

MASS MORTALITY OF ATLANTIC PUFFINS *FRATERCULA ARCTICA* OFF CENTRAL NORWAY, SPRING 2002: CAUSES AND CONSEQUENCES

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Anker-Nilssen T., Aarvak T. & Bangjord G. 2003. Mass mortality of Atlantic Puffins *Fratercula arctica* off Central Norway, spring 2002: causes and consequences. *Atlantic Seabirds* 5(2): 57-72. In late March and early April 2002, at least 300 dead or dying Atlantic Puffins *Fratercula arctica* were reported beached on the coast of Central Norway between 62°30' and 65°00'N. Post-mortem examinations of 30 individuals, 93% of which were adult birds, revealed that they had starved. No signs of injuries, parasites, diseases or external contamination were found, but levels of accumulated contaminants were not measured. The most likely origin of these birds were breeding sites at or in the vicinity of Røst (c. 450 000 pairs in 2001) 400-600 km further north. Based on a large difference between expected and observed adult survival rate for Atlantic Puffins at Røst between 2001 and 2002, it is possible that as many as 100,000 puffins died in this unusual but seemingly minor incident.

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INTRODUCTION

The Atlantic Puffin *Fratercula arctica* is the most abundant seabird in Norway with a total breeding population of 1.5-2 million pairs, most of which breed in colonies along the Norwegian Sea (Anker-Nilssen 1991; unpubl. data). The largest colonies in this area are in the Røst archipelago (c. 67°30'N 12°00'E), where breeding numbers decreased by 73%, from almost 1.5 million pairs in 1979 to less than 0.4 million pairs in 2002 (Anker-Nilssen & Røstad 1993; Anker-Nilssen & Aarvak 2003). This massive decline was primarily explained by frequent reproductive failures due to shortage of young herring *Clupea harengus* after the Norwegian spring-spawning stock collapsed in the late 1960s (e.g. Anker-Nilssen 1992; Durant *et al.* 2003) and, occasionally, reduced survival of adults (Anker-Nilssen & Aarvak 2003). North and south of the Norwegian Sea, chick diet is mainly based on other prey species, and populations have been stable or slightly increasing (Barrett *et al.* 1987; Barrett 2001, 2002; Lorentsen 2003).

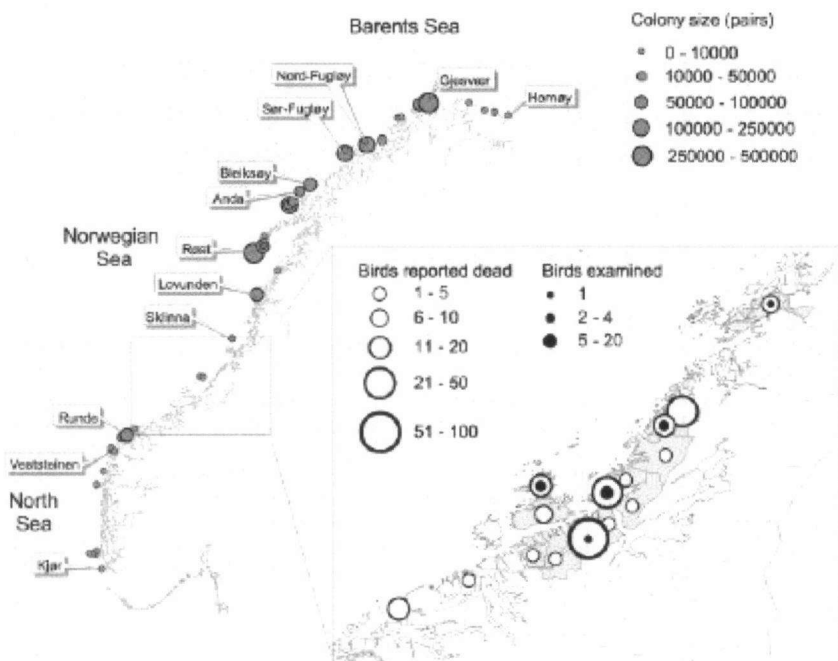


Figure 1. Geographical position of Norwegian colonies of Atlantic Puffins mentioned in the text, the area where Puffins were beached (box), and indications of the distribution by municipality (grey areas) of numbers of individuals reported dead (white circles, $n = 206$) and examined (black circles, $n = 30$).

Figuur 1. Ligging van de Noorse kolonies van Papegaaiduiker die in de tekst worden genoemd, het gebied waar Papegaaiduikers aanspoelden en de verspreiding per gemeente (grijs) van het aantal gemelde slachtoffers (witte rondjes, $n = 206$) en het aantal onderzochte slachtoffers (zwarte rondjes, $n = 30$).

No factors other than those directly or indirectly affecting food supply during the breeding season have been documented to affect population parameters of Atlantic Puffins in Norway (Anker-Nilssen & Tatarinkova 2000). However, the movements and diets of these birds outside the breeding season and, consequently, the environmental conditions they experience at that time of year, are not well known (Anker-Nilssen *et al.* in prep.). It is therefore difficult to assess to what degree factors such as various sources of pollution and extreme weather events affect the highly variable survival of adults between breeding seasons (Anker-Nilssen & Aarvak 2003). The distribution of non-breeding Atlantic Puffins is more pelagic and less aggregated than that of other auks

(Harris 2002). This probably explains why there are few incidents reporting large numbers of beached Atlantic Puffins (Camphuysen 2003). However, it is difficult to determine if this is mainly because they (for the same reasons) are less likely to be hit (e.g. by oil spills) or less likely to beach in significant numbers if they die at sea.

Massive die-offs (wrecks) of emaciated seabirds are known to occur irregularly but relatively frequently in many areas of the NE Atlantic (Blake 1984). Long periods of starvation and extreme weather events (or a combination of both) are the most likely reasons for such incidents, although it is usually impossible to identify the actual cause for any given event. Unfortunately, the possibility that the birds had initially been exposed to hazardous chemicals, or something else rendering them unable to feed, is rarely examined as such causes are both difficult and expensive to establish.

Also, the possible consequences of the incidents at the population level are rarely explored in any detail (Harris *et al.* 2000). One reason is that it may be difficult to determine the origin of wrecked seabirds. For most auks in the NE Atlantic, however, morphometric data for breeding birds are available from a large number of colonies throughout most of the birds' breeding range. These species form geographical races that are relatively distinct in size and often there is also a clinal increase in size with increasing latitude or decreasing sea temperatures in their breeding areas (Barrett *et al.* 1985; Anker-Nilssen *et al.* 1988; Barrett *et al.* 1997; Moen 1991). Thus, by comparing the sizes of wrecked adult birds with those measured at their colonies, it may be possible to identify the core areas from which they originated. Often, a large proportion of beached auks are immatures that have not yet reached the size of adults, making the use of biometry less applicable, but such incidents are less likely to be the most severe in terms of their effects on breeding numbers (Harris *et al.* 2000). Moen (1991) explored differences in body size and allozyme patterns within and among five Atlantic Puffin colonies, and found that they exhibited significant differences in size without significant differences in genetic structure. Thus, differences in body size might to a large degree be phenotypic rather than genotypic. As more refined genetic methods are not available to explore differences on small spatial scales (e.g. Moum & Árnason 2001), biometric comparison is still the most precise and cost effective way to assess the origin of dead birds outside the breeding season.

In late March and early April 2002, many dead and moribund Atlantic Puffins were beached on the coast of Trøndelag, Central Norway. The first birds were found on 26 March and from numerous reports received daily by local authorities it was soon realised that the extent of the incident was extraordinary, with varying numbers of dead puffins found along the whole coastline between 62°30'N and 65°00'N (Fig. 1). Large numbers of adult

puffins are rarely observed close to the coast in this area and to the best of our knowledge, massive wrecks of puffins have never previously been registered so far north. No other species were found dead in significant numbers, but many more live puffins were seen at sea close to the shores. No puffins were reported oiled, but many were described as behaving abnormally, seemingly confused and unable to escape approaching humans. With no systematic procedures, the environmental office of the county governor of Sør-Trøndelag registered reports of at least 300 dead Atlantic Puffins (with exact positions known for 206 individuals) and organised the collection of some of these birds. Based on post-mortem examinations and results from the regular monitoring of Norwegian Puffin colonies, this study aims to identify the most likely causes for the wreck, the location of the birds' breeding areas, and the consequences, if any, of the incident at the population level.

METHODS

Post-mortem examinations The external and internal morphology of 30 dead Atlantic Puffins collected during 1-9 April 2002 were examined following the procedures described by Jones *et al.* (1982). Age was determined by the number of bill grooves on the red outer part of the upper mandible (Petersen 1976). Wing length ($n = 28$) was measured as the maximum flattened cord to the nearest 1 mm using a stopped ruler. Culmen length ($n = 30$), total head length (head+bill, $n = 22$) and bill depth at gonys ($n = 26$) were measured to the nearest 0.1 mm with vernier callipers. Sex was determined by inspection of gonads (when present; $n = 19$). Whole carcasses ($n = 14$) were weighed to the nearest 1 g using an electronic balance. If intact and sufficiently fresh, the left breast muscle was carefully removed and weighed to the nearest 1 g ($n = 9$). Three of the adult birds were also autopsied by Kjell Handeland, National Veterinary Institute, Section for Wildlife Diseases, Oslo, who also undertook histological inspection of brain, eyes, lungs, heart muscle, liver and kidney.

Origin Biometric parameters reported by Barrett *et al.* (1985) for breeding Atlantic Puffins in 12 different Norwegian colonies (Fig. 1) were used as baseline reference data for comparisons. This was justified by the mean wing length of adult birds in our sample being close to the centre of the clinal distribution of this parameter with latitude along the Norwegian coast (Barrett *et al.* 1985). We improved the relevance of the cline by substituting latitude with mean sea surface temperature (SST) in April-August within 100 km of each colony during 1950-99, since SST is more likely to affect the morphology of seabirds than light conditions. SST data were provided by Steve Worley from the Hadley Centre for Climate Prediction and Research and summarized by

Table 1. Size parameters (mean \pm 1 SE) for adult Atlantic Puffins beached in Central Norway, spring 2002. Measurements in mm, mass in g. Sample sizes are indicated in brackets.

Tabel 1. Biometrische gegevens (gemiddelde \pm 1 SD) van adulte Papegaaiduikers die voorjaar 2002 zijn aangespoeld in centraal Noorwegen. Lengtes in mm, gewicht in g. Steekproefgrootte staat tussen haakjes.

| Sex | n | Wing | Head+bill | Culmen | Gonys | Body mass |
|---------|----|--------------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| Males | 11 | 174.6 \pm 1.45 (11) | 83.0 \pm 0.45 (10) | 47.9 \pm 0.35 (11) | 36.2 \pm 0.69 (10) | 339.8 \pm 9.8 (9) |
| Females | 7 | 168.3 \pm 1.91 (6) | 81.1 \pm 0.80 (5) | 45.3 \pm 1.00 (7) | 31.9 \pm 0.92 (7) | 329.3 \pm 23.3 (4) |
| All | 28 | 172.0 \pm 1.2 (24) | 82.2 \pm 0.4 (21) | 46.6 \pm 0.4 (28) | 34.1 \pm 0.6 (25) | 336.5 \pm 9.4 (13) |

David Irons, USFWS, Anchorage. Data from colonies outside Norway were excluded from this analysis because those Puffins are either smaller or larger than Norwegian birds (Barrett *et al.* 1985; Anker-Nilssen & Tatarinkova 2000) or, in the case of birds from the NW Atlantic and Iceland (Moen 1991), because they are not expected to visit this area in significant numbers (Harris 1984b; Gaston & Jones 1998).

Total mortality and population effects To assess the scale of the incident and its possible effects at the population level, we used data on population development collected by the Norwegian national monitoring programme for seabirds (Lorentsen 2003; NINA unpubl. data). Such data were available for five of the Norwegian colonies of Atlantic Puffins (Runde, Sklinna, Røst, Gjesvær and Hornøya). We also used annual data collected by Anker-Nilssen & Aarvak (2002, 2003 and unpubl.) on the adult survival and fledging success of Atlantic Puffins at Røst. They estimated survival and recapture rates from resightings of 390 colour-ringed individuals during 1990-2003 using the SURGE model (Lebreton *et al.* 1992) in program MARK (White 2002).

Statistical analyses Most data were analysed using the *Microsoft® Excel 2002* and *SPSS 11.0* software for Windows. Differences in mean wing length between samples were explored with the *t*-test procedure for small samples ($n < 30$) assuming unequal variances (Parker 1979) and adjusted by sequential Bonferroni correction.

Table 2. Mean wing lengths (mm \pm 1 SE) of adult Atlantic Puffins in colonies from south to north along the Norwegian coast (after Barrett et al. 1985) tested against the mean wing length of adults beached in Central Norway, spring 2002 (Table 1).

Table 2. Vergelijking van de gemiddelde vleugellengte (mm \pm 1 SD) van adulte Papagaaiduikers in kolonies van zuid naar noord langs de Noorse kust (naar Barrett et al. 1985) met de gemiddelde vleugellengte van adulte vogels die voorjaar 2002 zijn gestrand in centraal Noorwegen (tabel 1).

| Colony | Latitude | Longitude | Wing length | <i>n</i> | <i>t</i> | df | <i>P</i> | Bonferroni <i>P</i> |
|----------------|----------|-----------|------------------|----------|----------|------|----------|---------------------|
| Kjør | 58°53'N | 05°26'E | 163.8 \pm 0.46 | 57 | 6.382 | 30.0 | < 0.001 | < 0.01 |
| Veststeinen | 61°54'N | 04°52'E | 166.6 \pm 0.46 | 60 | 4.203 | 30.0 | < 0.001 | < 0.01 |
| Runde | 62°25'N | 05°38'E | 169.5 \pm 0.36 | 73 | 1.997 | 27.2 | 0.056 | n.s. |
| Sklinna | 65°13'N | 10°58'E | 170.0 \pm 0.46 | 70 | 1.557 | 30.0 | 0.130 | n.s. |
| Lovunden | 66°22'N | 12°20'E | 170.2 \pm 0.66 | 34 | 1.313 | 36.8 | 0.197 | n.s. |
| Hernyken, Røst | 67°26'N | 11°52'E | 172.9 \pm 0.26 | 229 | -0.730 | 25.1 | 0.472 | n.s. |
| Anda | 69°04'N | 15°10'E | 174.3 \pm 0.46 | 92 | -1.790 | 30.1 | 0.084 | n.s. |
| Bleiksey | 69°17'N | 15°52'E | 172.9 \pm 0.36 | 148 | -0.720 | 27.2 | 0.478 | n.s. |
| Sør-Fugløy | 70°06'N | 18°30'E | 174.5 \pm 0.66 | 46 | -1.340 | 37.4 | 0.188 | n.s. |
| Nord-Fugløy | 70°15'N | 20°15'E | 175.4 \pm 0.61 | 49 | -2.520 | 35.4 | 0.017 | n.s. |
| Gjesvær | 71°06'N | 25°23'E | 176.6 \pm 0.56 | 29 | -3.470 | 32.9 | 0.002 | < 0.01 |
| Hornøya | 70°23'N | 31°09'E | 177.6 \pm 0.26 | 328 | -4.560 | 25.1 | < 0.001 | < 0.01 |

RESULTS

Age and sex distribution Twenty-eight (93%) of the 30 dead Atlantic Puffins were adult birds (all having =3 bill grooves), two were immature in their 2nd (no bill grooves) and 3rd or 4th (1½ bill grooves) calendar year, respectively. In the further analyses we only use data for the adult birds. The sex ratio for the 18 adults that could be sexed (11? ?, 7? ?, Table 1) did not deviate significantly from 50:50 (Fisher's Exact test, $P = 0.315$).

Physical condition All birds examined were extremely emaciated, with visible traces of subcutaneous or deposited fat found in only one of 13 and one of 16 adults, respectively. The mean body mass of adults (339.8 g, Table 1, Fig. 2) was 29.6% lower than the body mass of adult Atlantic Puffins weighed in the colony at Røst one month later (482.9 g, SE = 5.4, $n = 27$) and 29.1% lower than the weighted mean for similar measurements in early May of nine other years between 1980 and 2001 (479.7 g, SE = 7.0, $n = 9$; Anker-Nilssen & Aarvak 2003). The total range in adult body mass at Røst in early May is 360–585 g (10 years, $n = 585$), with the lowest average registered for a small sample in 1996 (446.7 g, SE = 6.1, $n = 18$). However, the mean body mass of 29 adult Atlantic Puffins collected at sea 34 km west of Røst on 12 April 1996, i.e. at the same time of the year as the mass mortality occurred in 2002, had a mean body mass of 531.5 g (SE = 6.5, $n = 29$, range 475–632 g; Anker-Nilssen & Brøseth 1998).

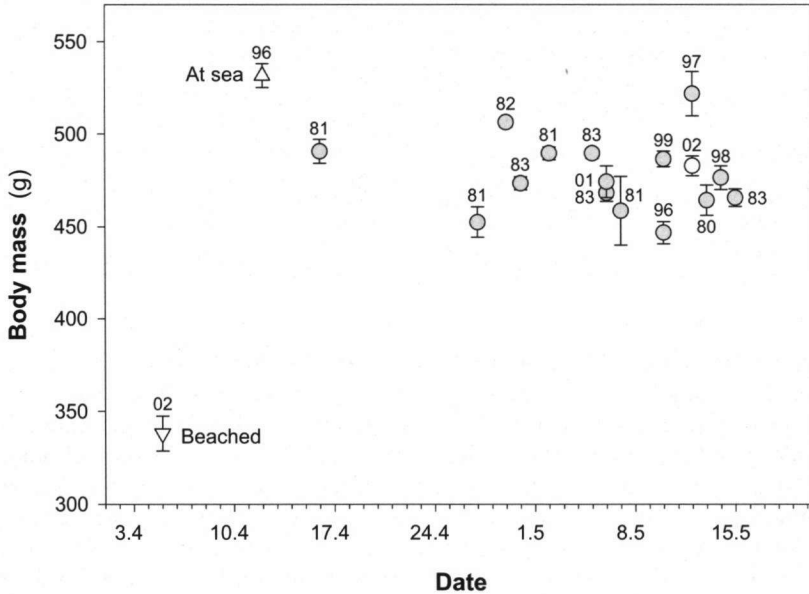


Figure 2. Mean body mass (± 1 SE) of adult Atlantic Puffins beached in Central Norway in early April 2002 (this study, $n = 13$), collected at sea 33 km WSW of Røst on 12 April 1996 (Anker-Nilssen & Brøseth 1998, $n = 29$) and measured in the colony at Heryken, Røst in April-May on different occasions in 1980-2001 (filled circles, n range 9-214, mean 67) and 2002 (open circle, $n = 27$) (Anker-Nilssen & Aarvak 2003).

Figuur 2. Gemiddeld lichaamsgewicht (± 1 SD) van volwassen Papegaaiduikers die begin april 2002 zijn aangespoeld in centraal Noorwegen (deze studie, $n = 13$), die 12 april 1996 op zee 33 km ten WZW van Røst zijn verzameld (Anker-Nilssen & Brøseth 1998, $n = 29$) en die op verschillende data in april-mei 1980-2001 (gesloten rondjes, spreiding $n = 9-214$, gemiddelde 67) en in 2002 (open rondje, $n = 27$) zijn gewogen in de kolonie in Heryken, Røst (Anker-Nilssen & Aarvak 2003).

Thus the beached birds were 63.9% lighter than the birds in that sample. Similarly, the weight of their left breast muscles (?? ? , 1? , mean 27.4 g, SE = 0.86) was 63.3% lower than for those collected at sea (15? ? , 14? ? , mean 43.3 g, SE = 0.61).

Table 3. Estimated annual population changes (%) in 1998-2003 of Atlantic Puffins in the five Norwegian colonies that are monitored, based on counts of apparently occupied burrows in sample plots (Lorentsen 2003; NINA unpubl. data).

Tabel 3. Geschatte jaarlijkse populatieverandering (%) in 1998-2003 van Papegaaiduiker in de vijf Noorse kolonies die met behulp van steekproefplots worden gemonitord (Lorentsen 2003; NINA ongepubl. data).

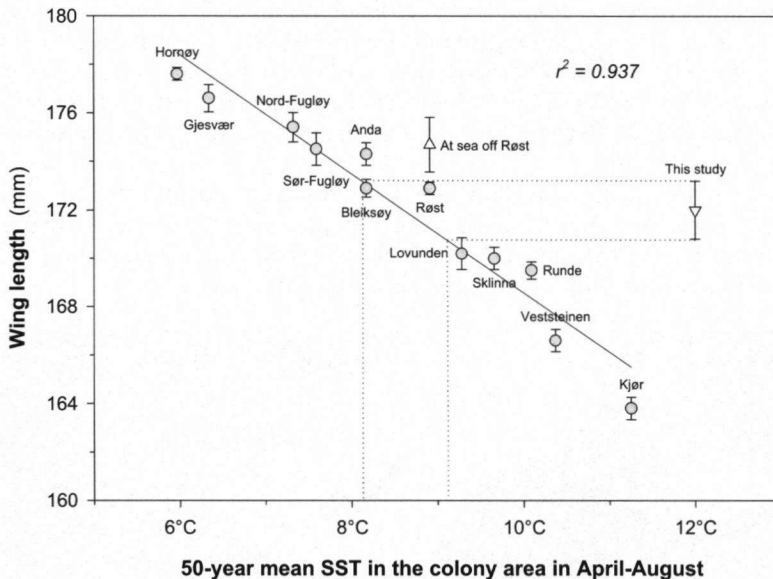
| Year interval | Runde | Sklinna | Røst | Gjesvær | Hornøya |
|---------------|-------|---------|-------|---------|---------|
| 1998-1999 | +3.6 | -5.7 | -2.7 | +16.0 | -5.9 |
| 1999-2000 | -1.5 | -7.8 | -0.9 | -4.5 | +20.0 |
| 2000-2001 | -11.8 | +3.8 | -9.6 | +3.6 | -2.7 |
| 2001-2002 | +3.9 | -20.0 | -15.0 | -1.9 | +8.2 |
| 2002-2003 | +7.5 | +5.7 | +6.1 | -46.0 | +4.5 |

Histological status The veterinary examination of three adults (2? ? , 1?) revealed a total absence of body fat and an atrophied skeleton musculature. No pathogens were isolated by bacteriological sampling of their liver and intestine, nor did they have any substantial load of internal parasites. Tissues of brain, eye, lung, heart, liver and kidney were all judged to be normal by microscopic examinations. The overall conclusion was that the birds were emaciated and had starved to death. This is supported by the fact that the one emaciated individual that was kept in captivity regained full health after one week's feeding (A.O. Folkestad *pers. comm.*).

Origin Mean wing length of the adult Atlantic Puffins that beached was significantly different from similar measurements of adults in colonies south of Runde (62°25'N) and north of Nord-Fugløy (70°15'N), and closest to those for Røst and Bleiksøy (Table 2, Fig. 3). Two birds were still in active moult with their longest primaries not fully regrown, so their wing lengths (142 and 145 mm) were omitted from all statistical analyses.

Total mortality and population effects Estimating the total mortality from only the carcasses recovered is not possible. No standardised beached bird surveys were carried out, and an unknown (but presumably large) proportion of the victims that died at sea never beached.

Since wing length comparisons enabled us to locate the most likely source populations of the birds affected, we can estimate the magnitude of unexplained mortality for the source populations between 2001 and 2002 by simply comparing the expected and observed population development in colonies that are monitored. For the Røst population, Anker-Nilssen & Aarvak



50-year mean SST in the colony area in April-August
 Figure 3. Mean wing length (± 1 SE) of adult Atlantic Puffins beached in Central Norway, spring 2002 (this study, $n = 28$) compared with those of adult birds from different colonies in Norway (filled circles, after Barrett et al. 1985) and adult birds collected at sea 33 km WSW of Røst on 12 April 1996 ($n = 29$). A linear regression line has been fitted to the colony data ($F = 149.5$, $P < 0.0001$).

Figuur 3. Gemiddelde vleugellengte (± 1 SD) volwassen Papegaaiduikers die voorjaar 2002 zijn aangespoeld in centraal Noorwegen (deze studie, $n = 28$) vergeleken met de vleugellengte van adulte vogels van verschillende kolonies in Noorwegen (dichte rondjes, naar Barrett et al. 1985) en met de vleugellengte van adulte vogels die 12 april 1996 op zee 33 km ten WZW van Røst zijn verzameld ($n = 29$). Een lineaire regressielijn is weergegeven voor de gegevens van de kolonies ($F = 149.5$, $P < 0.0001$).

(2003) found a significant relationship between the annual adult survival rate and fledging success in the preceding year. Using their best fitted model for this relationship (quadratic function, $r^2_{11} = 0.65$, $P = 0.015$) the observed fledging success in 2001 (84.4%, Anker-Nilssen & Aarvak 2002) would predict an adult survival rate of 95.3% (95% CI: 91.4-99.2) between 2001 and 2002. However, the true survival rate was estimated at only 84.7% (recapture data from 2003 included, $SE = 2.38$; Anker-Nilssen & Aarvak unpubl. data), i.e. a mortality rate three times higher than predicted. The observed decrease in breeding numbers

between the two years (15.0%, Table 3) fits this estimate perfectly, as no native recruitment was expected due to the age of first breeding in this colony typically being 5-7 years, and all years in the period 1994-1998 being ones of almost complete breeding failure. Translated into number of birds this corresponds to an unexpected loss of 92 000 adults for this colony alone, the total size of which was estimated at 382 676 pairs (SE = 16 073) in 2002 (Anker-Nilssen & Aarvak 2002).

Breeding numbers at Sklinna also decreased markedly between 2001 and 2002 (Table 3). However, the Sklinna population of Atlantic Puffins is relatively small (c. 3 800 pairs in 2000, T. Nygård *pers. comm.*), suggesting that only a small fraction of the victims originated from this colony.

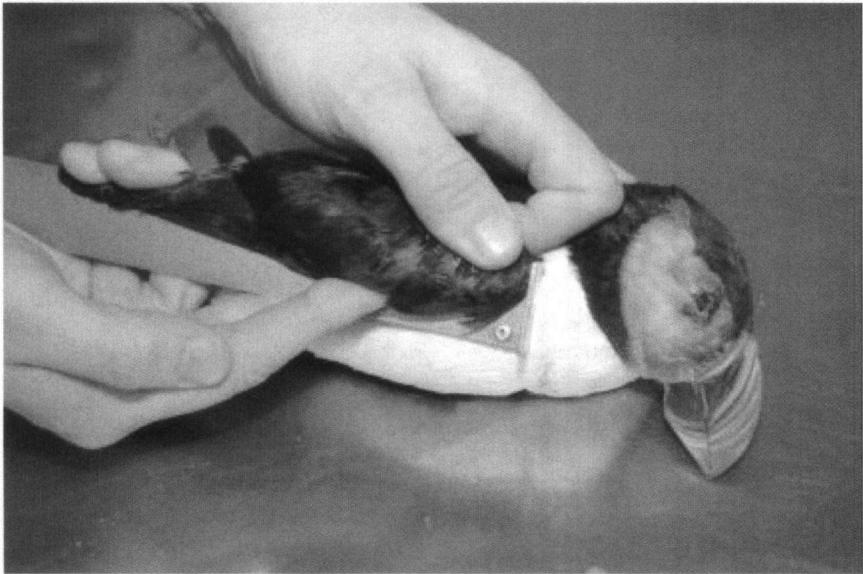


Figure 4. Wing length is the key parameter used to identify the origin of adult Atlantic Puffins from Norwegian colonies. Although the incident occurred in early April, every second adult (as this one) still possessed traces of the winter plumage.

Figuur 4. De vleugellengte is de belangrijkste maat om de herkomst te bepalen van volwassen Papegaaiduikers uit Noorse kolonies. Hoewel het beschreven incident begin april plaatsvond vertoonde een op de twee adulte vogels (zoals deze) nog sporen van het winterkleed.

DISCUSSION

Causes of mortality As there were no signs of bacteriological disease or heavy parasitic burden, we consider it most likely that the birds had starved to death due to prolonged exposure to poor feeding conditions at sea. However, no tests were undertaken to explore if the birds had accumulated any abnormal levels of environmental contaminants, and it is therefore impossible to rule out intake of hazardous compounds as the primary cause for the incident. However, high contaminant levels in emaciated individuals would not necessarily imply that this was the primary cause of death. On the contrary, fat-soluble chemicals (e.g. polychlorinated compounds such as PCBs) that are stored in the fat, will be released and circulated into the blood only during periods of physiological stress caused by food shortage, moult or migration. Thus, when all fat has been used the bird is already extremely distressed and the chemicals might directly result in death (Harris 1984a).

In winter 2001/2002, the string jellyfish *Apolemia uvaria* (Siphonophora) invaded the NE Atlantic and killed salmon *Salmo salar* in farms along the Norwegian coast (Fosså & Asplin 2002). At an early stage, the marine scientist Karl Tangen, OCEANOR, Trondheim, suggested that the puffins could have been blinded from contact with this jellyfish and therefore were unable to locate their prey. We found no support for this explanation because (1) histological examination of eye tissue revealed no abnormal conditions, and (2) the bird that was restored to health was able to pick up from the ground shrimps presented to it (A.O. Folkestad *pers. comm.*); we realise, however, that these observations are based on extremely small samples.

Origin Our analysis strongly indicates that the majority of the beached Atlantic Puffins originated from breeding colonies on the Norwegian coast, primarily from those between Lovunden and Bleiksøy in the northern part of Nordland county (Fig. 1, 3 and 4). The wing lengths of the sample birds resembled most closely those breeding at Røst in the centre of this area, but inter-observer variability in such measurements (Barrett *et al.* 1989) must be borne in mind. The wing lengths of Røst birds in the sample reported by Barrett *et al.* (1985) were measured by TAN and a different observer in 1981, and adjusted for differences between the two (Anker-Nilssen 1983). To simulate that all birds were measured by TAN, this value (Table 2, Fig. 3) should be increased by 0.95 mm, corresponding to half of the significant difference between the two ($t_{519} = 5.264$, $P < 0.001$, Anker-Nilssen 1983). The beached birds were all measured by TAa. However, in 2001 and 2002, 15 breeding adults at Røst were measured by both TAa and TAN, with the mean wing length measured by TAa being 1.43 mm shorter than that measured by TAN (paired sample *t*-test, $t_{14} = 3.647$, $P =$

0.003). Adjusting for both these sources of bias in absolute terms, the sample of dead birds is 0.5 mm (1.43 minus 0.95) closer in size to the birds from Røst than indicated in figure 3, i.e. their wing lengths were only 0.4 mm shorter (corresponding to only one third of the SE of their mean wing length).

Total mortality and population effects Atlantic Puffins at Røst visit their breeding sites regularly from early April, after which they probably remain relatively close to the colonies for the rest of the breeding season. However, foraging ranges of up to 140 and 200 km have been documented within the chick period (Anker-Nilssen & Lorentsen 1990; Anker-Nilssen *et al.* in prep.), and it is not unlikely they are far more mobile during the pre-laying period. Our study indicates that large numbers of Atlantic Puffins from this area died from starvation at the coast some 400–500 km to the south just at the onset of the breeding season. As this is immediately north of the main spawning grounds for Norwegian spring-spawning herring (Sætre *et al.* 2002), this area is expected to have the highest abundance of first-year herring at that time of year. Young herring, which drift northwards with the Norwegian Coastal Current to their main nursery areas in the Barents Sea (Dragesund 1970; Sætre *et al.* 2002), is the key determinant of reproductive success for Atlantic Puffins in the NE Norwegian Sea (e.g. Barrett *et al.* 1987; Anker-Nilssen 1992; Durant *et al.* 2003), and possibly also important for the survival of adults from this area when they visit the Barents Sea soon after breeding (Anker-Nilssen & Aarvak 2003; Anker-Nilssen *et al.* in prep.). However, it is not known to what extent they depend on herring earlier in the season. Both the timing and the centre of gravity of herring hatching varies substantially between years (Sætre *et al.* 2002), suggesting the availability of larval herring off Central Norway in March–April is also variable. Moreover, the distribution of herring larvae in April 2002 indicated that an unusually large proportion of the 2002 year class hatched at the northernmost spawning grounds much closer to Røst (Føyn *et al.* 2002). The stomach contents of birds sampled at sea off Røst on 12 April 1996, when the herring year class was moderate, indicated they had mainly fed on *Polychaeta* worms (P. Fossum *et al.* unpubl. data), but few herring spawned that far north in that year (P. Fossum *pers. comm.*).

Mean body mass of the starved individuals was 30% lower than that of adult Atlantic Puffins caught in the colony at Røst just one month later, the latter being close to the overall mean for that time of year. This suggests that those birds appearing in the colony had not been severely exposed to the incident, or they had been able to find sufficient food to fully recover during April and early May. Moreover, the record high resighting rates of colour-ringed birds in June–July 2002 (99.2%, 95% CI: 96.4–99.8), which was an extraordinarily productive breeding season (Anker-Nilssen & Aarvak 2003), indicated that very few birds

refrained from breeding in 2002. Furthermore, it is unlikely that sub-lethal effects lasted beyond the breeding season of 2003 (for which the model cannot distinguish between survival and recapture rates), since both the Røst and Sklinna populations then increased by 6% (Table 3). Consequently, if this was a major incident, most of the puffins affected probably never recovered.

For obvious reasons, it is impossible to conclude that a starvation incident off Central Norway in spring 2002 was the main reason for the unexpectedly poor survival of adult Atlantic Puffins from Røst between 2001 and 2002 and the parallel severe decreases in breeding numbers at Røst and Sklinna. However, if it were, it would imply that close to 100 000 adult Atlantic Puffins died in this wreck. If other colonies of Atlantic Puffins on this part of the coast were also affected, the total number of birds that died could easily be closer to 150 000. In this context, it is important to note that the total number of birds reported beached corresponds to only 0.3% of the more conservative of these estimates. Such a small fraction is intriguing and suggests that wrecks of very pelagic seabirds merit more attention than those of more coastal species.

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MASSALE STERFTE VAN PAPEGAAIDUIKERS *FRATERCULA ARCTICA* IN CENTRAAL NOORWEGEN, VOORJAAR 2002: OORZAKEN EN GEVOLGEN

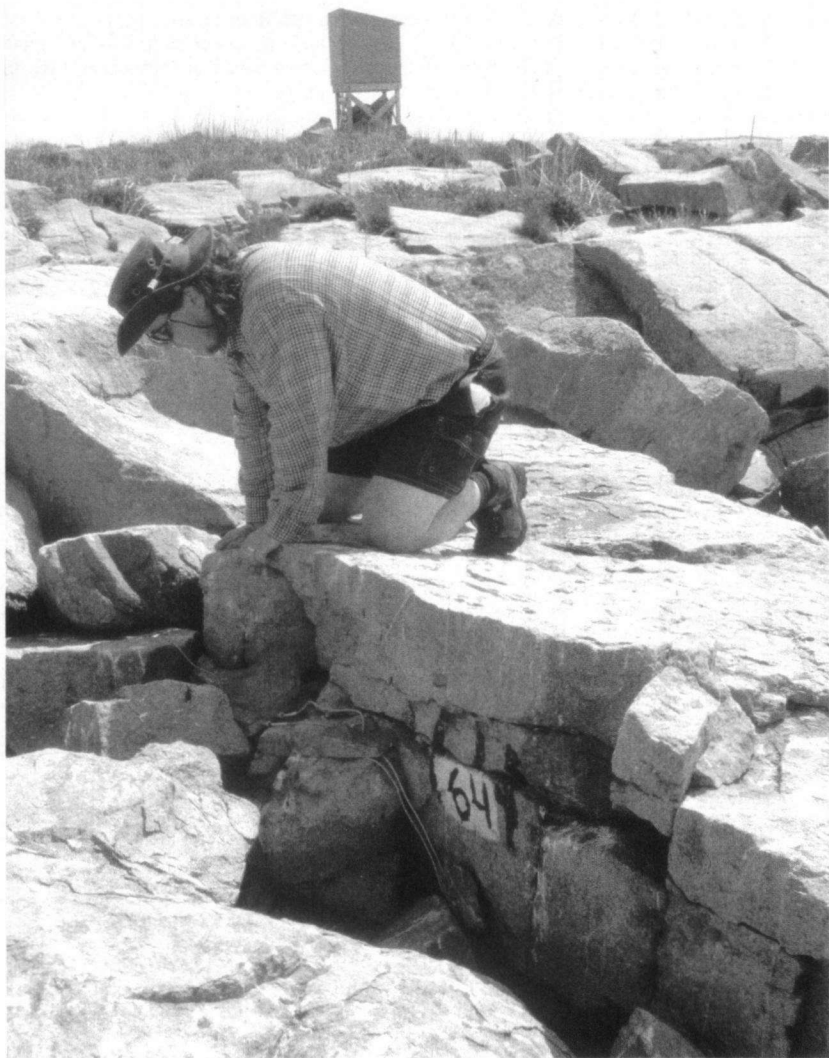
Eind maart, begin april 2002 werden minstens 300 dode of stervende Papegaaiduikers *Fratercula arctica* gemeld die op de kust van centraal Noorwegen waren aangespoeld (figuur 1). Post-mortem onderzoek van 30 slachtoffers, waarvan 93% adult was, bracht aan het licht dat ze waren verhongerd (figuur 2). Er werden geen sporen van verwondingen, parasieten, ziektes of externe besmettingen gevonden; gehalten van contaminanten werden niet bepaald. De slachtoffers waren waarschijnlijk afkomstig van de kolonies op of in de omgeving van Røst (ca 450,000 paar in 2001) 400-600 km noordelijker (figuur 1 & 3, tabel 2). Gebaseerd op een groot verschil in waargenomen en verwachte overleving van volwassen vogels op Røst tussen 2001 en 2002, zijn mogelijk 100,000 Papegaaiduikers omgekomen bij dit ongewone en ogenschijnlijk onbeduidend incident.

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The senior author inspecting a Razorbill nest site at Machias Seal Island. De hoofdauteur inspecteert een nest van een Alk op Machias Seal Island (A. Diamond)