



Post-fledging movements, mortality and migration of juvenile northern gannets

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ABSTRACT: Studying the at-sea movements and behaviour of juvenile seabirds is logistically challenging, but new technologies now allow tracking birds on their first migration, giving a more complete picture of population-level spatial ecology. We investigated the post-fledging migration of juvenile northern gannets *Morus bassanus* from the world's largest colony, at Bass Rock, Scotland. We first examined the movements and survival of 38 juveniles over their initial days at sea with GPS precision for up to 53 d post-fledging. We then compared their migration journeys with those of 35 adults tracked with geolocators. Almost one-third of juveniles died within 2 mo of leaving the colony, and this mortality was often associated with apparent uncertainties in their direction of migration, including marked, abrupt and often repeated changes in bearing within the North Sea. Both juveniles and adults then migrated as far as the Canary Current Large Marine Ecosystem (CCLME) off the Atlantic coast of West Africa, initially taking both clockwise and counter-clockwise routes around the UK. Juveniles covered a distance each day similar to that of adults, but they reached the CCLME much more quickly, mainly because they travelled more directly, staying close to the coast throughout most of their migration, whereas adults additionally spent long periods over relatively restricted areas of ocean further offshore. The CCLME is a hotspot of unregulated fishing activity, and our findings highlight the importance of this region across different age-classes of birds, echoing previous calls that the regional strengthening of marine conservation should be a high priority.

KEY WORDS: Mortality · Migration · GPS tracking · Northern gannet · *Morus bassanus* · Juvenile

1. INTRODUCTION

Young animals typically have much higher mortality than adults, and understanding this difference is fundamental to the study of population structure, size and dynamics (Charlesworth 1980, Stearns 1992, Genovart et al. 2018). The main hypothesis invoked to explain higher mortality in early life is that a lack of experience and learning, combined with physical immaturity, results in poor proficiency in skills such as foraging and predator avoidance (Sullivan 1989,

Daunt et al. 2007, Riotte-Lambert & Weimerskirch 2013). In many species, an additional major challenge in early life is completing an autumnal migration to regions with more favourable climates and higher winter food availability (Alerstam et al. 2003, Rotics et al. 2016, Breed et al. 2018, Sergio et al. 2019).

Juveniles make autumn migrations along routes and to destinations of which they have no prior experience, with those that make the journey alone having to rely solely on innate navigation capabilities

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that may be less well developed than in adults (Mueller et al. 2013, Sergio et al. 2019). Inferior navigation can lead to less efficient travel, as seen in juvenile Scopoli's shearwaters *Calonectris diomedea*, whose first autumn migrations are longer and more sinuous than those of adults (Péron & Grémillet 2013) and in golden eagles *Aquila chrysaetos*, which transition from vector-oriented migrations (travelling north–south) as juveniles to goal-oriented migrations (travelling to a previously visited destination) as adults (Miller et al. 2016). Understanding the movements of naïve individuals has been identified as a priority area for marine research due to a need to better understand how juveniles disperse from natal areas, make use of different marine habitats and overlap with potential threats (Hazen et al. 2012, Riotte-Lambert & Weimerskirch 2013). Studying the at-sea movements and behaviour of juvenile seabirds remains logistically challenging, but new technologies now allow tracking of birds on their first migration, allowing a more complete picture of population-level spatial ecology (de Grissac et al. 2016, Afán et al. 2019, Borrmann et al. 2021).

Northern gannets *Morus bassanus* (hereafter termed gannets) typically breed for the first time aged 5 yr (Nelson 2002) and forage in neritic waters (Wakefield et al. 2015). At the end of the breeding season, adults at European colonies migrate south as far as the Atlantic coast of West Africa (Kubetzki et al. 2009, Deakin et al. 2019, Grecian et al. 2019), with evidence of oriented chain migration (where populations move uniformly southwards) by birds from different colonies (Fort et al. 2012). Juveniles are independent of their parents after fledging (Nelson 2002) and therefore need to learn critical foraging, flight and navigation skills without parental guidance, possibly contributing to high mortality during their first year (Wanless et al. 2006). They may remain on the water for several days post-fledging while they lose mass and gain sufficient strength to take off from the water surface (Wanless & Okill 1994), yet little is known about their subsequent movements or behaviour. Ring recoveries, together with tracks of 4 juveniles from a colony in the English Channel, suggest that like adults they may migrate as far south as West Africa (Nelson 2002, Grémillet et al. 2015), while juvenile gannets tracked from 2 colonies in northeast Canada dispersed widely and overwintered from the mid-Atlantic region to the Gulf of Mexico (Spiegel et al. 2017). However, the development of directed movements, migration routes and speeds of travel have not previously been examined. Here we investigate the post-fledging movements and migration of

juvenile gannets from the world's largest colony (Murray et al. 2014), at Bass Rock, Scotland (56° 6' N, 2° 36' W). We tracked birds with GPS precision for up to 53 d post-fledging, allowing us first to examine the movements and survival of juveniles over their initial days at sea, and then to compare their migration journeys with those of adults tracked with geolocators from the same colony, specifically examining migration routes and speeds of travel.

2. MATERIALS AND METHODS

2.1. Sampling of birds

Forty-two juvenile gannets that had left their nest sites but were still at the colony were captured using a 6 m telescopic pole fitted with a metal noose or by hand on 5 October 2018 ($n = 21$) or 20 September 2019 ($n = 21$), prior to departing to sea. Most gannet chicks at Bass Rock currently fledge in mid-to-late September each year (2–3 wk later than in the 1960s; Nelson 2002). Hence, sampling was around the peak of fledging in 2019 and slightly after the peak in 2018. Each bird was weighed (to the nearest 25 g using a spring balance) and fitted with a metal British Trust for Ornithology (BTO) ring inscribed with a unique identification number. A solar powered Argos GPS-platform terminal transmitter (GPS-PTT; Microwave Telemetry), weighing 45 g (2018) or 30 g (2019) was then attached to the upper side of the 3 central tail feathers using Tesa © tape and cable ties (additional weight = 4 g). Each GPS-PTT was programmed to record a GPS location once an hour between 06:00 and 20:00 h, and locations were relayed to the Argos satellite system every 24 h. Handling time of birds was no longer than 20 min, after which time birds were released at the colony. The weight of the GPS-PTT in each case was <2% of body mass, which was considered sufficiently small to minimise risk of adverse effects (Phillips et al. 2003, Cleasby et al. 2015, Bodey et al. 2018).

Adult gannets attending a separate sample of chicks at Bass Rock during July and August 2018 ($n = 26$) and 2019 ($n = 36$) were caught using the same method as juveniles, weighed and fitted with a metal BTO ring. A combined geolocation–immersion logger (Mk 3006 British Antarctic Survey, $n = 58$; Initgeo C65, Migrate Technology Ltd, $n = 4$) attached with 2 cable ties to a plastic ring was then fitted to the tarsus of each bird. The total mass of the attachment was <10 g (~0.3% of adult body mass). On release all birds returned to their

chick and resumed normal behaviour almost immediately. Geolocators were then recovered (60%) between April and August in the years following device deployment.

2.2. Track reconstruction

Argos locations from GPS-PTTs on juveniles were filtered by speed and location class (LC) to remove erroneous locations using the R package 'argosfilter' (Freitas 2012, Langston et al. 2013; speeds $>25 \text{ ms}^{-1}$ and LC Z were removed). GPS (precise to $<100 \text{ m}$) and Argos PTT location classes 3, 2, 1, A and B (precision <250 to $>1500 \text{ m}$; Argos 2016) were then combined to reconstruct movements. All locations with duplicated dates and times were screened, and only the duplicate with greater precision was retained. A total of 15 834 valid locations was received of which 6780 (43%) were GPS and 9054 (57%) were ARGOS PTT. GPS locations were not obtained overnight, but average speeds between 20:00 and 06:00 h indicated that, like adults (Hamer et al. 2000, Furness et al. 2018), juveniles did not fly at night. Hence, overnight travel speeds were removed from the analysis.

Geolocators on adults recorded light intensity and time, which were used to generate a location at dawn and dusk each day using the R package 'GeoLight' (Lisovski & Hahn 2012). Data from 21 d before and 14 d after the autumn equinox were removed due to unreliable estimates of latitude during this period. Each location was then re-estimated using an iterative forward-step selection framework to create a cloud of 2000 possible locations in each case. Locations within each cloud of points were weighted according to daily median sea surface temperature (SST) recorded by the logger and daily mean National Oceanic and Atmospheric Administration (NOAA) SST data at 0.25° resolution (Reynolds et al. 2007, Physical Sciences Division 2019) using the R package 'probGLS' (Merkel et al. 2016). The most probable track was then obtained using the geographic median position from each weighted location cloud. A test of this approach using data for 2 species of albatross in the Southern Ocean indicated a median error of 145–185 km compared to locations obtained using GPS (Merkel et al. 2016). Nonetheless, while the lower precision of the geocator data may have resulted in greater variance in estimates of daily distances travelled by adults than by juveniles in our study, it would not have biased the comparison of mean distances travelled.

2.3. Juvenile fledging and survival at sea

Juveniles were considered to have fledged once GPS data identified them as being $\geq 0.5 \text{ km}$ from the colony, with subsequent flight indicated by a speed of $\geq 3.5 \text{ km h}^{-1}$ between consecutive GPS locations (Wakefield et al. 2013). Birds were considered to have died if: (1) GPS data indicated they did not fledge or take flight from the water once fledged; (2) subsequent GPS data indicated one or more complete days of inactivity with no movement (if on land) or only slow drifting of location (if at sea) before the signal was lost, and/or; (3) they were recovered post-mortem by a member of the public. In contrast, occasions when the signal was lost suddenly during normal activity of the bird were assumed to have resulted from failure of the tag or attachment. All birds recovered post-mortem had shown no movement or slow drifting at the coast for at least a complete day prior to the final data transmission.

2.4. Migration patterns of juveniles and adults

We investigated the development of flight activity among juveniles by estimating mean hourly displacement per day once birds were first airborne, calculated as the sum of straight-line distances between consecutive GPS locations during daylight hours divided by the number of hours. We then compared the migration of adults and juveniles by inspecting maps of their journeys. To compare migration parameters (time in days, distance in km, etc.), we used the subset of birds of each age-class that were tracked beyond the Strait of Gibraltar (36.20° N) to the coast of West Africa. This ensured that our comparison was not confounded by differences in the migration goals of birds (Kubetzki et al. 2009, Grecian et al. 2019). In each case, the time taken in migration was estimated in days from the first day birds took flight from the water (juveniles) or from when they left the colony for the winter (adults) until their first day south of the Strait of Gibraltar. Adult departure dates were determined from immersion data indicating when the bird last spent time at the colony overnight (birds do not fly in darkness, so an absence of immersion in salt water overnight indicated time spent on land, presumably at the colony). Departure was then confirmed from geocator data after 6 October each year (see Section 2.2 above), indicating the bird was always remote from the colony at both dawn and dusk each day. The total distance travelled was calculated as the cumulative

distance between each consecutive location. To compare distances and travel speeds of juveniles and adults, the combined GPS-PTT data for juveniles were subsampled to include only the first and last location recorded each day. Daily distance travelled (km d^{-1}) was then estimated by dividing the total distance travelled by the number of travel days. We used a general linear mixed model (LMM) using restricted maximum-likelihood (REML), specified in the R-3.5.1 package 'nlme' (R Core Team 2016, Pinheiro et al. 2018) to test for the effects of travel direction, age-class, year and their interactions on the distances travelled per day and the number of days spent travelling to the Strait of Gibraltar. Models included bird identity as a random effect to account for repeated measures. The number of days spent travelling was right skewed and so was log-transformed prior to analysis. Model selection was based on Akaike's information criterion adjusted for small sample size (AIC_c), with the top model ($\Delta\text{AIC}_c > 2$) refitted to obtain *p* values in each case (Burnham & Anderson 2002). All values are presented as mean \pm SD.

3. RESULTS

3.1. Collection of data

We tracked 38 juveniles for up to 53 d post-fledging (*n* = 17 in 2018, 21 in 2019; 4 tags or attachments failed within 3 d of deployment or before the bird fledged in 2018 and so did not provide useful data). There was no difference between years in the number of days juveniles were tracked at sea (in 2018, 25 ± 13.5 d, *n* = 17; in 2019, 30 ± 14.5 d, *n* = 21; $F_{1,36} = 1.3$, *p* = 0.3) or the average distance travelled per day (in 2018, 59.2 ± 49.3 km, *n* = 17; in 2019, 61.2 ± 44.2 km, *n* = 21; $F_{1,36} = 0.02$, *p* = 0.9). We obtained geolocator data from 35 adults (in 2018–2019, *n* = 21; in 2019–2020, *n* = 14), with data obtained from 7 individuals in both years. Mean departure dates of adults were similar each year (21 September in 2018, 25 September in 2019), corresponding broadly with the peak in chick fledging, although the latest recorded adult departure was not until 15 October each year. Of the 38 juveniles tracked, 11 birds (29%) died before completing migration (6 in 2018, 5 in 2019; see Table S1 in Supplement for details; www.int-res.com/articles/suppl/m671p207_supp.pdf), 12 birds (44% of survivors) were tracked to the Canary Current Large Marine Ecosystem (CCLME) off the coast of West Africa, and 15 birds (56% of survivors) were travelling rapidly at intermediate locations between Bass

Rock and the Strait of Gibraltar when their signal was lost, presumably due to failure of the transmitter or attachment (Fig. 1). There was no difference in pre-fledging body masses between the 11 birds considered to have died before completing migration (3348 ± 251 g) and the remaining 27 birds (3373 ± 362 g; $t_{36} = 0.2$, *p* = 0.8). Of the 35 adults tracked, 23 (66%) travelled as far as West Africa and 12 (34%) overwintered at intermediate locations, with overall movements ranging as far north as the southern Norwegian Sea and as far west as the mid-Atlantic ridge (Fig. 1).

3.2. Initial movements of juveniles at sea

After fledging, one juvenile died without ever becoming airborne from the sea, while the remaining 37 birds next took flight after 2–9 d (mean = 4 d), then in most cases spent a further 3–4 d interspersing short flights with periods resting on the water. Consequently, the mean hourly displacement of juveniles during hours of daylight increased significantly from a mean of 13.5 km ($\text{SD} \pm 9.26$) during the initial 5 d after first becoming airborne from the water to 21.1 ± 11.3 km during the following 5 d (paired *t*-test; $t_{25} = 2.70$, *p* = 0.012; 26 birds had sufficient data to calculate speeds accurately over this period) then changed little thereafter (19.4 ± 12.6 km over the following 5 d).

3.3. Direction, speed and directness of travel

Juveniles and adults migrated in both clockwise and counter-clockwise directions around the UK (juveniles: 17 clockwise, 16 counter-clockwise; adults: 17 clockwise, 8 counter-clockwise). However, juveniles stayed close to the coast except when south of Ireland and crossing the Bay of Biscay (75% of all locations for juveniles were ≤ 15 km from the nearest coastline), whereas adults were apparently located further offshore at all stages of migration, including over winter (Figs. 1 & 2).

Despite initial slow travel, on average juveniles that were tracked to the Strait of Gibraltar covered distances per day very similar to those of adults once they had first become airborne from the sea (334 ± 136 and 347 ± 162 km, respectively; $F_{1,19} = 0.15$, *p* = 0.7). There was no significant difference between years or directions of travel (clockwise or counter-clockwise) in distances travelled per day by adults or juveniles (Table S2 & S3; *p* > 0.1 in each case). Despite travelling similar distances to adults per day,

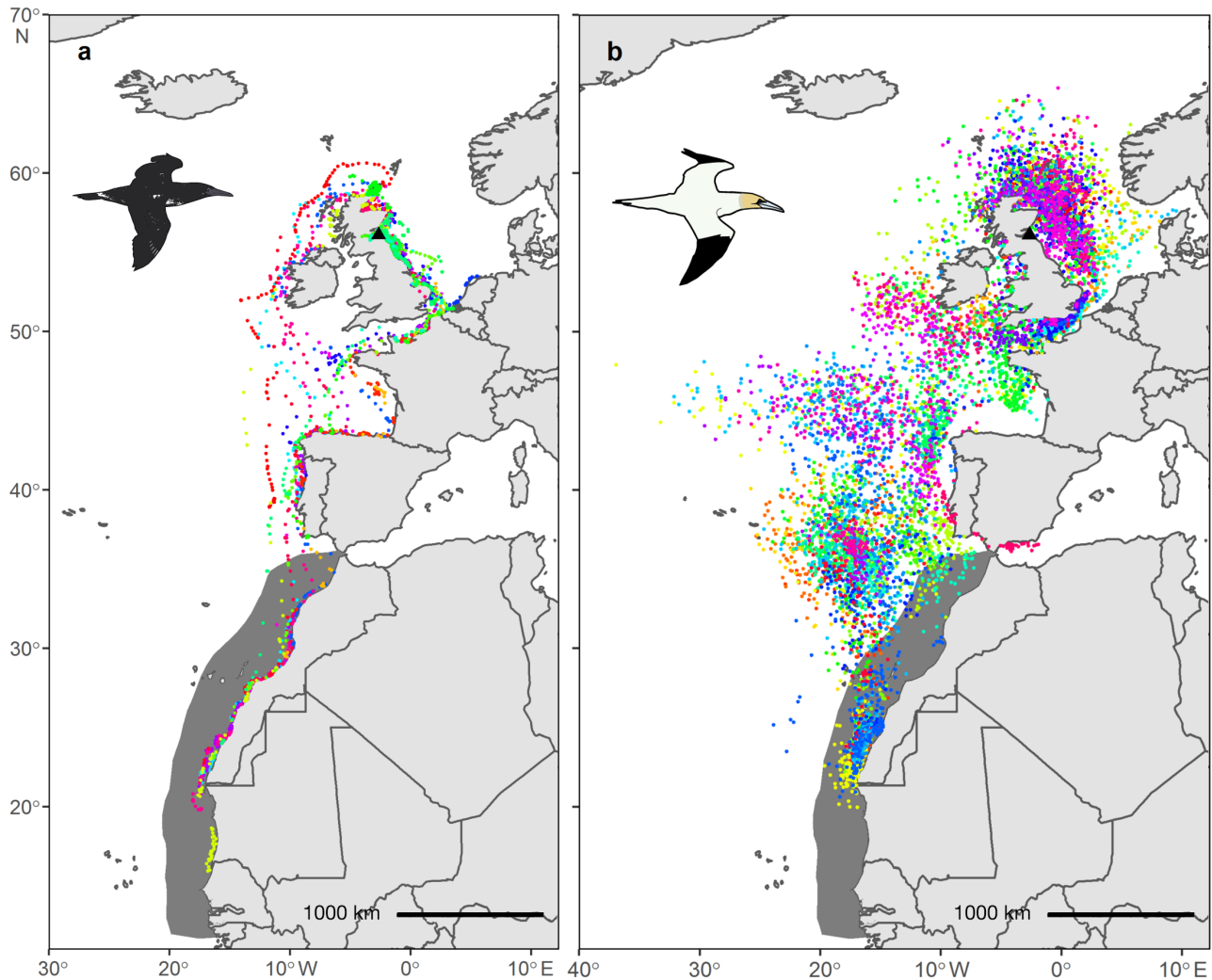


Fig. 1. (a) GPS locations of 41 juvenile gannets tracked from Bass Rock (black triangle) between September and November 2018 and 2019; (b) GLS locations of 35 adults tracked from Bass Rock between September and January 2018–19 and 2019–20. Individual birds identified by colour. Shaded area in (a) and (b) shows the Canary Current Large Marine Ecosystem

juveniles took many fewer days than adults to pass the Strait of Gibraltar (juveniles, 22 ± 10 d; adults, 68 ± 32 d; $F_{1,23} = 52.7$, $p < 0.001$). This difference in journey times was mainly because, in addition to periods of rapid direct travel, adults apparently spent longer periods (more than a month in some cases) over relatively restricted areas of ocean en route to the CCLME whereas juveniles did not. In particular, adults appeared to spend time northeast of Bass Rock and in an area of ocean roughly between Iberia, Madeira and the Azores Islands (Figs. 1 & 2). Adults also took significantly fewer days to reach the Strait of Gibraltar in 2018 than in 2019 (Table 1; $F_{1,23} = 15.47$, $p < 0.001$), but the direction of travel had no significant effect on the number of days taken by juveniles or adults, and there was no significant dif-

ference between years in the number of days taken by juveniles (Table S2 & S3).

3.4. Juvenile mortality

Of the 11 juveniles that died during migration, 4 apparently failed to navigate effectively, heading west from Bass Rock and either circling the Firth of Forth for several days or, in one case, heading overland before dying. A further 5 birds had uncertain migration routes characterised by multiple abrupt changes in direction (Fig. 3). Such apparently flawed migration did not necessarily result in birds dying, but overall, mortality was higher among such birds (10 of 21 individuals) than among those that migrated without any

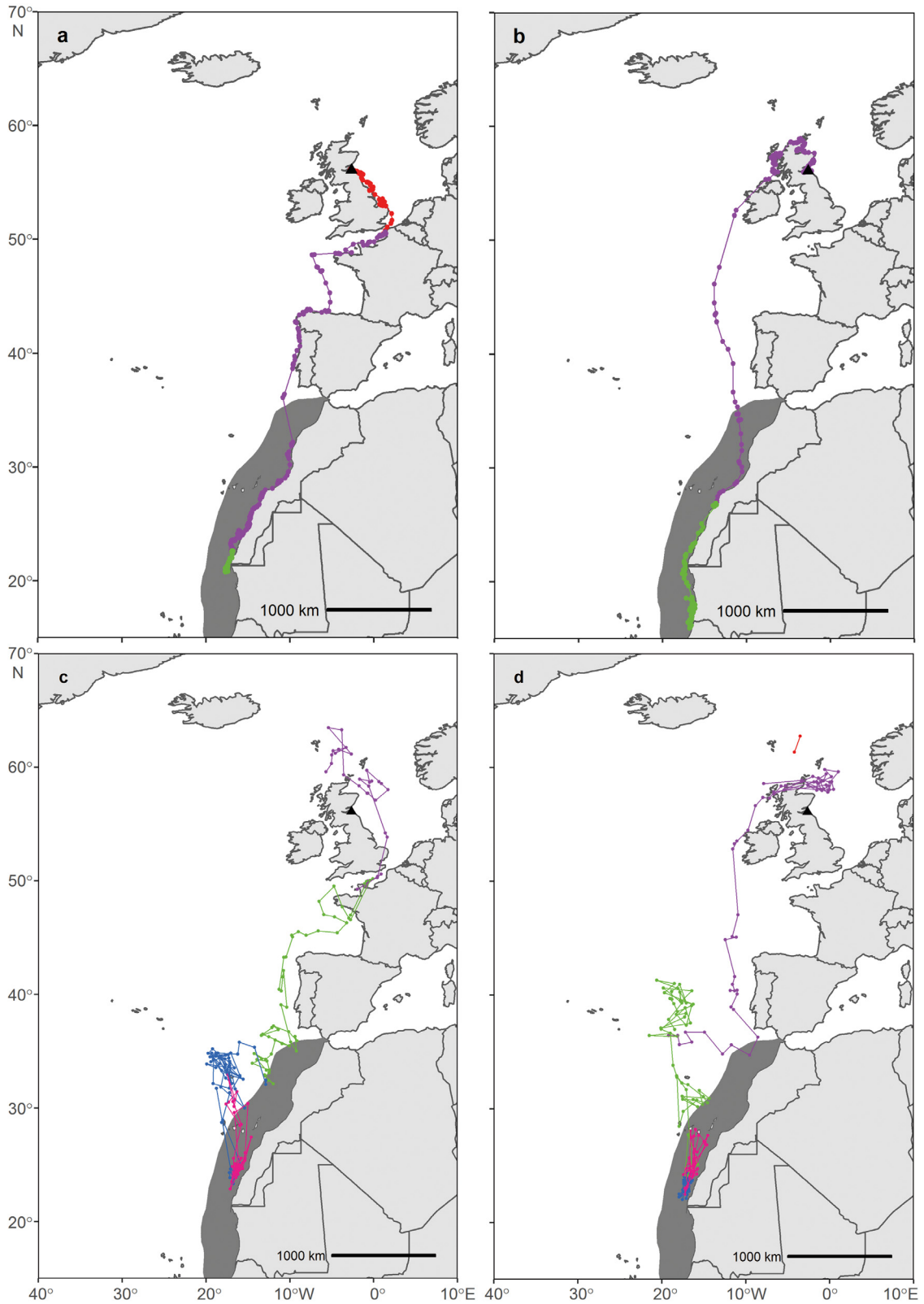


Fig. 2. Examples of (a,c) clockwise and (b,d) counter-clockwise migration routes of (a,b) juvenile and (c,d) adult gannets from Bass Rock. Locations coloured according to month: red = September, purple = October, green = November, blue = December, pink = January. Shaded area: Canary Current Large Marine Ecosystem, black triangle: Bass Rock

Table 1. Mean (SD) migration summary for juvenile and adult gannets from Bass Rock, Scotland, travelling to the Strait of Gibraltar via the English Channel (clockwise) or via Scotland and the west coast of Ireland (counter-clockwise). Travel direction of 3 adults could not be determined

	2018		2019	
	Juveniles	Adults	Juveniles	Adults
Birds (n)	5	12	7	4
Days to reach Strait of Gibraltar	27 (12)	54 (19)	18 (7)	112 (16)
Distance (km) d ⁻¹	265.5 (110.0)	386.5 (150.0)	382.7 (138.0)	229.8 (157.1)

a key destination for juvenile gannets migrating from Bass Rock. Our data reveal strong similarities between juveniles and adults in the large-scale pattern of migration, including the use of both clockwise and counter-clockwise routes around the UK and Ireland. However, there were also clear differences between age-classes in finer-scale movements and speeds of travel. These included marked and abrupt changes in the direction of travel of some juveniles within the North Sea, with potential implications for post-fledging survival and a marked restriction of juveniles to waters within 15 km of the coast throughout much of their migration and off West Africa, with implications for potential interactions with offshore wind farms and marine fisheries.

4.1. Fledging, flight characteristics and mortality at sea

A number of studies of seabirds have recorded a positive relationship between nestling body mass and post-fledging survival (Perrins et al. 1973, Coulson & Porter 1985, Dann 1988). In contrast, we recorded no such relationship, probably because most fledglings were in good condition when tagged (body mass of all but 5 birds exceeded the average adult body mass of ~3 kg; Table S1). In addition, large fat deposits may prevent birds from achieving the strength-to-weight ratio required to take off from the water surface (Montevecchi et al. 1984, Navarro 1992). In accordance with this notion, we found that aerial dispersal from the colony after fledging began only after a delay of up to 9 d,

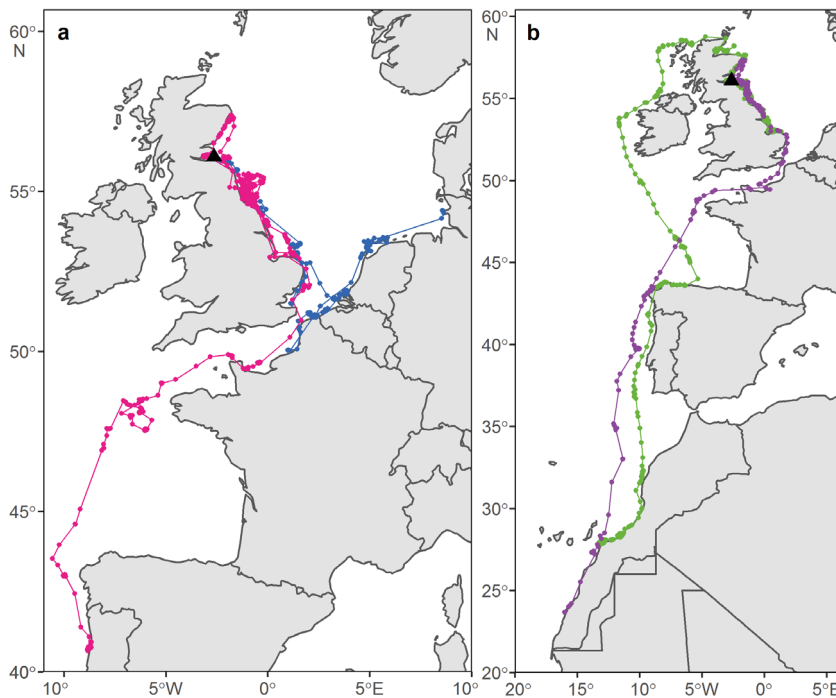


Fig. 3. Examples of juvenile gannets with non-monotonic travel. (a) Bird 1 (pink) travelled between the coasts of Aberdeenshire and Norfolk with several changes in direction over a period of 31 d before eventually heading southwards through the English Channel and dying on the North West coast of Portugal; Bird 2 (blue) initially travelled south along the North Sea coast to the Thames Estuary then made several changes in direction in the southern North Sea before travelling north along the Dutch coast to the Wadden Sea and dying on the North Frisian Coast. (b) Bird 3 (green) travelled ~400 km south over 7 d to the north coast of Norfolk before making an about turn, returning to the colony over the next 9 d then continuing north to reach West Africa via the west coast of Ireland; Bird 4 (purple) headed north to Peterhead then reversed its direction of travel reaching West Africa via the English Channel. Tracks reconstructed using GPS and PTT locations. Black triangle: Bass Rock

abrupt changes in direction (1 of 16 individuals; χ^2 using Fisher's exact test; $\chi^2_1 = 7.4$, $p = 0.01$).

4. DISCUSSION

The results of our study highlight the importance of the CCLME along the Atlantic coast of West Africa as

during which time birds were drifting on the water, a similar period to that observed in juvenile wandering albatrosses *Diomedea exulans* (Weimerskirch et al. 2006). This delay, together with adverse effects of greater body mass on manoeuvrability and energy expenditure during flight (Amélineau et al. 2014), may result in a non-linear relationship or no relationship between pre-fledging body mass and sub-

sequent survival, as reported in Atlantic puffins *Fratercula arctica* (Harris & Rothery 1985) and shy albatrosses *Thalassarche cauta* (Alderman et al. 2010). Moreover, in wandering albatrosses, male chicks in poorer condition at fledging had higher subsequent survival, probably due to benefits of lower wing loading among young birds (Weimerskirch et al. 2000). In our study, once birds had become airborne from the sea, they increased their mean hourly displacement during daylight hours over the following 5–10 d, consistent with an increasing capacity for sustained flight. Thereafter, they travelled daily distances very similar to those of adults, suggesting that they acquired some components of flight capability relatively quickly, as also found in great frigatebirds *Fregata minor* (Corbeau et al. 2020) but in contrast to brown boobies *Sula leucogaster*, which have a long duration of post-fledging parental care during which they only gradually acquire efficient flight (Yoda et al. 2004).

About 60% of gannets die within their first year at sea (Wanless et al. 2006), and our satellite data suggest that a high proportion of this mortality occurs within a short period after fledging; almost one-third of juveniles died within 2 mo of leaving the colony, with over half of this mortality (60%) occurring close to the colony within the first few days at sea. This pattern of mortality is similar to that found in ring recovery data; from 1600 birds ringed as chicks at Bass Rock, 589 birds (37%) were found dead before the end of October of the same year (Table 23 in Nelson 2002). In our study, birds were sampled slightly after the peak of fledging in 2018, but there was no indication that this led to the selection of lower quality individuals, as post-fledging mortality was very similar in the 2 yr studied (Table S1), as were distances travelled per day (Table 1). High mortality during the first few months after attaining independence has also been recorded in several other species of seabird (Daunt et al. 2007, Guo et al. 2010, Afán et al. 2019). For instance, 49% of shy albatrosses satellite-tagged in Tasmania were assumed to have died within 5 d of fledging, probably due largely to foraging failure of naïve birds (Alderman et al. 2010).

High levels of post-fledging mortality emphasise the critical importance to juveniles of gaining proficiency in flight, foraging and navigational skills. In our study, juvenile mortality was often associated with uncertainties in the direction of migration, including marked, abrupt and often repeated changes in bearing within the North Sea. Such

changes may have resulted from birds experiencing poor foraging success or encountering unfavourable wind conditions, potentially including both strong head winds that may have impeded progress (Lane et al. 2019) and light winds that may entail greater energy expenditure during flight in flap-gliding species such as gannets (Amélineau et al. 2014). Another possibility is that at least some juveniles followed adults, potentially allowing them to learn migration routes and foraging areas (Mueller et al. 2013), with some birds making inappropriate choices such as following adults still engaged in central-place foraging from the colony. Evidence for social learning in gannets has been recorded during the breeding season, when younger birds may follow more experienced birds to and from colonies (Wakefield et al. 2019). However, we found no indication of juveniles following adults on migration. Rather, adults departing at a similar time to juveniles headed mainly into the northern North Sea following the breeding season whereas juveniles travelled northwards and southwards mainly along the coast, probably using topography to aid their navigation (Pollonara et al. 2015). Moreover, abrupt changes in direction were not always associated with mortality, and juveniles may simply have been motivated to explore their natal area or search for foraging grounds before orienting to their migratory direction (Catry et al. 2011, Syposz et al. 2021).

4.2. Characteristics of migration

Of the 27 juveniles presumed not to have died before completing their migration, 44% were tracked to the CCLME and the remainder were travelling rapidly at intermediate locations between Bass Rock and the Strait of Gibraltar when their signal was lost. The CCLME is among the most productive marine ecosystems globally (Sambe et al. 2016) and is a key wintering ground for a suite of European seabirds (Camphuysen & van der Meer 2005, González-Solís et al. 2007, Grecian et al. 2016), including adult gannets (Grémillet et al. 2015, Grecian et al. 2019, this study). Our data highlight that it is also an important destination of juvenile gannets on their first migration. However, we also found that about one-third of adults did not migrate as far south as West Africa, in keeping with previous studies at this colony and elsewhere (Kubetzki et al. 2009, Grecian et al. 2016, Deakin et al. 2019, Grecian et al. 2019). This raises the possibility that some juveniles whose signal was lost north of Gibraltar may also have

remained in European waters. This suggestion is supported to some extent by aerial survey data indicating the presence of young birds (aged 1–3 yr) in the Bay of Biscay over winter (Pettex et al. 2019), although the origin of these birds and the proportion of juveniles present were not known.

Although juveniles travelling to the Atlantic coast of West Africa moved a distance each day similar to that of adults, they reached the CCLME much more quickly than adults. It might have been expected that adults would migrate more quickly and efficiently than juveniles due to their greater age and experience (Thorup et al. 2003, Riotte-Lambert & Weimerskirch 2013, de Grissac et al. 2016). However, the shorter journey times of juveniles in our study resulted mainly from them travelling more directly and staying close to the coast throughout most of their migration and off West Africa whereas adults additionally spent long periods (more than a month in some cases) over relatively restricted areas of ocean further offshore, particularly during October and November. This included time spent over the European continental shelf and deeper waters to the northeast of Bass Rock and over deep waters between the Atlantic coasts of Portugal and West Africa and the mid-Atlantic ridge, in areas of ocean with high productivity that are also visited over winter by a range of other species (Catry et al. 2011, Grecian et al. 2016) and by adult gannets from other European colonies (Fort et al. 2012). Hence, shorter journey times were probably due to juveniles having less flexibility than adults to explore offshore waters during their migration, possibly due to poorer knowledge of and experience with oceanographic conditions, poorer navigational skills or a benefit of less competition with adults (Votier et al. 2011, 2017, Grecian et al. 2018, Pettex et al. 2019). Wind speeds and wave heights increase with increasing distance from the Atlantic coast of West Africa (Semedo 2018), and so by staying close to the African coast, juveniles may also have avoided more taxing weather conditions further offshore.

Gannets from European populations face a number of potential threats during migration and over winter, including adverse interactions with offshore wind installations and marine fisheries. The southern North Sea holds the world's highest concentration of operational and planned offshore wind farms, presenting a potential risk to birds through both collision mortality and barrier effects (Furness et al. 2013, Garthe et al. 2017, Lane et al. 2020). Our data indicate that while both juveniles and adults migrate through this area in autumn, adults are potentially more likely to

encounter wind turbines, as a result of apparently migrating further offshore, thus placing them at much greater risk than juveniles of adverse effects. In addition, our data indicate that both juvenile and adult gannets from Bass Rock winter within the CCLME, as also found in a small sample of birds tracked from a colony in the English Channel (Grémillet et al. 2015). This region experiences among the highest fishing effort globally and is a hotspot of illegal, unreported and unregulated fisheries, posing substantial threats to birds from depletion of prey stocks and both incidental and intentional bycatch in fishing gear (Laurans et al. 2004, Camphuysen & van der Meer 2005, Agnew et al. 2009). Our data highlight the vulnerability of juveniles to these threats in addition to adults, as also found in Scopoli's shearwater (Afán et al. 2019). The impact of juvenile mortality on overall population size is less severe than that of adult mortality, but younger birds are more vulnerable to bycatch (Belda & Sanchez 2001, Watkins et al. 2008) as well as being potentially more affected than adults by depletion of prey. Our findings highlight the importance of this region across different age-classes of birds, echoing previous calls that the regional strengthening of marine conservation should be a high priority (Grémillet et al. 2015, Grecian et al. 2016, Afán et al. 2019).

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