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East or west? Migration routes and wintering sites of Northern Gannets *Morus bassanus* from south-eastern Iceland

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Abstract Northern Gannets (*Morus bassanus*) are distributed in eastern and western North Atlantic breeding populations. The species' colonies in Iceland lie between the European and North American colonies. To better understand their migratory patterns and to explore potential connections between the western and eastern populations, geo-location devices were used to track the migrations of Northern Gannets from Iceland. Findings support ringing records in demonstrating a primarily south-eastward movement following the breeding season, with no tracked birds wintering in western Atlantic waters. Fifteen successfully tracked adult birds wintered over a range of about 5000 km on continental shelf seas from NW Scotland to NW Africa with areas of concentration off Africa and in the Celtic Sea. Direct distance from the colony to the most distant point reached ranged from 1200 to 6100 km. Trips amounted to 16,100–33,500 km over the entire migration/winter period. While birds heading for NW Africa mostly showed a relatively straight migration direction, several round trips were recorded in (N)W Europe. Migration trips and over-winter colony absence lasted between 126 and 189 days. Birds departed from the colony from 9 to 24 September and returned from 19 January to 27 March. Timing and duration of migration and wintering periods varied substantially among individuals. Gannets staying in the waters of NW Africa experienced much higher sea surface temperatures than birds wintering further north, suggesting higher thermostatic costs for the latter.

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Introduction

Studies of migration movements have until recently depended on analyses of low levels of recoveries of ringed birds (Berthold 2001). Recovery rates have been generally low for marine species and are biased towards coastal areas with high human occupancy (Gaston et al. 2008). Recent developments in lightweight bird-borne tracking devices have surmounted many of these limitations and revolutionized understanding of the movement ecology of marine birds (Burger and Shaffer 2008; Wilson and Vandenabeele 2012).

Northern Gannets *Morus bassanus* occur in two major populations, one in the eastern and one in the western North Atlantic Ocean. Their migration patterns have been assessed through long-term ringing studies (Nelson 2002; Wernham et al. 2002) and more recently through the use of geo-location tracking devices (Kubetzki et al. 2009; Montevecchi et al. 2011; Fort et al. 2012; Fifield et al. 2014).

Overall, findings indicate that Northern Gannets are essentially coastal shelf migrants on both sides of the Atlantic Ocean with a low level of contact between these populations (Fifield et al. 2014). Research on the eastern Atlantic population has also revealed that the gannets exhibit a 'chain'-type migration whereby birds from more northerly situated colonies winter in more northerly areas than do birds from more southerly situated colonies (Fort et al. 2012).

The species' colonies in Iceland are the westernmost of the eastern population and are situated nearest the North American colonies. Rings from gannets banded in four colonies in Iceland have been recovered in the eastern Atlantic region, though one was recovered in northwest Greenland (Petersen 1998), suggesting that Icelandic gannets migrate primarily south-eastwards, but that some birds may move westward. Recent studies of migrations by Great Skuas *Stercorarius skua* breeding in Iceland found that some individuals wintered in Europe while others wintered in North America (Magnusdottir et al. 2012), suggesting that Icelandic seabirds of some species may choose either a south-eastern or south-western post-breeding migration direction. To better understand Northern Gannet migratory patterns and to explore potential connections between the western and eastern populations, the first applications of bird-borne geo-location devices were used to track the migratory behaviour of Northern Gannets from Iceland. Our objectives are to document the migration routes, wintering areas and spatial and temporal movement patterns of Northern Gannets from an Icelandic colony and to compare these findings with ringing data and with the migration patterns of Northern Gannets from colonies in the eastern and western North Atlantic.

Materials and methods

Study site, field work

Field work was conducted at the Northern Gannet colony on Skrúður (64°53′N, 13°37′W), eastern Iceland. 28 chick-rearing adults were equipped with geo-location loggers (see below) on 8 July 2010. Thirteen birds with loggers were recaptured in summer 2011; four more birds were recaptured in summer 2012. A few birds were seen with the metal bands partially open suggesting that several of the other birds lost the band with the logger attached. Fifteen devices delivered full data sets from summer 2010 to late spring 2011, covering the gannets' entire migratory period. Two devices malfunctioned.

Devices

We used geo-location data loggers (GeoLT) from Earth & Ocean Technologies (Kiel, Germany) to estimate the daily positions of the birds. The loggers were housed in a pressure-tight seawater-resistant casing (diameter, 14 mm; length, 38/45 mm [2 versions]); 8.2 g, equivalent to ca. 0.3 % of the bird body mass) and attached to a custom-built leg band. The main sensor of the device was a light sensor, allowing geographic position to be calculated from day length and time of local midday and midnight (Wilson et al. 1992; Kubetzki et al. 2009; Fifield et al. 2014). Light levels were measured every 30 s, allowing the device to operate for 1 year while providing two positional fixes per day.

In addition, the GeoLT recorded ambient temperature (i.e. air or sea surface temperature, depending on its position) every 120 s throughout deployment. This was done by a temperature sensor with a measuring range from 0 to 32 °C, a resolution of 0.125 K, an accuracy of 0.2 K and a 90 % response time of <4 min.

Geo-locator position estimation

Geographic positions were calculated from raw light curves using MultiTrace Geolocation from Jensen Software Systems (Laboe, Germany). Analysis followed principally the protocols described by Kubetzki et al. (2009) and Fifield et al. (2014).

Light levels were calibrated for sunrise and sunset from known locations (colony) and then applied to the whole data set. Since our focus was on migratory movements rather than at-colony activity, analysis was restricted to the period from colony departure to colony return. Colony attendance was derived from logger temperature profiles (for details see e.g. Wilson et al. 1995; Garthe et al. 2003). The error in the light-based latitude can be more than twice the corresponding longitude error estimated by geo-locators (Phillips et al. 2004; Teo et al. 2004; Shaffer et al. 2005). Light-based latitude cannot be estimated during the solar equinoxes, when day length is the same at all latitudes (Hill 1994). However, light-based latitude estimates can be improved (or recovered during equinoxes) by reconciling geo-locator-measured sea surface temperatures (SSTs) with remotely sensed satellite SSTs (Teo et al. 2004; Shaffer et al. 2005). The algorithm for this procedure was implemented in MATLAB (Mathworks, Natick, MA) and was used to adjust gannet daily latitude estimates accordingly (Fifield et al. 2014). The SST-corrected positions were filtered to remove positions requiring unreasonable speeds. Missing positions (e.g. due to failure of light-based geo-location during equinoxes and/or failure of the SST correction algorithm) were linearly interpolated between surrounding positions (Guilford et al. 2009). The proportion of missing positions of all positions varied between 5 and 22 % per track, with an overall mean of 12 ± 5 %. Tracks of individual birds were finally smoothed whereby the coordinates of each smoothed position were the weighted mean (in a 1:2:1 ratio) of the previous (*1), current (*2) and subsequent (*1) position's coordinates.

Further data analysis

Latitude was chosen as the best indicator of migratory movements, as all birds migrated more or less south. A smoothed latitude value was determined for each bird, for each 5-day period from the date of colony departure until the date of colony return. December has previously been determined as the most suitable time to define gannet 'winter home range' in the eastern Atlantic, as most larger scale movements of gannets had ceased by then (Kubetzki et al. 2009; Fort et al. 2012). Mean winter region position was thus defined as the centroid (mean latitude and longitude) of all locations obtained during the period 1–31 December.

Two definitions of the 'non-breeding period' were considered. The duration of trip version 1 ranges from the last night in the colony in autumn to the first night in the colony the following year. The duration of trip version 2 ranges from the first day the respective individual has exceeded a distance of 500 km from the colony (and has thus left the colony surroundings) until the day it returned to a distance of <500 km from the colony the following year (and has just reached the colony surroundings again). The 500-km threshold is consistent with the maximum recorded distance of breeding adult gannets during foraging trips from colonies, mean distance 92 km, mean maximum distance 229 km, longest ever recorded 590 km (Thaxter et al. 2012).

Sea surface temperatures (SSTs) were measured in the middle of the inactive period of the bird overnight. Temperature signals were stable overnight except for some short periods when the birds were flying. Those extended swimming periods gave best results as the temperature sensor in the device was fully adapted to the SST.

Results

Northern Gannets from Iceland moved eastward and southward to a broad range of wintering sites, ranging from NW Scotland to NW Africa (Table 1; Fig. 1, Online Resource 1). In total, seven birds (=47 %) spent their winter in Africa while eight birds (=53 %) wintered in Europe, with primary wintering sites being off NW Africa and the Celtic Sea area. No birds entered North American waters during post-breeding or return migrations. The direct distance from the colony to the most distant point reached ranged from 1200 to 6100 km. Trips amounted to 16,100–33,500 km over the entire migration/winter period (mean = 22,600 km; Table 1). While birds heading for NW Africa mostly showed a relatively straight migration direction (e.g. Fig. 2a; Online Resource 1), several birds performed round trips as shown in Fig. 2b, c using different migration routes in autumn and spring. Only one bird did not move further south than NW Scotland (Fig. 2b). All birds spent most time on the continental shelf and/or near the shelf break zones (Online Resource 1).

Migration trips and over-winter colony absence (the 'non-breeding period') lasted on average (±SD) 169 ± 17 days and ranged between 126 and 189 days (Table 1). All birds finally departed the colony region (here defined as >500 km from the colony, a distance that could be flown when permanently on the wing on an average migration/winter day) for 99–166 days, mean ± SD = 125 ± 22 days.

Birds departed from the colony from 9 to 24 September (median for the last night in the colony = 20 September). However, birds often remained near the colony for some weeks despite not returning to land. The time between colony departure and first moving more than 500 km from the colony varied from 0 to 22 days (Table 1), median 12 days, and was shorter for birds departing later in September. All birds had left the colony vicinity by 10 October. Timing and duration of migration and wintering periods varied considerably among individuals (Fig. 3). Birds heading to NW Africa stayed at their southerly position from <2 to 17 weeks. They also had different temporal schedules. For example, one individual stayed only <2 weeks from mid- to end November before returning north while another individual arrived after mid-December (Fig. 3). Birds returned to the colony for the first time overnight from 19 January to 27 March (median = 8 March). Return dates to the region varied from 12 January to 18 March (median = 30 January). Birds returning to the colony vicinity in January remained overnight in the colony earlier than birds returning in February or March, but the interval between arriving back in the vicinity and staying overnight in the colony was shorter for individuals returning later in spring (Table 1).

Gannets staying in the waters of NW Africa experienced much higher sea surface temperatures than gannets wintering further north (Fig. 4). Water temperatures did not differ very much around Britain and Ireland, but sea surface temperatures near the breeding colony in Iceland when birds returned in January or February were frequently as low as 0–3 °C.

Table 1 Summary of data for the 15 individually tagged Northern Gannets over the winter 2010–2011

Bird ID	Last night in colony	First night in colony	First day >500 km off colony	First day <500 km off colony	Total trip duration version 1 (days)	Total trip duration version 2 (days)	Winter region (December positions)	Maximum distance from colony (km)	Total distance flown (km)
023	18 Sept	02 Mar	10 Oct	21 Feb	165	134	Iberia/W Africa	5800	25,800
092	21 Sept	07 Mar	09 Oct	30 Jan	167	113	W Africa	4800	19,800
116	21 Sept	08 Mar	10 Oct	24 Jan	168	106	North Sea/Channel	1900	16,100
127	20 Sept	16 Mar	09 Oct	04 Feb	177	118	W Africa	5000	20,100
134	16 Sept	21 Mar	07 Oct	15 Jan	186	100	NW Scotland	1200	23,200
140	23 Sept	07 Mar	05 Oct	12 Jan	165	99	Celtic Sea/W Ireland	2100	20,900
141	23 Sept	16 Mar	30 Sept	01 Feb	174	124	North Sea to Bay of Biscay	2200	27,100
143	22 Sept	06 Mar	28 Sept	12 Jan	165	106	Celtic Sea	1800	19,600
144	20 Sept	13 Feb	25 Sept	21 Jan	146	118	Gibraltar to W Ireland	5700	28,700
145	24 Sept	20 Mar	08 Oct	05 Mar	177	148	W Africa	5000	22,800
147	19 Sept	27 Mar	03 Oct	18 Mar	189	166	W Africa	6100	33,600
150	09 Sept	24 Feb	21 Sept	16 Jan	168	117	Channel/Celtic Sea	1900	20,400
151	15 Sept	19 Jan	15 Sept	18 Jan	126	125	Biscay/W Ireland	2400	18,900
154	19 Sept	21 Mar	27 Sept	23 Feb	183	149	W Africa	4700	22,100
155	19 Sept	19 Mar	24 Sept	26 Feb	181	155	Gibraltar	3700	19,800

Trip version 1 ranges from the last night in the colony in autumn to the first night in the colony the following year. Trip version 2 ranges from the first day the respective individual exceeded a distance of 500 km from the colony until the day it returned to a distance of <500 km from the colony the following year. Distances were rounded to the nearest 100 km

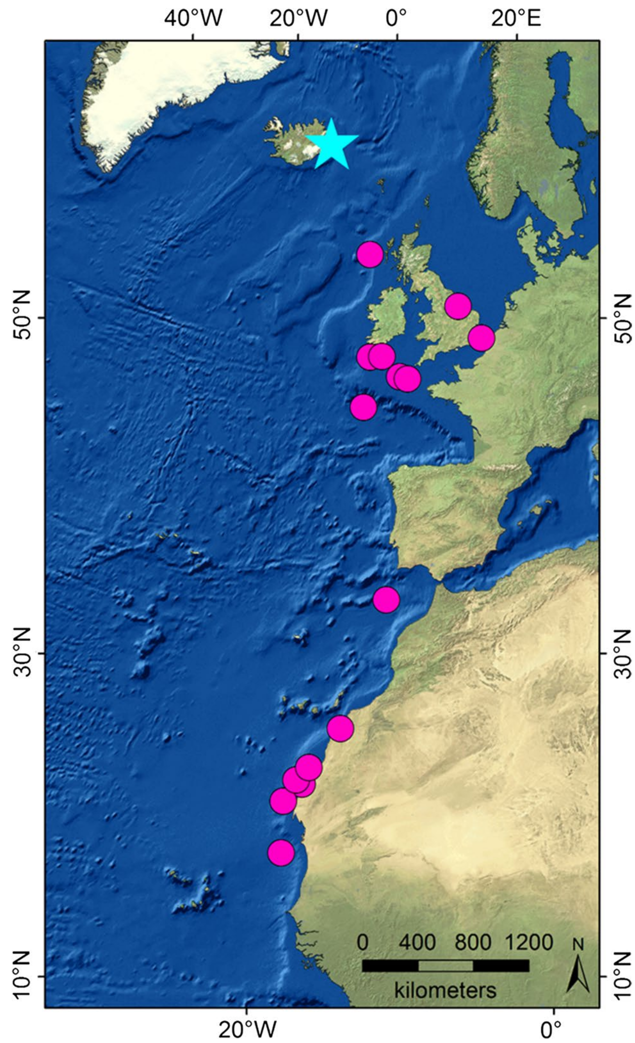

Fig. 1 Average December positions for all birds tracked (for details see text)

Discussion

Migration of gannets from Iceland

Northern Gannets moved eastward and southward from Iceland during September. Our geo-locator tracks concur with ringing recoveries of gannets from colonies in Iceland which also indicate predominately south-eastward movements from Iceland in autumn (Petersen 1998). Birds wintered from as far north as NW Scotland south to NW Africa, spanning a winter range of nearly 5000 km. No tracked birds moved through, or wintered in, eastern North American waters (Atlantic, Gulf of Mexico). This is consistent with the migratory behaviour of adult gannets from European colonies. Recoveries of gannets ringed in the Faroes also show no examples of birds from that population migrating to the western Atlantic; all recoveries are from Europe or West Africa (Hammer et al. 2014). The same is true for gannets ringed in the British Isles (Wernham et al. 2002) and for gannets tracked from European colonies from Norway to France (Fort et al. 2012). However, a small proportion of gannets breeding in North American colonies cross the Atlantic in autumn to overwinter off West Africa (as shown by geo-location data loggers, Fifield et al. 2014), so there is some mixing of these populations in winter, but apparently only in the east Atlantic.

The movements of adults from Iceland are consistent with data presented by Fort et al. (2012) for adults from colonies between Norway and France. Although there is much overlap, Icelandic birds tended to winter further north than birds from Britain and France. Interestingly, birds from Iceland wintered off Africa at a much higher proportion than birds from Norway in spite of comparable latitude of their breeding sites. While two birds from Iceland had their December range centred in the North Sea, six were centred in areas west of Britain and Ireland. In contrast, tracked adults from two Norwegian colonies which wintered around the British Isles were mainly in the southern North Sea during December, with fewer records west of the British Isles (Fort et al. 2012; Fig. 1). These differences in spatial distribution are important in relation to potential risks of collision with offshore wind farm turbines, since gannets are among the species thought to be at highest risk of collision mortality (Furness et al. 2013; Furness and Wanless 2014). Most offshore wind farms that have been constructed or given planning consent are in the southern North Sea. Tracking data indicate that most of the gannets in the southern North Sea in winter are from Norwegian colonies. While some Icelandic birds winter in the North Sea, more are found west of the British Isles, and off West Africa and southern Europe, where there are no offshore wind farms at present. But risks due to economic activities also occur elsewhere on their migratory routes. Gannets wintering in waters off West Africa are at risk from competition with fisheries, as well as intentional and incidental mortality by fishing gear (Gremillet et al. 2015).

Migration phenology

Departure from Skrúður was on average 2.5 weeks earlier than from Bass Rock (Scotland; median = 7 Oct; Garthe et al. unpubl. data). Data for North American colonies were determined differently (Fifield et al. 2014), but suggest that birds from Iceland were also starting at least 2 weeks earlier than birds from North America. The median for the return to the colony was only 2 days earlier for Skrúður as compared to Bass Rock, but the birds breeding in Iceland exhibited generally a much higher proportion of birds returning home much earlier, i.e. late winter. These patterns in European gannets differ markedly from gannets in eastern North

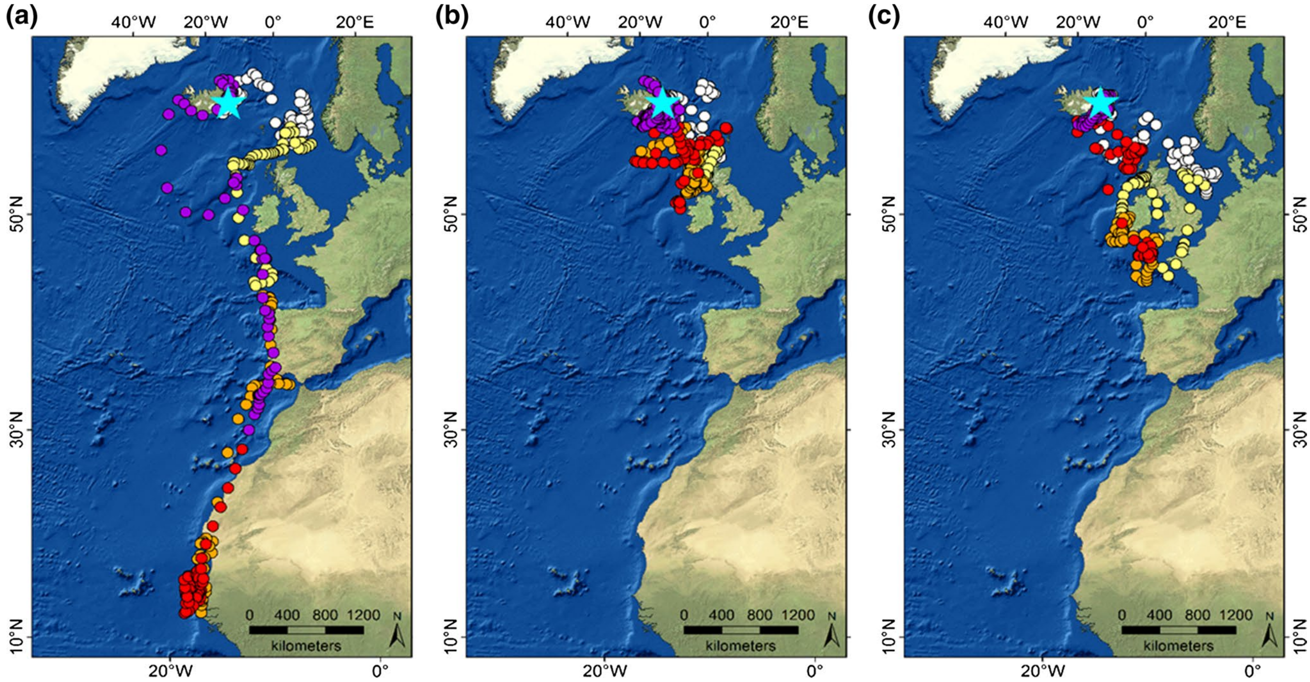

Fig. 2 Three examples of individual tracks of Northern Gannets tracked over the winter 2010–2011. **a** ind. 023, **b** ind. 134, **c** ind. 140. Table 1 provides more information on these birds. *Different colours* of the positions of the birds represent different periods of the winter movement; *white* September + October, *yellow* November, *orange* December, *red* January, *purple* February + March

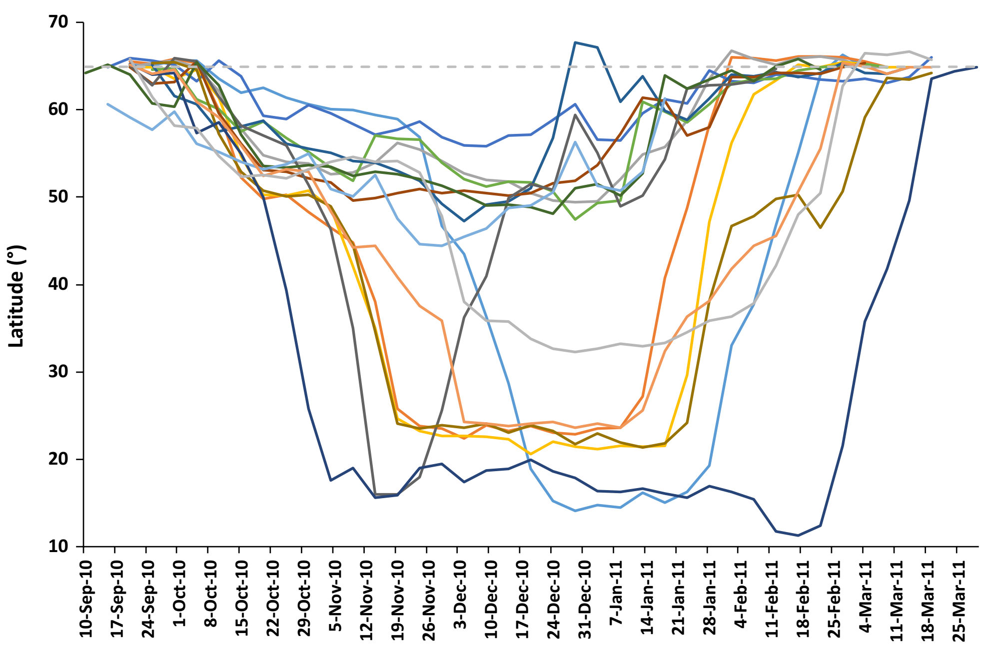

Fig. 3 Timing of movements of individual gannets showing mean latitude for each bird during standardized 5-day periods. The *dotted line* indicates latitude of the Skrúður colony

America which did not even come close their breeding colonies before early April, and usually mid-April, because of cold weather and sea ice (Fifield et al. 2014).

The wintering population of gannets in Iceland has been estimated at 100–1000 individuals mainly distributed from the south-west to the south-east coast (Petersen 1998). Since 2011

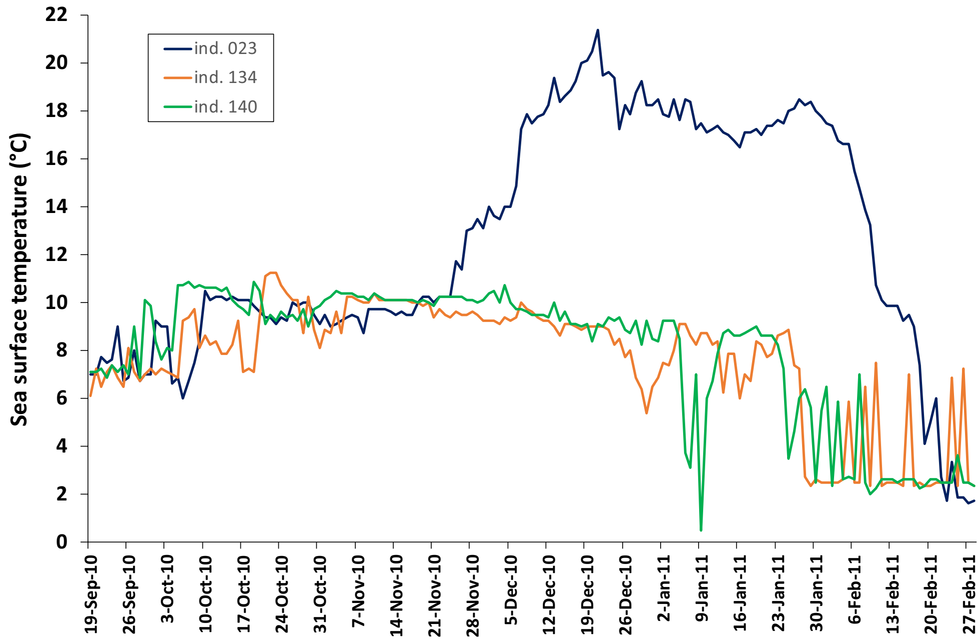

Fig. 4 Sea surface temperature experienced by three individually tracked Northern Gannets over the whole migratory period in winter 2010–2011: *Ind. 023* migrating to Africa (*blue colour*), *ind. 134* wintering north-west of Scotland (*red colour*), *ind. 140* wintering in the Celtic Sea (*green colour*). See Table 1 for more information on these birds

increasing number of gannets have been found in annual Icelandic Christmas Bird Count surveys, ranging roughly from 2 to 5 thousand individuals (CBC—IINH website). Only a fraction of the coastline is covered in these land based surveys indicating that the wintering population could be much larger. The origin of these wintering birds is unknown, but may be related to breeding birds returning early to Icelandic waters.

Birds returning early to Icelandic waters experienced very low water temperatures, suggesting substantially elevated thermal costs (Garthe et al. 2012), that were obviously compensated by sufficient prey availability. Only anecdotal data are available on gannet diet during this time period, but potential prey in south-eastern Iceland in February and March includes capelin (*Mallotus villosus*). This capelin population migrates in January from feeding grounds in north-eastern Greenland eastwards along the north coast of Iceland towards the spawning areas. Spawning takes place in February/March while the stock continues from the south-eastern coast westwards along the south coast of Iceland (Barbaro et al. 2009; Pálsson et al. 2012). Timing of this event coincides with the early return of gannets to Skrúður. The Icelandic summer-spawning stock of Atlantic herring (*Clupea harengus*) was known to form wintering schools in the fjords of eastern Iceland and start leaving for feeding migration in late February. The wintering grounds for this herring population have, however, changed during the past decades, and from 2006/2007 the majority of wintering schools have been found off the western part of the country (Óskarsson et al. 2009; ICES 2015). The commercial fishing of wintering herring reflects this pattern with around 90 % of the catches from western Iceland since 2007/2008 (ICES 2015). The fishing activity, and the behaviour of herring winter schools to stay deep in the sea, makes this species less likely to be an important prey item for early returning gannets in our study compared to the capelin. Flexibility in their choice of size and species of fish is well known in Northern Gannets and enables them to respond to such changes in prey fields (e.g. Hamer et al. 2007; Montevecchi et al. 2009; Garthe et al. 2011). Breeding gannets at Skrúður depend nonetheless on herring and mackerel (*Scomber scombrus*) for chick rearing (Vigfusdottir et al. 2009).

Colonies of Northern Gannets in Iceland

Of the six gannet colonies in Iceland, the very old colonies are located off the coast of south-western Iceland at Eldey Island and in the Westman Islands. The Skrúður colony in south-eastern Iceland was relatively recently established in 1943. From 1999 to 2008, the colony grew rapidly (6.3 % per annum, A. Garðarsson unpubl. data), and it is evident that the colony has continued to increase since then.

The relatively recent northward expansion of the species' breeding range along the Norwegian coast and to inside the Arctic Circle has been sourced by birds of European origin (Barrett and Folkestad 1996), including Iceland (Barrett

2008). Hence, it is conceivable that establishment of the Skrúður colony in south-eastern Iceland was also at least to some degree sourced by gannets from European colonies of origin. In consequence, autumn migratory movements with an eastwardly component might be expected.

It is possible that there are some spatial associations between the older Icelandic colonies and North American colonies. One gannet ringed in a colony in western Iceland migrated westward to NW Greenland (Petersen 1998), and a gannet banded in Canada was recovered in south-western Iceland (Fifield et al. 2014). These old colonies may have provided 'stepping stones' for the species' radiation from the eastern to the western Atlantic. Studies of population genetics are underway that could help unravel some of the current uncertainty about the species' radiation and the ages of colonies in the eastern, western and Icelandic Atlantic Ocean (V.L. Friesen pers. comm., Taylor and Friesen 2012). Our next immediate objective is to apply geo-location devices to track the migratory movements of Northern Gannets from these older, more westerly situated Icelandic colonies.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards All applicable international, national and institutional guidelines for the care and use of animals were followed.

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