Status, origin, and population level impacts of Atlantic Puffins killed in a mass mortality event in southwest Norway early 2016

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Abstract

The typical life history of long-lived seabirds makes their populations extra sensitive to decreases in adult survival. It is therefore important to uncover the extent, causes and consequences of any incident that involves massive die-offs of such species. Towards the end of a stormy winter, large numbers of dead Atlantic Puffins *Fratercula arctica* were beached in Vest-Agder and Rogaland counties, southwest Norway in February and March 2016. There were also reports of smaller numbers of birds found further north along the Norwegian coast, but it was not possible to assess the total extent of the wreck directly. The first birds stranded on 31 January, the day after the storm *Gertrude* (in Norway named *Tor*) caused the strongest winds ever recorded in Norway. Post-mortem examinations of 200 carcasses collected in the two counties over the following two months indicated that 59% of the birds were adults, whereas 9% were first-winter birds. Virological examination of three birds tested negative for Influenza A. All birds were emaciated and lacked significant fat deposits, and had presumably starved to death. Most birds, especially among adults, were in the last stage of primary moult, and had probably been flightless only a few weeks earlier. This may help explain why the different age groups were so disproportionately affected. The mean wing length of adults not in active moult indicated the birds originated mainly from colonies on the east coast of the UK. This conclusion was in accordance with the origins of eight ringed birds found dead in connection with the incident, seven of which were adults with a mean age of at least 21.6 years. It also fits well with results from recent tracking studies of birds with geolocators. The apparent survival of adult birds breeding on the Isle of May, southeast Scotland, was much lower between 2015 and 2016 than in most other years, which, unlike what has been possible for many other incidents, demonstrates that this wreck probably had a serious impact on the population level.

Introduction

Many seabirds are characterised by long life spans and delayed maturity, and spread their reproduction across many years. This is particularly true for the most numerous species breeding at higher latitudes, indicating this way of life has proven successful over the longer term in variable environments where food is not always plentiful close to the colonies. Such a life history does, however, also make the populations very sensitive to changes in adult survival (e.g. Cairns 1987, 1992).

The Atlantic Puffin *Fratercula arctica* (hereafter 'Puffin'), is a typical species in this context, laying single-egg clutches only and rarely breeding before five years old (e.g. Harris & Wanless 2011). Although probably still the most numerous seabird in the northeast Atlantic (e.g. Barrett *et al*. 2006; Mitchell *et al*. 2004), the Puffin is now rated as Vulnerable on the *IUCN Red List of Threatened Species* (BirdLife International 2017) following decades of substantial population decrease in several of its historical strongholds (e.g. Harris & Wanless 2011). Many of these negative trends may be explained by long-term recruitment failures (e.g. Durant *et al*. 2003; Erpur Snær Hansen pers. comm.) and no big differences in adult survival rates among colonies have yet been documented (Harris *et al*. 2005). Nevertheless, occasional events of reduced survival may have important effects on any seabird population (e.g. Frederiksen *et al*. 2008), warranting that mass mortality events should be examined to uncover their extents and causes, and to identify what populations, age classes and sexes are affected.

A more pelagic and dispersed distribution of Puffins outside the breeding season may explain why they are less numerous victims of coastal oil spills than for instance Common Guillemots *Uria aalge* (e.g. ICES 2005). Incidents involving substantial numbers of emaciated Puffins washed up dead on beaches have, however, been registered in most parts of the European distribution range, although most often in UK waters where beached birds surveys (BBS) are most extensive. Harris & Wanless (2011) list 23 wrecks of Puffins in the east Atlantic since 1856, of which 12 occurred in the last 40 years (i.e. the period when Puffin population trends have been monitored with reasonable accuracy) and five in the last ten years (2002–2011) covered by that review. Subsequently, there was an extensive wreck in the Bay of Biscay and southwestern UK waters in midwinter 2013/2014 (Morley *et al*. 2016), and two episodes in southwest Norway; one in February 2003 (Aarvak & Anker-Nilssen 2005) that overlapped in time with the one reported from the southern North Sea (Camphuysen 2003), and one in February–March 2016 (this study). With one exception from Norfolk in May 1856 (see Harris & Wanless 2011), all timed reports of wrecks involving significant numbers of Puffins are from outside the breeding season, and we are not aware of any similar incidents in the west Atlantic where Puffins are much less numerous.

Here we report results of investigations carried out following an extensive wreck of Puffins recorded on beaches in Vest-Agder and Rogaland counties in southwest Norway in late winter 2015/16. These areas have been subject to regular BBS since the 1990s, enabling us to evaluate the relative magnitude of the event. Our primary aims are to shed light on possible reasons for the wreck, document the age and sex distribution and body condition of the birds that were hit, and uncover the breeding areas from which they most likely originated.

Methods

Information on environmental conditions: Information on weather conditions (max 10-minute wind speed, wave height, daily rainfall and air temperature extremes) in southwest Norway and the northeastern part of the North Sea in the months and days prior to and during the wreck was found on the official web sites of the UK Met Office in Exeter (www.metoffice.gov.uk) and the Norwegian Meteorological Institute in Oslo (www.met.no).

Collection and handling of birds: A total of 200 dead Puffins was collected by volunteers from local branches of the Norwegian Ornithological Society. Hereof, 141 (70.5%) were found at Lista in Farsund municipality, Vest-Agder; the remainder 59 were collected on beaches along the coast of Rogaland county (Figure 1). They were all stored in a freezer until later thawed and examined using standard protocols. About half (73) of the Lista birds were examined at the Lista Nature Museum on 4–5 April 2016, where most of them were later preserved as part of the museum's collection of bird skins. All the other 127 birds were examined at NINA's laboratory facilities in Trondheim, 122 of them on 26–29 April 2016.

As part of a regular monitoring of beached birds that has run relatively unchanged since winter 2008/09, a selection of beaches covering 19 km of coastline in Rogaland county was surveyed by volunteer ornithologists once every fortnight from October/November to April. All dead or dying birds found were registered, identified to species level and inspected for plumage oiling.

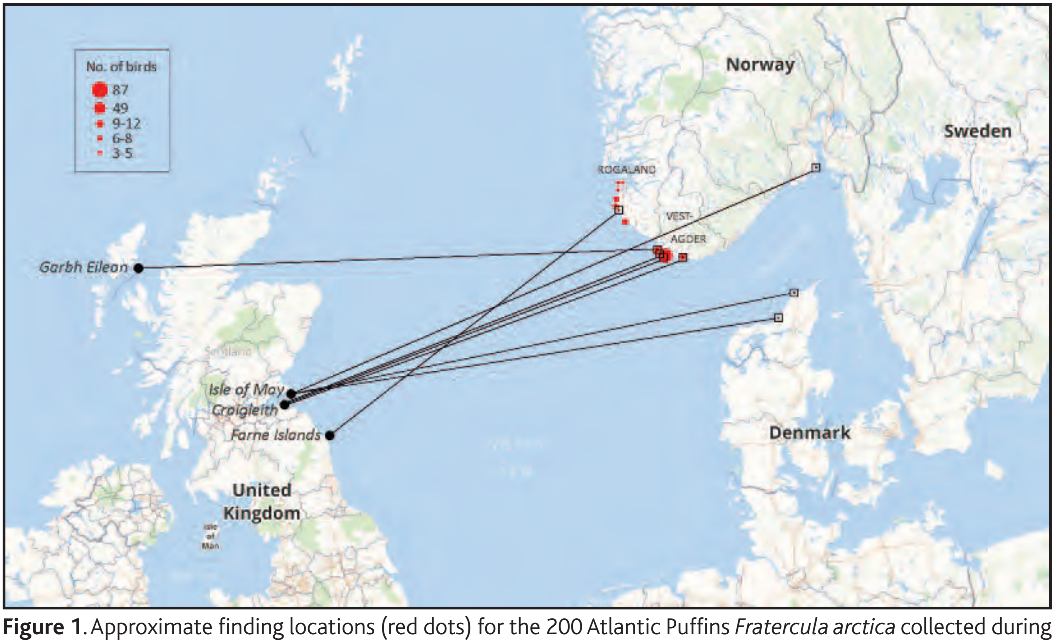

Figure 1. Approximate finding locations (red dots) for the 200 Atlantic Puffins *Fratercula arctica* collected during a wreck of Puffins in Vest-Agder and Rogaland counties, southwest Norway in February–March 2016 and examined in this study. The map also shows the finding locations (dotted squares) and colonies of origin (black dots) of eight ringed Puffins found dead in the eastern North Sea area in the same period (cf. Table 5).

Post-mortem examinations: On 21 April 2016, three birds randomly selected among intact corpses from the Lista sample already measured externally by ML, were sent frozen to the Norwegian Veterinary Institute (NVI) for autopsy and virological testing. All other post-mortem examinations were carried out as described by Camphuysen *et al*. (2007). One person (ML) took all the biometric measurements and made all external and internal assessments of the birds' plumage, state and condition. The freshness of each carcass was assessed on a six-graded categorical scale. Unless the carcass was damaged, a variety of size measurements were collected, including wing length (maximum flattened cord) to the nearest 1 mm and bill depth at gonys and head+bill length to the nearest 0.1 mm. All intact corpses were also weighed on an electronic balance to the nearest 1 g.

To assess the status of flight feather moult, the longest primary (usually P10) of each bird was pulled out, wrapped in aluminium foil and stored individually in a sealed plastic bag. The shaft end of each feather was later inspected to determine if it was soft and "open", indicating it was still growing when the bird died, or hard and "closed", indicating it was fully grown. The method and its apparent value in the context of assessing the origin of birds from wing length measurements, is documented in more detail by Heubeck *et al*. (2011) who used it to control for the effect of moult on wing lengths of Razorbills *Alca torda* beached in the Skagerrak wreck in 2007. We applied the same approach here.

Ageing was done by counting the bill grooves on the bird's upper mandible. Incomplete grooves were counted as 0.25, 0.5 or 0.75, relative to the length of a full groove. In addition, the presence and size of bursa Fabricii was recorded. Physical condition was assessed by inspection of the breast muscle, and ranking of sub-cutaneous and intestinal fat deposits on a 0–3 scale (see Camphuysen *et al*. 2007 for details). If possible, the thickness of sub-cutaneous fat was also measured to the nearest 0.1 mm using vernier calipers. When present and in a reasonably fresh condition, the stomach of each bird (n = 89) was taken out and stored frozen at NINA in case it was needed for further analyses.

Whenever possible (116 cases), sex was determined by gonadal inspection and the diameter of the largest follicle or the length and breadth of the left testis measured to the nearest 0.1 mm. In most other cases, this sexing method was impossible because of scavenging or decay of internal organs. We therefore tried to sex 86 birds at NINA's genetic laboratory as detailed below, using either the primary feather sampled for inspection of their moulting status (84 cases) or tissue from their stomach samples (2 cases). This included all 15 first-winter birds, nine of which had also been sexed by gonadal inspection, and the three birds sent to the NVI. This sexing method only proved successful in 62 (72%) of the cases, probably because of degradation of DNA from decay, which on average was rated more than one category lower for the birds with the successful samples. These samples still increased the total number of birds sexed from 116 (58%) to 172 (86%) and confirmed the sexing by gonadal inspection of first-winter birds in five of six cases. The sixth case proved to be a female in heavy decay that on inspection was noted to have a pinkish-grey, "floating" organ, which erroneously was assumed to be a testis. Testing new samples from further up the shaft of 14 feathers that did not reveal the sex in the first attempt, were all again unsuccessful.

Molecular sex determination: The tip (5–10 mm) of each feather calamus was digested overnight at 56°C in 350 µL lysis buffer and 25 µL proteinase K, during which they were pulse-vortexed twice. Genomic DNA was extracted with the E-Z 96 Tissue DNA Kit (Omega Bio-tek, Norcross, GA, USA) following the manufacturer's protocol. Sex was determined using the universal primers M5 (Bantock *et al*. 2008) and P8 (Griffiths *et al*. 1998). The M5 primer was 6FAM fluoro-labelled. Polymerase chain reaction (PCR) was performed with a multiplex PCR kit (Qiagen, Hilden, Germany) following the manufacturer's protocol, but using 8.4 µL reaction volume. PCR products (1 µL) were mixed with GeneScan 500 LIZ (Applied Biosystems, Foster City, CA, USA) size standard (0.14 µL) and Hi-Di formamide (6.16 µL). Alleles were separated using capillary electrophoresis on an ABI 3130xl Genetic Analyzer and sizes assigned using GeneMapper software (Applied Biosystems). A single allele amplifies in males and two alleles amplify in females.

Survival of adults: The survival of adult Puffins registered to have bred at least once on the Isle of May (56°11'N, 02°33'W) in the Firth of Forth, east Scotland is monitored annually by repeated field observations of about 150–200 uniquely colour-ringed individuals (Harris & Wanless 2011). The annual sightings (1) or non-sightings (0) of the altogether 622 such individuals registered from 1991 up to and including 2017 were analysed by applying the four basic Cormack-Jolly-Seber (CJS) models in Program MARK v. 8.0 (Cooch & White 2017) using the SIN link function with no environmental covariates and adjusting the model results by c-hat. The validity of the models was assessed using model likelihood and the Akaike selection criterion corrected for small samples (AICc). We did not control for trap happiness, which is likely to have slightly overestimated the survival and recapture rates and explain the low goodness of fit of the top ranked model ($P = 0.94$ with 100 simulations) as previously documented in more detail for an earlier part of this time series (Harris *et al*. 2005).

Other statistical analyses: Chi-square tests for differences in distributions of categorical variables among age and sex groups were calculated as described by Zar (1984) in a Microsoft Excel spreadsheet, using the Yates correction for continuity (Yates 1934) for all 2×2 and 2×1 contingency tables. All other statistical analyses were made using IBM SPSS Statistics (v. 23.0, IBM Corp. 2015). Means are presented with their standard errors. One-way ANOVAs were used to test for differences in size and body mass between age groups, whereas sexual differences in such measurements were tested with independent-samples t-tests assuming equal variances and their statistical significance indicated by 2-tailed P values using 0.05 as the alpha level. To reduce the risk of making type-I errors when performing many similar t-tests on biometrical data, we applied the sequential Bonferroni method for assessing levels of significance as originally developed by Holm (1979).

Results

Environmental circumstances: The first dead bird was found on 30 January and the last on 11 April, but most (close to 80%) were collected during February. Median date of collection was 18 February. During most of the wreck, wind speeds and wave heights in the area were close to normal, but nine winter storms had hit the North Sea during the 2–3 months prior to the incident. This is not an unusual frequency of storms for that time of year, but both in November and December 2015, mean wind speeds and wave heights were above the long-term average in the northern North Sea and waters west of Shetland. On 28–30 January 2016, the storm *Gertrude* (in Norway named *Tor*) swept across these waters and caused mean 10-minute wind speeds at up to 91 knots (169 km/h) and wave heights of up to 14 m in the UK sector. On the Norwegian west coast, the southwest winds on 29 January reached a 10-minute mean of up to 95 knots (176 km/h), which in fact is the strongest mean wind force ever measured in Norway.

In winter 2015/16, the regular BBS in Rogaland recorded 257 dead birds of which 68 (26.5%) were Puffins. All but one of these Puffins were found between 6 February and 27 March. This number may not be directly comparable to the results from previous winters, because some beaches were likely visited more often and by other people during the wreck, and we do not know to what extent the Puffins they collected were included in the overall account. Still, this is the highest proportion of Puffins found in the Rogaland BBS scheme to date, and twice as high as in the preceding winter (22 of 168) and five times higher than in winter 2011/12 (15 of 339). In the other five winters of the survey, there were only between 0–2 Puffins among the 202–342 dead birds registered in each year.

Age and sex distribution, body condition and moulting status: Of the 144 birds with reasonably intact heads, all but one were in winter plumage. The odd individual was an adult bird with four bill grooves that was in transition to breeding plumage.

More than half (59%) of the corpses examined had more than two bill grooves, which is typical for adult birds (Table 1). Only 15 individuals (9%) lacked any evident bill grooves and were therefore assumed to be first-winter birds. All but one of them possessed a cloacal bursa Fabricii. As expected, all the adults lacked a bursa, but this character could not be assessed for 31 (30.6%) birds due to scavenging of internal organs. For most (23 of 31) adult females and one female with two bill grooves, the condition of the oviduct indicated they had bred, although it is impossible to say when.

The sex ratio did not vary significantly between age groups (Table 2, $\chi^2_3 = 4.543$, P = 0.209), but there was a predominance of males among the first-winter birds ($\chi^2_1 = 4.923$, P = 0.027) (Table 1).

Of the 158 birds inspected for moult of wing feathers, 89 individuals (56%) were actively growing their longest primaries and 31 (20%) had completed this moult, whereas 38 birds (24%) still retained their old primaries (Table 2). However, this

Table 1. Age and sex distribution (in numbers and %) of Atlantic Puffins *Fratercula arctica* found dead in southwest Norway in February–March 2016. Age was coarsely assessed from the number of grooves on their upper mandibles. The presence of cloacal bursa Fabricii, which is typical of immature auks, is also indicated for the carcasses that were intact, together with a simple index of its size (length × breadth, mm²).

Bill grooves	Putative age	No. of birds (%)	Prevalence of bursa (%)	Bursa index (± 1 SE)	Males : Females (% males)
< 0.5	1st winter	15 (8.7%)	6 : 1 (85.7%)	65.7 ± 10.9	11 : 2 (85.0%)
0.5–1.0	2nd winter	25 (14.5%)	13 : 1 (92.9%)	58.1 ± 4.4	11 : 9 (55.0%)
1.5–2	3rd–4th winter	31 (18.0%)	11 : 9 (55.0%)	43.6 ± 5.8	15 : 14 (52.0%)
> 2	Adult	101 (58.7%)	0 : 70 (0.0%)	0 ± 0.0	50 : 40 (55.6%)

Table 2. Distribution (in numbers and %) of moulting status for the longest primary flight feather among Atlantic Puffins *Fratercula arctica* found dead in southwest Norway in February–March 2016, divided by their putative age as assessed by number of bill grooves (cf. Table 1). Old = old feather not yet moulted, In growth = new feather in active growth, New = new feather fully grown.

Bill grooves	Putative age	All birds (%) Old : In growth : New	No. of males (%) Old : In growth : New	No. of females (%) Old : In growth : New
< 0.5	1st winter	11 (73) : 1 (7) : 3 (20)	8 (67) : 1 (8) : 3 (25)	1 (100) : 0 (0) : 0 (0)
0.5–1.0	2nd winter	9 (50) : 2 (11) : 7 (39)	4 (44) : 1 (11) : 4 (44)	3 (50) : 1 (17) : 2 (33)
1.5–2	3rd–4th winter	5 (19) : 15 (56) : 7 (26)	3 (21) : 5 (36) : 6 (43)	2 (17) : 9 (75) : 1 (8)
> 2	Adult	13 (13) : 71 (72) : 14 (14)	7 (14) : 36 (72) : 7 (14)	5 (13) : 31 (79) : 3 (8)

Table 3. Mean (± 1 SE) size measurements (mm) and body mass (g) of Atlantic Puffins *Fratercula arctica* found dead in southwest Norway in February–March 2016, divided by their putative age as assessed by number of bill grooves (cf. Table 1). All incomplete or fouled carcasses were excluded from analysis of body mass, but the results include birds with a wet plumage. The last column also indicates the statistical level of significance when applying the sequential Bonferroni method to all test results indicated in Tables 3 and 4 (*** = P < 0.001, ** = P < 0.01, * = P < 0.05, ns = not significant).

Variable	Putative age	All (n)	Males (n)	Females (n)	t-test P (t)
Culmen	1st winter	35.9 ± 0.6 (15)	36.5 ± 0.5 (11)	33.0 ± 2.0 (2)	0.020 (2.725) ns
	2nd winter	37.2 ± 0.6 (25)	38.3 ± 0.8 (11)	35.5 ± 1.0 (9)	0.028 (2.397) ns
	3rd–4th winter	39.1 ± 0.5 (30)	39.7 ± 0.7 (15)	38.4 ± 0.6 (14)	0.186 (1.356) ns
	Adult	41.9 ± 0.2 (97)	42.9 ± 0.2 (50)	40.7 ± 0.2 (38)	< 0.001 (6.952) ***
Head+bill length	1st winter	78.7 ± 0.5 (13)	78.8 ± 0.4 (9)	77.2 ± 1.0 (2)	0.103 (1.812) ns
	2nd winter	79.1 ± 0.4 (22)	79.5 ± 0.6 (10)	77.8 ± 0.5 (8)	0.069 (1.947) ns
	3rd–4th winter	78.5 ± 0.4 (29)	79.7 ± 0.5 (15)	77.2 ± 0.3 (13)	< 0.001 (4.014) ***
	Adult	79.6 ± 0.2 (95)	80.7 ± 0.3 (49)	78.1 ± 0.2 (38)	< 0.001 (6.844) ***
Gonys depth	1st winter	21.7 ± 0.5 (14)	22.1 ± 0.6 (10)	21.1 ± 0.3 (2)	0.544 (0.629) ns
	2nd winter	23.7 ± 0.6 (23)	25.2 ± 0.9 (10)	22.5 ± 1.0 (8)	0.079 (1.876) ns
	3rd–4th winter	27.5 ± 0.7 (28)	27.3 ± 1.0 (14)	27.5 ± 1.0 (13)	0.875 (−0.159) ns
	Adult	32.5 ± 0.2 (96)	33.6 ± 0.2 (50)	31.1 ± 0.3 (38)	< 0.001 (7.248) ***
Body mass	1st winter	273.7 ± 12.4 (3)	273.7 ± 12.4 (3)	(0)	
	2nd winter	241.3 ± 10.5 (12)	230.0 ± 21.4 (5)	245.3 ± 11.0 (6)	0.520 (−0.670) ns
	3rd–4th winter	269.0 ± 4.6 (16)	273.9 ± 6.9 (10)	260.8 ± 2.9 (6)	0.181 (1.407) ns
	Adult	286.0 ± 5.8 (42)	298.8 ± 6.6 (24)	268.8 ± 9.1 (18)	0.005 (2.748) ***

pattern differed clearly between age groups (χ^2_6 = 48.27, P < 0.001), with a strong increase with age in the proportion of birds being in active moult of flight feathers. There was no significant difference in moulting status between the sexes within each age group (χ^2_2 range 0.218–4.789, P range 0.897–0.091).

Body condition and possible causes of death: The vast majority of the birds appeared to be severely emaciated, with no subcutaneous or internal fat deposits visible in 89% (n = 116) and 92% (n = 104) of the cases, respectively. Only two birds (both adults) were scored higher than 1 on these characters, both only for subcutaneous fat. In all cases inspected (n = 100), the condition of the pectoral (breast) muscle was judged as either slightly emaciated (10%), emaciated (85%) or strongly emaciated (5%) with no evident variation between age groups (χ^2_6 = 9.964, P = 0.126). Mean body mass did not exceed 300 g in any sex/age group, with adult males weighing on average 30 g more than adult females (Table 3).

Two first-winter males (no bill grooves) and one immature female (1.5 bill grooves) inspected by veterinarian Knut Madslien at the NVI, were all reported to exhibit moderate breast muscle atrophy and therefore assumed to have died from emaciation (body mass 240–278 g). Virological examination of swab samples from their oesophagus and cloaca tested negative for Influenza A virus, but the carcasses were noticeably autolytic (K. Madslien, *in litt.*) and had been found and stored frozen. Considering also the low sample size, this test could thus not rule out that pathogens had been at play.

Body size and area of origin: Size and body mass increased significantly with age for all parameters listed here (Tables 3–4) except head+bill ($F_{3,155}$ = 2.495, P = 0.062; in all other cases P < 0.001 except for body mass $F_{3,69}$ = 5.598, P = 0.002).

Table 4. Mean wing length (mm ± 1 SE) of Atlantic Puffins *Fratercula arctica* found dead in southwest Norway in February–March 2016, divided by the moulting stage of their longest primary (LP) wing feathers (cf. Table 2) and their putative age as assessed by number of bill grooves (cf. Table 1). No tests were statistically significant (sequential Bonferroni method applied, cf. Table 3).

LP feather	Putative age	All (n)	Males (n)	Females (n)	t-test P (t)
Old or	1st winter	148.9 ± 1.1 (14)	148.7 ± 1.4 (10)	149.0 ± 2.0 (2)	0.930 (−0.090)
New	2nd winter	151.7 ± 0.9 (22)	152.8 ± 1.4 (10)	150.8 ± 1.3 (8)	0.316 (1.035)
	3rd–4th winter	155.8 ± 2.2 (15)	154.9 ± 2.0 (10)	157.6 ± 4.3 (5)	0.526 (−0.652)
	Adult	163.0 ± 0.9 (29)	163.5 ± 1.5 (14)	162.0 ± 1.4 (9)	0.510 (0.669)
In growth	1st winter	146 (1)	146 (1)	(0)	
	2nd winter	150.5 ± 0.5 (2)	150 (1)	151 (1)	
	3rd–4th winter	156.9 ± 1.0 (15)	156.4 ± 1.6 (5)	157.0 ± 1.5 (9)	0.804 (−0.254)
	Adult	160.6 ± 1.5 (69)	159.4 ± 2.7 (36)	161.7 ± 1.0 (30)	0.464 (−0.736)
All	1st winter	148.7 ± 1.0 (15)	148.5 ± 1.3 (11)	149.0 ± 2.0 (2)	0.868 (−0.170)
	2nd winter	151.6 ± 0.8 (24)	152.5 ± 1.3 (11)	150.8 ± 1.2 (9)	0.337 (0.986)
	3rd–4th winter	156.4 ± 1.1 (30)	155.4 ± 1.4 (15)	157.2 ± 1.7 (14)	0.422 (−0.815)
	Adult	161.3 ± 1.1 (99)	160.6 ± 2.0 (50)	161.8 ± 1.0 (39)	0.613 (−0.507)

Table 5. Details of eight ringed Atlantic Puffins *Fratercula arctica* recovered in Norway (NO) and Denmark (DK) in first half of 2016 as reported to the British and Norwegian ringing schemes. Except for ringing of nestlings, ages are given in calendar years (y). County names are indicated in parentheses (VA = Vest-Agder, RO = Rogaland, VF = Vestfold). Three of the birds (marked with an asterisk) were among those collected in this study.

Ringing colony location / Year, age	Found 2016; date, municipality, location	Age
1. Farne Islands, Northumberland 55°36'N, 01°40'W		
2015, pullus	17/4, Hå (RO) NO 58°39'N, 05°34'E	2y
2. Craigleith, Firth of Forth 56°04'N, 02°43'W		
1985, pullus	20/2, Farsund (VA) NO 58°05'N, 06°36'E *	32y
1997, 4y+	17/2, Farsund (VA) NO 58°04'N, 06°43'E *	23y+
2000, pullus	6/2, Lindesnes (VA) NO 58°03'N, 07°10'E	17y
3. Isle of May, Firth of Forth 56°11'N, 02°33'W		
2002, 4y+	31/1, Nordjyllands Amt, DK 57°33'N, 09°54'E	18y+
2005, pullus	28/2, Nordjyllands Amt, DK 57°15'N, 09°35'E	12y
2005, 4y+	21/3, Nøtterøy (VF) NO 59°12'N, 10°30'E	15y+
4. Garbh Eilean, Western Isles 57°54'N, 06°22'W		
1985, 3y+	14/2, Farsund (VA) NO 58°08'N, 06°36'E *	34y+

Sexual differences were also evident within each age group, especially for adult birds, but no such differences were found for wing length, nor when divided into different moulting stages. Within each age group, we therefore pooled birds with old or fully re-grown flight feathers before further analyses (Table 4). We found no significant effect of decay on the wing length of moulting adults (independent-samples Kruskal-Wallis test, $P = 0.424$, $n = 97$), indicating that the feather shafts were unaffected by this process.

When excluding birds in active moult, the mean wing length of adult Puffins found dead in this incident (163.0 mm) was between 1.0 and 14.8 mm shorter than any published estimate for breeding birds in Norway, where 12 colonies spread across the entire distribution range show a strong clinal increase in wing length from southwest to northeast (Barrett *et al*. 1985) that almost perfectly matches the average summer sea surface temperature within 100 km of each colony (Anker-Nilssen *et al*. 2003). Compared to the wing lengths of British Puffins (see e.g. Barrett *et al*. 1985) however, it corresponds very well with those of birds breeding on the Farne Islands and Isle of May at the northeast coast of UK, whereas it is somewhat larger than those breeding elsewhere in Britain, including colonies in the Channel Islands, Wales, and the Western Isles, and most colonies in Shetland. With the clear exception of Hermaness at the northern tip of Shetland, mean wing lengths in these colonies are all around 160 mm or less (see e.g. Barrett *et al*. 1985).

In the first half of 2016, eight ringed Puffins were recovered in the area likely to be impacted by this incident (Table 5). All were from colonies in the UK. Their age distribution, seven adults and one first-winter bird, also agreed well with the sample we examined. Interestingly, the mean age of these adults were at least 21.6

(SD = 8.5) years and two were well above 30 years old. The recovery of one bird from the Western Isles also shows that Puffins from most of the Scottish breeding range may possible have been involved, especially when considering that birds killed offshore in northern UK waters during strong southwesterly winds would have been less likely to turn up at any beaches.

Survival of adults from the Isle of May: After adjusting for low over-dispersion (median c-hat = 1.282), the best CJS model accounted for virtually all the variation in the data set (corrected Akaike information criterion QAICc weight > 0.999, second best model ΔQAICc = 43.1) and showed that both survival and resighting rates varied significantly among years. The analysis, which also included the resightings of colour-ringed birds in 2017, estimated an apparent overwinter survival probability of only 0.742 (SE = 0.04, 95% confidence interval 0.653–0.815) in the interval between breeding seasons 2015 and 2016 (Figure 2). The probability of resighting any colour-ringed Puffin estimated to be alive in 2016 was however high (0.951), indicating that the birds that survived the incident returned to the colony in ordinary numbers in the breeding season following the wreck.

Discussion

As detailed in the Introduction, the frequency of Puffin wrecks appears to have increased in recent years, with almost one third of the 26 incidents recorded since the mid-1800s having occurred in the last 15 years. Unfortunately, it has most often proved difficult to track the effects of these incidents in the colonies most likely affected, but the die-off of adult birds off central Norway in March–April 2002 was associated with a much lower survival rate than normal for birds from

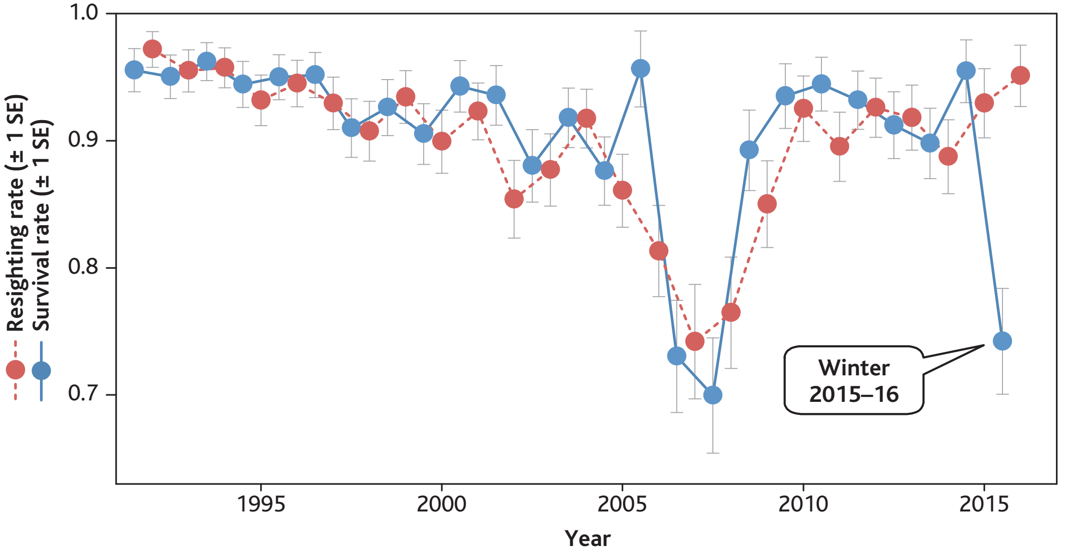

Figure 2. Annual variation in the apparent survival rate of adult Atlantic Puffins breeding on the Isle of May and the resighting probability of the birds estimated to be alive in each breeding season since 1991, as calculated using the CJS model in Program MARK (see details in Methods). Error bars indicate ± 1 SE.

Figure 3. One of the hundreds of adult Atlantic puffins *Fratercula arctica* that washed up on the sandy beaches at Lista on the southernmost part of the Norwegian coast in early 2016. This picture was taken on 24 February. © *Tor Oddvar Hansen*.

Røst (Anker-Nilssen *et al*. 2003). Harsh weather conditions in February–March 1994 were shown to have a devastating effect on the survival of European Shags *Phalacrocorax aristotelis* causing a population crash on the Isle of May, whereas the Common Guillemots from the same colony were seemingly unaffected, even if many more guillemots than shags were found dead during that incident (Harris & Wanless 1996). Massive die-offs of Common Guillemots after four oil spills in the winter areas of birds from Skomer in Wales could, however, all be traced as substantial reductions in adult survival rates at that colony (Votier *et al*. 2005).

The larger proportion of birds in active moult of flight feathers among adults than younger birds may help explain why adults seemingly were killed in higher numbers than the other age classes combined. Apparently, most adults were close to finishing (or had recently finished) their growth of primary wing feathers, indicating their flight and diving skills had been greatly reduced for a number of weeks immediately prior to the wreck. This is likely to have affected their foraging capacity considerably, thereby reducing their ability to sustain their energy demands through a period of bad weather and/or poor food availability.

The moulting of primaries in adult Puffins has been documented to occur most often in October or March, with fewer birds moulting in mid winter (Harris *et al*. 2014). This could be an advantageous strategy as it avoids compromising foraging ability during periods of poor food supply when light is most limited. In our study however, the majority of the adults examined were still in the last phase of this moult when they died, with only 2.4 mm of the length growth remaining (corresponding to 1.5% of a full-grown wing). This indicates that most of them had been flightless sometime in January, which is very different from those incidents examined by Harris *et al*. (2014), even if the results are not directly comparable as we assessed moult from inspecting the shaft end of the longest feather, not by the presence/absence of its waxy sheath. For the youngest age groups, our results are in better accordance with their results, as 73% (12) of the first-winter birds and 50% (9) of the second-winter birds had not yet undertaken the moult of primaries.

As for the Razorbills wrecked in the Skagerrak in 2007 (Heubeck *et al*. 2011), our study also demonstrates another important reason for carefully checking if the longest primary of adult birds was fully grown. Even if this bias only would have reduced the mean wing length estimate of the Puffins by 1.7 mm (1.0%), it would have acted to make our assessment of origin less accurate and more biased towards areas in the southwestern UK.

Several other results also support our conclusion that the majority of the adults originated from colonies on the east coast of the UK. Besides the recoveries of ringed birds (Table 5), tracking of Puffins with geolocator loggers (GLS) has shown that birds from Isle of May usually stay within the northeast parts of the North Sea in late winter (Harris *et al*. 2013), whereas birds from Skomer in Wales move west or south without entering the North Sea (Fayet *et al*. 2016). GLS tracking has not been performed for Puffins breeding on the Norwegian side of the North Sea, but birds from colonies further north do not appear to enter the North Sea regularly, although birds from Sklinna have been located there in late winter or spring (Norwegian SEATRACK project, www.seapop.no/en/seatrack).

Considering the wind directions and what is known about the key areas for UK Puffins at that time of year, it is likely that only a very small proportion of the birds that were killed was ever found. We also received reports of small numbers of dead/dying Puffins from other parts of the Norwegian coast, both inside the Skagerrak (including one of the birds from the Isle of May) and along the west coast as far north as to the Lofoten Islands, where seven seemingly adult birds were beached at Røst (67°32’N, 12°05’E) in the second week of February (Arnold Wilhelmsen pers. comm.). It is difficult to assess the overall extent of this incident or estimate its population level effects with any certainty. However, the survival analysis showed that at least for adults on the Isle of May, overwinter survival (0.74) was seriously lower than the more normal rate of around 0.93 per annum documented over the 1990s for five colonies spread across the northeast Atlantic (Harris *et al*. 2005). Although we have no information as to whether the proportion of adults breeding in 2016 differed from normal, the high resighting probability in 2016 (0.95) makes it is unlikely that many birds avoided showing up in the colony in the breeding season immediately after the wreck event. As Puffins are also known to be extremely faithful to their breeding site (e.g. Harris & Wanless 2011), we therefore do not expect the low survival estimate over winter 2015/16 will change much when resighting data from future years are added. Survival of adults at this colony was similarly low over the winters 2006/07 and 2007/08, which were followed by a decline in the breeding population of about 30% (Harris & Wanless 2011). It still remains to be seen whether the wreck in winter 2015/16 will also be reflected by a distinct decline in Puffin numbers at the colonies in northeast England and Scotland.

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