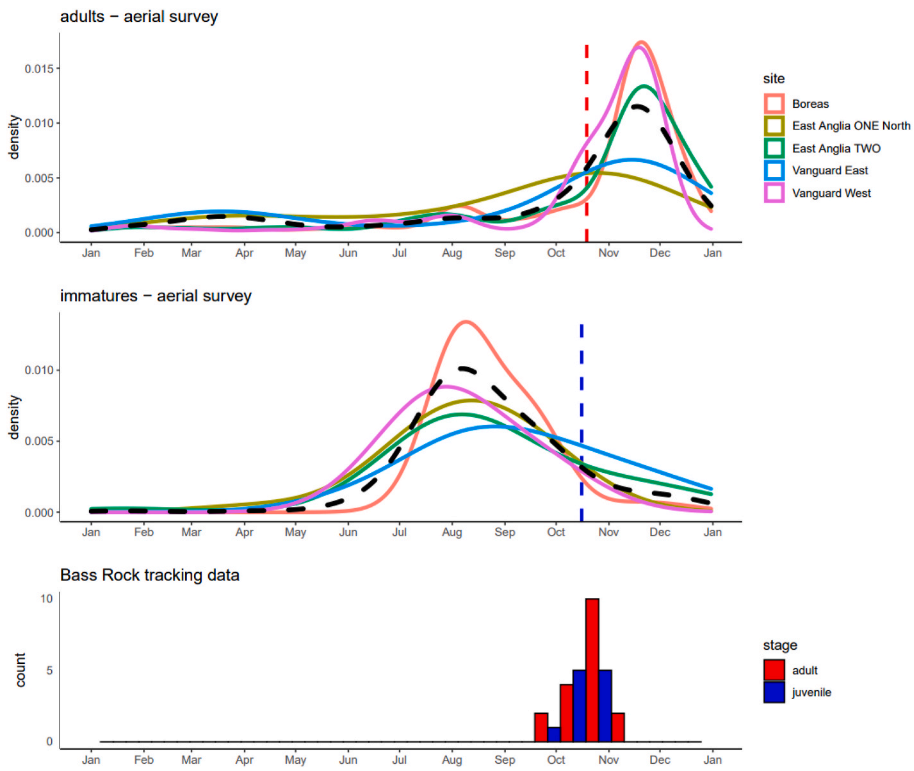

Fig. 4. Density plots of adults (top) and immatures (middle) from aerial survey data, displaying smoothed counts throughout the year. Individual OWF sites represented by different colours with the dashed black line showing the general trend for all five sites combined. The bottom figure is counts of tracked birds travelling south through the North Sea, at the midpoint in time between entering and leaving the designated high-risk area, with the median date represented on the upper plots for the respective stage (adults; red dashed-line = 19th October, juveniles; blue dashed-line = 16th October). X-axes ticks represent the beginning of the labelled month. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

identified as adults (n = 3542), 5.1% as immatures (n = 198) and 1.3% as juveniles (n = 46). Age could not be reliably determined for 4.5% of birds (n = 161).

Seasonal peaks in abundance were evident for both adults and juveniles (Fig. 4). Peak counts of juveniles occurred in August (n = 92) whereas peak counts of adults occurred in November (n = 1761). Similar seasonal patterns are seen across surveyed OWF in Fig. 4. A much smaller peak of adults was also detected in March (n = 166).

When compared with tracking data it is clear that tagged adults from Bass Rock were present in the HRA earlier than the peak seen in digital aerial surveys, whereas tracked juveniles were much later than the peak detected in surveys for immature gannets. The proportion of juveniles in counts in individual OWF sites showed an inverse relationship to increasing distance from the shore (Figure A.2), showing spatial consistency with what the tracking data appear to show.

3.3. European Seabirds at sea

The 30 year period (1980–2010) for which ESAS data were examined comprised a total of 168,993 counts of gannets, of which 15% (n = 24,790) were classed as immature. These data show differences in seasonal abundance of gannets in different areas of the North Sea. Gannets are generally more numerous on the UK side of the North Sea than on the continental side, and are in higher abundance during the summer in the northern area, whereas in the UK southern North Sea (box 5) peak numbers of gannets are seen in October–November (Fig. 5 A). In the UK southern North Sea, the majority of gannets present in April to September (the breeding season) were immatures, whereas in October to March, the majority were adults (Fig. 5 B).

4. Discussion

Tracking and survey data for gannets displayed marked spatio-temporal differences between age classes in the usage of space with a high concentration of OWF sites in the southern North Sea. Adults from Bass Rock were apparently more likely than juveniles to travel on paths that intersected current or planned OWFs, placing them at greater potential collision risk, during their autumn migration. At sea surveys indicate that immature birds travel through the southern North Sea on migration, and potentially foraging trips, but much earlier in the year than adults. As we are confident that our tracking data are representative of the timing of adult gannet migrations from Bass Rock, it is likely that the November peak from survey data consists predominantly of birds from colonies further north than Bass Rock (Fort et al., 2012).

The collision risk to juvenile gannets fledged from Bass Rock was much lower than for adults migrating from this colony, as juveniles tended to migrate much closer to the shore through the southern North Sea. Previous studies at Bass Rock have shown that upon leaving the colony, many adults went northwards to waters around Norway for a short period in early autumn (Kubetzki et al., 2009; Furness et al., 2018), before heading south again. Mackerel (*Scomber scombrus*) stocks in Norwegian waters during autumn may result in their use as a staging ground after the breeding season and before heading to wintering grounds. Similar patterns of movement were seen in our tracked adults. To fly south through the Strait of Dover the adults apparently took the most direct route from Norwegian North Sea waters (see Figure A3 for comparison of adult and juvenile tracks), thus increasing their contact with OWF sites. How this translates to actual risk from OWFs is still not clear, but our data suggest highest risk for immature gannets in summer, highest risk for adult gannets in October–November, and generally low risk for juveniles.

Tracking data suggest that breeding adult gannets may avoid OWFs operating within their foraging ranges (Peschko et al., 2021). If they also avoid OWFs during migration, then potential energetic consequences (barrier effect) might need to be given more consideration. However, it seems likely that any deviations from their default course would have only negligible effects on fitness, given that gannets may migrate over 1, 000 km from colony to wintering areas. Moreover, the magnitude of barrier effects will be higher during the breeding season than during migration (Masden et al., 2010; Warwick-Evans et al., 2017) owing to repeated avoidance and higher overall energetic demand when acting as a centrally placed forager.

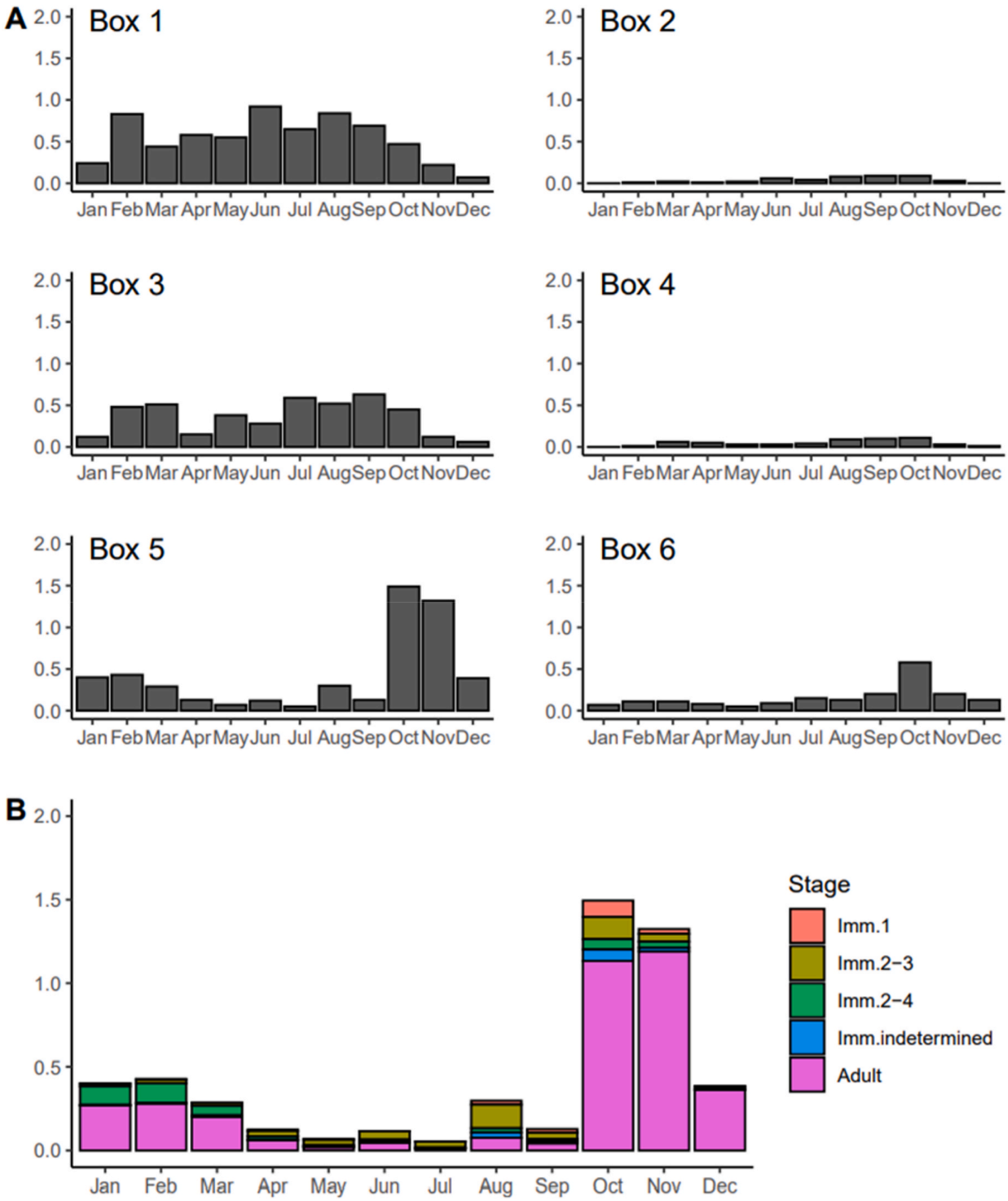

Fig. 5. **A**: Seasonal variation in gannet densities in different parts of the North Sea as indicated by ESAS data (see Fig. 1 for location of each Box). **B**: Densities of each age class of gannets in Box 5 each month.

Tracked juveniles and adults from Bass Rock passed through the southern North Sea at a similar time of year in around mid-late October. The peak of immature counts from aerial surveys of prospective OWF sites was much earlier than this, in keeping with the notion of immatures (excluding juveniles) leaving the colony earlier than adults (Nelson, 2002), after acting as central place foragers over the summer (Votier et al., 2017; Grecian et al., 2018). Lacking experience, juveniles will potentially benefit by learning from adults through local enhancement (Thiebault et al., 2014; Wakefield et al., 2019) and following their direction during the post-breeding migration (Nelson, 2002). It is uncertain, however, whether or not juveniles and immatures react to encountering OWFs in the same way. Juveniles may be more likely to enter OWFs, due to lack of experience, or perhaps less likely, if they are more cautious. Our study provides more support for the latter, given how tracked juveniles apparently hugged the coast on their journey.

A large proportion of gannets in ESAS data for the southern North Sea during the summer months were immature birds, some of which may have been acting as central place foragers from breeding colonies further north and in the English Channel. The southern North Sea around the Strait of Dover is not an area regularly visited by breeding adults on foraging trips (Wakefield et al., 2013), but may be within range of immatures, which range much further than adults from the colony (Votier et al., 2017; Grecian et al., 2018). ESAS data indicating a high proportion of immature gannets in the southern North Sea did not, however, match results from the digital aerial surveys, raising the possibility that the boat-based surveys employed in acquiring ESAS data may have attracted immatures more than adults, hence skewing the data. This seems unlikely, however, because vessels used in ESAS do not include those that catch or discard fish, so should be of little interest to gannets. Rather, the pixel size of our digital aerial survey data (2 cm) probably meant that residual black feathers on the wing and tail of some 3rd year and 4th year birds were not visible, resulting in them being recorded as adults and hence underestimating the proportion of immature birds present, as also found by Pettex et al. (2019).

A recent study in which currently-available GLS data processing methods were tested using birds synchronously double-tagged with GLS and GPS devices (Halpin et al., 2021) has confirmed that we used the optimal available method for open-ocean foraging species (processing data using the ProbGLS package with SST refinement). Nonetheless, differences in the error estimates for different tracking methods are large. Hence, we have been cautious when interpreting results, particularly where we compare GLS with GPS-PTT data, making sure to draw inferences only on large-scale movements and the timing of migration, which we have confidence in. The independent evidence from the ESAS survey data, which match the patterns observed in our tracking data provides further confidence. Nonetheless, we recommend using the same devices across age groups for future studies, ideally at GPS-level precision where funding is not prohibitive.

Adults tracked from Bass Rock passed through the southern North Sea around a month earlier than the peak numbers of adults counted at OWF sites there. This could indicate that the latter was due mainly to birds from colonies further north, such as Shetland, Orkney, Iceland, and Norway, many of which may spend the winter in the North Sea (Fort et al., 2012; Furness et al., 2018). This pulse seen in the digital aerial survey data were also seen for the ESAS data in the southern North Sea, whereas ESAS data from other areas in the North Sea display very different patterns, with the eastern North Sea and German Bight having relatively low numbers throughout the year. The North Sea along the northeast coast of the UK sees higher numbers during the summer months, presumably mainly breeding birds from colonies such as Bass Rock and Bempton Cliffs (Wakefield et al., 2013), emphasising the southern North Sea's importance as a migratory bottle-neck for gannets and an area of high collision risk during autumn. Looking to the future, it is possible that the number of gannets migrating through or wintering in the North Sea may increase as a result of increasing numbers in the more northern colonies (Murray et al., 2015; Barrett et al., 2017). This trend, together with declining numbers in the southernmost colony (Grémillet et al., 2020), may also indicate a northwards shift in breeding distribution, as predicted from bio-climate modelling (Russell et al., 2015) and proximately linked to northwards movements of the distribution of key prey species such as Atlantic Mackerel due to warming oceans (Berge et al., 2015).

Our results confirm the southern North Sea as being of particular importance in terms of the potential collision risks to gannets from OWFs during the autumn migration period each year. Combining different data sources have allowed for unique insights that would have otherwise gone unnoticed. We ascertain that adults heading south from the large breeding colony at Bass Rock were at higher risk than juveniles of encountering OWFs, as a result of migrating further from the coast. The majority of birds present in the high-risk area from November onwards each year were probably from colonies further north than Bass Rock, and a metapopulation approach to understanding which sites contribute to these numbers would aid considerably in apportioning risk to specific colonies.

Declaration of competing interest

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

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Birds were ringed and loggers deployed with permits and approval from the British Trust for Ornithology. Telemetry data will be made available free of charge through the BirdLife International Seabird Tracking Database: http://www.seabirdtracking.org to accompany publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2021.105457.

Author contributions

Christopher J. Pollock: Conceptualisation, Methodology, Investigation, Formal analysis, Writing – original draft. **Jude V. Lane:** Data collection, Formal analysis, Methodology, Writing – review & editing. **Lila Buckingham:** Formal analysis, Writing – review & editing. **Stefan Garthe:** Formal analysis, Writing - review & editing. **Ruth Jeavons:** Data collection, Writing – review & editing. **Robert W. Furness:** Conceptualisation, Methodology, Data collection, Writing – review & editing, Supervision. **Keith C. Hamer:** Conceptualisation, Methodology, Data collection, Writing – review & editing, Supervision.

References

Argos, 2016. Argos user's manual; worldwide tracking and environmental monitoring by satellite. www.argossystem.org/wp-content/ uploads/ 2016/ 08/ r363 _ 9 _ argos _ users _ manual-v1.6.6.pdf.

Barrett, R.T., Strøm, H., Melnikov, M., 2017. On the polar edge: the status of the northern gannet (Morus bassanus) in the Barents Sea in 2015-16. Polar Res. 36, 1390384. https://doi.org/10.1080/17518369.2017.1390384.

Berge, J., Heggland, K., Lønne, O.J., Cottier, F., Hop, H., Gabrielsen, G.W., Nøttestad, L., Misund, O.A., 2015. First records of atlantic mackerel (Scomber scombrus) from the svalbard archipelago, Norway, with possible explanations for the extensions of its distribution. Arctic 68, 54–61. https://doi.org/10.14430/arctic4455.

Calenge, C., Calenge, M.C., 2018. Package 'adehabitatLT'.

Cleasby, I.R., Wakefield, E.D., Bearhop, S., Bodey, T.W., Votier, S.C., Hamer, K.C., 2015. Three-dimensional tracking of a wide-ranging marine predator: flight heights and vulnerability to offshore wind farms. J. Appl. Ecol. 52, 1474–1482. https://doi.org/10.1111/1365-2664.12529.

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., Taylor, P., 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird. Conserv. Int. 22, 1–34. https://doi.org/10.1017/S0959270912000020.

deCastro, M., Salvador, S., Gómez-Gesteira, M., Costoya, X., Carvalho, D., Sanz-Larruga, F.J., Gimeno, L., 2019. Europe, China and the United States: three different approaches to the development of offshore wind energy. Renew. Sustain. Energy Rev. 109, 55–70. https://doi.org/10.1016/j.rser.2019.04.025.

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G., Croxall, J.P., 2019. Threats to seabirds: a global assessment. Biol. Conserv. 237, 525–537. https://doi.org/10.1016/j.biocon.2019.06.033.

Dierschke, V., Furness, R.W., Garthe, S., 2016. Seabirds and offshore wind farms in European waters: avoidance and attraction. Biol. Conserv. 202, 59–68. https://doi.org/10.1016/j.biocon.2016.08.016.

Fort, J., Pettex, E., Tremblay, Y., Lorentsen, S.-H., Garthe, S., Votier, S., Pons, J.B., Siorat, F., Furness, R.W., Grecian, W.J., Bearhop, S., Montevecchi, W.A., Grémillet, D., 2012. Meta-population evidence of oriented chain migration in northern gannets (Morus bassanus). Front. Ecol. Environ. 10, 237–242. https://doi.org/10.1890/110194.

Freitas, C., 2010. Package Argosfilter: Argos Locations Filter. R package version 0.62.
Furness, R.W., Hallgrimsson, G.T., Montevecchi, W.A., Fifield, D., Kubetzki, U., Mendel, B., Garthe, S., 2018. Adult Gannet migrations frequently loop clockwise around Britain and Ireland. Ringing Migr. 1–9 https://doi.org/10.1080/03078698.2018.1472971.
Furness, R.W., Wade, H.M., Masden, E.A., 2013. Assessing vulnerability of marine bird populations to offshore wind farms. J. Environ. Manag. 119, 56–66. https://doi.org/10.1016/j.jenvman.2013.01.025.
Garthe, S., Guse, N., Montevecchi, W.A., Rail, J.-F., Grégoire, F., 2014. The daily catch: flight altitude and diving behavior of northern gannets feeding on Atlantic mackerel. J. Sea Res. 85, 456–462. https://doi.org/10.1016/j.seares.2013.07.020.
Garthe, S., Markones, N., Corman, A.-M., 2017. Possible impacts of offshore wind farms on seabirds: a pilot study in Northern Gannets in the southern North Sea. J. Ornithol. 158, 345–349. https://doi.org/10.1007/s10336-016-1402-y.
Grecian, W.J., Lane, J., Michelot, T., Wade, H.M., Hamer, K.C., 2018. Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. J. R. Soc. Interface. https://doi.org/10.1098/rsif.2018.0084.
Grecian, W.J., Williams, H.J., Votier, S.C., Bearhop, S., Cleasby, I.R., Grémillet, D., Hamer, K.C., Le Nuz, M., Lescroël, A., Newton, J., Others, 2019. Individual spatial consistency and dietary flexibility in the migratory behavior of northern gannets wintering in the Northeast Atlantic. Front. Ecol. Evol. https://doi.org/10.3389/fevo.2019.00214.
Grémillet, D., Péron, C., Lescroël, A., Fort, J., Patrick, S.C., Besnard, A., Provost, P., 2020. No way home: collapse in northern gannet survival rates point to critical marine ecosystem perturbation. Mar. Biol. 167, 189. https://doi.org/10.1007/s00227-020-03801-y.
Gremillet, D., Peron, C., Provost, P., Lescroel, A., 2015. Adult and juvenile European seabirds at risk from marine plundering off West Africa. Biol. Conserv. 182, 143–147. https://doi.org/10.1016/j.biocon.2014.12.001.
Halpin, L.R., Ross, J.D., Ramos, R., Mott, R., Carlile, N., Golding, N., Reyes-González, J. M., Militão, T., De Felipe, F., Zajková, Z., Cruz-Flores, M., Saldanha, S., Morera-Pujol, V., Navarro-Herrero, L., Zango, L., González-Solís, J., Clarke, R.H., 2021. Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. Methods Ecol. Evol. https://doi.org/10.1111/2041-210x.13698.
Kubetzki, U., Garthe, S., Fifield, D., Mendel, B., Furness, R.W., 2009. Individual migratory schedules and wintering areas of northern gannets. Mar. Ecol. Prog. Ser. 391, 257–266. https://doi.org/10.3354/meps08254.
Lane, J.V., Jeavons, R., Deakin, Z., Sherley, R.B., Pollock, C.J., Wanless, R.J., Hamer, K. C., 2020. Vulnerability of northern gannets to offshore wind farms; seasonal and sex-specific collision risk and demographic consequences. Mar. Environ. Res. 162, 105196. https://doi.org/10.1016/j.marenvres.2020.105196.
Lane, J.V., Pollock, C.J., Jeavons, R., Sheddan, M., Furness, R.W., Hamer, K.C., 2021. Post fledging movements, mortality and migration of juvenile northern gannets. Mar. Ecol. Prog. Ser. 671, 207–218. https://doi.org/10.3354/meps13804.
Lane, J.V., Spracklen, D.V., Hamer, K.C., 2019. Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. Mar. Ecol. Prog. Ser. 628, 183–193. https://doi.org/10.3354/meps13089.
Langston, R.H., Teuten, E., Butler, A., 2013. Foraging Ranges of Northern Gannets Morus Bassanus in Relation to Proposed Offshore Wind Farms in the UK: 2010–2012. RSPB Report to DECC.
Lisovski, S., Bauer, S., Briedis, M., Davidson, S.C., Dhanjal-Adams, K.L., Hallworth, M.T., Karagicheva, J., Meier, C.M., Merkel, B., Ouwehand, J., Pedersen, L., Rakhimberdiev, E., Roberto-Charron, A., Seavy, N.E., Sumner, M.D., Taylor, C.M., Wotherspoon, S.J., Bridge, E.S., 2019. Light-level geolocator analyses: a user's guide. J. Anim. Ecol. https://doi.org/10.1111/1365-2656.13036.
Lisovski, S., Hahn, S., 2012. GeoLight- processing and analysing light-based geolocator data in R. Methods Ecol. Evol. 3, 1055–1059. https://doi.org/10.1111/j.2041-210X.2012.00248.x.
Masden, E.A., Haydon, D.T., Fox, A.D., Furness, R.W., 2010. Barriers to movement: modelling energetic costs of avoiding marine wind farms amongst breeding seabirds. Mar. Pollut. Bull. 60, 1085–1091. https://doi.org/10.1016/j.marpolbul.2010.01.016.
Merkel, B., Phillips, R.A., Descamps, S., Yoccoz, N.G., Moe, B., Strøm, H., 2016. A probabilistic algorithm to process geolocation data. Mov Ecol 4, 26. https://doi.org/10.1186/s40462-016-0091-8.
Murray, S., Harris, M.P., Wanless, S., 2015. The status of the gannet in Scotland in 2013-14. Scott. Birds 35.
Nelson, B., 2002. The Atlantic Gannet. Fenix Books.
Pebesma, E.J., 2018. Simple features for R: standardized support for spatial vector data. R J 10, 439.
Peschko, V., Mendel, B., Mercker, M., Dierschke, J., Garthe, S., 2021. Northern gannets (Morus bassanus) are strongly affected by operating offshore wind farms during the breeding season. J. Environ. Manag. 279, 111509. https://doi.org/10.1016/j.jenvman.2020.111509.
Pettex, E., Lambert, C., Fort, J., Dorémus, G., Ridoux, V., 2019. Spatial segregation between immatures and adults in a pelagic seabird suggests age-related competition. J. Avian Biol. https://doi.org/10.1111/jav.01935.
Phillips, R.A., Xavier, J.C., Croxall, J.P., 2003. Effects of Satellite Transmitters on Albatrosses and Petrels. Auk. https://doi.org/10.1093/auk/120.4.1082.
Physical Sciences Division, 2019. NOAA High Resolution SST Data. https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html. Accessed on 09/12/2020.
Reynolds, R.W., Smith, T.M., Liu, C., Chelton, D.B., Casey, K.S., Schlax, M.G., 2007. Daily high-resolution-blended analyses for sea surface temperature. J. Clim. 20, 5473–5496. https://doi.org/10.1175/2007JCLI1824.1.
Russell, D.J.F., Wanless, S., Collingham, Y.C., Huntley, B., Hamer, K.C., 2015. Predicted future European breeding distributions of British seabird species under climate change and unlimited/no dispersal scanearios. Diversity 7, 342–359. https://doi.org/10.3390/d7040342.
Stone, C.J., Webb, A., Barton, C., Ratcliffe, N., Reed, T.C., Tasker, M.L., Camphuysen, C. J., Pienkowski, M.W., Consult, O., 1995. An Atlas of Seabird Distribution in North-West European Waters.
Thiebault, A., Mullers, R.H.E., Pistorius, P.A., Tremblay, Y., 2014. Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. Behav. Ecol. 25, 1302–1310. https://doi.org/10.1093/beheco/aru132.
Votier, S.C., Fayet, A.L., Bearhop, S., Bodey, T.W., Clark, B.L., Grecian, J., Guilford, T., Hamer, K.C., Jeglinski, J.W.E., Morgan, G., Wakefield, E., Patrick, S.C., 2017. Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. Proc. Biol. Sci. 284 https://doi.org/10.1098/rspb.2017.1068. https://doi.org/10.1098/rspb.2017.1068.
Votier, S.C., James Grecian, W., Patrick, S., Newton, J., 2011. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. Mar. Biol. 158, 355–362. https://doi.org/10.1007/s00227-010-1563-9.
Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green, J.A., Grémillet, D., Jackson, A.L., Jessopp, M.J., Kane, A., Langston, R.H.W., Lescroël, A., Murray, S., Le Nuz, M., Patrick, S.C., Péron, C., Soanes, L.M., Wanless, S., Votier, S.C., Hamer, K.C., 2013. Space partitioning without territoriality in gannets. Science 341, 68–70. https://doi.org/10.1126/science.1236077.
Wakefield, E.D., Furness, R.W., Lane, J.V., Jeglinski, J.W.E., Pinder, S.J., 2019. Immature gannets follow adults in commuting flocks providing a potential mechanism for social learning. J. Avian Biol. 50, 1. https://doi.org/10.1111/jav.02164.
Warwick-Evans, V., Atkinson, P.W., Walkington, I., Green, J.A., 2017. Predicting the impacts of wind farms on seabirds: an individual-based model. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.12996.