New Finds, Sites and Radiocarbon Dates of Skeletal Remains of the Great Auk Pinguinus impennis from the Netherlands

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The Great Auk *Pinguinus impennis* was a large, flightless alcid, endemic to the North Atlantic Ocean. It became extinct around 1844. Skeletal remains are used to document its (pre-)historic range. While these remains were considered rare from the southern North Sea, over the past five years 91 (sub-)fossil specimens have been recovered by citizen scientist fossil collectors from Dutch beaches that were nourished with sediments dredged from the bottom of the North Sea. Some of this material is now stored in museum collections. This paper lists the new remains and documents them through measurements and photographs. The material was recovered from fourteen new localities and one previously known locality in The Netherlands and has yielded four radiocarbon dates (1425–1300 BC till beyond 48,000 cal BP) which significantly increase the Great Auk's temporal range in this area. The sheer volume of remains alters our image of the Great Auk in the southern part of the North Sea from a rare bird to most likely a common or regular wintering bird over the past millennia.

Key words: citizen science, extinct birds, fossil collectors, palaeontology, radiocarbon dates

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The Great Auk *Pinguinus impennis* was a large, flightless alcid, endemic to the low-arctic and boreal waters of the North Atlantic Ocean. In historical times, its most significant breeding colony was on Funk Island, NE of Newfoundland, Canada. A well-documented smaller breeding colony occurred on Geirfuglasker, Reykjanes, SW of Iceland. This island disappeared due to tectonics in 1831, the Great Auks then moving to the nearby island of Eldey (Fuller 1999). Smaller breeding colonies are generally poorly documented, but certain ones did include Bird Rocks, N of Magdalen Islands (Quebec), Penguin Islands, SW of Newfoundland (Montevecchi & Kirk 1996), Paamiut, SW Greenland (Meldgaard 1988), two more islands named Geirfuglasker, one of the Vestmannaeyjar archipelago, S of Iceland, and one near the island of Papey, E of Iceland, and the islands of St Kilda, Scotland (Fuller 1999). Nettleship & Evans (1985) also include Papa Westray, Orkney Islands (Scotland) as a certain breeding colony, but Fuller (1999) dismisses this based on historical evidence. It is likely that during prehistory small and vulnerable breeding colonies have been extirpated by hunter-gatherers leaving no or few traces, limiting our knowledge of the more recent natural breeding range of the species (Bengtson 1984, Bourne 1993, Serjeantson 2001). The historical winter range crudely documented through observations of live specimens seems to have ranged from off SW Greenland at least north to around Nuuk (Meldgaard 1988), south to at least Massachusetts (Brown 1985) and from mid-Norway to around the northern part of the British Isles (Fuller 1999).

A few centuries of overexploitation for their meat, feathers, eggs, chicks and finally, when the species became rare, natural history specimens resulted in their extinction around 1844 with the last authentic record from Eldey, SW Iceland, where two adult Great Auks were killed and their egg was broken by collectors (Fuller 1999, Gaskell 2000, Thomas *et al.* 2019). All that remains of the Great Auk are 78 skins, 75 eggs, a larger volume of (isolated) skeletal remains and an incomplete ecological knowledge (Fuller 1999). Their robust skeletal remains, with typical adaptations for underwater flight (Smith & Clarke 2011), are generally easily recognized and have been recovered from numerous deposits of various ages and origins, including Pleistocene and Holocene natural deposits and kitchen middens of (pre-)historical peoples at both sides of the Atlantic Ocean (Greenway 1967, Tyrberg 1998, Fuller 1999). These (sub-)fossils provide an image of the distribution of the species over geological time, which was much larger than their historically documented one of the past couple of centuries (e.g. Grieve 1885, Burness & Montevecchi 1992, Serjeantson 2001). Specimens have been found as far south as Porto Santo (Madeira, Portugal) at 33°N (Pleistocene; Pieper 1985, Pimenta *et al.* 2008), Morocco at 34°N (5800 to 7000 BP; Campmas *et al.* 2010), Bermuda at 32°N (Middle Pleistocene; Olson 2003) and Florida at just over 26°N (e.g. 1000 BC: Brodkorb 1960, 1000 AD: Fradkin 1980) or as far north as Greenland at just above 68°N (2400 BC till 1600 BC; Meldgaard 1988) and Norway above 70°N (Holocene; Christiani 1916, Greenway 1967).

Through records from The Netherlands, the Great Auk is known to have occurred at least occasionally in the southern North Sea, i.e. between the United Kingdom and The Netherlands and Belgium. Dutch records are mainly confined to remains recovered during archaeological excavations from Roman contexts (c. 2000 years old). Groot (2005) lists four Roman sites yielding four bones and one partial skeleton (van Wijngaarden-Bakker 1978) and a specimen reported and illustrated by Kompanje & Kerkhoff (1991) from Maasvlakte beach (near Rotterdam) that they tentatively dated as Holocene. Currant & Stewart (2000) report, but do not describe nor illustrate, two specimens from the beach of Cadzand (near the Dutch-Belgian border). Groot (2005) notices the lack of Great Auk remains in Dutch excavations predating or postdating the Roman period and uses this lack of finds as an indication that Great Auks did not frequent Dutch waters before the Roman time nor thereafter. During an exploratory study on dredged fossil avian remains from the North Sea (Langeveld *et al.* 2017) the first Great Auk remains described in the present paper were discovered. Comparison with literature (e.g. Owen 1866, Cohen & Serjeantson 1996, Kilmer & Steadman 2016) and specimens (details below) confirmed the identification. Reaching out to the large and skilled community of Dutch citizen scientist fossil collectors active on dredged beaches through various publications (Langeveld 2015a–c, 2016a–c, Langeveld & Mol 2015, Langeveld & Passchier 2015, Cadée 2016, Mol & Langeveld 2016, Cardol & Langeveld 2019, Twigt & Langeveld 2019), oral and poster presentations at paleontological societies (Langeveld & Mol 2016), public identification sessions (e.g. Mol *et al.* 2015), private collection visits, exhibitions in a local palaeontological and a regional natural history museum and even use of social media, yielded a continuous flow of new specimens from 30 citizen scientists. This paper now finally summarizes all new specimens identified by the author over the past five years: 91 specimens from fourteen new localities and one previously known locality, documented through photographs (since not all of them are in museum collections), their measurements and four radiocarbon dates.

METHODS

Study area

This study is confined to remains of Great Auks found in The Netherlands, bordering the southern North Sea. Since about two thirds of the country lies below sea level, The Netherlands has an extensive history in land reclamation, including nourishing beaches or the shoreface with dredged sand from the North Sea and even using dredged sediments to build completely new peninsulas and other structures that protect the coast from rising sea levels. Over the past years, the Dutch government has had deposited at least five million cubic meters of sediment annually along the coast and on the beaches from various near-shore sand source areas (Stive *et al.* 2013, Rijkswaterstaat 2019). The suction dredged sediments are usually sandy and Pleistocene or Holocene in age and, especially in the southern half of the country, fossiliferous. This has not gone unnoticed with private fossil collectors. Over the decades, a significant and dedicated community of citizen scientists has emerged that collects and documents the dredged fossils (and archaeological artefacts) and saves them from weathering and erosion, ultimately making them available for scientific study through their own research or loans and donations to museums and universities (Mol 2016, Mol *et al.* 2018). It is this community of citizen scientist fossil collectors that has yielded the abundant Great Auk material described here.

Material studied

Most recently found specimens discussed in this paper are kept in over 25 private collections and as not all collectors assign catalogue numbers to their specimens, each specimen was assigned an ID number by the author, listed in Table S1, to allow matching of particular specimens with their photographs and measurements. Some collectors donated (some of their) specimens to the Natural History Museum Rotterdam (Rotterdam, The Netherlands); two were donated to Naturalis Biodiversity Center (Leiden, The Netherlands). Great Auk material studied for comparative purposes consisted of specimen v53 of the Amsterdam Centre for Ancient Studies and Archaeology (University of Amsterdam and VU Amsterdam, The Netherlands). This is the partial skeleton described by van Wijngaarden-Bakker (1978) from a Roman setting near Velsen, The Netherlands. Specimens NHMUK A151, a mounted, partially composed, skeleton from Funk Island with the skull and right wing detached and NHMUK A857, an isolated humerus from Caithness, Scotland, United Kingdom were studied at the Natural History Museum, London, United Kingdom. Isolated scapulae and tarsometatarsi from Funk Island (specimens USNM 623465 and USNM 623680 of the Smithsonian National Museum of Natural History, Washington D.C., USA) were also studied. To differentiate Great Auk remains from those of its living relatives, osteological material of a number of recent Alcidae species was studied at the Natural History

Stuffed adult Great Auk in summer plumage, possibly originating from the coasts of Scotland. In the collection of the Muséum national d'Histoire naturelle, Paris (photo Bram Langeveld, 15 September 2016).

Museum Rotterdam and the Groningen Institute of Archaeology, University of Groningen, Groningen, The Netherlands.

Measurements

Measurements were taken with Vernier callipers following von den Driesch (1976). Measurements were taken only on the most complete specimens showing no or very little weathering. Measurements below 70 mm were taken to the nearest 0.1 mm; those above to the nearest millimetre. Statistics were run in PAST 3.25 (Hammer *et al.* 2001).

RESULTS

Specimens

A total of 91 post-cranial skeletal remains were identified (Table S1, Figures 1–4). Humeri, or fragments thereof, were by far the most common (59 specimens), followed by coracoids (16) and ulnae (10). Furthermore, two epistrophei (maximum length of vertebral body: 10.7 mm and 12.6 mm), one cervical vertebra fragment, one thoracic vertebra (maximum length of vertebral body: 14.0 mm, BFcd: 7.1 mm), one radius (GL: 57.4 mm, SC: 2.8 mm) and one damaged scapula (Dic: 15.0 mm) were collected. Citizen scientist Henk Mulder collected 13 specimens during at least 3500 hours of fossil collecting; this equals roughly 270 hours per Great Auk specimen.

Many specimens were fragmented, but none of them showed traces that could be attributed to ancient humans. Instead, most of the damage seemed fresh and was probably caused by the sand dredging process through which most fossils recovered from nourished beaches have been damaged (Hendriks 2010, pers. obs.). Comparison with specimen NHMUK A151 showed that even dredged specimens that were not obviously damaged were all, without exception, weathered or polished to some degree, especially at the articular surfaces. Hence, in many specimens only one or two measurements could be reliably taken and these measurements are all slight underestimates of the original dimensions of the bone and should not be used to infer any size differences between the Dutch specimens and other samples, except for greatest length of the bones where this effect of wear is minimal due to the large size of this measurement. The measurements however do provide clear evidence that the material should be ascribed to Great Auk: their size matches the comparative material and lies far above the range of extant Alcidae (Table 1).

Table 1. Measurements (in mm) of bones of Great Auks *Pinguinus impennis* and other alcids. Comparative: comparative material from museum collections, beach: specimens recovered from Dutch beaches, Bp: width at proximal end, SC: smallest width of the shaft, Bd: width at distal end, GL: greatest length of the bone, Lm: medial length, BF: width of the facies articularis basalis.

Humerus

Great Auk *Pinguinus impennis*, comparative

ID	Bp	SC	Bd	GL
A151	24.0	9.5	15.0	99
A857	23.8	9.0	15.1	99
v53	26.1	11.6	16.2	107
v53	26.2	11.4	16.2	107

Great Auk *Pinguinus impennis*, beach

ID	Bp	SC	Bd	GL
4		9.4		
6	26.3			
7	25.6			
8		9.5		
13	23.1			
14	23.8			
16		9.6		
17	25.9			
21		9.6		
25		10.0		100
26		10.1		99
27			14.9	
32		10.4		
34		9.3	14.5	
35	22.3			
39	25.2	10.0	15.3	102
41	26.8			
42		11.5		109
43	26.8	10.9	16.9	107
44	24.0	9.9	15.0	103
47		10.6	15.6	
49		11.4	15.7	
52	25.5			
53	24.3			
60		10.6		
61	24.5	10.7	15.4	108
64		9.2		
65		9.9		
66			15.0	
73	26.0	10.9	16.7	113
74		10.2		
76		9.8		
86		10.7		
90		10.4	14.0	

Common Guillemot *Uria aalge* (*n* = 13)

	Bp	SC	Bd	GL
Mean	18.1	7.8	11.9	85.5
SD	0.3	0.2	0.2	2.3

Razorbill *Alca torda* (*n* = 11)

	Bp	SC	Bd	GL
Mean	16.2	6.8	10.6	73.2
SD	0.5	0.2	0.3	2.1

Thick-billed Murre *Uria lomvia* (*n* = 3)

	Bp	SC	Bd	GL
Mean	17.6	7.2	11.9	87.0
SD	0.4	0.3	0.1	1.0

Black Guillemot *Cepphus grylle* (*n* = 3)

	Bp	SC	Bd	GL
Mean	14.9	4.8	9.1	61.5
SD	0.5	0.2	0.2	2.0

Atlantic Puffin *Fratercula arctica* (*n* = 4)

	Bp	SC	Bd	GL
Mean	14.7	5.2	9.9	64.8
SD	0.2	0.1	0.1	2.1

Ulna

Great Auk *Pinguinus impennis*, comparative

ID	Bp	SC	GL
A151	10.0	4.2	56.1

Great Auk *Pinguinus impennis*, beach

ID	Bp	SC	GL
1	8.3	4.0	
24	8.9		
30	9.7	4.2	
48	10.0		
56	9.5	4.2	
57	9.3	4.2	54.5
88	9.2	4.1	56.3

Common Guillemot *Uria aalge* (*n* = 10)

	Bp	SC	GL
Mean	8.1	3.9	63.9
SD	0.2	0.1	1.7

Razorbill *Alca torda* (*n* = 8)

	Bp	SC	GL
Mean	7.3	3.4	58.7
SD	0.2	0.1	1.7

Thick-billed Murre *Uria lomvia* (*n* = 2)

	Bp	SC	GL
Mean	8.3	3.9	68.2
SD	0.2	0.2	0.1

Black Guillemot *Cepphus grylle* (*n* = 2)

	Bp	SC	GL
Mean	6.8	3.1	53.3
SD	0.1	0.0	0.5

Atlantic Puffin *Fratercula arctica* (*n* = 4)

	Bp	SC	GL
Mean	6.5	3.0	50.6
SD	0.2	0.1	1.2

Coracoid

Great Auk *Pinguinus impennis*, comparative

ID	GL	Lm	BF
v53	66.1	60.0	25.9
v53	66.3	60.2	26.0

Great Auk *Pinguinus impennis*, beach

ID	GL	Lm	BF
22	62.3	59.2	21.9
68			19.8
89			22.3

Common Guillemot *Uria aalge* (*n* = 9)

	GL	Lm	BF
Mean	43.6	40.3	15.4
SD	1.7	1.6	0.7

Razorbill *Alca torda* (*n* = 7)

	GL	Lm	BF
Mean	38.9	35.2	13.7
SD	1.1	1.2	0.4

Thick-billed Murre *Uria lomvia* (*n* = 2)

	GL	Lm	BF
Mean	41.2	37.8	16.0
SD	0.8	1.1	0.4

Black Guillemot *Cepphus grylle* (*n* = 3)

	GL	Lm	BF
Mean	33.3	30.4	12.1
SD	0.9	0.8	0.7

Atlantic Puffin *Fratercula arctica* (*n* = 4)

	GL	Lm	BF
Mean	37.2	35.4	9.9
SD	0.7	0.5	0.6

Figure 1. Humeri of Great Auks *Pinguinus impennis* collected from sediments dredged from the southern North Sea. ID numbers correspond to Table S1.

Localities

Great Auk bones were recovered from fifteen beach localities along the shore of The Netherlands, fourteen of which are new (Figure 5). The southernmost specimen was collected just north of the Dutch-Belgian border at Het Zwin (Cadzand; Currant & Stewart (2000) already report two specimens from this locality), the northernmost specimen was recovered from the Zandvoort beach near Amsterdam. By far the most productive Dutch Great Auk locality, with 52 specimens, is the Zandmotor near The Hague. This artificial peninsula was created in 2011 with 21.5 million cubic meters of dredged sediment (Stive *et al.* 2013) from just north of the Eurogeul (Langeveld 2013), the dredged navigational channel to the port of Rotterdam that exposes fossiliferous Late Pleistocene and Holocene deposits (Mol *et al.* 2006). The Zandmotor quickly became a popular locality for fossil collectors; a Late Pleistocene and Holocene fauna is recovered there (van der Valk *et al.* 2011, Mol & Langeveld 2018). A comparable locality is Maasvlakte 2. Here, an artificial peninsula was created to facilitate extension of the Rotterdam port. Early/Middle and Late Pleistocene as well as Holocene fossiliferous sediments from just south of the Eurogeul were used (Busschers *et al.* 2012, Kuitems *et al.* 2015, Mol & Langeveld 2016). Despite

Figure 2. Coracoids of Great Auks *Pinguinus impennis* collected from sediments dredged from the southern North Sea. ID numbers correspond to Table S1.

comparable search effort by collectors, only nine specimens were recovered from Maasvlakte 2. The beach of Dishoek is the most productive locality of the province of Zeeland, with ten records. This beach was nourished with sand dredged from the locality S7AA, which is about 15 km offshore of the city of Domburg (Cardol & Langeveld 2019). Furthermore, three specimens were collected at a shell grit plant at Yerseke, from material originating from the Steenbanken in the North Sea, ca. 20 km north of the western edge of the island of Walcheren, Zeeland. From the beaches of Noordwijk and Zandvoort only one specimen each was recovered.

Figure 3. Ulnae of Great Auks *Pinguinus impennis* collected from sediments dredged from the southern North Sea. ID numbers correspond to Table S1.

Figure 4. Various skeletal remains of Great Auks *Pinguinus impennis* collected from sediments dredged from the southern North Sea. ID numbers correspond to Table S1.

Figure 5. Map of The Netherlands and the adjacent North Sea with localities where Great Auk *Pinguinus impennis* remains were collected. 1: Velsen, 2: Zandvoort beach, 3: Noordwijk beach, 4: Katwijk beach, 5: Den Haag, 6: Zandmotor beach, 7: 's-Gravenzande beach, 8: Hoek van Holland beach, 9: Schipluiden, 10: Vlaardingen, 11: Maasvlakte beach, 12: Maasvlakte 2 beach, 13: Banjaardstrand beach, 14: Oostkapelle beach, 15: Westkapelle (towards Domburg) beach, 16: Steenbanken (dredged; processed at Yerseke shell plant), 17: Zoutelande beach, 18: Dishoek beach, 19: De Kaloot beach, 20: Het Zwin (Cadzand) beach (based on Currant & Stewart 2000, Groot 2005 and the present paper).

This may be due to a lower search effort there, since these are not popular fossil localities, but it could also be due to a genuine rarity of Great Auk material on these sites. Not a single Great Auk bone from a beach north of Zandvoort was found.

Radiocarbon dates

Four specimens were successfully radiocarbon dated at the Centre for Isotope Research of the University of Groningen (Groningen, The Netherlands). Specimens with different colours (indicating differing depositional environments) and from various sites were selected. None of the dated specimens was treated with any preservatives. The obtained dates were 1425–1300 BC till beyond 48,000 cal BP (calendar years before 1950; Table 2) and significantly increase the temporal range of the Great Auk in the southern North Sea. A further four specimens (ID numbers 2, 6, 21, 23) had insufficient collagen quality for radiocarbon dating.

DISCUSSION

All specimens from dredged and even natural beaches were not retrieved from their primary context. The locality where a specimen was collected cannot therefore be considered to be the exact locality where the specimen was preserved. Dutch law dictates that sand sourced from the North Sea for beach nourishments has to be taken from a water depth of at least 20 metres. Sand source areas are usually designated at that depth as close to the beach as possible to limit transportation costs (e.g. Langeveld 2013). Most of the material that naturally washes up on beaches is from the direct vicinity of that beach (de Bruyne & van der Valk 1991). Hence, the localities where the bones were collected indeed do approximate the original place of deposition of the birds' remains. But still, these localities do not have to be (close to) the localities where the animals actually lived and died. Dead birds remain afloat for extensive periods of time: Schäfer (1962) found dead European Herring Gulls *Larus argentatus* to sink only after 38 days at which point most of the skeleton was still articulated. Extant Atlantic Puffins *Fratercula arctica* rarely occur close to the Dutch shore and are much more common in the central North Sea in winter (Camphuysen & Leopold 1994), but dead specimens do beach regularly on Dutch shores, sometimes in significant numbers (Camphuysen 2003). These must have been transported as dead specimens over a significant distance. Within the North Sea residual currents follow a cyclonic path down the English east coast, across the

Table 2. Radiocarbon dates of Great Auk *Pinguinus impennis* specimens from the southern North Sea.

ID	Collection	Element	Locality	Lab number	Result BP	cal BP/BC
22	NMR9989-4370	Coracoid sin.	Zandmotor	GrA-65546	3505 ± 45	1425–1300 BC
4	RMNH.5070466	Damaged humerus dex.	Zandmotor	GrA-64384	6480 ± 40	7000–6890 cal BP
15	RMNH.5070467	Proximal humerus sin.	Hoek van Holland	GrA-64453	43,290 ± 380	46,460–45,690 cal BP
43	NMR9989-5959	Humerus dex.	Yerseke	GrM-17850	>45,000	>48,000 cal BP

North Sea and up the coasts of Belgium and The Netherlands (Sündermann & Pohlmann 2011, Vindenes *et al.* 2018). Currents thus may wash birds that died in the central or southern North Sea up on the Dutch coast. Hence, the abundant Great Auk material presented here at least shows that the species once commonly lived (and died) in the central and/or southern part of the North Sea between The Netherlands and the United Kingdom.

The southern North Sea record of the Great Auk is rather poor; the eight specimens reported by van Wijngaarden-Bakker (1978), Kompanje & Kerkhoff (1991), Currant & Stewart (2000) and Groot (2005) until recently made up the entire record. Although the Great Auk has an abundant record in the United Kingdom, none of those finds originates from the southern North Sea. The British records are predominantly located on the northern islands of Scotland and along the west coast (Burness & Montevecchi 1992, Serjeantson 2001). Great Auk records closest to the southern North Sea are the upper mandible from a cave near Whitburn, NE England (Grieve 1885), medieval material from Holy Island, Lindisfarne, NE England (O'Sullivan & Young 1995), a Middle Pleistocene humerus fragment from Boxgrove, S England (Harrison & Stewart 1999), material from a Roman setting on the Isle of Portland, S England (Maltby & Hamilton-Dyer 2012) and a Late Pleistocene humerus fragment from La Cotte de St. Brelade, Jersey, Channel Islands (Andrews 1920). In Denmark, the species commonly occurs in Mesolithic shell middens (e.g. Grieve 1885, Hørring 1934, Greenway 1967, Burness & Montevecchi 1992), but these middens are confined to the northern and eastern coasts of Denmark and lacking on the western (North Sea) coast (Andersen 2000). In fact, the scarcity of Great Auk records from the southern North Sea thus far may well be explained by the complete absence of (accessible) shell middens or similar deposits on its coasts (Gutiérrez-Zugasti *et al.* 2011), as more to the south the Great Auk does occur in such middens on the coast of Brittany (France; Schulting *et al.* 2004). No Great Auk bones are reported from Belgium. Based on the scarcity of the material known at that time, Groot (2005) hypothesized that a climate deterioration caused rare Great Auks to strand on the Dutch coast during Roman times. With the wealth of material presented here, we can now alter this image of the occurrence of the Great Auk in the southern North Sea. The abundance of new material (91 specimens) and localities (fourteen new sites) where it has been recovered, as well as the broad range of radiocarbon dates (1425–1300 BC till beyond 48,000 cal BP) show that the Great Auk was more common in the southern North Sea than previously assumed and that it was present over a much longer time period.

The abundance of humeri (59 of 91 specimens) relative to other skeletal parts may be due to their readily recognizable morphology, their size and their strong build with thick bone walls (Smith 2013) and thus high preservation potential. Based on the relatively smooth bone surface and fully ossified ends (Tumarkin-Deratzian *et al.* 2006, Watanabe & Matsuoka 2013) none of the specimens could be classified as a chick; they represent juveniles, sub-adults or adults in which the long bones had reached their maximum length. In our material, the maximum length could be reliably measured in eight specimens (Table 1): mean length is 105.1 ± 4.9 mm (± SD). A Shapiro-Wilk test showed that these data are normally distributed ($W = 0.9505$, $P = 0.71$) and thus they were compared using a *t*-test with published data. Burness & Montevecchi (1992) studied the size of the Great Auk from across the Atlantic and provided data on humerus length. They found material from Funk Island to be statistically significantly larger (mean humerus length ± SD: 104.4 ± 1.69 mm, $n = 82$) than that from Scandinavia (100.0 ± 1.82 mm, $n = 15$). Livezey (1988) also provides measurements of material from Funk Island. He found a humerus length of 106.1 ± 7.3 mm ($n = 69$). There was no significant difference between the two reported means of the Funk Island material ($t = 0.420$, $P = 0.687$ and $t = –0.565$, $P = 0.590$, respectively) and our data. There was however a significant difference between our data and the Holocene Scandinavian material ($t = 2.969$, $P = 0.02$). This can be explained in several ways: it could be that the population that frequented the North Sea was distinct from the population that was collected from Scandinavia, but recent more extensive morphometric and genetic evidence accumulated from almost exclusively Holocene specimens from across the entire range of the Great Auk suggests that there was actually very little genetic population structure and significant spatial size differences were in fact lacking in the species (Thomas 2018). Given the large spread in geological age of our specimens, it is more likely that body size variation over geological time must be blamed for this apparent pattern. More Pleistocene specimens from across the species' range must be collected and studied to further investigate this.

Exact dates are available for only four of 91 specimens and range from 1425–1300 BC till beyond 48,000 cal BP; this spans at least part of the Pleistocene and most of the Holocene. The North Sea changed significantly over this time, due to sea level variations forced by land ice build-up and melting. Based on relative sea level reconstructions, the sand source areas that had been dry land from at least 80,000 BP were inundated by the North Sea from about 8000 BP onwards (Beets & van der Spek 2000, Hijma *et al.* 2012). The Great Auk dated to beyond 48,000 cal BP may well be of early Late Pleistocene age (Eemian interglacial, sea level higher than today) or older. The two younger dates, 1425–1300 BC and 7000–6890 cal BP, fit well with sea level reconstructions and show that Great Auks entered the North Sea soon after inundation under a temperature regime that was roughly comparable to that of today (Berendsen 2011). The specimen dated to 46,460–45,690 cal BP is more difficult to explain given the sea level reconstructions, but various arctic marine mammals from the southern North Sea date to this same period (e.g. Post 2005, Mol *et al.* 2006) and more research is needed to unite these data (more detailed discussion in Hijma *et al.* (2012)). The Holocene Dutch coastline probably did not meet the breeding requirements of the flightless and on land mostly defenceless Great Auk, due to the lack of suitably isolated (rocky) islands (Bengtson 1984). During the genesis of the North Sea, various isolated and now submerged or eroded islands must have been available for centuries to some millennia, but these were composed of soft sediment (e.g. Sturt *et al.* 2013). It thus seems highly unlikely that the remains represent breeding individuals. While wintering, Great Auks seem to have preferred shallow areas (depth < 75 m) where they took both benthic and pelagic fish (Bradstreet & Brown 1985, Brown 1985). Olson *et al.* (1979) inferred food choice by studying fish remains from sediments rich in Great Auk bones from Funk Island and found an abundance of remains of the clupeid fish *Brevoortia* of 140–190 mm length. This genus does not occur in the eastern Atlantic, however the North Sea is rich in the closely related Herring *Clupea harengus* (Simmonds 2007) which is also a known food species (Fuller 1999) and fossil marine fish remains are common from the sand source areas (Langeveld *et al.* 2016). Being a relatively shallow, sheltered and productive area (de Wolf 1990, Joint & Pomroy 1993), the southern North Sea thus may have provided rich and suitable wintering grounds for a Great Auk population that bred near Iceland or another, unknown, eastern Atlantic population as is indeed the case for extant Alcidae (Camphuysen & Leopold 1994).

Horn *et al.* (2019) found high quality preservation of ancient collagen in some of the Great Auk bones presented here. This shows promise for future genetic or other ancient biomolecular studies on the Great Auk specimens that were added to museum collections during this study, which could yield more palaeobiological details on the North Sea Great Auks. The two reported specimens that were dated in the Pleistocene are furthermore important, since in contrast to the species' rich Holocene record, its Pleistocene record is rather poor (Tyrberg 1998, 2008, Harrison & Stewart 1999).

In conclusion, the sheer volume of skeletal remains and broad range of radiocarbon dates presented here alters our image of the Great Auk in the southern part of the North Sea from a rare bird to most likely a common or regular wintering bird over the past millennia. This fills in an almost completely blank spot in the species' distribution and adds to our understanding of the ecology of this extinct bird.

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SAMENVATTING

De Reuzenalk *Pinguinus impennis* was een grote, niet-vliegende alk van de Noord-Atlantische Oceaan. De soort stierf rond 1844 uit. Skeletresten worden gebruikt om de (pre)historische verspreiding te reconstrueren. Resten uit Nederland en de aangrenzende zuidelijke Noordzee worden als zeldzaam beschouwd. De afgelopen vijf jaar zijn van Nederlandse stranden die waren opgespoten met zand uit de Noordzee 91 (sub)fossiele botten van de Reuzenalk door amateurwetenschappers verzameld. Een deel hiervan wordt nu bewaard in museumcollecties. Dit artikel somt alle nieuwe resten op, beeldt ze af en geeft afmetingen van de resten. Het materiaal werd op 14 nieuwe vindplaatsen en één al bekende vindplaats verzameld. Er werden vier ^{14}C-dateringen uitgevoerd (1425–1300 BC tot meer dan 48.000 cal BP) die de verspreiding in de tijd van de Reuzenalk in de zuidelijke Noordzee oprekken. De grote hoeveelheid resten verandert ons beeld van de Reuzenalk in de zuidelijke Noordzee van een zeldzame dwaalgast naar waarschijnlijk een algemene of geregelde wintergast gedurende de afgelopen millennia.

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SUPPLEMENTARY MATERIAL

Table S1. Great Auk *Pinguinus impennis* specimens from the southern North Sea. dex. = right side, sin. = left side, nn = not numbered. NMR: Natural History Museum Rotterdam, RMNH: Naturalis Biodiversity Center.

ID number	Collection	Element	Locality
1	Henk Mulder nn	Ulna dex.	Zandmotor
2	Henk Mulder nn	Proximal humerus sin.	Zandmotor
3	NMR9989-4878	Proximal humerus sin.	Hoek van Holland
4	RMNH.5070466 (cast NMR9989-4879)	Defect humerus dex.	Zandmotor
5	NMR9989-6032	Proximal humerus sin.	Maasvlakte 2
6	Wilco Sliedrecht nn (cast NMR9989-4880)	Proximal humerus sin.	Maasvlakte 2
7	NMR9989-5960	Proximal humerus sin.	Maasvlakte 2
8	Ivan van Marrewijk nn	Distal humerus dex.	Zandmotor
9	Ivan van Marrewijk nn	Proximal coracoid dex.	Zandmotor
10	Ivan van Marrewijk nn	Proximal coracoid sin.	Zandmotor
11	Cèdric Heins nn	Proximal humerus dex.	Maasvlakte 2
12	André Cardol 148	Proximal ulna dex.	Dishoek
13	Johan Passchier NW40 (cast NMR9989-6030)	Proximal humerus sin.	Noordwijk
14	NMR9989-6150	Proximal humerus dex.	Zandmotor
15	RMNH.5070467 (cast NMR9989-4881)	Proximal humerus sin.	Hoek van Holland
16	NMR9989-6148	Distal humerus dex.	Zoutelande
17	NMR9989-4372	Proximal humerus dex.	Maasvlakte 2
18	Rick van Bragt nn	Proximal humerus sin.	Zandmotor
19	Rick van Bragt nn	Fragment coracoid dex.	Zandmotor
20	NMR9989-6149	Distal humerus dex.	Zoutelande
21	NMR9989-4366	Distal humerus dex.	Zandmotor
22	NMR9989-4370	Coracoid sin.	Zandmotor
23	NMR9989-4365	Defect humerus dex.	Zandmotor
24	Rick van Bragt nn	Proximal ulna dex.	Zandmotor
25	Dick Duineveld nn	Humerus dex.	Zandmotor
26	Erik Spithoven nn	Humerus dex.	Maasvlakte 2
27	Rick van Bragt nn	Distal humerus dex.	Zandmotor
28	Dick Duineveld nn	Humerus sin.	Zandmotor
29	NMR9989-4884	Proximal coracoid sin.	Zandmotor
30	NMR9989-4885	Ulna sin.	Zandmotor
31	Dick Duineveld nn	Fragment coracoid dex.	Zandmotor
32	Ivan van Marrewijk nn	Distal humerus sin.	Zandmotor
33	Jan Meulmeester 50.29	Distal coracoid sin.	De Kaloot
34	Maarten Schoemaker nn	Distal humerus sin.	Zandmotor
35	Henk Mulder nn	Proximal humerus sin.	Zandmotor
36	Ivan van Marrewijk nn	Proximal humerus sin.	Zandmotor
37	Willy van Wingerden nn	Proximal humerus dex.	Zandmotor
38	Rick van Bragt nn	Proximal humerus sin.	's-Gravenzande
39	Dick Duineveld nn	Humerus sin.	Zandmotor
40	Bram Goetheer nn	Defect humerus dex.	De Kaloot
41	Bram Goetheer nn	Proximal humerus sin.	Steenbanken (Yerseke)
42	Bram Goetheer nn	Humerus sin.	Steenbanken (Yerseke)
43	NMR9989-5959	Humerus dex.	Steenbanken (Yerseke)
44	Henk Mulder nn	Humerus sin.	Zandmotor
45	Henk Mulder nn	Coracoid sin.	Zandmotor
46	Patrick Ouwehand nn	Proximal humerus sin.	Katwijk

Table S1. Continued.

ID number	Collection	Element	Locality
47	Peter and Ingrid de Bruijn 2877	Distal humerus dex.	Maasvlakte 2
48	Willy van Wingerden nn	Proximal ulna sin.	Zandmotor
49	Dick Duineveld nn	Distal humerus sin.	Zandmotor
50	NMR9989-5211	Proximal humerus sin.	Zandmotor
51	Jan Meulmeester 50.52	Proximal humerus dex.	Oostkapelle
52	Willy van Wingerden nn	Proximal humerus dex.	Zandmotor
53	Willy van Wingerden nn	Proximal humerus sin.	Zandmotor
54	Willy van Wingerden nn	Distal humerus sin.	Zandmotor
55	Willy van Wingerden nn	Distal humerus sin.	Zandmotor
56	Willy van Wingerden nn	Ulna sin.	Zandmotor
57	Willy van Wingerden nn	Ulna dex.	Zandmotor
58	Willy van Wingerden nn	Proximal coracoid dex.	Zandmotor
59	André Cardol 48	Proximal humerus dex.	Dishoek
60	André Cardol 46	Distal humerus sin.	Dishoek
61	André Cardol 47	Humerus sin.	Dishoek
62	NMR9989-6031	Coracoid sin.	Zandmotor
63	Ivan van Marrewijk nn	Proximal humerus dex.	Zandmotor
64	NMR9989-6033	Humerus sin.	Zandvoort
65	Roel van Reijmersdal nn	Humerus sin.	Zoutelande
66	Roel van Reijmersdal nn	Distal humerus sin.	Zoutelande
67	Willy van Wingerden nn	Proximal ulna sin.	Zandmotor
68	Willy van Wingerden nn	Coracoid dex.	Zandmotor
69	André Cardol 49	Proximal coracoid dex.	Dishoek
70	André Cardol 60	Proximal coracoid dex.	Dishoek
71	NMR9989-6133	Radius dex.	Dishoek
72	Henk Mulder nn	Proximal coracoid dex.	Zandmotor
73	Jan Hengst nn	Humerus dex.	Westkapelle (towards Domburg)
74	Lex Kattenwinkel nn	Distal humerus sin.	Het Zwin (Cadzand)
75	Henk Mulder nn	Proximal humerus dex.	Zandmotor
76	Henk Mulder nn	Distal humerus sin.	Zandmotor
77	NMR9989-6132	Thoracic vertebra	Dishoek
78	NMR9989-6134	Cervical vertebra fragment	Dishoek
79	NMR9989-6135	Epistropheus	Banjaardstrand
80	Willy van Wingerden nn	Proximal humerus dex.	Zandmotor
81	Willy van Wingerden nn	Scapula sin.	Zandmotor
82	Rick van Bragt nn	Proximal ulna dex.	Zandmotor
83	Nicolai Jansen 182	Proximal humerus sin.	Maasvlakte 2
84	Arie Twigt nn	Epistropheus	Katwijk
85	Michiel Bil nn	Coracoid sin.	Dishoek
86	Dick Duineveld nn	Humerus sin.	Zandmotor
87	Dick Duineveld nn	Proximal humerus sin.	Zandmotor
88	Dick Duineveld nn	Ulna dex.	Zandmotor
89	Henk Mulder nn	Coracoid dex.	Zandmotor
90	Henk Mulder nn	Distal humerus sin.	Zandmotor
91	Cèdric Heins nn	Proximal humerus sin.	Maasvlakte 2