The seabird wreck in the Bay of Biscay and Southwest Approaches in 2014: A review of reported mortality

Tim I. Morley[1*], Annette L. Fayet[2], Helene Jessop[3], Paul Veron[4], Merlin Veron[5], Jacquie Clark[6] and Matt J. Wood[7]

* *Correspondence author. Email: t.i.m-eee09@hotmail.co.uk*

[1] *Alderney Wildlife Trust, Slades, 48 Victoria Street, Alderney, GY9 3TA, Channel Islands;*

[2] *Department of Zoology, University of Oxford, Oxford OX1 3PS, UK;*

[3] *RSPB, Keble House, Southernay Gardens, Exeter, Devon, EX1 1NT, UK;*

[4] *Mermaid Cottage, Mannez Lighthouse, Alderney, GY9 3YJ, Channel Islands;*

[5] *Le Grand Verger, Rue Des Marais, Vale, Guernsey, GY6 8AU, Channel Islands;*

[6] *British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK;*

[7] *School of Natural & Social Sciences, University of Gloucestershire, Cheltenham GL50 4AZ, UK.*

Abstract

Between December 2013 and February 2014, a series of storm events occurred in areas of the North Atlantic frequented by migratory seabirds. Prolonged exposure to sustained storm conditions was followed by an unprecedented level of seabird mortality, apparently due to starvation, exhaustion and drowning. A total of 54,982 wrecked birds was recorded along European coastlines of the northeast Atlantic over the winter; 94% of which were dead. The majority of birds found were recorded on the French coastline (79.6%), and the most impacted species was the Atlantic Puffin *Fratercula arctica* (53.6%). In this paper, we describe the conditions surrounding this wreck event and report the numbers of wrecked and stranded seabirds by combining reports from multiple affected countries.

Introduction

Seabird wrecks occur when large numbers of dead, injured or exhausted seabirds wash up on coastlines with no obvious cause of death (Birkhead 2014). Such events are extremely hard to quantify because most mortality occurs at sea. Even when birds do wash ashore they often do so in inaccessible locations, such as at the bottom of steep cliff shorelines. Despite these challenges, it is important to attempt to quantify the magnitude of wreck events and put them into context with other wrecks to inform long-term studies of seabird population dynamics, because they can have large impacts on seabird populations (Votier *et al*. 2005, 2008; Mesquita *et al*. 2015).

Between December 2013 and February 2014 a succession of extreme and persistent weather events generated such severe conditions that a number of seabird species, usually wintering in the open ocean, were adversely affected. Although no individual storm was an exceptional event, the clustering and persistence of the storms was highly unusual (Slingo *et al.* 2014). The storms occurred from the first week of December 2013, through January and into early February 2014 causing record wind gusts (> 60 knots) and rainfall in the UK (Slingo *et al.* 2014). A notable feature of the storms was the long peak wave period and high wave height, resulting in waves carrying a large amount of energy causing substantial damage to northeast Atlantic coasts; presumably conditions at sea for wintering seabirds must have been similarly extreme. Conditions also included an unusually strong North Atlantic jet stream and a prolonged series of storm events, with winds gusting in excess of 100 mph; the worst recorded for a century (Slingo *et al.* 2014).

Tracking studies have shown that several seabird species including Atlantic Puffin *Fratercula arctica,* hereafter 'Puffin' (Guilford *et al*. 2011; Jessopp *et al*. 2013; Fayet *et al*. 2016), Common Guillemot *Uria aalge*, hereafter 'Guillemot' (Stone *et al*. 1995), Northern Gannets *Morus bassanus,* hereafter 'Gannet', from the UK and Norway (Veron & Lawlor 2009; Fort *et al*. 2012), and Black-legged Kittiwakes *Rissa tridactyla*, hereafter 'Kittiwake', from Western Europe (Frederiksen *et al*. 2012), would have been in the Celtic Sea, Bay of Biscay and/or western English Channel

Table 1. Known survey effort within affected areas.

Country	Date	Location	Distance	Source
United Kingdom	22–23 February	Accessible coastline throughout the UK excluding the southwest England region*	1,984 km	Schmitt 2014
Channel Islands: Alderney	Regular surveys from 10 February to 22 March	6.51 km of accessible coastline	77.18 km total	Broadhurst & Morley 2014
Channel Islands: Guernsey	22 February to 8 March	Accessible coastline	96 km total	C. Veron, pers. comm.
Channel Islands: Jersey	16–23 February, 2–9 March	Accessible coastline	Variations in personnel make total distance incalculable	G. Young & C. Sellares, pers. comm.
France	Six weekends from 1 February to 9 March 2014	French Atlantic coastline	Surveys conducted across 2,773.7 km but not all was accessible	Farque *et al.* 2014
Spain	Some areas regular, others intermittent	Atlantic and northern Spanish coastlines	Varying effort in different locations makes distance incalculable	C. Torrell, pers. comm.
Portugal	14–27 March	12.7 km of accessible coastline between Sao Jacinto and Torreira, northwest Portugal	22.7 km total	T. van Nus, pers comm.

* SW region could not be surveyed on the designated days due to weather

during late winter (January–February), and therefore at risk of being affected by the storm events during this period. Large numbers of dead and injured seabirds were subsequently washed ashore over much of the northeast Atlantic coast of Europe, as ocean currents and wind carried dead and moribund birds ashore.

This paper attempts to give a detailed report of the mortality associated with the 2013/14 seabird wreck by combining beached bird surveys from across the entire affected area. Information will be provided on the origin of the species most affected by the wreck using ring recovery data; note that data were available from the UK only for this review. We also report evidence on cause of death from post-mortem examinations of dead seabirds.

Methods

Survey of stranded seabirds: The methods used by different organisations or volunteers in different countries were sufficiently similar to warrant comparison. Typically, a designated route along an accessible coastal area, usually sandy beaches but including all accessible coastline habitats, is walked by surveyors standing a distance apart that allows the maximum amount of beach area to be covered in one transect as they scanned the location for specimens. This methodology accords very closely with that of the Royal Society for the Protection of Birds' (RSPB) 'Beached Bird Survey' which coincided with the 2013/14 wreck, conducted on its annual schedule in the UK on 22–23 February (Schmitt 2014). Not all surveys in all areas of the UK (Figure 1) would have been through the RSPB scheme, due to the reactive approach to seabird wrecks, but many of them were (Table 1).

Besides the survey effort described in Table 1, additional data were gathered from members of the public. These records were subsequently confirmed and verified by the relevant organisation, minimising the chances of double-counting individuals by cross-checking against previous reports from the same location and confirming identification from photos where available. All these data are included in the totals given. Despite the coordinated Beached Bird Survey in parts of the UK and France, and continued major survey effort across multiple locations providing a considerable amount of data on the seabird wreck, the challenges involved in collating and continuing surveys across such a large area, the varying search effort between organisations around the period of the wreck, the discovery of only a proportion of the fatalities occurring at sea and the varying time that different species of seabird corpses will remain afloat, are likely to result in a substantial underestimation of mortality.

Post-mortem examinations: To determine cause of death, staff from the Groupe Ornithologique Normand, Alderney Wildlife Trust and Alderney Animal Welfare conducted a necropsy workshop in Alderney on 22–23 March 2014. Subcutaneous fat (between the feathers on the breast), fat deposits around the distal part of the gut, curvature of pectoral muscle extending from the sternum and presence of spume in the lungs were recorded, alongside general information on the state of the specimens, to determine any potential cause of death (Broadhurst & Morley 2014).

Ringing recoveries: Ringing recoveries reported to the British Trust for Ornithology (BTO) over the wreck period were analysed. Only recoveries occurring between December 2013 and March 2014 were included. We limited the analysis to the recoveries made in the area affected by the storms, including the French, Spanish and Portuguese Atlantic coasts, the coast along the English

Figure 1. Location of survey areas recorded during the seabird wreck event (red line).

Channel, and the Irish and British coast of the Celtic and Irish Seas (Figure 1). Note, all recoveries originated from British colonies (Figure 2). Causes of death for inland recoveries are uncertain, with factors other than the storms potentially impacting the birds, whilst the death of many birds recovered during the time period of the wreck was not linked to the storms (e.g. disease or shot); all these recoveries were excluded from the results.

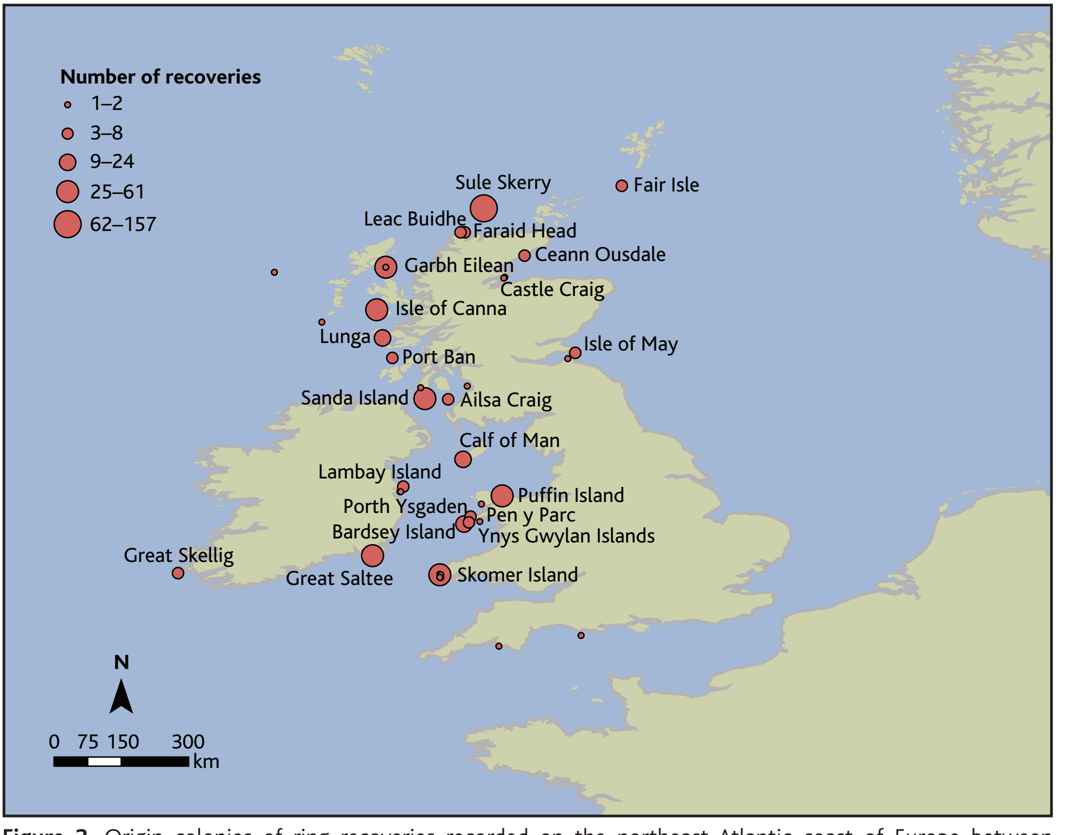


Figure 2. Origin colonies of ring recoveries recorded on the northeast Atlantic coast of Europe between December 2013 and March 2014, for the four main species affected (Puffin *Fratercula arctica*, Guillemot *Uria aalge*, Razorbill *Alca torda* and Shag *Phalacrocorax aristotelis*); colonies with more than one recovery labelled.

Results

Estimates of mortality: In total, 54,982 birds were found during the survey period; of these 3,243 (5.9%) were live birds. The majority of the birds was found in France (79.6%) and Puffins were by far the species most impacted (53.6%; Table 2). Of the live birds retrieved, 3,014 (93%) were found in France, most likely due to currents and proximity to this coastline during the storm events. Of these a third subsequently died in transit, a third died in care and a third were successfully released back into the wild (Farque *et al*. 2014). The only other locations in which live birds were recorded were in Guernsey (18 Guillemots and one Gannet), southwest England (209 birds) and Wales (one Guillemot).

Table 2. Numbers of wrecked seabirds (live strandings and dead birds combined) recorded on the northeast Atlantic coast of Europe from January to April 2014.

Species	Portugal	Spain	France	Channel Islands	SW England	Wales	Rest of UK & Ireland[1]	Total
Gannet	5	67	305	8	33	5	4	427
Fulmar	1	4	131	4	3	7	15	165
Shag		12	47	110	22	1	0	192
Kittiwake	5	51	868	31	29	20	73	1,077
Puffin	121	277	28,745	119	115	25	42	29,444
Razorbill	9	99	1,197	468	902	234	911	3,820
Guillemot	0	1,538	11,801	441	1,311	139	713	15,943
Auk *spp*.	1	85	254	16	590	2	2	950
Other seabirds	14	105	229	43	53	7	33	484
Non-seabirds	6	12	176	48	5	0	5	252
Unidentified	1	3	0	2	276[2]	217	1,729	2,228
Total	163	2,253	43,753	1,290	3,339	657	3,527	54,982

[1] Region encompasses data from Ireland, Northern Ireland, Scotland, Shetland and England (except the southwest region).
[2] Value includes 209 live birds retrieved but species composition was not recorded, likely mostly auks.

Post-mortem examinations: Necropsy analyses conducted on a sample of 12 Guillemots in Alderney showed that 58% had emaciated pectoral muscles, 92% had no stomach contents (no data available for the final bird), 83% had no fat on the chest and 50% had some or no fat in the intestine, indicating that starvation was the most likely cause of death (Broadhurst & Morley 2014). In addition, specimens of Guillemot and Razorbill *Alca torda*, hereafter 'Razorbill', were collected on Chesil Beach, Dorset, on 2 March 2014 (P. Read pers. comm.). Although data on time since stranding were unavailable, the mean (± SD) masses were 451.9 ± 53.9 g (n = 44) for the Razorbills and 601.5 ± 85.5 g (n = 17) for the Guillemots. Winter weight of healthy individuals is difficult to attain, but Guillemots are likely in the range of 900–1,200 g (Hope Jones *et al*. 1984). Values for Razorbill are harder to come by still but likely higher than the average weight of the wreck individuals. Furthermore, live birds collected in France were emaciated and extremely weak, typically weighing less than half that of a healthy adult (O. Le Gall, pers. comm.).

The Animal Health and Veterinary Laboratories Agency (AHVLA) also necropsied 27 seabirds from the wreck, primarily Razorbills and Guillemots, all of which were emaciated (AHVLA 2014). The presence of spume (frothy water) in the lungs was noted by the AHVLA (AHVLA 2014) and recorded in three specimens in the Alderney Guillemot autopsy (Broadhurst & Morley 2014).

Finally, only 10 (3.3%) out of 300 wrecked Puffins whose wings were examined were in moult to such an extent that they would have been flightless (M.P. Harris pers. comm.).

Ring recovery data: Since the first recovery of a ringed Puffin was made in 1935/36, the BTO have recorded an average of 11.5 recoveries of ringed Puffins washed ashore dead in the UK per winter (November to April) up until 2012/13; a maximum of 127 recoveries were reported in the winter of 1982/83. Additionally,

Table 3. Recovery locations of ringed seabirds found wrecked on the northeast Atlantic coast of Europe between December 2013 and March 2014, as registered by the British Trust for Ornithology.

Species	Portugal	Spain	Channel France	UK & Islands	Ireland	Total
Gannet	1	1	2		6	10
Fulmar					2	2
Shag					50	50
Cormorant		1	1		9	11
Kittiwake		1			7	8
Herring Gull					7	7
Great Black-backed Gull					4	4
Lesser Black-backed Gull	2	1				3
Black-headed Gull					4	4
Puffin	1	5	205	1	4	216
Razorbill	1	2	26	1	126	156
Guillemot		6	90	3	44	143
Black Guillemot					17	17
Total	5	17	324	5	280	631

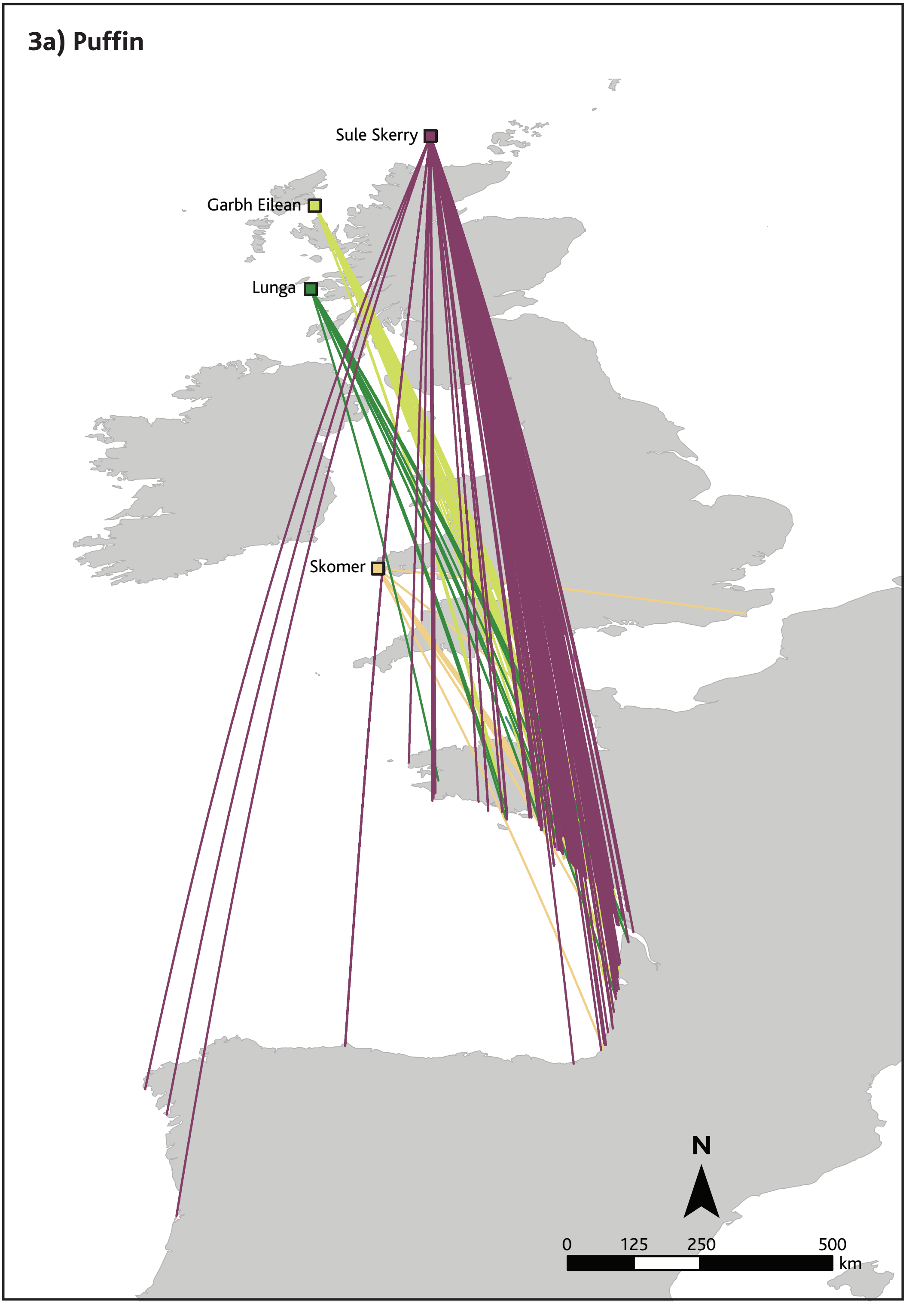
Table 4. Ringing locations of ringed seabirds wrecked on the northeast Atlantic coast of Europe between December 2013 and March 2014, as registered by the British Trust for Ornithology.

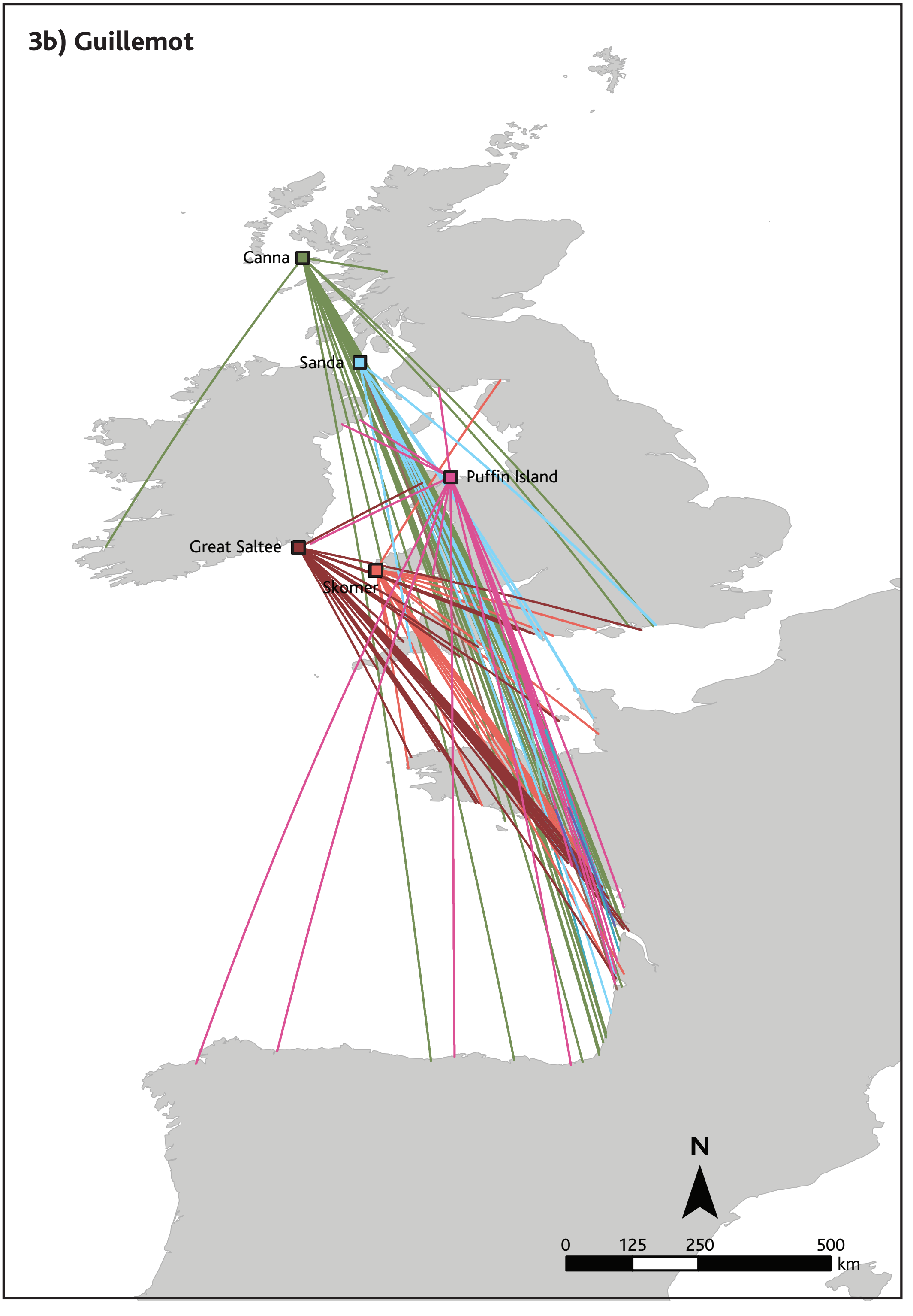
Species	Ireland	Northern Ireland and England	Scotland	Wales	Isle of Man	Rest of Europe*	Total
Gannet	4		4	1		1	10
Fulmar	1					1	2
Shag	7	2	4	27	10		50
Cormorant	2	1	2	6			11
Kittiwake			2	1		5	8
Herring Gull		2	1	1	3		7
Great Black-backed Gull						4	4
Lesser Black-backed Gull		1	2				3
Black-headed Gull	1	1				2	4
Puffin	5		196	15			216
Razorbill	29		72	50	5		156
Guillemot	29		74	40			143
Black Guillemot	11	6					17
Total	89	13	357	141	18	13	631

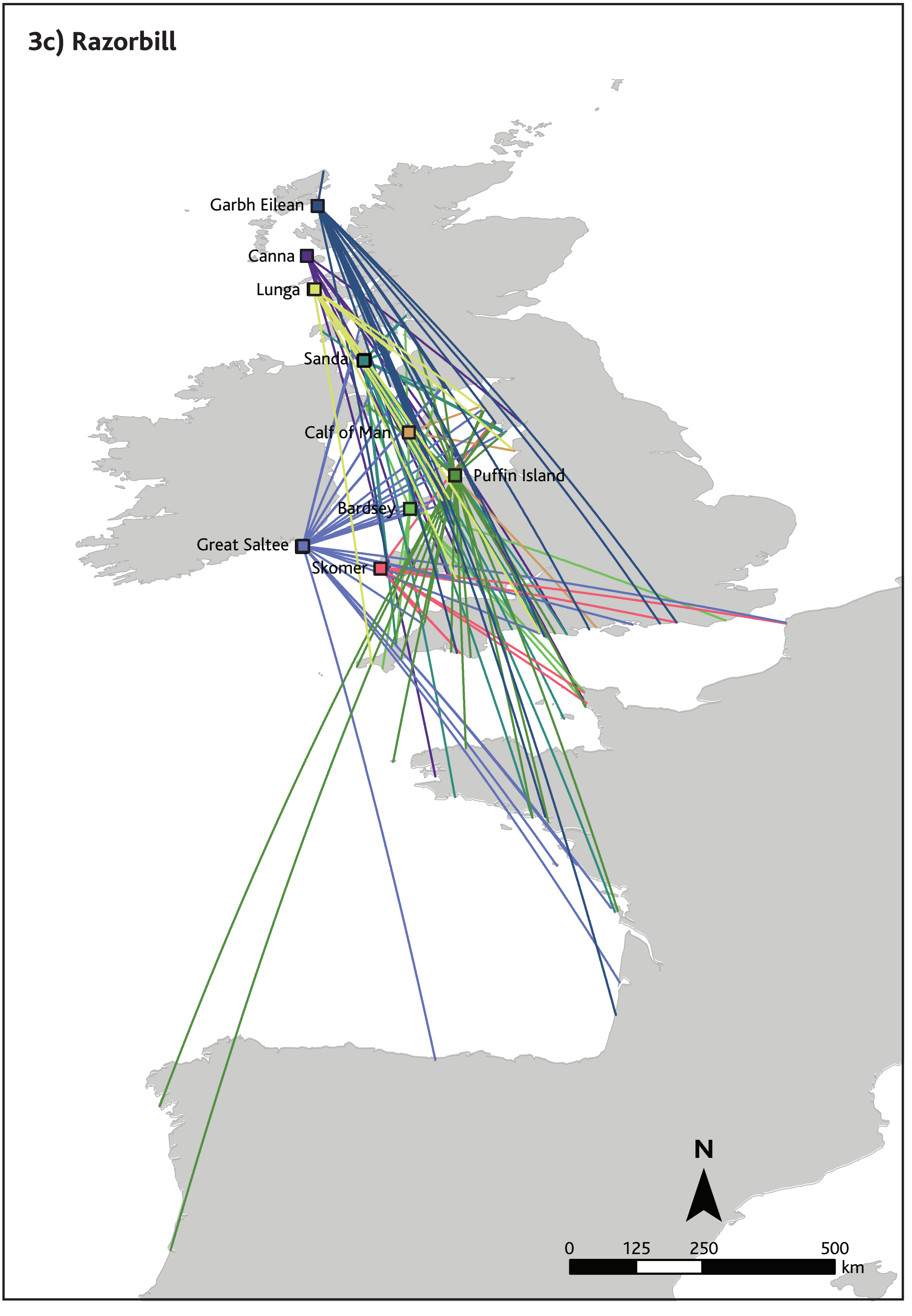
* Including data from Belgium, France, Finland, Iceland and Norway.

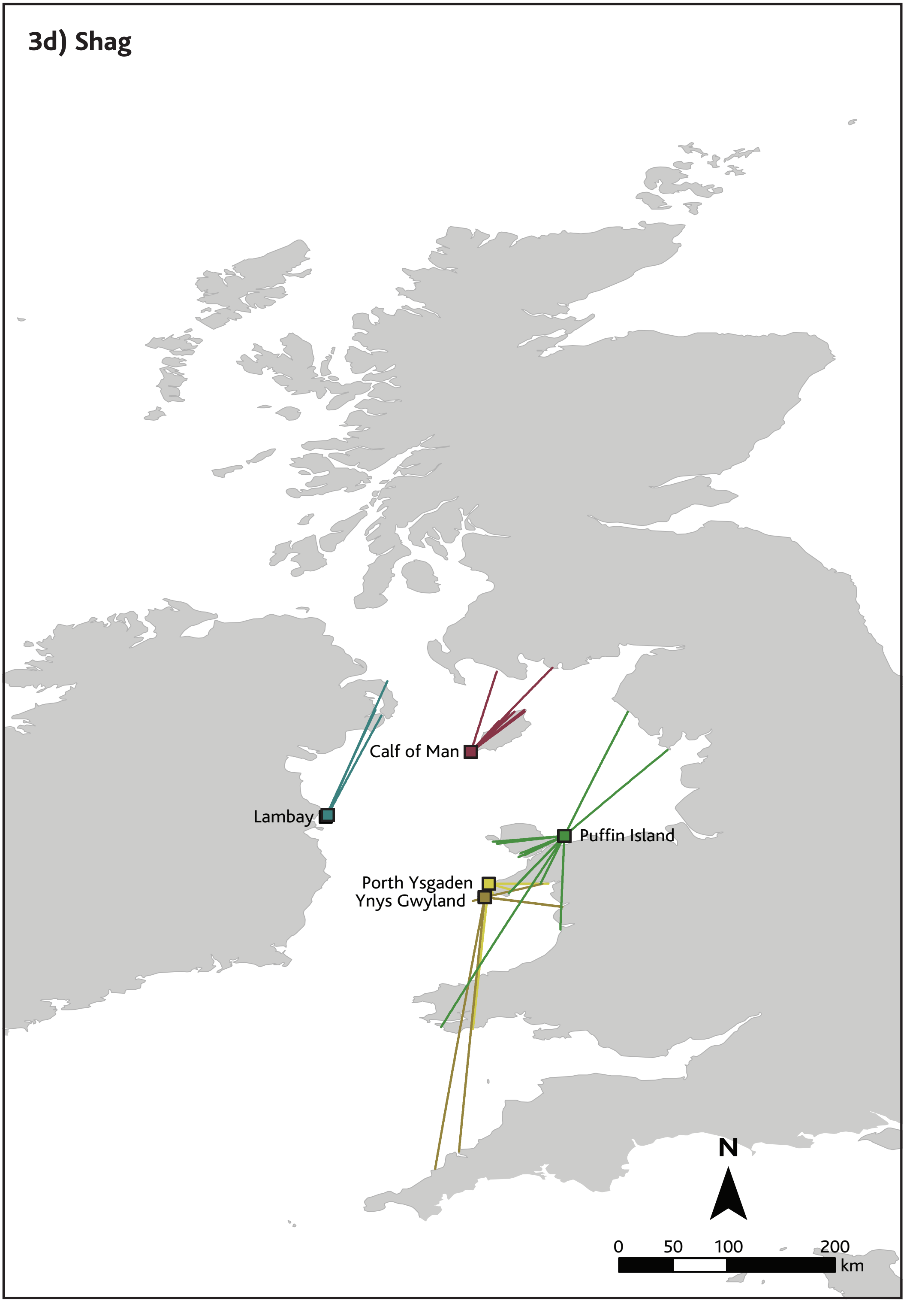
recoveries of dead ringed Puffins from France and Spain would normally equal two or three a year (Grantham & Stancliffe 2014). However, during the wreck, 631 ringed birds were recovered, including 216 Puffins, of which 205 were from France (Tables 3 and 4). The recoveries were spread across the entire impacted area, but

Figure 3 (overleaf). Colony origin of ringed auks and Shags *Phalacrocorax aristotelis* (for colonies contributing more than 5 recoveries) recovered on the northeast Atlantic coast of Europe between December 2013 and March 2014, as registered by the British Trust for Ornithology.


3a) Puffin
Sule Skerry
Garbh Eilean
Lunga
Skomer
N
0
125
250
500
km


3b) Guillemot
Canna
Sanda
Puffin Island
Great Saltee
Skomer
N
0
125
250
500
km


3c) Razorbill
Garbh Eilean
Canna
Lunga
Sanda
Calf of Man
Puffin Island
Bardsey
Great Saltee
Skomer
N
0
125
250
500
km


3d) Shag
Calf of Man
Lambay
Puffin Island
Porth Ysgaden
Ynys Gwyland
N
0
50
100
200
km

certain UK colonies were seemingly represented in higher numbers than others (Figures 2 and 3). Data were filtered to remove any ring recoveries during the wreck time period that were not attributable to the storm conditions; therefore, we only included recoveries of birds with 'unknown' (53.57%) or 'natural' (42.95%; predominantly attributed to 'violent weather') recorded as the cause of death. Ring recoveries of oiled birds (3.49%) were also recorded within the wreck event as specimens from other locations showed signs of oiling without it necessarily being the final cause of mortality (AHVLA 2014; Broadhurst & Morley 2014).

Discussion

A total of 54,982 birds was recorded during the 2013/14 northeast Atlantic seabird wreck, 79.6% of which were found in France. This number is likely to be a large underestimate of the final death toll, due to the limited surveying across all regions impacted. Also, many birds that perish in storms may not be washed ashore, the proportion of which can only be estimated by drift experiments made during the incident (Weise 2003). However, with such a large level of mortality (94% of the birds, of which 53.6% were Puffins, were found dead), it is important to consider potential factors that may have affected the severity of the wreck event.

Causes of mortality: The ringing recoveries recorded by the BTO attribute 42.3% of mortality to 'violent weather'; this is the likely overall cause, but more specifically several independent lines of evidence point to starvation as the most likely direct explanation for the extensive mortality observed in the 2013/14 seabird wreck. Autopsy data from Alderney (Broadhurst & Morley 2014), Chesil Beach (P. Read pers. comm.) and the AHVLA (AHVLA 2014) all show marked levels of emaciated body condition in analysed specimens. The recording of weight of dead birds comes with the caveat that many corpses are found in a desiccated state, potentially overestimating the amount of weight loss. However, the Alderney autopsy states that 50% of specimens were fresh and 25% rather fresh, reducing the likelihood of desiccation after death being a major factor for these results. Although starvation is the main factor in cause of mortality, evidence of drowning, such as spume in lungs, was also noted in some specimens (AHVLA 2014; Broadhurst & Morley 2014).

Many factors are likely to affect the susceptibility of different species or individuals to death from starvation or drowning. Seabirds spend a significant amount of time and energy foraging in winter, particularly in November and December, to regain body condition for the breeding season (e.g. Daunt *et al*. 2006; Fort *et al*. 2009), so challenging winter conditions sustained over several weeks or, as in this case, months are likely to affect the birds' foraging opportunities with possible consequences on their future condition, survival and reproductive ability. For example, European Shags *Phalacrocorax aristotelis*, hereafter 'Shags', have been shown to forage less during times of high wind speeds, with males foraging for shorter times than females which could have consequences for sex-specific survival rates (Lewis *et al*. 2015), and they may even halt diving altogether during high onshore gales (Frederiksen *et al*. 2008).

Additionally, the continued turbid water conditions associated with storms may create poor visibility for foraging. This is a particular issue for auks which have less flexible foraging strategies than Shags (Watanuki *et al.* 2008; Cook & Burton 2010) and spend more energy on longer, deeper dives (Elliott *et al.* 2013; Elliott & Gaston 2014) to pass through the turbid surface conditions, possibly causing the energetic cost of foraging to outweigh the nutritional gain from successful catches. The fact that the overwhelming majority (91.3%) of retrieved birds during the 2013/14 seabird wreck belonged to the auk family supports difficult foraging conditions as a major contributor to mortality.

In addition to considering the weather conditions, the habits of the species found must also be considered; susceptibility may vary between pelagic and inshore species and between long- and short-ranging species. Pelagic seabirds were the most impacted during the wreck, accounting for 92.5% of all findings (auks alone were 91.3%), whilst inshore species contributed just 3.3% of all findings (Table 2) suggesting they were less susceptible to the conditions created by the storms. Findings from a small number of Puffins carrying geolocation loggers also suggest that the migratory patterns of some individuals may make them more susceptible to suffer from a wreck than others (A. Fayet *et al.* unpubl. data). Moult stage could be another factor adding to birds' susceptibility to a wreck event. For example, Puffins shed all their main wing feathers synchronously during the winter (Harris & Yule 1977) and are then unable to fly for a few weeks (Harris 2014; Harris *et al.* 2014). However, the small number of moulting Puffins found suggests moult was not an important factor in this wreck (M.P. Harris pers. comm.). Nevertheless, it cannot be totally disregarded, given the variability in the timing of Puffin moult (Harris *et al.* 2014) and the role of post-moult feather growth in the Razorbill wreck in 2007 (Heubeck *et al.* 2011).

Besides differences in foraging, migratory strategies, and habitat use, the physiological differences between species could also have affected mortality rates. For instance, the partially wettable plumage of Shags (Grémillet *et al.* 1998) increases mortality in times of low ambient temperature, most likely through hypothermia (Frederiksen *et al.* 2008). The ability to survive through a wreck event may also be linked to body size, with larger-bodied species retaining greater energy reserves. Finally, metabolism could also play a role, as suggested by Hope Jones *et al.* (1984) who discovered a higher percentage of Razorbills to have lower fat reserves on autopsy than Guillemots following the 1983 seabird wreck. However, the small samples examined of these species from the 2013/14 wreck are insufficient to provide any further evidence on the role of metabolism, particularly as weight loss was high for both species. A recent study of some specimens showed, however, that high concentrations of mercury (known to increase stress) may have acted as an aggravating mortality factor during the event (Fort *et al.* 2015).

Impacts of mortality: Whilst the majority of wreck birds were located in France (Tables 2 and 3), most ringed birds were from breeding colonies in Scotland, Wales and Ireland (Table 4). This is to be expected as most of the large seabird colonies where BTO-licensed ringers operate are in these locations, but it does highlight the possibility that reproductive success, recruitment or survival of birds from these colonies were impacted by the wreck. Furthermore, whilst the scale of the wreck event is staggering in terms of numbers, it is not the first event of this scale. For example, in February and March 1994, 20,000–50,000 Guillemots and 3,000–5,000 Shags were reported washed ashore in emaciated states due to storm events (Harris & Wanless 1996), and in February 1983 prolonged storms across Western Europe resulted in 34,000 seabirds washing ashore in the northeast UK alone with another 24,000 across Western Europe (Underwood & Stowe 1984). Therefore, the regularity of wrecks impacting on a particular species or colony should also be considered when trying to uncover any longer-term effects at the population level.

In summary, the seabird wreck along the Atlantic coastline of northwest Europe in winter 2013/14 was an extreme example of weather-induced mortality from starvation in seabird populations. The subsequent impacts on population numbers and productivity are likely to be detectable in multiple species and colonies (M.J. Wood *et al.,* unpubl data; T.R. Birkhead, pers. comm.). Whilst any individual wreck can have significant consequences for the populations involved, the frequency of wreck events is also likely to be an important factor. The potential of climate change to increase the frequency and strength of storms (Slingo *et al.* 2014; Fischer & Knutti 2015) can have severe implications for seabird populations in the future, and the vulnerability of species to extreme events needs to be accounted for in future predictions of ecological impacts of climate change (Frederiksen *et al.* 2008).

Acknowledgements

We would like thank the hundreds of dedicated staff, volunteers and members of the public across Western Europe who responded to the wreck event with efforts to survey its impact. We would like to thank the organisations across Europe that contributed to the response to and recording of the wreck, including: Ligue pour la Protection des Oiseaux (LPO), RSPB, Cornwall, Devon and Dorset Wildlife Trusts (and the Cornwall Marine Strandings Network and DoWT staff at Chesil Beach, Dorset in particular), RSPCA, South Devon Seabird Trust, BTO Ringing Scheme, National Trust, Natural England, SEO Birdlife, Alderney Wildlife Trust, Durrell Wildlife Conservation Trust, States of Jersey, States of Guernsey, other county Wildlife Trusts and Sussex Ornithological Society. We would particularly like to thank the following people for their specific help in supplying data and details on responses to the wreck event in their location: Mike Harris (CEH, Scotland), Glyn Young (Durrell Conservation Trust, Jersey), Cristina Sellares (National Trust, Jersey), Catherine Veron (La Société Guernesiaise, Guernsey), Janice Dockerill (Environment Department, Guernsey), Anne-Isabelle Boulon (Living Islands, Alderney), Ed Stubbings (Warden Skomer Island, Wales), Bee Bueche (Warden Skomer Island, Wales), Pembrokeshire Bird Group (Wales), Phil Read (Chesil Beach, Dorset), John Walmsley (Newgale Beach, Wales), Tim van Nus (Portugal), Olivier le Gall (LPO, France), Amélie Boue (LPO, France) and Albert Cama Torrell (Spain). We are also grateful to Martin Heubeck, Viola Ross-Smith, Richard Sherley and two anonymous referees, whose comments greatly improved this paper.

References

AHVLA 2014. 'AHVLA Disease Surveillance Report, May 2014.' (https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/350618/pub-survreport-0514.pdf). Animal Health and Veterinary Laboratories Agency (AHVLA). Updated May 2014. Accessed 24 August 2016.

Birkhead, T. 2014. 'The Seabird Wreck of 2014.' (http://myriadbirds.com/2014/03/03/wrecks/). Updated 3 March 2014. Accessed 24 August 2016.

Broadhurst, M. & Morley, T. 2014. 'Alderney Wildlife Trust: Annual Ramsar Project Review 2014'. (http://www.alderneywildlife.org/sites/default/files/annual_ramsar_project_report_2014_final.pdf). Alderney Wildlife Trust. Updated October 2014. Accessed 24 August 2016.

Cook, A. S. C. P. & Burton, N. H. K. 2010. 'A review of the potential impacts of marine aggregate extraction on seabirds. Marine Environment Protection Fund Project 09/P130'. (https://www.bto.org/sites/default/files/shared_documents/publications/research-reports/2010/rr563.pdf). Marine Aggregate Levy Sustainability Fund. Updated August 2010. Accessed 24 August 2016.

Daunt, F., Afanasyev, V., Silk, J. R. D. & Wanless, S. 2006. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behavioural Ecology and Sociobiology* 59: 381–388.

Elliott, K. H. & Gaston, A. J. 2014. Dive behaviour and daily energy expenditure in Thick-billed Murres *Uria lomvia* after leaving the breeding colony. *Marine Ornithology* 42: 183–189.

Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakmane, J. R. & Davorena, G. K. 2013. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proceedings of the National Academy of Sciences* 110: 9380–9384.

Farque, P-A., Boue, A., Dugue, A-L. & Micol, T. 2014. 'Echouage massif d'oiseaux marins durant l'hiver 2014 sur la facade atlantique.' (http://www.lpo.fr/images/actualites/2014/echouages/bilan_echouages_2014_lpo_final1.pdf). Ligue pour la Protection des Oiseaux (LPO) and Birdlife International. Updated July 2014. Accessed 24 August 2016.

Fayet, A. L., Freeman, R., Shoji, A., Boyle, D., Kirk, H. L., Dean, B. J., Perrins, C. M. & Guilford, T. 2016. Drivers and fitness consequences of dispersive migration in a pelagic seabird. *Behavioral Ecology* 27: 1061–1072.

Fischer, E. M. & Knutti, R. 2015. Anthropogenic contribution to global occurrence of heavy-precipitation and high-temperature extremes. *Nature Climate Change* 5: 560–565.

Fort, J., Lacoue-Labarthe, T., Nguyen, H. L., Boué, A., Spitz, J. & Bustamante, P. 2015. Mercury in wintering seabirds, an aggravating factor to winter wrecks? *Science of The Total Environment* 527–528: 448–454.

Fort, J., Pettex, E., Tremblay, Y., Lorentsen, S-H., Garthe, S., Votier, S., Pons, J. B., Siorat, F., Furness, R. W., Grecian, W. J., Bearhop, S., Montevecchi, W. A. & Grémillet, D. 2012. Meta-population evidence of oriented chain migration in northern gannets (*Morus bassanus*). *Frontiers in Ecology and the Environment* 10: 237–242.

Fort, J., Porter, W. P. & Grémillet, D. 2009. Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. *Journal of Experimental Biology* 212: 2483–2490.

Frederiksen, M., Børge, M., Daunt, F., Phillips, R. A., Barrett, R. T., Bogdanova, M. I., Boulinier, T., Chardine, J. W., Chastel, O., Chivers, L. S., Christensen-Dalsgaard, S., Clément-Chastel, C., Colhoun, K., Freeman, R., Gaston, A. J., González-Solís, J., Goutte, A., Grémillet, D., Guilford, T., Jensen, G. H., Krasnov, Y., Lorentsen, S-H., Mallory, M. L., Newell, M., Olsen, B., Shaw, D., Steen, H., Strøm, H., Systad, G. H., Thórarinsson, T. L. & Anker-Nilssen, T. 2012. Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions* 18: 530–542.

Frederiksen, M., Daunt, F., Harris, M. P. & Wanless, S. 2008. The demographic impact of extreme events: stochaistic weather drives survivial and population dynamics in a long lived seabird. *Journal of Animal Ecology* 77: 1020–1029.

Grantham, M. & Stancliffe, P. 2014. 'British Puffins caught up in Biscay storms.' (http://www.bto.org/news-events/press-releases/british-puffins-caught-biscay-storms). British Trust for Ornithology. Updated February 2014. Accessed 24 August 2016.

Grémillet, D., Tuschy, I. & Kierspel, M. 1998. Body temperature and insulation in diving Great Cormorants and European Shags. *Functional Ecology* 12: 386–394.

Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R. & Perrins, C. 2011. A Dispersive Migration in the Atlantic Puffin and Its Implications for Migratory Navigation. *PLoS ONE* 6: e21336.

Harris, M. P. 2014. Ageing Atlantic puffins *Fratercula arctica* in summer and winter. *Seabird* 27: 22–40.

Harris, M. P. & Wanless, S. 1996. Differential responses of Guillemot *Uria aalge* and Shag *Phalacrocorax aristotelis* to a late winter wreck. *Bird Study* 43: 220–230.

Harris, M. P. & Yule, R. F. 1977. The moult of the Puffin *Fratercula artica*. *Ibis* 119: 535–541.

Harris, M. P., Wanless, S. & Jensen, J-K. 2014. When are Atlantic Puffins *Fratercula Arctica* in the North Sea and around the Faroe Islands flightless? *Bird Study* 61: 182–192.

Heubeck, M., Aarvak, T., Isaksen, K., Johnsen, A., Petersen, I. K. & Anker-Nilssen, T. 2011. Mass mortality of adult Razorbills *Alca torda* in the Skagerrak and North Sea area, autumn 2007. *Seabird* 24: 11–32.

Hope Jones, P., Barrett, C. F., Mudge, G. P. & Harris, M. P. 1984. Physical condition of auks beached in eastern Britain during the wreck of February 1983. *Bird Study* 31: 95–98.

Jessopp, M. J., Cronin, M., Doyle, T. K., Wilson, M., McQuatters-Gollop, A., Newton, S. & Phillips, R.A. 2013. Transatlantic migration by post-breeding puffins: a strategy to exploit a temporarily abundant food resource? *Marine Biology* 160: 2755–2762.

Lewis, S., Phillips, R. A., Burthe, S. J., Wanless, S. & Daunt, F. 2015. Contrasting responses of male and female foraging effort to year-round wind conditions. *Journal of Animal Ecology* 84: 1490–1496.

Mesquita, M. D. S., Erikstad, K. E., Sandvik, H., Barrett, R. T., Reiertsen, T. K., Anker-Nilssen, T., Hodges, K. I., & Bader, J. 2015. There is more to climate than the North Atlantic Oscillation: a new perspective from climate dynamics to explain the variability in population growth rates of a long-lived seabird. *Frontiers in Ecology and Evolution* 3: 43.

Schmitt, S. 2014. 'The UK Beached Bird Survey 2014.' (http://www.rspb.org.uk/Images/schmitt_2014_tcm9-389064.pdf) Royal Society for the Protection of Birds. Accessed 24 August 2016.

Slingo, J., Belcher, S., Scaife, A., McCarthy, M., Saulter, A., McBeath, K., Jenkins, A., Huntingford, C., Marsh, T., Hannaford, J. & Parr, S. 2014. 'The Recent Storms and Floods in the UK.' (http://www.metoffice.gov.uk/media/pdf/g/e/Recent_Storms_Briefing_Final_SLR_20140210.pdf) Meteorological Office and the Centre for Ecology and Hydrology. Updated February 2014. Accessed 24 August 2016.

Stone, C. J., Webb, A., Barton, C., Ratcliffe, T. C., Reed, M. L., Camphuysen, K. C. J. & Pienkowski, M. W. 1995. *An atlas of seabird distribution in north-west European waters*. Joint Nature Conservation Committee (JNCC), Aberdeen.

Underwood, L. A. & Stowe, T. J. 1984. Massive wreck of seabirds in Eastern Britain, 1983. *Bird Study* 31: 79–88.

Veron, P. K. & Lawlor, M. P. 2009. The dispersal and migration of the Northern Gannet *Morus bassanus* from Channel Islands breeding colonies. *Seabird* 22: 37–47.

Votier, S. C., Birkhead, T. R., Oro, D., Trinder, M., Grantham, M. J., Clark, J. A., McCleery, R.H. & Hatchwell, B. J. 2008. Recruitment and Survival of Immature Seabirds in Relation to Oil Spills and Climate Variability. *Journal of Animal Ecology*, 77: 974–983.

Votier, S. C., Hatchwell, B. J., Beckerman, A., McCleery, R. H., Hunter, F. M., Pellatt, J., Trinder, M. & Birkhead, T. R. 2005. Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecology Letters* 8: 1157–1164.

Watanuki, Y., Daunt, F., Takahashi, A., Newell, M., Wanless, S., Sato, K. & Miyazaki, N. 2008. Microhabitat use and prey capture of a bottom-feeding top predator, the European shag, shown by camera loggers. *Marine Ecology Progress Series* 356: 283–293.

Weise, F. K. 2003. Sinking rates of dead birds: improving estimates of seabird mortality due to oiling. *Marine Ornithology* 31: 65–70.