

Seabirds as samplers of the marine environment – a case study in Northern Gannets

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Abstract. Understanding distribution patterns, activities, and foraging behaviours of seabirds require interdisciplinary approaches. In this paper, we provide examples of the data and analytical procedures from a new study in the German Bight, 10 North Sea, tracking Northern Gannets (*Morus bassanus*) at their breeding colony on the island of Helgoland. Individual adult Northern Gannets were equipped with different types of data loggers for several weeks, measuring geographic positions and other parameters mostly at 3-5 min intervals. Birds flew in all directions from the island to search for food, but most flights targeted areas to the (N)NW of Helgoland. Foraging trips were remarkably variable in duration and distance; most trips lasted 1–15 h and extended from 3–80 km from the breeding colony on Helgoland. Dives of gannets were generally shallow, with 15 more than half of the dives only reaching depths of 1–3 m. The maximum dive depth was 11.4 m. Gannets showed a clear diurnal rhythm in their diving activity, with dives being almost completely restricted to the daylight period. Most flight activity at sea occurred at an altitude between the sea surface and 40 m. Gannets mostly stayed away from the wind farms and passed around them much more frequently than flying through them. Detailed information on individual animals may provide important insights into various processes, based on multi-layer information.

Abstract. Understanding distribution patterns, activities, and foraging behaviours of seabirds require interdisciplinary approaches. In this paper, we provide examples of the data and analytical procedures from a new study in the German Bight, North Sea, tracking Northern Gannets (*Morus bassanus*) at their breeding colony on the island of Helgoland. Individual adult Northern Gannets were equipped with different types of data loggers for several weeks, measuring geographic positions and other parameters mostly at 3-5 min intervals. Birds flew in all directions from the island to search for food, but most flights targeted areas to the (N)NW of Helgoland. Foraging trips were remarkably variable in duration and distance; most trips lasted 1–15 h and extended from 3–80 km from the breeding colony on Helgoland. Dives of gannets were generally shallow, with more than half of the dives only reaching depths of 1–3 m. The maximum dive depth was 11.4 m. Gannets showed a clear diurnal rhythm in their diving activity, with dives being almost completely restricted to the daylight period. Most flight activity at sea occurred at an altitude between the sea surface and 40 m. Gannets mostly stayed away from the wind farms and passed around them much more frequently than flying through them. Detailed information on individual animals may provide important insights into various processes, based on multi-layer information.

1 Introduction

Seabirds are marine animals that live mostly at or near the air–water interface. The dynamics of both these media may consequently have strongly influences on seabird ecology (Schneider 1991). Many studies in the world’s oceans have shown that the physical environment has a substantial influence on seabird distributions (e.g. Haney & McGillivray, 1985, Briggs et al., 1987, Hunt, 1990). Physical processes are particularly relevant to seabirds when they cause predictable prey aggregations, either regular or irregular. However, other opportunities (such as fisheries discards; e.g. Ryan & Moloney, 1988, Garthe et al., 1996) and constraints (such as the need to breed on land; e.g. Schneider & Hunt, 1984, Wilson et al., 1995) may also influence seabird distributions and related behaviours. Furthermore, it is important to note that scale is an essential feature in the marine system, markedly affecting quantitative relations between abiotic and biotic variables (Schneider 1994). Thus, general seabird distribution patterns often correspond best with physical phenomena at large scales, whereas smaller scale patterns are associated with biological features such as foraging range, social interactions, and prey availability (Schneider & Duffy, 1985, Hunt & Schneider, 1987). Most behaviours at sea are directly related to foraging (e.g. searching, feeding) or the result of foraging-related constraints (waiting for food to become available, digesting, commuting). Several external and internal characteristics and limitations influence foraging activities, e.g. diurnal rhythms, flight manoeuvrability, feeding techniques, prey-detection capabilities, social attractions, learning and age-dependent skills, foraging ranges, and dietary preferences (Furness & Monaghan, 1987, Shealer, 2002).

For decades, studies of seabird biology were mainly land-based, with a particular focus on the breeding period. Although there were understandable logistic reasons for this, it has led to severe biases in our understanding of seabird ecology. Two subsequent approaches focusing on the behaviours of seabirds at sea have allowed significant progress in our understanding of seabird ecology. One such approach involved studying seabird distributions at sea from boats. Whereas early

work was targeted towards establishing the distribution patterns of seabirds (e.g. Brown, 1986, Tasker et al., 1987), later studies concentrated on improving our understanding of the underlying factors, including habitat parameters, mainly hydrographic features measured synoptically at sea or by remote techniques, and food availability, assessed by detecting and possibly quantifying prey at sea (e.g. Haney, 1991, Decker & Hunt, 1996). The second approach was to equip seabirds with telemetric devices and/or data-logging units (e.g. Jouventin & Weimerskirch, 1990, Wilson et al., 2002, Wilson & Vandenabeele, 2012). These devices record the bird's position and/or other parameters such as temperature and depth while the bird is at sea. Because seabirds are fast-moving and wide-ranging animals, this approach also enables us to study them in logistically inaccessible areas. Furthermore, it allows information on individual birds to be collected, in contrast to boat-based observations, which involve larger samples of birds, but where single individuals cannot be tracked over larger areas or time spans.

Understanding patterns in distributions, activities, and foraging behaviours of seabirds requires interdisciplinary approaches. The physical properties of the sea establish the basic habitat parameters with which both the seabirds and their prey have to cope, while biological conditions influence the birds' food supply (e.g. by prey behaviour) and foraging behaviours. Furthermore, anthropogenic activities may also influence different aspects of the marine environment, both directly on individual seabirds, and indirectly by affecting habitat conditions and prey availability. A combination of these methodological and conceptual approaches will further our understanding of the ecology of seabirds within the study area.

In this paper, we provide an overview of a new study in the German Bight, North Sea, connected to the Coastal Observing System for Northern and Arctic Seas (COSYNA) network. We started tracking Northern Gannets (*Morus bassanus*) at their breeding colony on the island of Helgoland in 2014. Here we provide examples of the data and analytical procedures based on selected data sets from 2015, and explain the value and perspectives of such studies, especially in relation to coastal observation systems such as COSYNA.

2 Methods

2.1 Field experiments

Field experiments were conducted on the island of Helgoland (54° 11' N, 7° 55' E) in the southeastern North Sea (Fig. 1). A total of 14 adult Northern Gannets that were either incubating or rearing chicks were caught on 12–13 May, 17–18 June, or 22–23 July 2015. All birds were equipped with data loggers. Ten gannets each received a Bird Solar GPS logger (e-obs GmbH, Munich, Germany) and the other four birds were equipped with both a CatLog-S GPS logger (Catnip Technologies, Hong Kong, China) and a precision temperature–depth (PTD) logger (Earth & Ocean Technologies, Kiel, Germany). All loggers were attached to the base of the four innermost tail feathers using TESA® tape (Beiersdorf AG GmbH, Hamburg, Germany). Data obtained from these loggers covered durations of 0.4–10.9 weeks (Fig. 2).

The total masses of the attached devices (including sealing, base plate, and tape) were 48 g (Bird Solar) and 64 g (CatLog-S plus PTD), representing 1.5% and 1.9%, respectively, of the mean gannet body mass of 3,286 g (Wanless & Okill, 1994). This is well below the potential threshold of 3% (Phillips et al., 2003, but see Vandenabeele et al., 2012). Although

attachments to the tail may have a negative influence 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 detectable effects on bird behaviour 

2.2 Technology

2.2.1 Bird Solar GPS logger

- 5 These loggers recorded date, time, position (latitude, longitude), ground speed, heading and acceleration. The sampling interval was mostly set to 3–5 min, and the accelerometer to 0.25–3 min. The onboard memories were 32 and 64 MB, respectively. The outer diameters of the device were $63 \times 22 \times 16$ mm, plus base plates and an antenna of 76 mm for data transfer. Data could be downloaded remotely using a hand-held device when approaching the birds in the colony.

2.2.2 CatLog-S GPS logger

- 10 These devices recorded date, time, and position (latitude, longitude) and were set at an interval of 5 min. Dimensions varied slightly according to battery type, but were about $50 \times 35 \times 8$ mm. The plate was encased by a heatable plastic housing. Data were retrieved by recapturing the bird and downloading data from the device.

2.2.3 PTD loggers

- 15 These loggers had 2 MB onboard memory and measured date, time, pressure, and internal and external temperatures (Earth & Ocean Technologies). Temperature measurements were obtained from an external, fast-responding, temperature sensor that allowed sampling of the water column with minimal time lag in thermal signals. The streamlined lightweight carbon-fibre-composite casing (outer diameter 19 mm, length 80 mm) weighed about 23 g. Recording intervals for temperature and pressure were set at 3 s. Data could be retrieved by recapturing the bird and downloading the data from the device.

2.3 Northern Gannets

- 20 The Northern Gannet is the largest seabird species in the North Atlantic. It is a goose-sized bird with a body mass of 2.3–3.6 kg and breeds in colonies of up to several tens of thousands of pairs. Northern Gannets spend their entire life at sea, except for breeding on land. They usually start breeding at 5–6 years old, and may live to 20 years or older. They lay one egg that is incubated for 6 weeks, followed by a chick-rearing period of about 13 weeks. Only one adult of the pair is usually at the nest at any one time during incubation or chick guarding, while the other is at sea (Nelson, 2002, Bauer et al., 2005). Apart from
25 short flights to collect nesting material or due to disturbance/interactions at the nest site, gannets carry out foraging trips to collect food for themselves and their offspring. They usually forage using so-called plunge dives, which are initiated when flying (and searching) at a few to several tens of metres above the sea surface (Nelson, 2002, Garthe et al., 2014). Two different dive types can be distinguished in this species (Garthe et al., 2000). U-shaped dives occur when the birds remain at a largely

constant depth for a period after plunging into the water, with little vertical movement, before returning to the sea surface. In contrast, V-shaped dives are usually short and shallow, with the ascent almost immediately following the descent. 

Northern Gannets have recently been studied intensively by satellite telemetry and data loggers in various places, thus allowing comparisons among regions and populations to be investigated comprehensively. 

5 3 Products and analyses

3.1 Flight patterns

Figures 3a and 3b show the flight patterns of two adult Northern Gannets that were typical of 13 of the 14 individuals tracked in 2015. Birds flew in all directions from the island to search for food, but most flights targeted areas to the (N)NW of Helgoland. Foraging trips (defined in this paper as absences from the nest site of at least 20 min and of at least 2.0 km direct distance) were remarkably variable in duration and distance; most trips lasted 1–15 h and extended from 3–80 km from the breeding colony on Helgoland. One individual's behaviour differed from that of the other gannets by repeatedly flying far north to forage in the Skagerrak (Fig. 3c). These long-distance foraging trips were almost identical in their structures ($n = 3$; duration = 44.3–59.3 h, most distant location = 375–388 km, total distance flown = 971–1019 km) and were interspersed with 'normal' foraging trips into the German Bight.

15 3.2 Diving behaviour

Dives of gannets breeding on Helgoland and foraging in the German Bight (defined as south of 55° 30' N) were generally shallow, with more than half of the dives only reaching depths of 1–3 m (Fig. 4). The maximum dive depth was 11.4 m, and the median dive depth was 2.2 m ($n = 4$ individuals, $n = 2,376$ dives). Most dives were V-shaped, though the measuring interval of 3 s did not allow a precise determination of the proportions of U- and V-shaped dives (see Garthe et al., 2000). The measuring interval of 3 s might also mask the deepest parts of some dives and may thus underestimate dive depth in general. We therefore re-analysed a random sample of 100 dives from Garthe et al. (2014), where gannets exhibited a similar high percentage of V-shaped dives, using both 1 s and 3 s intervals (10 individuals, 10 dives each). Scaling down to 3 s missed 10% of the dives, while the median detected dive depth was only slightly smaller (4.3 vs. 4.5 m). These subtle differences demonstrate the validity of 3 s measuring intervals to determine the dive-depth pattern.

25 These dives were shallow compared with previous studies conducted in the northwestern North Sea (Lewis et al., 2002), the English Channel (Grémillet et al., 2006), the northwest Atlantic (Garthe et al., 2000), and the Gulf of St. Lawrence, Canada (Garthe et al., 2007).

Gannets showed a clear diurnal rhythm in their diving activity (Fig. 5). Dives were almost completely restricted to the daylight period, with the remaining dives occurring around dawn and dusk. No dives were recorded between 22:09 and 30 05:21 Central European Summer Time (CEST). This pattern fits well previous studies (Garthe et al., 2000, Garthe et al., 2003).

3.3 Flight altitudes

The altitudes of flying birds are important in relation to their migratory movements, prey-searching behaviour, and potential overlap with technical installations at sea.

The BirdSolar GPS loggers calculated height above the ellipsoid when connecting with satellites during positional
5 fixes, and altitude measurements were therefore corrected for geoid height (39.1 m at colony location). Altitude estimates are improved when connection time to the satellite is increased (e.g. Corman & Garthe, 2014), and we therefore used pulses of GPS fixes over 11–15 s and analysed the last and assumed best altitude measurement from each pulse. Figure 6 shows non-smoothed altitude measurements for one foraging trip of 22.7 h. Colony attendance was derived from positional fixes and known nest position, on-water periods were determined from ground speed ($< 3 \text{ km h}^{-1}$) and positional fixes. Although values
10 fluctuated slightly even for fixed places such as the nest site in the colony and the sea surface, the measurements appeared reasonable and showed that most flight activity occurred at an altitude between the sea surface and 40 m, with maximum values in this study when birds were commuting to/from the colony. Measurements in the colony and on water can be used to calibrate altitude measurements because of their relatively well-known heights.

Flight heights of gannets have also been determined by radar measurements (e.g. Krijgsveld et al., 2011), visual
15 observations (e.g. Johnston et al., 2014), and from pressure sensors (Garthe et al., 2014, Cleasby et al., 2015). Overall, flight heights of gannets tend to be low, with relatively few flights above 50 m and very few recorded above 100 m, though no comprehensive analysis has yet been published.

3.4 Behavioural patterns

Animal movements can be tracked using motions sensors. Many data loggers contain accelerometers that ideally cover all
20 three axes (x, y, z)  frequent measurements allow behavioural differentiation at a fine scale (e.g. Sakamoto et al., 2009).

Figure 5  shows an example of accelerometer measurements of a Northern Gannet at a 0.25 min interval over 24 h. Recordings start when the bird is on its nest, with very little activity, obviously sleeping. After about 3 h, the bird remains on its nest but its activity increases, coinciding with dawn. A few hours later, the bird leaves the nest and flies off, followed by a period of about 10 h of mostly flying, interrupted by a few shorter swimming periods. Towards the end of the recording period,
25 the bird settles down on the sea surface and remains floating there overnight (Fig. 7).

To determine the relevance of certain sea areas and to improve our understanding of the flight patterns of the birds, it is necessary to know when and where the birds are feeding actively. Because gannets almost always obtain food by plunge diving, observing dives provides a good proxy for determining feeding areas. Figure 8 shows the flight tracks and dive locations of the gannet that flew repeatedly towards the Skagerrak. It shows that the gannet was foraging intensively in the Skagerrak,
30 while longer passages on outbound and inbound flights were long-distance flights without much foraging activity.

3.5 Overlap with human pressures

The ability to track seabird movements at small spatial and temporal scales makes it possible to study the potential impacts of human activities at sea comprehensively. Eleven offshore wind farms have been built and became operational in the German Bight between 2008 and April 2016, and a further five are currently under construction. Another 19 wind farms have been given consent, and several tens more have been applied for. The impact of wind farms on seabirds, which is currently a hot topic in conservation biology and environmental policy (e.g. Furness et al., 2013, Masden et al., 2015), can thus be studied comprehensively in German North Sea waters.

The flight tracks of the gannets shown in Fig. 1 were projected on top of the wind farms that were operational or under construction during the tracking period. Three gannets mostly stayed away from the wind farms and passed around them much more frequently than flying through them (Fig. 9). Wind farms further from Helgoland were not entered, but gannets visited the wider wind farm sites. Focusing on the three wind farms north of Helgoland, five of the 14 gannets tracked in 2015 did not enter them, four only flew into the wind farms once, while four visited them occasionally and one frequently.

4 Conclusions and perspectives

Tracking free-living animals such as seabirds can open up new dimensions in biological, ecological, and environmental research (Kays et al., 2015). The latest developments in microelectronics can even provide real-time data transfer through mobile-phone networks (e.g. Gilbert et al., 2016). Information collected by data loggers can be used for various purposes, including applied topics, such as assessing the possible effects of wind farms, as well as fundamental research. In a review of offshore wind-farm studies, Bailey et al. (2014) concluded that traditional visual surveys of birds and mammals from ships and aircraft were unlikely to have enough power to detect changes in behaviour or fine-scale spatial or temporal shifts in distribution, given that observers can only be in one place at a time and can only reliably survey in calm sea conditions during daylight hours. Other techniques such as GPS tracking are thus likely to provide more useful data in many cases (Bailey et al., 2014).

Substantial added-value information can be retrieved by combining geographic-position information with other parameters. For birds feeding under water, pressure sensors are essential to characterise foraging areas, allowing diving activity to be described comprehensively (e.g. Boyd, 1997, Ronconi & Burger, 2011). Pressure sensors and/or high-rate GPS measurements can also be used to estimate flight heights (Corman & Garthe, 2014, Scales et al., 2014). Further detailed behavioural and energetic information can be derived from three-dimensional accelerometer measurements (Gómez Laich et al., 2008, Sakamoto et al., 2009), making this a topical research interest.

Detailed information on individual animals may also provide important insights into various processes, based on multi-layer information. From an animal habitat-selection perspective, information on the physical environment used by the animal is important, allowing habitats to be described and even generalised by different types of habitat models (e.g. Barbet-Massin et al., 2012, Schwemmer et al., 2016). Project consortia such as COSYNA can provide comprehensive and relevant

information (Baschek et al., this issue), while information on foraging animals such as seabirds, which exhibit distinct prey-search behaviours, may also inform physical oceanographers on the location of physical features, especially small-scale physical features such as fronts (e.g. Sabarros et al., 2014, Scales et al., 2014). 

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References

- Bailey H., Brookes K. L., and Thompson, P. M.: Assessing environmental impacts of offshore wind farms: lessons learned and recommendations for the future, *Aquat. Biosyst.*, 10, 8, 2014.
- Barbet-Massin, M., Jiguet, F., Albert, C. H., and Thuiller, W.: Selecting pseudo-absences for species distribution models: how, 5 where and how many?, *Meth. Ecol. Evol.*, 3, 327–338, 2012.
- Baschek et al. this issue XXX
- Bauer, H.-G., Bezzel, E., and Fiedler, W.: *Das Kompendium der Vögel Mitteleuropas. Alles über Biologie, Gefährdung und Schutz. Vol. 1: Nonpasseriformes – Nichtsperlingsvögel.* Aula-Verlag, Wiebelsheim, Germany, 2005.
- Boyd, I. L.: The behavioural and physiological ecology of diving, *Trends Ecol. Evol.*, 12, 213-217, 1997.
- 10 Briggs, K. T., Tyler, W. B., Lewis, D. B., and Carlson, D. R.: Bird communities at sea off California: 1975 to 1983, *Stud. Avian Biol.*, 11, 1–74, 1987.
- Brown, R. G. B.: *Revised Atlas of Eastern Canadian Seabirds. I. Shipboard surveys,* Canadian Wildlife Service, Dartmouth, Canada, 1986.
- Cleasby, I. R., Wakefield, E. D., Bearhop, S., Bodey, T. W., Votier, S. C., and Hamer, K. C. 2015. Three-dimensional tracking 15 of a wide-ranging marine predator: flight heights and vulnerability to offshore wind farms, *J. Appl. Ecol.*, 52, 1474–1482, 2015.
- Corman, A.-M. and Garthe, S. What flight heights tell us about foraging and potential conflicts with wind farms: a case study in lesser black-backed gulls (*Larus fuscus*), *J. Ornithol.*, 155, 1037–1043, 2014.
- Decker, M. B. and Hunt, G. L. Jr.: Foraging by murre (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, 20 USA, *Mar. Ecol. Prog. Ser.*, 139, 1–10, 1996.
- Furness, R. W. and Monaghan, P.: *Seabird Ecology,* Blackie, Glasgow, 1987.
- Furness, R. W., Wade, H, and Masden E. A.: Assessing vulnerability of seabird populations to offshore wind farms, *J. Environ. Manage.*, 119, 56–66, 2013.
- Garthe, S., Camphuysen, C. J., and Furness, R.W.: Amounts of discards by commercial fisheries and their significance as food 25 for seabirds in the North Sea, *Mar. Ecol. Prog. Ser.*, 136, 1–11, 1996.
- Garthe, S., Benvenuti, S., and Montevecchi, W. A.: Pursuit-plunging by Northern Gannets (*Sula bassana*) feeding on Capelin (*Mallotus villosus*), *Proc. R. Soc. London Biol. Sci.*, 267, 1717–1722, 2000.
- Garthe, S., Benvenuti, S., and Montevecchi, W. A.: Temporal patterns of foraging activities of northern gannets, *Morus bassanus*, in the northwest Atlantic Ocean, *Can. J. Zool.*, 81, 453–461, 2003.
- 30 Garthe, S., Montevecchi, W. A., Chapdelaine, G., Rail, J.-F., and Hedd, A.: Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields, *Mar. Biol.*, 151, 687–694, 2007.

- Garthe, S., Guse, N., Montevecchi, W.A., Rail, J.-F., and Grégoire, F.: The daily catch: Flight altitude and diving behavior of northern gannets feeding on Atlantic mackerel, *J. Sea Res.*, 85, 456–462, 2014.
- Gilbert, N. I., Correia, R. A., Silva, J. P., Pacheco, C., Catry, I., Atkinson, P. W., Gill, J. A., and Franco, A. M. A.: Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population, *Movement Ecol.*, 4(7), 2016.
- Gómez Laich, A., Wilson, R. P., Quintana, F., and Shepard, E. L. C.: Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers, *Endang. Spec. Res.*, 10, 29–27, 2008.
- Grémillet, D., Pichegru, L., Siorat, F., and Georges, J.-Y.: Conservation implications of the apparent mismatch between population dynamics and foraging effort in French Northern Gannets from the English Channel, *Mar. Ecol. Prog. Ser.*, 319, 15–25, 2006.
- Haney, J. C.: Influence of pycnocline topography and water-column structure on marine distributions of alcids (Aves: Alcidae) in Anadyr Strait, northern Bering Sea, Alaska, *Mar. Biol.*, 110, 419–435, 1991.
- Haney, J. C. and McGillivray, P. A.: Midshelf fronts in the South Atlantic Bight and their influence on seabird distribution and seasonal abundance, *Biol. Oceanogr.*, 3, 401–430, 1985.
- Hunt, G. L. Jr.: The pelagic distribution of marine birds in a heterogeneous environment, *Polar Res.*, 8, 43–54, 1990.
- Hunt, G. L. Jr. and Schneider, D. C.: Scale-dependent processes in the physical and biological environment of marine birds, in: *Seabirds: Feeding Ecology and Role in Marine Ecosystems*, edited by: Croxall, J. P., Cambridge University Press, Cambridge, 7–41, 1987.
- Johnston, A., Cook, A. S. C. P., Wright, L. J., Humphreys, E. M., and Burton, N. H. K.: Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines, *J. Appl. Ecol.*, 51, 31–41, 2014.
- Jouventin, P. and Weimerskirch, H.: Satellite tracking of Wandering Albatrosses, *Nature*, 343, 746–748, 1990.
- Kays, R., Crofoot, M. C., Jetz, W., and Wikelski, M.: Terrestrial animal tracking as an eye on life and planet, *Science*, 348, aaa2478, 2015.
- Krijgsveld, K. L., Fijn, R. C., Japink, M., van Horssen, P. W., Heunks, C., Collier, M. P., Poot, M. J. M., Beuker, D., and Dirksen, S. Effect Studies Offshore Wind Farm Egmond aan Zee: Final report on fluxes, flight altitudes and behaviour of flying birds, Bureau Waardenburg Report, 10–219, 2011.
- Lewis, S., Benvenuti, S., Dall’Antonia, L., Griffiths, R., Money, L., Sherratt, T. N., Wanless, S., and Hamer, K. C.: Sex-specific foraging behaviour in a monomorphic seabird, *Proc. R. Soc. London B*, 269, 1687–1693, 2002.
- Masden, E. A., McCluskie, A., Owen, E., and Langston, R. H. W.: Renewable energy developments in an uncertain world: The case of offshore wind and birds in the UK, *Mar. Policy*, 51, 169–172, 2015.
- Nelson, J. B.: *The Atlantic Gannet*, Fenix Books, Norfolk, 2002.
- Phillips, R. A., Xavier, J. C., and Croxall, J. P.: Effects of satellite transmitters on albatrosses and petrels, *Auk*, 120, 1082–1090, 2003.

- Ronconi, R. A., Burger, A. E.: Foraging space as a limited resource: inter- and intra-specific competition among sympatric pursuit-diving seabirds, *Can. J. Zool.*, 89, 356-368, 2011.
- Ryan, P. G. and Moloney, C. L.: Effect of trawling on bird and seal distributions in the southern Benguela region, *Mar. Ecol. Prog. Ser.*, 45, 1–11, 1988.
- 5 Sabarros, P. S., Grémillet, D., Demarcq, H., Moseley, H., Pichegru, L., Mullers, R. H. E., Stenseth, N. C., and Machu, E.: Fine-scale recognition and use of mesoscale fronts by foraging Cape gannets in the Benguela upwelling region, *Deep-Sea Res. II*, 107, 77–84, 2014.
- Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F., and Wanless, S.: Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE* 4(4), e5379, 2009.
- 10 Scales, K. L., Miller, P. I., Embling, C. B., Ingram, S. N., Pirotta, E., and Votier, S. C.: Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird, *J. R. Soc. Interface*, 11, 20140679, 2014.
- Schneider, D. C.: The role of fluid dynamics in the ecology of marine birds, *Oceanogr. Mar. Biol. Annu. Rev.*, 29, 487–521, 1991.
- 15 Schneider, D. C.: *Quantitative Ecology. Spatial and Temporal Scaling*, Academic Press, San Diego, 1994.
- Schneider, D. C. and Duffy, D. C.: Scale-dependent variability in seabird abundance, *Mar. Ecol. Prog. Ser.*, 25, 211–218, 1985.
- Schneider, D. and Hunt, G. L. Jr.: A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska, in: *Marine Birds: their Feeding Ecology and Commercial Fisheries Relationships*, Nettleship, D. N., Sanger, G. A., and Springer, P. F., (Eds.), *Can. Wildl. Serv. Spec. Publ.*, Canadian Wildlife Service, 86–95, 1984.
- 20 Schwemmer, P., Güpner, F., Adler, S., Klingbeil, K., and Garthe, S.: Modelling small-scale foraging habitat use in breeding Eurasian oystercatchers (*Haematopus ostralegus*) in relation to prey distribution and environmental predictors, *Ecol. Model.*, 320, 322–333, 2016.
- Shealer, D. A.: Foraging behavior and food of seabirds, in: *Biology of Marine Birds*, Schreiber, E. A. and Burger, J., (Eds.), CRC Press, Boca Raton, 137–177, 2002.
- 25 Tasker, M. L., Webb, A., Hall, A. J., Pienkowski, M. W., and Langslow, D. R.: *Seabirds in the North Sea. Final report of phase 2 of the Nature Conservancy Council Seabirds at Sea Project November 1983–October 1986*, Nature Conservancy Council, Peterborough, 1987.
- Vandenabeele, S. P., Shepard, E. L. C., Grogan, A., and Wilson, R. P.: When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints, *Mar. Biol.*, 159, 1–14, 2012.
- 30 Vandenabeele, S. P., Grundy, E., Friswell, M. I., Grogan, A., Votier, S. C., and Wilson, R. P.: Excess baggage for birds: Inappropriate placement of tags on gannets changes flight patterns, *PLoS ONE*, 9(3), e92657, 2014.
- Wanless, S. and Okill, J. D.: Body measurements and flight performance of adult and juvenile Gannets *Morus bassanus*, *Ring. Migr.*, 15, 101–103, 1994.

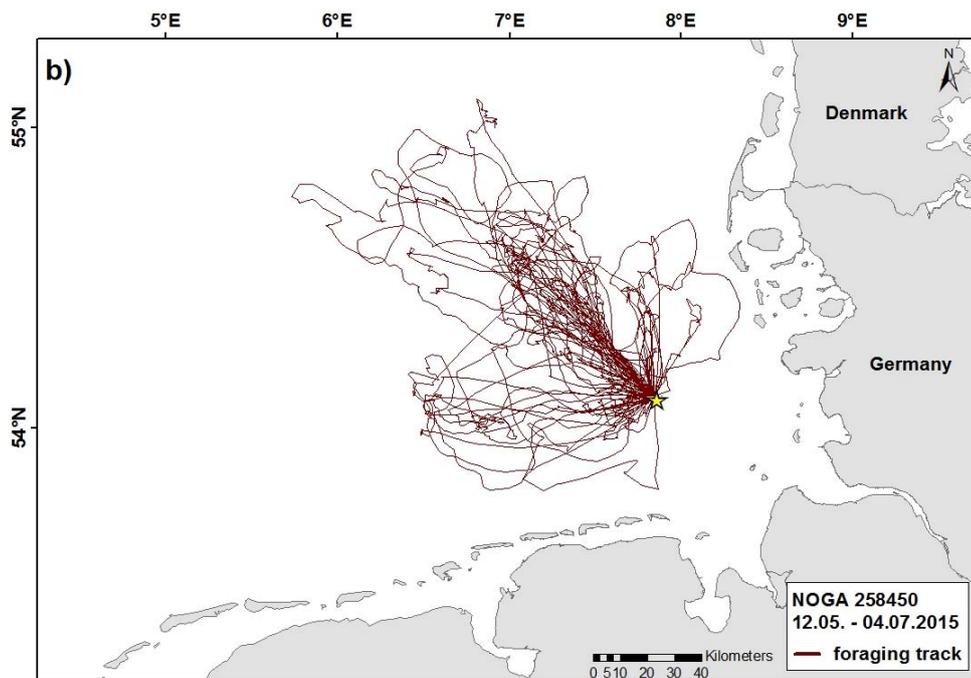
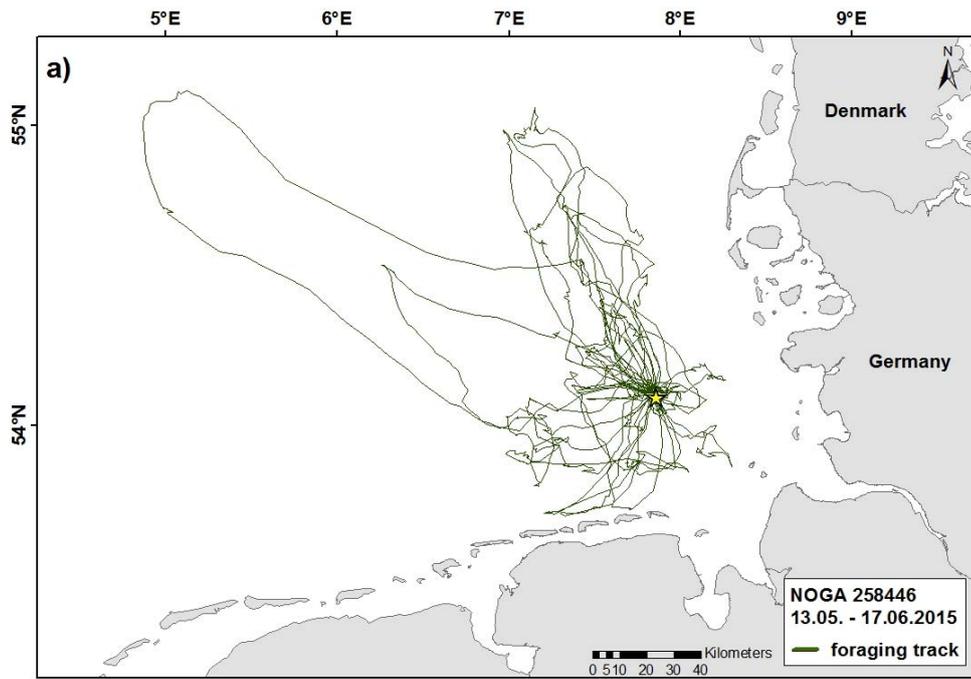
- Wilson, R. P. and Vandenabeele, S. P.: Technological innovation in archival tags used in seabird research, *Mar. Ecol. Prog. Ser.*, 451, 245–262, 2012.
- Wilson, R. P., Scolaro, J. A., Peters, G., Laurenti, S., Kierspel, M., Gallelli, H. & Upton, J.: Foraging areas of Magellanic Penguins *Spheniscus magellanicus* breeding at San Lorenzo, Argentina, during the incubation period, *Mar. Ecol. Prog. Ser.*, 129, 1–6, 1995.
- 5 Wilson, R. P., Grémillet, D., Syder, J., Kierspel, M. A. M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J. A., Bost, C.-A., Plötz, J. & Nel, D.: Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables, *Mar. Ecol. Prog. Ser.*, 228, 241–261, 2002.



Figure 1. Breeding colony of Northern Gannets on the island of Helgoland. Photo: S. Garthe.



5 **Figure 2.** Flying Northern Gannets with a Bird Solar GPS Logger attached to the tail feathers. Photo: K. Borkenhagen.



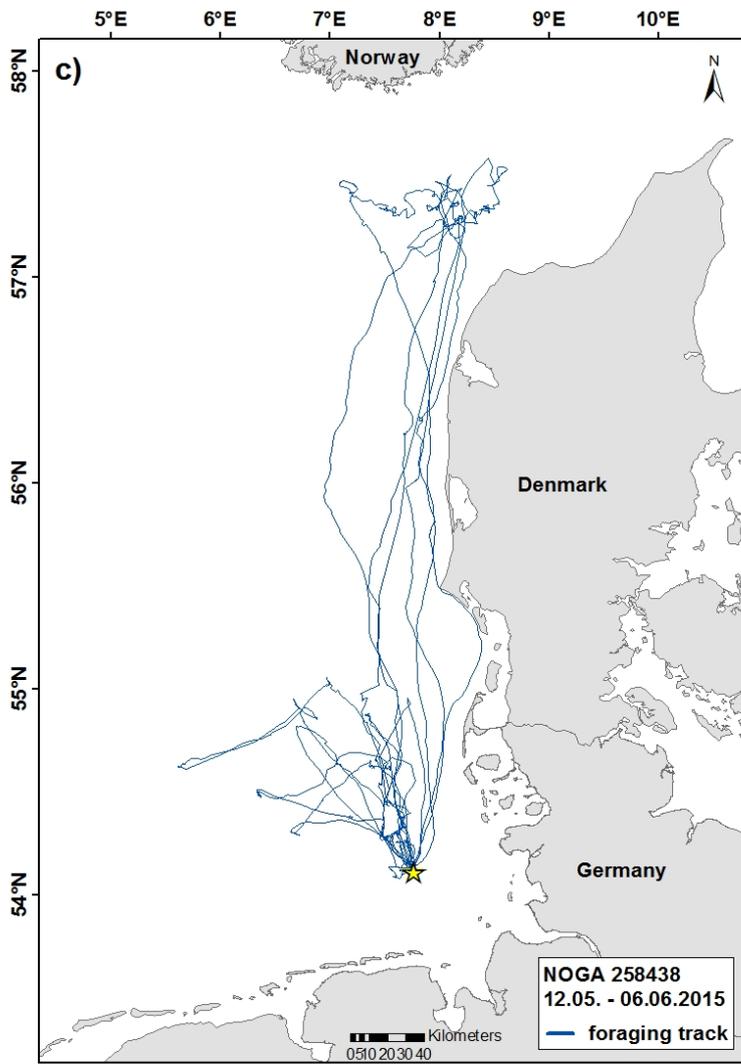


Figure 3. Flight patterns of three Northern Gannets (NOGA) breeding on Helgoland in 2015. Birds were tracked over 8 (a), 5 (b), and 3.5 (c) weeks, respectively.

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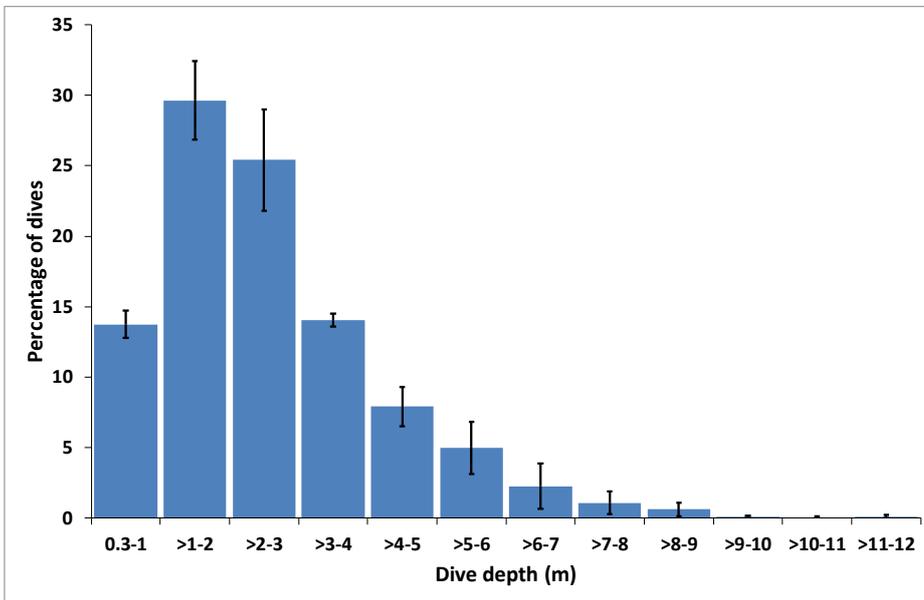


Figure 4. Dive depths of Northern Gannets in the German Bight, 2015. Data are based on dive recordings of four adults breeding on Helgoland. Vertical bars show mean values, extended lines show standard errors. Immersions of < 0.3 m were excluded as potentially indicating bathing and other behaviours.

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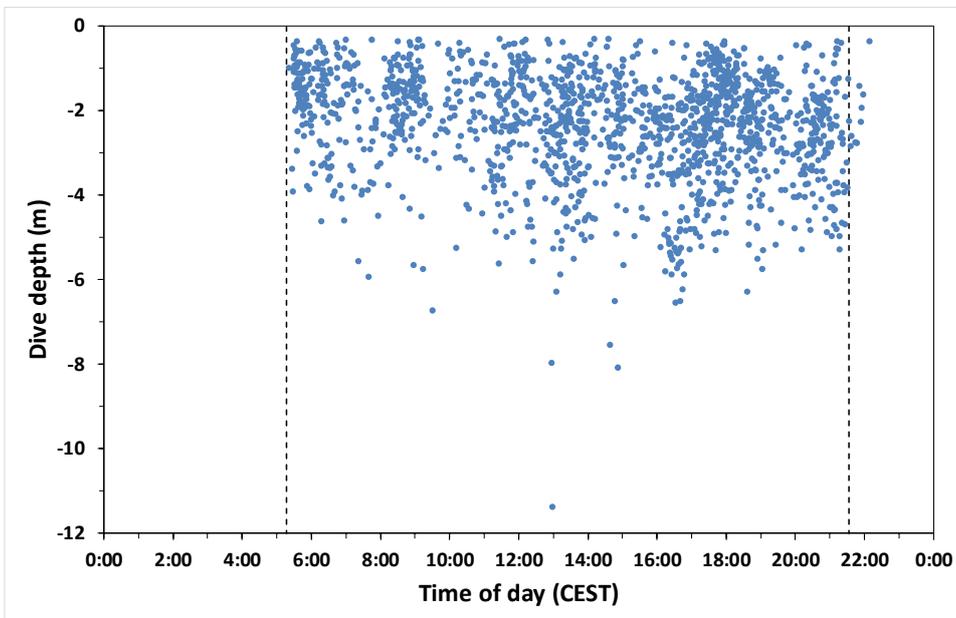


Figure 5. Diurnal rhythm in diving activity of Northern Gannets in the German Bight, 2015. Data are for the period 12–31 May 2015 and are based on dive recordings of three adults breeding on Helgoland. Each dot represents one dive, showing the maximum depth during the dive. Vertical dashed lines indicate sunrise and sunset for the median day of the period covered.

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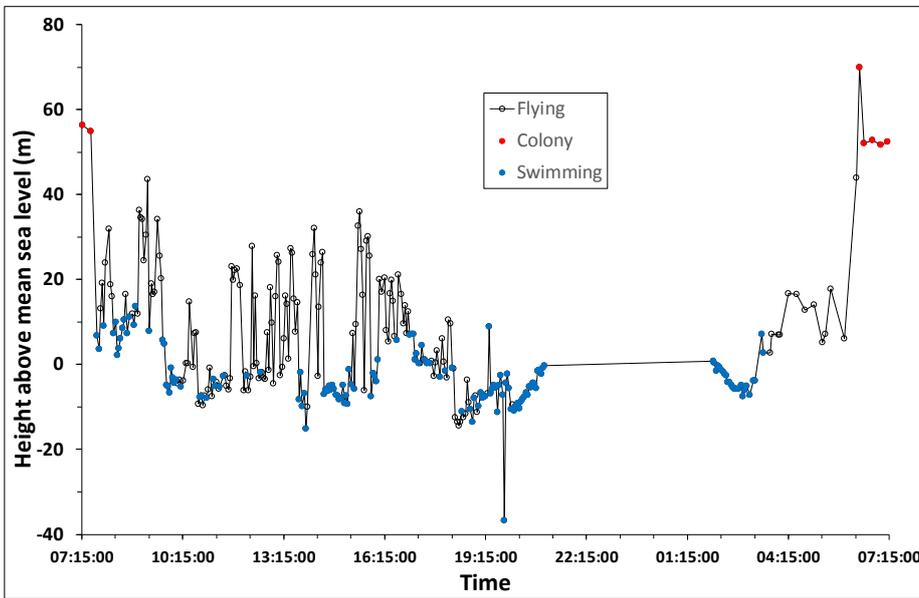


Figure 6. Altitude measurements for a Northern Gannet tracked in summer 2015 on Helgoland. Altitude measurements are related to activities 'in colony' (before and after the 22.7 h foraging trip), swimming, and flying. For details see text. Please note that this device was switched-off during the core darkness hours to save energy, and because birds are known to either stay at the nest site or rest at the sea surface during this period (as here).

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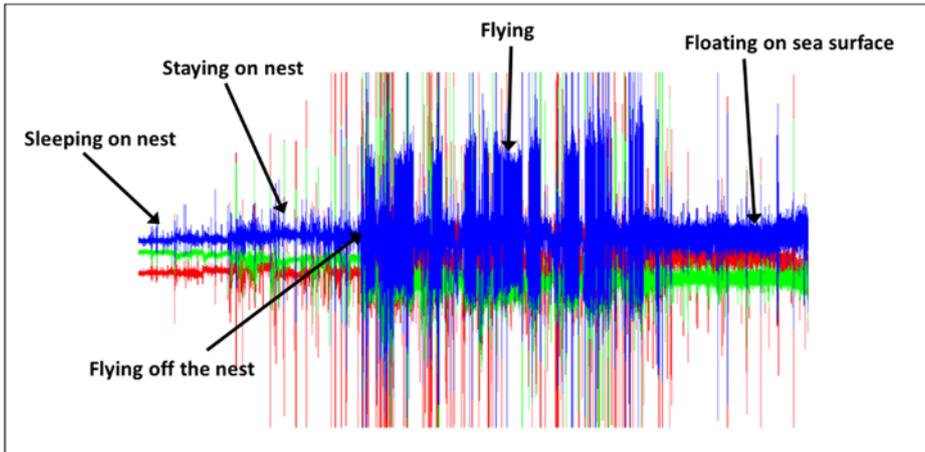


Figure 7 Accelerometer measurements for a Northern Gannet breeding on Helgoland. This example shows the values for the three different axes (red = x, green = y, blue = z) over 24 h, from 02:00 to 02:00 CEST on the next day. Different activities are indicated by arrows; higher peak indicate greater movement.

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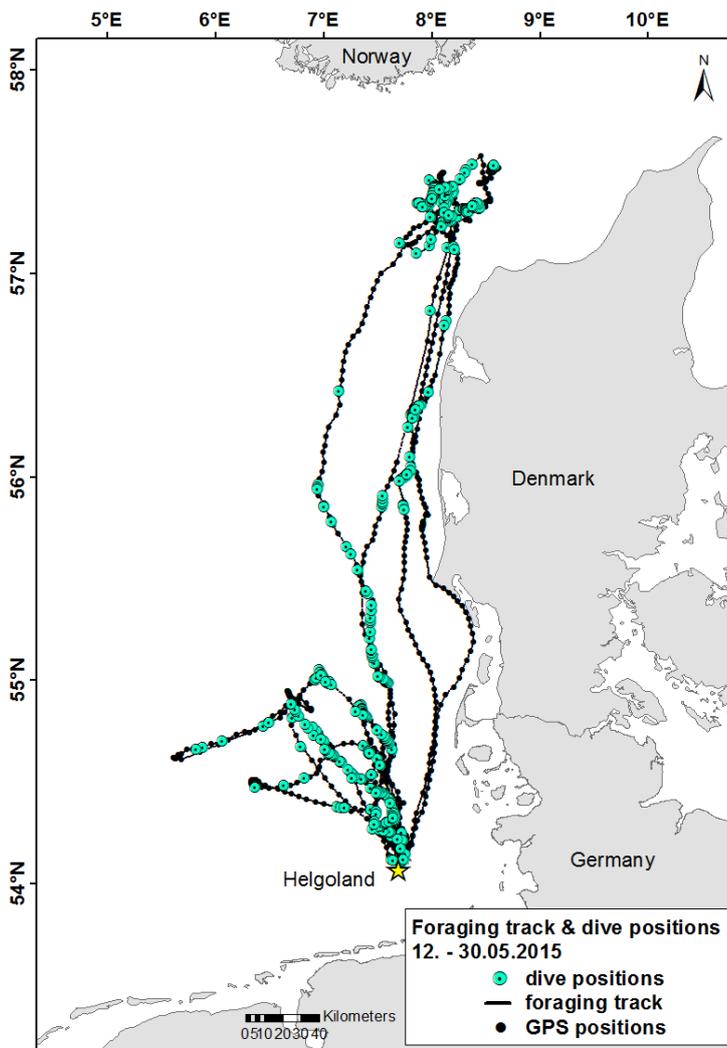


Figure 8. Foraging tracks and dive positions for the Northern Gannet shown in Fig. 3c. Please note that the data set is smaller than in Fig. 1c because only the synoptic GPS + pressure data are shown (the memory of the PTD logger was full after about 18 days).

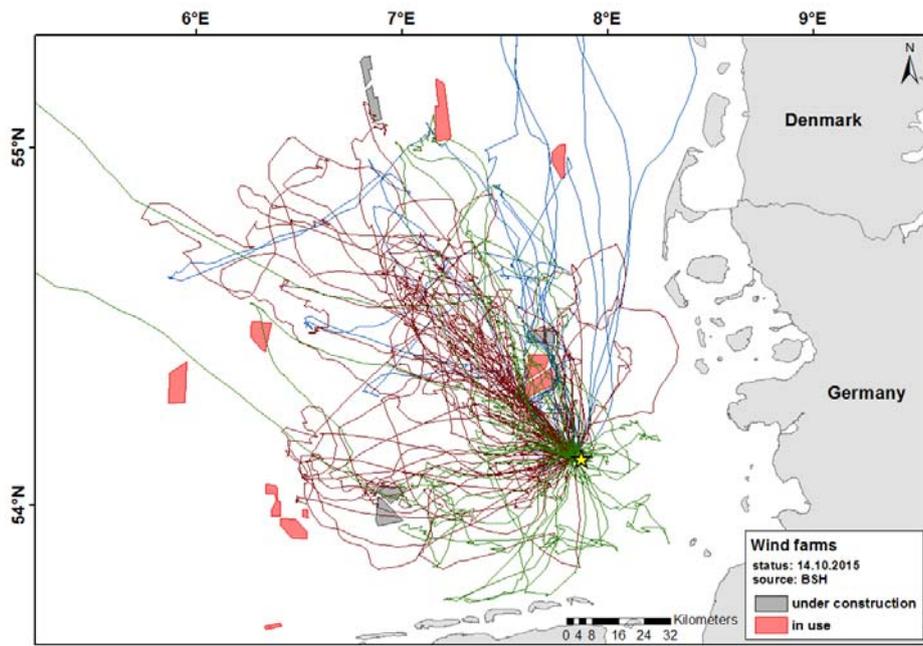


Figure 9. Overlap of flight patterns for the three Northern Gannets shown in Fig. 3 with the locations of wind farms in the German Bight. Information on the location and status of wind farms was collated from the Federal Maritime and Hydrographic Agency (BSH, pers. comm.) and from the Global Offshore Wind Farms Database (<http://www.4coffshore.com/offshorewind/>).

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