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The great auk in Norway: From common to locally extinct

Anne Karin Hufthammer¹  | Karl Ove Hufthammer² 

¹Department of Natural History, The University Museum, University of Bergen, Bergen, Norway

²Unaffiliated, Bergen, Norway

Correspondence

Anne Karin Hufthammer, Department of Natural History, The University Museum, University of Bergen, PB 7800, Bergen, Norway.

Email: anne.hufthammer@uib.no

Abstract

A total of 477 bones of the great auk (*Pinguinus impennis*) from 53 localities and 55 periods in Norway are studied. All but two, are archaeological sites from the Holocene, mainly from 6000–2000 cal years BP. The two non-anthropogenic sites date to the Ice Age: probably 36,000–34,500 and 14,690–12,890 years BP. The bones are mainly unburned and well preserved but fractured. Except for the open-air sites in northern Norway, the bones are mainly from rock-shelters and caves. In combining archive data, chronological information, and morphometrical studies, we suggest the great auk disappeared from the most southern part of Norway (and Sweden and Denmark) prior to 4000 years BP: a decline in distribution 2000 years ago: It became absent from the Norwegian coast 1000 years ago. Data suggest that it was distributed on the coast and in the fjord systems in winter and early spring. The presence of bones of juveniles/subadults indicates that it was also distributed in northern Norway in the autumn. To evaluate possible size differences, in time and space, nine bone elements have been measured according to standard recommendations. Multiple imputation was used to handle missing data before any statistical analysis. Analyses indicate that bones from Nordland are larger than from the rest of the country, while bones from the northernmost sites are smaller. At some localities, size differences, especially in total length of the bones, are found. It has not been verified if this is due to individual variation or sexual differences. The great auk became extinct in the 19th century. The study supports the theory that human predation at breeding sites was the main cause of its extinction.

KEYWORDS

distribution, extinction, great auk, Norway

1 | INTRODUCTION

The great auk (*Pinguinus impennis*), the only flightless bird in the North Atlantic in the Holocene, became extinct in the mid-19th century. The last certain observation was on June 3, 1844, when a breeding pair was killed on Eldey, a few miles south of mainland Iceland. Its rarity and later extinction, as well as flightlessness, size, and appearance

have made the bird of particular interest for scientists, collectors, and the public for hundreds of years. Numerous publications have sought to describe the bird's features, ecology, and distribution and discussed the causal factors for its extinction.

Grieve, referring to observations at St Kilda in 1697 (Martin, 1753 cited by Grieve, 1885, p. 65), states that the bird was the size of a “solan goose.” Solan goose is another name for northern gannet

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(*Morus bassanus*), an approximately 90-cm-tall bird. Fleming, a British naturalist who observed the bird alive, noted approximately the same size: The bird was 3 ft tall (Grieve, 1885 p. 69). Fuller (1999) gives a slightly smaller average size: 75–80 cm, while other authors have described the great auk as being the size of a goose (e.g., Serjeantson, 2001).

There is, in general, little sexual dimorphism in alcids. This might be because they are all monogamous with biparental care (Winkler et al., 2020) and a low level of mating competition may constrain the sexes to similar sizes (Serrano-Meneses & Székely, 2006). In general, male body size, measured both as body mass and wing length, has been more variable during evolution than female body size (Lindfors et al., 2003). According to Fuller (1999), the sexes of great auk were apparently identical, though there might be slight external differences. Livezey (1988), however, found that samples from Funk Island, off Newfoundland, suggest bimodality in sample distribution of several measurements, especially bill length, and measurements taken by Lucas in 1890 also suggest sexual differences in length of femur.

In the Holocene, the breeding grounds were on islands and remote skerries, in the boreal and low Arctic zones on both sides of the North Atlantic (e.g., Burness & Montevecchi, 1992; Langeveld, 2020; Meldgaard, 1988; Serjeantson, 2001). Burness and Montevecchi (1992) compared measurements of great auk bones from the west Atlantic (Funk Island) and the east Atlantic (Norway). They suggest that birds breeding in the northwest were larger than those in the east Atlantic and that the great auks from low Arctic regions were larger than conspecifics from boreal regions. Furthermore, they suggest that there was no exchange between western and eastern Atlantic populations. In contrast, Thomas et al. (2019) suggest that there were no barriers to interbreeding across the species range.

Being flightless, the great auk had specific demands for breeding places, foremost they needed to be distant from possible predators, but reachable by walking. Fuller (1999) suggests that they bred in large colonies for protection, as do most penguin species. Bengtson (1984), on the other hand, argues that they bred in small colonies. Also, Meldgaard (1988), who studied the great auk in Greenland, suggests that the bird bred in small colonies on remote skerries. For the east Atlantic, Grieve (1885) suggests strong breeding colonies at St Kilda, near Iceland, and probably on the Faroes and the Orkney Islands.

A study from Funk Island on remnants of the great auk's digestive tract, suggests that the birds preyed on several species, mainly fish (Olson et al., 1979). Moreover, a predominance of high-calorie oily species, such as capelin and species from the herring family, was detected.

The great auk was vulnerable to predation during the breeding period, mainly by mammals. As is common for species in the Alcidae family, its fecundity was probably low, with few eggs, and most likely one, laid per pair (Grieve, 1885, p. 7) and reached sexual maturity slowly. If an egg was lost, no replacement was laid that year (Martin,

1753 cited by Grieve, 1885, p. 65). The breeding period was short, lasting from mid-May to the end of June (Fuller, 1999; Grieve, 1885, p. 65). Except for during breeding, great auks spent their time at sea.

Their range through the non-breeding months was wide. In the east Atlantic, great auk bones dated to 5800–7000 years ago have been found as far south as Morocco (Campmas et al., 2010). They were, however, by far most frequent in the North Atlantic. At localities bordering the North Sea, high numbers of great auk bones have been recovered. Curren and Stewart (2000), Groot (2005), and Langeveld (2020) have reported great auk remains from 20 localities in the Netherlands. In the British Isles, bones have been found at 51 sites/periods, mainly on the Hebrides and the Orkneys. The sites date from the Mesolithic to the Norse period (8th–11th C) (Best, 2013). Bones have also been reported from four sites on the Swedish west coast and 15 sites in Denmark, mainly on the coast of the Kattegat (Petersen, 2009). Most of these southern Scandinavian sites are more than 4000 years old. Great auk skeletal elements have been found on localities along the entire Norwegian coast—from 58° to 71°N (Figure 1).

Thomas et al. (2019) sequenced the complete mitochondrial genome of 41 individuals across the species' geographical range and found high haplotype diversity. This indicates constant population size through time, with no evidence of a population decline. Six of the 41 bones in the study are from Norway. Four of these, all humeri, are included in the current study.

By combining archive data, chronological information, and morphometrical studies of the bones, this paper will discuss morphological variation and distribution as well as causal factors for the distribution and the disappearance of the great auk from the Norwegian coast.

2 | MATERIAL

The bones included in this study are from the Osteological collection at The University Museum, University of Bergen. The collection holds bone assemblages from more than 1850 localities in Norway, mainly from archaeological sites.

Great auk bones—477 bones in total—have been found in 53 localities (Figure 1 and Table 1). Due to human handling and/or taphonomy during deposition, most bones are heavily fragmented. Preservation conditions for unburned bones are particularly good under cold conditions, for example, in northern Norway. There, well-preserved bones are found at open-air sites (Localities 1–12, Figure 1 and Table 1). At sites further south, the bones are mainly from caves and rock shelters where they have been protected from the wind and weather. (The Norwegian word for rock shelter is “helleren,” and for cave, it is “hulen” or “hola.”) All but two bone assemblages are from the Holocene and are found at archaeological sites. The two which are from the last Ice Age (Weichselian/Devensian), are probably naturally deposited.

FIGURE 1 Localities with great auk bones. The locality numbers match those in Table 1. The localities in Sweden and Denmark are after Petersen (2009). [Colour figure can be viewed at wileyonlinelibrary.com]



3 | METHODS

Many of the archaeological sites have been in use for a long time (Table S1). The time frame of the settlement phases, and hence the age of the bones, has in general been assessed by radiocarbon dating, archaeological chronology, or artifacts, or a combination of these three.

With regard to the great auk, there is no mention of differences in size in the written sources, but Fuller (1999) assumes that the differences between the sexes were minor, if any. To explore size

differences the following bones have been measured according to recommendations by von den Driesch (1976): scapula, coracoid, humerus, radius, ulna, carpometacarpus, femur, tibiotarsus, and tarsometatarsus. Any ontogenetic features in the bones that relate to juvenile or subadult age were recorded with reference to observations by Watanabe (2017).

We present the data as means, 95% confidence intervals, and standard deviations. We explore whether there are geographical or temporal gradients by calculating Spearman's correlation between the measurement and the longitude, latitude, and age of the site.

TABLE 1 Localities included in the study along with bone element distribution for each site, bones that are known of but have not been studied, total number of great auk bones for each site, and the percentage of great auk bones compared with total number of marine birds at the locality

Locality No., with reference to Figure 1	Accession No. locality	Cranium, quadratum, mandibula	Vertebrae	Scapula, coracoideum, furcula	Sternum	Humerus, radius, ulna	Carpometacarpus	Phalanges manus	Os coxae	Femur, tibiotarsus	Tarsometatarsus	Bones reported, not seen	NISP great auk bones	NISP marine birds	% great auk of total marine birds
1	JS 349 Advik					3				2			5	196	2.6
2	JS 358 Grasbakken, hus 4			1		4							5	266	1.9
3	JS 370 Grasbakken, hus 1, 3, 4											14	14	3245	0.4
4	JS 371, Nyelv, Lossoas hus,	5		5	1	13	4			2			30	780	3.8
5	JS 382 Grasbakken, hus 9, 11, 12			1		1				2			4	294	1.4
6	JS 400 Nyelv 1938			1		3							4	36	11.1
7	JS 480 Mestersanden											1	1	139	0.7
8	JS 611 Nyelv 1978											11	11	420	2.6
9	JS 734 Mortensnes (forminne 8)											3	3	132	2.3
10	JS 748 Karlebotnbakken											26	26	403	6.5
11	JS 832 Bergeby			3		3	1				1		8	268	3
12	JS 603 Iversfjord	2		2	1	7	1				2		15	250	6
13	JS 812 Føre									1			1	10	10
14	JS 523, JS 528, JS 532 Storbåthelleren	9		28	9	33	5			15	3		10	1862	5.6
15	JS 910 Nordland I	1				3							4	1153	0.3
16	JS 874 Helvete Trenyken	1								1	1		3	128	2.3
17	JS 684 Stjørhelleren	2	1			10	1			4	1		19	144	13.2
18	JS260 Kirkhelleren	2		1	1	8	1		1	7	6		27	861	3.1
19	JS 14 Aakvik	1		1		2							4	135	3
20	JS 264 Flatåsen II					5				1	1		7	343	2
21	JS 8 Solsemhulen			1		2							3	24	12.5
22	JS 10 Absalohelleren			1									1	22	4.5
23	JS 12 Einhol III			1									1	7	
24	JS 13 Sandhelleren									1			1	23	4.3
25	JS 5 Hestneshulen	1											1	46	2.2
26	JS 403 Boshelleren			2	2	2				1			7	79	8.9
27	JS 194 Møyslåtten			1									1	6	
28	JS 16 Laksevaagen			1									1	9	
29	JS 104 Valsethulen			1									1	5	
30	JS 153 Laksevaagen II									1			1	1	
31	JS 719 Sør-Dalahelleren											1	1	8	
32	JS 6 Sauehelleren		1	2	1	1				1			6	86	7
33	JS 7 Lillehelleren					1							1	45	2
34	JS 427, JS 440 Skjonghelleren											4	4	301	1.3
34	JS 948 Skjonghelleren			1		1							2	1080	0.2
35	JS 305 Dollsteinhøla					1							1	137	0.7
36	JS 445, JS 487 Grønehelleren			1	1	17	1			2	3		25	108	23.1
37	JS 495 Søre-Leirvika											1	1	1	
38	JS 728 Kotedalen											2	2	43	4.7
38	JS 728 Kotedalen											34	34	1180	2.9
39	JS 390 Follese					1							1	1	
40	JS 901 Hetlevik					1							1	3	
41	JS 259 Blomvåg			1		2				1			4	110	3.6
42	JS 1 Ruskeneset					1		1		2			4	58	6.9
43	JS 258 Skipshelleren				1		1			1			3	435	0.7
44	JS 199 Rundøyno			1	1	1	1						4	8	
45	JS 257 Ostrabakken	2	2	4	3	7	1			7			26	45	58
46	JS 428 Setrehelleren					3	1				1		5	79	6.3
47	JS 944 Kobbeshelleren			2		1	1						4	97	4.1
48	JS 797 Austbø	1											1	53	1.9
49	JS 112, JS 412 Vistehøla	1	1	6	1	14			1		1		25	294	8.5
50	JS 238 Tuen av Vågamo											7	7	32	21.9
51	JS 626 Auve									1			1	171	0.6
52	JS 521 Frebergsvik											1	1	32	3.1
53	JS 560 Tørkop			1			1						2	35	5.7

Note: Two localities are recorded twice because the bones are from different time periods and excavations at the same locality. Locality No. refers to numbers attributed to each locality in Figure 1.

Spearman's correlation was chosen so that we could capture any monotonic associations, not just linear ones.

Due to the bones' condition, there were many incomplete measurements. To reduce any bias caused by missing data and to improve the precision and the statistical power, we used multiple imputation. For each bone element, we generated 50 imputations using the multivariate imputation by chained equations (MICE) algorithm (van Buuren, 2018). For this, we used the R package "mice" version 3.14.0 (van Buuren & Groothuis-Oudshoorn, 2011) and "miceadds" version 3.12–26 (Robitzsch & Grund, 2022). The imputation method was set to "norm" (Bayesian linear regression), the number of iterations to 40, and otherwise, default settings were used. The included variables were the measurements, side (left/right), latitude, longitude, and the log-transformed estimated age of the bone. The chronological age was set to the middle value of the estimated age range. We report descriptive data and correlations (all pooled from the imputed data using Rubin's rules) only for the bones and measurements where there were sufficient values to fit reliable imputation models. For each bone element, we report the number of bones, and for each measurement, the number of complete values. All statistical analyses were performed using R version 4.2.0 (R Core Team, 2022).

Age and sex are essential knowledge in most paleoecological studies of fossil assemblages. For example, occurrence of immature

individuals can be evidence for breeding places in the vicinity (Watanabe, 2017) and reveal breeding strategies of extinct animals (Turvey & Holdaway, 2005). Therefore, all bones, including those that have not been measured, have been recorded as being from a juvenile/subadult or not.

The postnatal ontogeny of avian skeletons is little known (Watanabe, 2017). The avian skeleton reaches maturity early. Unlike mammals, birds do not have growing points between the epiphysis and diaphysis, but grow by apposition from the shaft to the end (Serjeantson, 2009, p. 17). Watanabe (2017), who studied the ontogenesis of six long bones in four avian species, found that for most species longitudinal growth of the bones seems to cease around the time of fledging. At that time, the limb bones will be of the same length as those of an adult individual. There are, however, exceptions: in large chicks and fledglings in alcids, bones that are not fully grown and with cartilaginous epiphysis have been observed (Gaston & Jones, 1998).

4 | RESULTS

The closest living relative to the great auk is the razorbill, and it may be the species with the closest resemblance to the great auk with regard to morphology and biogeography. In a previous study,

TABLE 2 Estimated means (with 95% confidence intervals) and standard deviations for four bone elements, along with Spearman's correlation between measurements and longitude, latitude, and bone age (radiocarbon date)

Bone element	Meas.	<i>n</i> ^a	Mean	95% CI	SD	Longitude		Latitude		Age	
						<i>R</i>	<i>P</i> value	<i>R</i>	<i>P</i> value	<i>R</i>	<i>P</i> value
Tarsometatarsus (<i>n</i> = 20)	GL	12	51.6	48.7 to 54.5	3.6	−0.2	0.44	−0.1	0.66	−0.1	0.61
	Bp	13	13.5	12.8 to 14.2	1.1	−0.2	0.51	−0.1	0.72	0.0	0.96
	SC	19	7.0	6.7 to 7.3	0.5	−0.2	0.55	0.0	0.91	0.4	0.11
	Bd	13	13.9	13.0 to 14.9	1.2	0.0	0.97	0.1	0.82	0.4	0.23
Humerus (<i>n</i> = 78)	GL	21	100.7	98.5 to 102.9	4.5	0.0	0.86	0.1	0.71	0.1	0.58
	Bp	40	24.5	24.2 to 24.8	1.0	−0.2	0.13	−0.1	0.33	0.0	0.99
	SC	54	10.0	9.9 to 10.1	0.5	−0.2	0.18	−0.1	0.42	0.0	0.92
	Bd	37	15.5	15.3 to 15.7	0.7	−0.3	0.08	−0.2	0.12	−0.1	0.40
Tibiotarsus (<i>n</i> = 34)	SC	29	6.1	6.0 to 6.3	0.5	−0.4	0.01	−0.4	0.04	0.2	0.27
	Bd	21	12.4	12.0 to 12.9	1.0	−0.3	0.11	−0.3	0.17	0.2	0.48
	Dd	21	11.7	11.4 to 12.1	0.9	−0.4	0.08	−0.3	0.14	0.1	0.59
Ulna (<i>n</i> = 36)	GL	19	55.9	54.4 to 57.4	2.4	0.0	0.92	0.0	0.98	0.1	0.78
	Bp	19	9.1	8.9 to 9.4	0.5	−0.2	0.41	−0.1	0.69	0.0	0.87
	SC	33	4.1	4.0 to 4.2	0.2	−0.3	0.16	−0.2	0.37	−0.1	0.61
	Did	23	10.2	10.0 to 10.4	0.5	−0.2	0.28	−0.3	0.15	0.1	0.82
	Dip	18	16.1	15.6 to 16.7	1.1	−0.4	0.04	−0.3	0.12	−0.1	0.50

Note: All estimates are based on multiple imputation.

Abbreviations: Bd, breadth distal; Bp, breadth proximal; CI, confidence interval; Dd, depth of distal end; Did, diagonal breadth of distal end; Dip, diagonal breadth of proximal end; GL, greatest length; Meas., measurement; *n*, number of recorded values; *R*, Spearman's rho; SC, smallest breadth of the corpus; SD, standard deviation.

^aThe estimates are based on results from multiple imputation, that is, they use data from *all* bones, not just the *n* bones that have complete data. Latitude and longitude refer to data in Table S3 and age to chronological age in Table S1.

Hufthammer (1982) measured the same bone elements as those of the great auk of 18 recent specimens of razorbill (*Alca torda*) (nine of each sex) and 30 recent specimens of thick-billed murre (*Uria lomvia*) (15 of each sex). Total length, particularly of the long bones, is an expression of size. An analysis of variance for both species displayed no significant difference in total length of the bones between the sexes. Haftorn (1971), however, reports that there are sexual differences in razorbill, in wing length as well as total body length.

Table S2 lists the measurements for the nine bone elements that are included in the study. Due to heavy fragmentation, the full set of measurements are provided for relatively few bones.

Table 2 shows descriptive data and the results of the Spearman's correlation test for four bone elements, based on multiple imputation. There are no signs of an association between age (radiocarbon date) and any of the measurements. There are a few signs of a north–south or east–west gradient. However, for tibiotarsus, there is some (weak) evidence (mainly for smallest breadth of the corpus [SC]), and there is also some evidence for differences in the diagonal breadth of the proximal end (Dip) of the ulna. We therefore explored the data

further, to try to identify any patterns. We found that the measurements from the two furthest northern counties differ from the other localities (Figure 2). In particular, the tibiotarsus measurements from Nordland are larger (especially for distal breadth [Bd] and depth of distal end [Dd]), with some signs of the Finnmark measurements being smaller (for Bd, Dd, and SC). Finnmark, not Nordland, is the most northern and eastern county, so while there is a geographical pattern, it is not a north–south/east–west gradient (except perhaps for SC), which explains the somewhat weak evidence from the correlation tests. For ulna, the diagonal breadth of distal end (Did) and Dip measurements from Finnmark are smaller than the measurements from the other counties.

According to criteria given by Watanabe (2017), 17 bones are identified as being from juvenile/subadult individuals. From Locality 1, two tibiotarsi; Locality 3, three tibiotarsi and one tarsometatarsus; Locality 12, one carpometacarpus; Locality 14, two coracoid, one scapula, one humerus, and one tibiotarsus; Locality 18, one humerus, one femur, and one tarsometatarsus; Locality 26, one radius; and from Locality 46, one carpometacarpus.

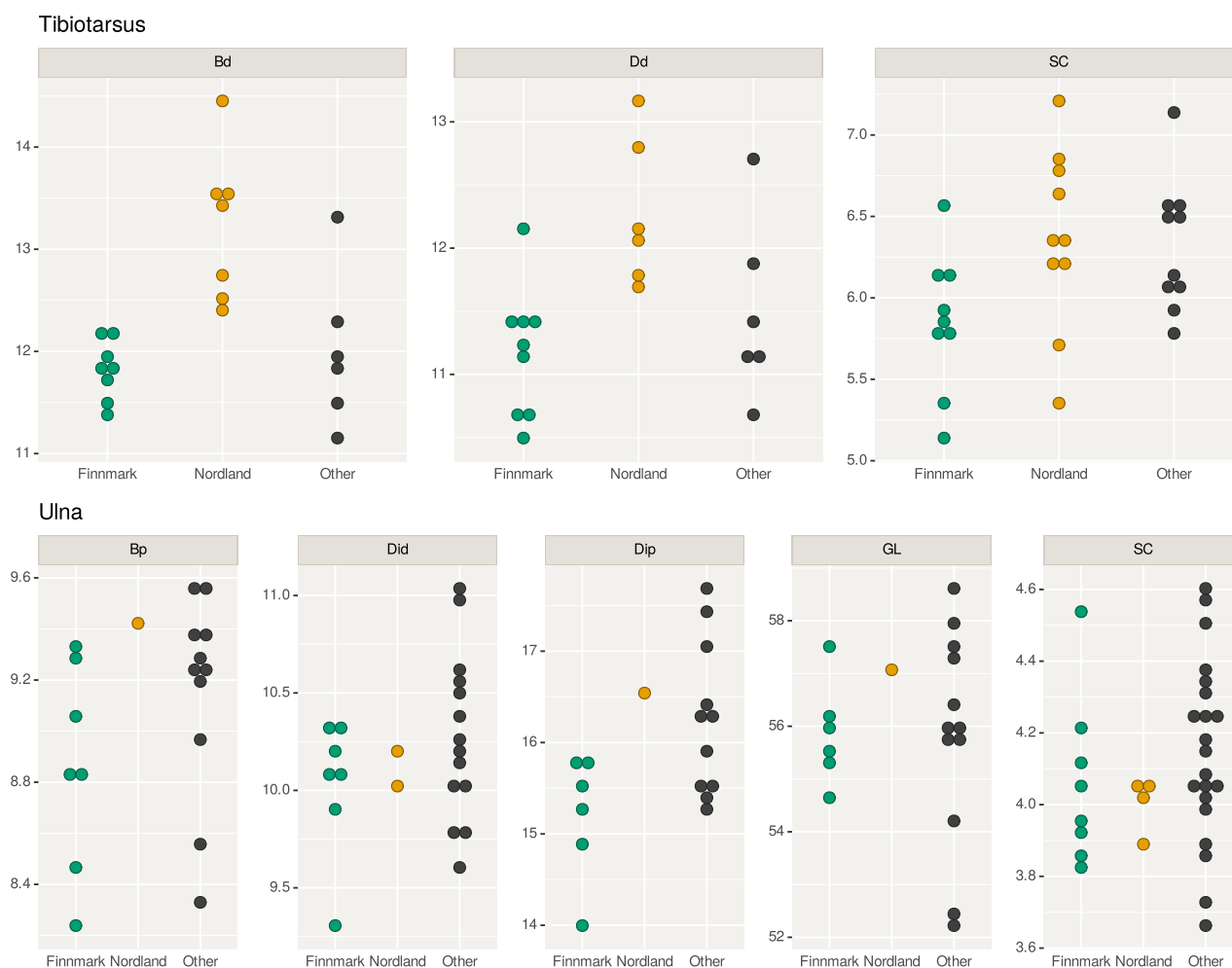


FIGURE 2 Dot chart showing measurements of tibiotarsus and ulna stratified by county (Finnmark, Nordland, and all other counties). For each panel, each dot corresponds to one bone. Only complete (not imputed) data are shown. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

5 | DISCUSSION

The oldest bones are from non-anthropogenic layers, from the middle Weichselian (Marine Isotope Stage 3) in the cave Skjonghelleren (34, Table 1). Imbedded in clay, thousands of bone fragments, mainly of birds from the Alcidae family, have been found in the cave (Larsen et al., 1987). The bones are probably waste refuse from polar fox (*Vulpes lagopus*) activity. Two bones of the great auk, a coracoid with severe pathology and a radius have been found, together with other bird bones dated to $31,670 \pm 410$ ^{14}C years BP. Calibrated age (2 sigma) is 34,155–32,506 BCE (Heaton et al., 2020; Stuiver et al., 2022), which implies that they are from the later part of Marine Isotope Stage 3. The open-air locality Blomvåg (41, Table 1) is the other non-anthropogenic Ice Age locality holding great auk bones. There, in clay sediments, bones of 34 species of birds, mammals, and fish have been identified (Lie, 1986). The bones are from the Bølling–Allerød interstadial: 14,690–12,890 years BP, a relatively warm period at the end of the Ice Age.

All bones that date to the Holocene, that is, younger than 11,700 years, have been found at archaeological localities. Except for the sites Tørkop (53), Frebergsvik (52), Viste (49), Skipshelleren (43), and the oldest layers at Kotedalen (38) which date to the older Stone Age, the majority are from the younger Stone Age and Bronze Age (5000–2500 years ago) (Figure 1 and Table S3).

In archaeological coastal sites in the British Isles (Scotland, Hebrides, and the Orkneys), great auk bones are present at all Mesolithic sites and 44% of the Neolithic sites (Best, 2013) but only at 8% of the sites from the Norse period (793–1066 CE). In southern Scandinavia—Sweden and Denmark—great auk bones are mostly found at sites that are older than 4000 cal years BP. In Sweden, great auk bones have largely been recovered on the west coast (Jonsson, 1995; Liljegren & Lagerås, 1993), and in Denmark, most sites are on the Kattegat coast (Petersen, 2009). The distribution in the very southern part of Norway demonstrates a similar pattern: great auk bones have only been found at sites that are at least 4000 years or older (Locations 50–53, Figure 1 and Table 1). On the western and northern coast, however, the distribution is very different from further south. There, most sites date to the younger Stone Age and to the Bronze Age (5000–2500 cal years BP).

The percentage of great auk bones is particularly high at Localities 36, 45, and 50 (Figure 1). All three are on the very outer coast, in the south of Norway. In general, locations with great auk bones are in coastal areas. Exceptions are the northernmost locality Iversfjord (12, Figure 1), localities in the inner area of the Varangerfjord (1–11, Figure 1), and Skipshelleren (43, Figure 1) which all are in fjord areas. The presence of great auk bones at those localities illustrates that the great auk was not only present on the Norwegian coast, but also migrated into the fjord systems, as they probably also did in Greenland (Meldgaard, 1988).

In nearly all sites, the percentage of great auk number of identified specimen (NISP) compared with marine birds is relatively low (Table 1). Except for the fact that the great auk in the southernmost regions of Norway is only found at sites that are older than

4000 years, there are no significant changes in distribution and frequencies until ca. 2000 years ago. Best (2013) reports a pattern of distribution and frequencies that is similar to that of Norway in the British Isles. She noticed a large decline in great auk numbers and distribution by the late Iron Age. However, she also noted that great auk NISP frequencies declined as a proportion of NISP avian assemblage over time, from 6% in the Mesolithic to 0.07% in the Norse period (Viking Age). The same decline has not been detected in Norway. In fact, the highest frequency of great auk bones, 58%, is found in Iron Age layers at the site Ostrabakken (45). There might be several explanations as to why there are few, or no, great auk bones at a site. Obviously, bones will be missing if the bird was not hunted or a prey of interest or if it was absent in the region when the site was in use. The oily fish species capelin (*Mallotus villosus*) and herring (*Clupea harengus*) were probably important prey for the great auk (Olson et al., 1979). Herring and capelin move in large schools and have extensive seasonal migrations along the Norwegian coast. Traditionally, both species migrate to the coast during winter and early spring for spawning, capelin from the Barents Sea to northern Norway (Finnmark) and herring to the western coast of Norway. Herring distribution varies a great deal. In recent years, they have been spawning from Nordland to Møre, but in the 19th century, they had a more southerly distribution, from Møre to Lindesnes. Assuming that herring, European sprat (*Sprattus sprattus*), and capelin were important prey, one may expect great auk in Norwegian waters during the winter and early spring, and thus that great auk bones might be found at sites that were occupied at that time of the year. Investigations have shown that the site Skipshelleren (43, Table 1), for example, was in use in late winter and early spring (Hufthammer et al., 2010), a time when the great auk may have followed the spring spawning herring or preyed on European sprat in the fjord area.

The presence of bones assessed as juveniles/subadults, though low in numbers, strongly indicates that great auk also visited the Norwegian coast in the autumn. Interestingly, most of these bones are from locations in northern Norway. This may indicate a closer proximity to the breeding area and/or that the auk preyed on a source that was available there in the autumn months. There are no data (e.g., neonatal bones) to indicate that great auk bred on the Norwegian coast.

The youngest date of great auk in Norway is 1545 ± 70 (TUa-1535) from the site Kobbhelleren (47, Figure 1). Calibrated age (1 sigma) is 914–1118 CE and median calibrated probability is 1018 CE (Heaton et al., 2020; Stuiver et al., 2022). This date shows that great auk was present along the Norwegian coast in the late Viking Age/early medieval. Because of its size and flightlessness, it is reasonable to believe that the great auk was a bird that aroused human interest in the past. Still, there is no mention in medieval written sources (e.g., the sagas, diplomas, and legal texts) of the bird being present in Norwegian waters, nor are any traces of great auk found in the many urban bone assemblages that date to the Middle Ages in Oslo, Tønsberg, Bergen, or Trondheim, or in any medieval farm midden in northern Norway. This strongly suggests that the great auk



FIGURE 3 Top left: The cave Kirkhelleren seen from the north. Top right: The interior of the cave, from the excavations in 1937–38. Photo: With permission from E.K. Jørgensen. Lower panel: Some of the great auk bones from the cave that illustrate their great variation, particularly in bone length. From the left, two tibiotarsi from the same square and layer, two humeri, two femora, and three tarsometatarsi. Photo: Adnan Icgic [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1002/oa.3161)]

has been absent from the Norwegian coast for the last 1000 years. Bengtson (1984) suggests that the great auk became extinct because of human predation. Judging from the frequencies and distribution pattern in Norway, he may very well be right, at least for the period 1000–1700 before present, a time of extensive human migration and, in the Viking Age, with ocean-going ships that reached remote areas. Human exploitation may also be the reason for the disappearance of the great auk from southern Scandinavian waters before 4000 years BP. The closest known and most likely breeding areas for the great auk that migrated to southern Scandinavia would be the Orkneys. There, a significant human expansion took place in the early Neolithic (Bunting et al., 2022). One might anticipate that an increased human population led to overexploitation of resources, such as hunting of the great auk at its breeding sites. This might have led to the conditions suggested by Bengtson (1984), with a desolation of certain breeding sites. Indeed, Serjeantson (2001) shows that there was a significant decline in the percentage of great auk in the Neolithic at two archaeological sites at Sanday, in the northeastern part of the archipelago.

In Nordland, the bone assemblages from the localities Storbåthelleren (14) and Kirkhelleren (18) (Figure 3) and in Finnmark at Advik, Grasbakken, and Iversfjord (1, 3, and 12) stand out. At these localities, relatively many bones have been recorded as immature. Considering that the bird skeleton matures early, it is rare to find juvenile/subadult individuals, particularly as it is difficult to assess if a bone is fully grown or not. The presence of juvenile/subadult

individuals may indicate proximity to breeding sites. Moreover, it shows that the great auk was distributed in those regions during the autumn.

The bones from Kirkhelleren (18) (Figure 3) also illustrate significant size differences in some bone elements. We have not been able to verify whether these differences are natural size variations within the population or due to sexual differences. An ongoing aDNA study will hopefully reveal that.

In general, there are too few complete bones and too few samples from each site to give a clear picture of size variations. However, based on imputed data correlated to latitude and longitude, some patterns regarding size appear. The great auk bones from sites on the coast of the county Nordland (Localities 13–20) are, in general, larger than the rest. In contrast, there are indications that the bones from Finnmark (Localities 1–12) are smaller than those from other parts of Norway. This suggests that the great auk in Finnmark originated from another population than those in Nordland.

6 | CONCLUSIONS

In total, 477 bones of the great auk have been found at 53 localities in Norway. All but two localities are from archaeological sites. The remaining two are naturally deposited bones from the Ice Age. One is probably 36,000–34,000 years old, while the other is 14,300–12,800 years.

The great auk disappeared from the southern part of Norway (and Sweden and Denmark) more than 4000 years ago. There seems to have been a further decline in the distribution of the great auk 2000 years ago with the species absent from the Norwegian coast for the last 1000 years.

The great auk was distributed along the coast and in the fjord systems. Assuming that oily fish were their preferred prey, it is thought that the great auk was found along the Norwegian coast in late winter/early spring.

Bones of juvenile/subadult individuals at localities in Nordland and Finnmark suggest proximity to breeding grounds and show that the great auk visited these regions in the autumn. In general, the bones from Nordland were larger than those from the rest of the country, while bones from the Finnmark localities were smaller. Differences in size, especially in total length of the bone, have been found between some localities. It has not been verified if this is due to individual variation or sexual differences.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supporting Information of this article.

ORCID

Anne Karin Hufthammer  <https://orcid.org/0000-0002-1570-9667>

Karl Ove Hufthammer  <https://orcid.org/0000-0003-3170-9496>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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