Quaternary bird remains from the southern North Sea

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Based on a literature survey and unpublished material fished by Dutch fishing vessels and collected by citizen scientists from Dutch beaches nourished with near-shore suction-dredged sediments, an overview is provided of the avian fossil record from the Quaternary (predominantly Late Pleistocene and Holocene) of the southern part of the North Sea. Previously recorded taxa are listed, in some cases with new specimens. Newly recorded taxa are: *Tetrao praeurogallus* Jánossy, 1969, *Gavia immer* (Brünnich, 1764), *Calonectris* sp./*Pterodroma* sp., *Ciconia nigra* (Linnaeus, 1758), *Pandion haliaetus* (Linnaeus, 1758), *Accipiter gentilis* (Linnaeus, 1758), *Stercorarius pomarinus* (Temminck, 1815), *Alle alle* (Linnaeus, 1758), *Uria aalge* (Pontoppidan, 1763) and *Bubo scandiacus* (Linnaeus, 1758). At least 44 species are now known.The fossil avifauna from the North Sea remains relatively poorly known, due to scarcity of sufficiently preserved material and comparatively low research effort. Lack of geological context hampers detailed interpretation of the material. Much work remains to be done, but it is clear that the specimens hold significant potential to refine our palaeoecological understanding of this drowned ecosystem.

Key words: Aves, beach nourishments, citizen scientists, Early Holocene, extinct birds, Late Pleistocene, Maasvlakte 2, Zandmotor

Introduction

Today, the southern North Sea, *viz.* the region between the United Kingdom in the West and The Netherlands and Belgium in the East, is a shallow sea on the continental shelf, with a depth not much exceeding 50 meters (De Wolf, 1990). During Pleistocene glacials the continental shelf was exposed repeatedly for long periods, mainly due to eustatic sea level drops caused by land ice build-up (Hijma *et al*., 2012; Cohen *et al*., 2014) and formed the habitat of terrestrial and freshwater species, with alternating cold-adapted faunas (with *e.g.* woolly mammoth) and temperate faunas (including *e.g.* hippopotamus). These faunas are documented through terrestrial mammal fossils recovered from the bottom of the North Sea (Mol *et al*., 2008); fossils of both temperate as well as arctic marine mammals are also known (Post, 2005). For over a century, Dutch (beam) trawlers have been retrieving these fossils and archaeological artefacts such as bone tools as bycatch (Staring, 1861; Maarleveld, 2020). Over 25 scientific expeditions with such ships have yielded a wealth of data (Mol & Post, 2010). Large museum and private collections of (mostly large) mammal fossils have thus been assembled, studied and published (*e.g.* Louwe Kooijmans, 1970; Drees, 1986; Van Kolfschoten & Laban, 1995; Reumer *et al*., 2003; Mol *et al*., 2003, 2006, 2008; Post, 2005), leading to a thorough understanding of past mammal faunas of the North Sea. Bird remains, however, are rarely collected this way (Langeveld & Tanis, 2015) and thus our knowledge of the Quaternary avifauna of this area is very poor.

The scarcity of bird remains from the North Sea is explained by the relatively small and slender bones passing through the wide-meshed fishing nets or not being noticed by fishermen. The material that is fished is dominated by tibiotarsi of *Meleagris gallopavo* (Linnaeus, 1758); *Gallus gallus domesticus* (Linnaeus, 1758) is also present. Their presence can be explained by ships dumping kitchen waste overboard. Furthermore, bones of *Anser* sp., *Anser/Branta* sp., *Cygnus* sp., *Cygnus olor* (Gmelin, 1789), *Phalacrocorax carbo* (cf. *carbo*) (Linnaeus, 1758) and *Haliaeetus albicilla* (Linnaeus, 1758) have been fished from the North Sea (Bosscha Erdbrink, 1993; Langeveld & Tanis, 2015; Langeveld & Mol, 2017). Camphuysen (2000) passingly mentions bones of *Gavia immer* (Brünnich, 1764) fished from the Brown Bank in the North Sea, but this could not be verified. Scager *et al*. (2017) mention unidentified Anatidae from the Oosterschelde estuary, bordering the southern North Sea. Over the past decades, Dutch large-scale land reclamation and coastal protection projects have regularly employed sandy sediments dredged from near-shore sand source areas in the North Sea for beach and shoreface nourishments (Stive *et al*., 2013). As this sediment may be fossiliferous, a very active and open community of citizen scientist fossil collectors has evolved. They spend thousands of hours collecting specimens on these beaches (Langeveld & Liscaljet, 2019), usually with great attention to detail (Mol, 2016; Mol *et al*., 2018; Curry, 2020; Haug *et al*., 2020). Over the years, this community has collected significant numbers of fossil bird bones of both large (*e.g.* Accipitridae) and smaller (*e.g.* Scolopacidae) bird

species, eventually allowing a closer study of the fossil avifauna of the southern North Sea. Previous identifications of bird material from these dredged sediments or of fossil bird bones washed up naturally on Dutch beaches were made by Currant & Stewart (2000), Stewart (2001), Langeveld (2015a-c, 2016a-d, 2020), Langeveld & Mol (2015, 2016), Langeveld & Passchier (2015), De Bruijn & de Bruijn (2016), Langeveld *et al*. (2016, 2017), Reehorst (2017), Cardol (2018), Mol & Langeveld (2018), Cardol & Langeveld (2019) and Twigt & Langeveld (2019). The taxa recorded in these studies are summarised in Table 1, together with the taxa that were fished and new records presented in this paper. Kompanje & Kerkhoff (1991) published bird remains from the Maasvlakte beach (port of Rotterdam). However, at the time they collected their specimens this locality comprised sediments dredged from various inland sources (Kompanje & Kerkhoff, 1991).

This paper discusses bird bones collected from beaches nourished with or built from sediments from the southern North Sea that are kept in various private collections and the collection of the Natural History Museum Rotterdam (NMR). Also included are some specimens in NMR that were collected by fishing vessels. First records of fossil specimens from the North Sea are capercaillie *Tetrao praeurogallus* Jánossy, 1969 (extinct), common loon *Gavia immer*, petrel *Calonectris* sp./*Pterodroma* sp., black stork *Ciconia nigra* (Linnaeus, 1758), western osprey *Pandion haliaetus* (Linnaeus, 1758), northern goshawk *Accipiter gentilis* (Linnaeus, 1758), pomarine jaeger *Stercorarius pomarinus* (Temminck, 1815), little auk *Alle alle* (Linnaeus, 1758), common guillemot *Uria aalge* (Pontoppidan, 1763) and snowy owl *Bubo scandiacus* (Linnaeus, 1758).

Study area

The majority of the studied material was collected from the beach of the artificial peninsula named Zandmotor. This structure (near Ter Heijde, South of The Hague) was built in 2011 using 21.5 million cubic meters of sediment and functions as coastal defence (Van der Valk *et al*., 2011; Stive *et al*., 2013). Another important site is the Maasvlakte 2 beach. This is the westernmost part of the port of Rotterdam constructed from 240 million cubic meters of sediment, completed in 2012 (Reumer *et al*., 2010; Kuitems *et al*., 2015). A third site is the beach of Hoek van Holland. This natural beach has an extensive history of sand nourishments. All three sites have been built from or nourished with sediments dredged from the Eurogeul area (Langeveld, 2013; Kuitems *et al*., 2015), a fossiliferous dredged navigational channel just off the coast of Rotterdam that traditionally yields Late Pleistocene and Early Holocene material (Mol *et al*., 2006, 2008, 2013, 2020; Langeveld *et al*., 2018) (Fig. 1). For Zandmotor and Hoek van Holland, Late Pleistocene and Holocene fluviatile and marine sediments were dredged up to 6 meters and 4 meters below seafloor, respectively. Due to deeper sand dredging (up to 20 meters below seafloor) into older deposits, Maasvlakte 2 additionally yields material from the Early or Middle Pleistocene (Busschers *et al*., 2013; Mol & Langeveld, 2014, 2016; Kuitems *et al*., 2015).

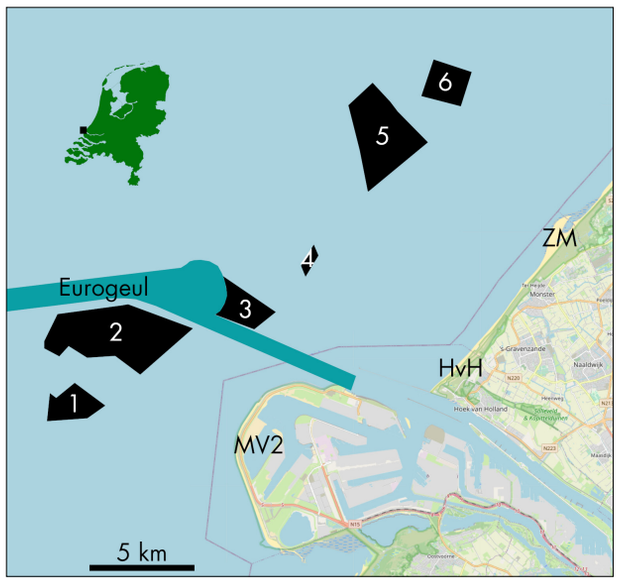

Figure 1. Main localities where bird bones were recovered and their sand source areas. Source areas (maximum sand dredging depth below seafloor) designated with 1 (10 m) and 2 (20 m) were used for Maasvlakte 2 (MV2), 3 (4 m) and 4 (unknown, but shallow) for Hoek van Holland (HvH), 5 (6 m) and 6 (6 m) for Zandmotor (ZM) (after Langeveld, 2013; Kuitems *et al*., 2015; map data: OpenStreetMap).

Other localities where some fossil bird bones treated here were collected are:

• southern North Sea	fished
• De Banjaard, Zeeland	beach
• Westkapelle, Zeeland	beach
• Yerseke, Zeeland	amongst shells dredged from the southern North Sea
• Zoutelande, Zeeland	beach
• Cadzand, Zeeland	beach

Methods

It is well known that bird bones may be hard to identify to low taxonomic level, *e.g.* species, due to the many closely related species with similar skeletal morphology (Romer, 1945) and extensive distribution ranges of many species; many experienced workers warn for overinterpretation of fragmentary or worn specimens (*e.g.* Ericson & Tyrberg, 2004; Bocheński, 2008; Serjeantson, 2009; Stewart & Jacobi, 2015). Hence, in this study, out of hundreds of (fragments of) specimens, only the most diagnostic and/or complete specimens have been identified, usually by a combination of direct comparison with reference collections and consultation of osteological literature deal-

Family	Species
Anatidae	*Cygnus olor* (Gmelin, 1789)[a]
	Anas sp. indet.[a]
	Anas querquedula Linnaeus, 1758 / *A. crecca* Linnaeus, 1758[a]
	Bucephala clangula (Linnaeus, 1758)[a]
	Clangula hyemalis (Linnaeus, 1758)[a]
	Melanitta nigra (Linnaeus, 1758)[a]
	Anser spp. (large geese)[a]
	Anser/*Branta* spp. 1 (medium geese)[a]
	Anser/*Branta* spp. 2 (small geese)[a]
	Anser cf. *djuktaiensis* Zelenkov & Kurochkin, 2014[a]
Phasianidae	*Lagopus lagopus* (Linnaeus, 1758)[b]
	**Tetrao praeurogallus* Jánossy, 1969
Gaviidae	*Gavia arctica* (Linnaeus, 1758)[a]
	**Gavia immer* (Brünnich, 1764)
	Gavia stellata (Pontoppidan, 1763)[a]
Procellariidae	**Calonectris* sp./*Pterodroma* sp.
	Puffinus sp.[a]
Podicipedidae	*Podiceps* cf. *cristatus* (Linnaeus, 1758)[c]
Ciconiidae	**Ciconia nigra* (Linnaeus, 1758)
Ardeidae	*Ardea* sp.[a]
Sulidae	*Morus bassanus* (Linnaeus, 1758)[a]
Phalacrocoracidae	*Phalacrocorax carbo* (Linnaeus, 1758)[a]
	Phalacrocorax carbo cf. *carbo* (Linnaeus, 1758)[d]
Pandionidae	**Pandion haliaetus* (Linnaeus, 1758)
Accipitridae	Accipitridae indet.[a]
	**Accipiter gentilis* (Linnaeus, 1758)
	Haliaeetus albicilla (Linnaeus, 1758)[e]
Rallidae	*Fulica atra* Linnaeus, 1758[a]
Gruidae	*Grus grus* (Linnaeus, 1758)[c]
Haematopodidae	*Haematopus ostralegus* Linnaeus, 1758[a]
Scolopacidae	*Calidris canutus* (Linnaeus, 1758)[a]
	Gallinago gallinago (Linnaeus, 1758)[a]
	Lymnocryptes minimus (Brünnich, 1764)[a]
	Numenius arquata (Linnaeus, 1758)[f]
Laridae	Laridae indet.[a]
	Chroicocephalus cf. *ridibundus* (Linnaeus, 1766)[a]
	Larus marinus Linnaeus, 1758[a]
Stercorariidae	**Stercorarius pomarinus* (Temminck, 1815)
Alcidae	*Alca torda* Linnaeus, 1758[a]
	**Alle alle* (Linnaeus, 1758)
	Pinguinus impennis (Linnaeus, 1758)[g]
	**Uria aalge* (Pontoppidan, 1763)
Strigidae	*Bubo bubo* (Linnaeus, 1758)[h]
	**Bubo scandiacus* (Linnaeus, 1758)
Passeriformes	Passeriformes indet.[f]

Table 1. All bird taxa known through fossils from the Pleistocene/Holocene of the southern North Sea. Identifications at family or genus level are only listed when they represent one or more other species in that family or genus. *: first reported in the present paper; a-h: previously published: a: Langeveld *et al*. (2017); b: Langeveld (2016a); c: De Bruijn & de Bruijn (2016); d: Langeveld & Mol (2017); e: Langeveld & Tanis (2015); f: Stewart (2001); g: summarised by Langeveld (2020); h: Langeveld *et al*. (2016).

ing with a specific bird family (Stewart & Hernández Carrasquilla, 1997). For comparative purposes the avian osteological collections of the Natural History Museum Rotterdam (The Netherlands; NMR; Langeveld *et al*., 2020) and of the Groningen Institute of Archaeology (University of Groningen, The Netherlands; GIA; Çakirlar *et al*., 2016) were used. Identifications are based on morphology and size. Anatomical terminology follows Baumel & Witmer (1993). Orientation follows Cohen & Serjeantson (1996). Taxonomy follows Gill & Donsker

(2020). Measurements follow Von den Driesch (1976) except for *Lagopus* Brisson, 1760 where they follow Kraft (1972), *Tetrao* Linnaeus, 1758 where they follow Erbersdobler (1968), Accipitridae where they follow Schmidt-Burger (1982) when noted and Strigidae tarsometatarsi where they follow Meijer *et al*. (2017). Following Scager *et al*. (2017), when no standard measurements could be taken due to damage to the specimens a maximum dimension of the fragment is provided as a very rough indication of taphonomy. All measurements were taken with Vernier or digital calipers with 0.1 mm accuracy. Following Sánchez-Marco (1999) and Stewart & Jacobi (2015), ecological characteristics of extant taxa were compiled from the literature (Del Hoyo *et al*., 1992, 1994, 1996, 1999) for interpretation: preferred nesting and non-breeding habitats, inhabited climatic zones and a classification into marine birds (species that spend at least part of their lifecycle on or near seas or oceans), freshwater birds (need to be near freshwater, whether for feeding, breeding or safety) and land birds (do not need proximity of open (fresh/marine) water or prefer drier areas); taxa were assigned to more than one category when necessary due to broad habitat preferences or diverging habitat preferences during different stages of their lifecycle.

Abbreviations

Anatomy

lig.	ligamentum (ligament)
m.	musculus (muscle)
n.	nervus (nerve)

Measurements

Bd/DW/TD	greatest width at distal end
Bp/BP/PW	greatest width at proximal end
DD (in Strigidae)/Td	distal depth
DD/Did	greatest diagonal at distal end
DS	depth of the shaft perpendicular to WS and measured at the same point
GL	greatest length
KT/SC/WS	smallest width of the diaphysis
LI	greatest length of the incisivum - apex praemaxillaris
Lm	medial length
LPF	length from proximal articulation to the foramen vasculare distale
LTD	length from attachment of tuberculum m. tibialis cranialis to distal end of trochlea III
SBO	smallest width between the orbits on the dorsal side

Collections (all in The Netherlands)

DD	private collection Dick Duineveld, The Hague
FB	private collection Frank de Boer, Capelle aan den IJssel
GIA	Groningen Institute of Archaeology (University of Groningen), Groningen
HKV	private collection Hans and Karin Verhulsdonck, Nijmegen
HM	private collection Henk Mulder, Monster
HS	private collection Henk ter Steege, Middelburg
HZ	private collection Heleen Zwennes, The Hague
JD	private collection Jeffrey Dolkens, The Hague
KT	private collection Kommer Tanis, Goedereede
NJ	private collection Nicolai Jansen, Spijkenisse
NMR	Natural History Museum Rotterdam, Rotterdam
RB	private collection Rick van Bragt, The Hague
RR	private collection Roel van Reijmersdal, Bosch en Duin
WW	private collection Willy van Wingerden, Honselersdijk

Results

A total of 46 previously unpublished specimens was identified to at least genus level; a further 30 specimens are listed at family level, since they are informative even at that level. Based on their state of preservation all specimens are more than *ca*. 1,000 years in age (details in Discussion). The specimens are briefly described and listed below.

Family Anatidae

Anatidae indet.

Material – Zandmotor: coll. NMR998900156723, NMR998900157263-66, 70-71, 7 coracoids (Pl. 1, fig. 1); coll. NMR998900157258-62, 67-69, 8 humeri; Hoek van Holland: coll. NMR998900159704, 1 distal fragment of a humerus; De Banjaard: coll. NMR998900156710, 1 coracoid; coll. NMR998900156711, 1 humerus.

The coracoids are characterised by the ridges for muscle attachments on the dorsal side of the blade which allow attribution to Anatidae (Cohen & Serjeantson, 1996). The size points to various ducks. Specific identification of any of this damaged material is however not possible with certainty (Stewart, 2004, 2010).

***Anas crecca* Linnaeus, 1758 / *A. querquedula* Linnaeus, 1758**

Material – Zandmotor: coll. NMR998900154389, 1 humerus (Pl. 1, fig. 2).

This well preserved anatid humerus is small with GL: 60.5 mm. At that size it is only attributable to *Anas crecca*, *A. querquedula* or *Mergellus albellus* Linnaeus, 1758. However, in the latter species the foramen pneumaticum has a smooth surface, whilst in the fossil some trabeculae are present, thus ruling out this species and leaving the other two, which are indistinguishable (Woelfle, 1967).

***Anser* sp.**

Material – Zandmotor: coll. HS, 1 distal humerus fragment; Hoek van Holland: coll. NMR998900154714, 1 distal humerus fragment; southern North Sea: coll. NMR998900153514, 1 humerus; coll. NMR9989-00153515, 1 tibiotarsus.

The humerus (Bp: 32.8, SC: 10.2, Bd: 23.3, GL: 158.2 mm) is completely preserved. The distal fragment NMR998900154714 (max. dimension: 40.9 mm) of a large humerus is heavily damaged, but the characteristics that are present (size, shape and location of the fossa m. brachialis and the tuberculum supracondylare) fit well with Anatidae. The other distal humerus fragment is well preserved with Bd: 25.7 mm. The tibiotarsus is slightly damaged at the proximal end (GL must have been *ca*. 145 mm, SC: 8.1, Bd: 16.8 mm). All specimens were morphologically indistinguishable from large *Anser* spp. in the comparative collections. Based on Bacher (1967), the specimens are too large to assign to *Branta* Scopoli, 1769 and too small to assign to *Cygnus* Garsault, 1764; they fit in the group of larger *Anser* Brisson, 1760 species but are not diagnostic at the species level.

***Cygnus olor* (Gmelin, 1789)**

Material – Maasvlakte 2: coll. RR RRMV.011, 1 distal fragment of a coracoid.

This small fragment (max. dimension: 37.8 mm) of a large and heavily built coracoid shows the characteristic ridges which allow attribution to Anatidae (Cohen & Serjeantson, 1996). The size points to *Cygnus*. Its heavy build matches *C. olor* better than *C. cygnus* (Linnaeus, 1758). Following Bacher (1967), the uninterrupted, smooth and slightly convex morphology of the linea transversa allows identification as *C. olor*.

Family Phasianidae

***Lagopus lagopus* (Linnaeus, 1758)**

Material – Zandmotor: coll. NMR998900006029, 1 humerus (Pl. 1, fig. 3); coll. HM, 1 distal fragment of a humerus; 1 ulna (Pl. 1, fig. 5); coll. RB: 1 distal fragment of a humerus (Pl. 1, fig. 4).

The complete humerus has the typical galliform stout build with GL: 62.1 mm and KT: 5.7 mm; the compact and arched distal humerus fragment in coll. HM has TD: 12.0 mm; the almost complete specimen in coll. RB has TD: 12.3 mm and KT: 6.3 mm. When compared to modern populations, these sizes allow attribution to *L. lagopus* based on Kraft (1972) and Stewart (2007). The well preserved and rather large ulna (GL: 61.8, DD: 8.3, KT: 3.9 mm) is heavily built and is notably curved only in its proximal halve. The condylus ventralis ulnae is conspicuous and protrudes strongly, characteristic for the Galliformes (Cohen & Serjeantson, 1996). Based on Stewart (2007) its dimensions allow attribution to *L. lagopus*.

***Tetrao praeurogallus* Jánossy, 1969**

Material – Maasvlakte 2: coll. KT 4364, 1 carpometacarpus (Pl. 1, fig. 6).

This well preserved galliform specimen (GL: 67.7, BP: 19.1, DD: 12.7 mm, smallest anterior-posterior depth of the diaphysis: 6.4 mm) was assigned to *Tetrao* based on morphology (typical deep notch in the ventral rim of the trochlea carpalis with its edges meeting at a right angle and a broad processus extensorius) following Tomek & Bocheński (2009). Its length agrees well with male *T. urogallus* Linnaeus, 1758 reported by Erbersdobler (1968), but its BP and DD are slightly lower (7% and 6%, respectively) than the minimum values observed there, while all dimensions of the specimen are clearly above the range of extant female *T. urogallus* reported by Erbersdobler (1968). The dimensions of this slender carpometacarpus match those of a carpometacarpus from the early Middle Pleistocene of Slovakia described by Jánossy (1969) as *Tetrao praeurogallus*.

Family Gaviidae

***Gavia arctica* (Linnaeus, 1758)**

Material – Zandmotor: coll. RB, 1 distal fragment of an ulna.

This specimen (max. dimension: 58.8 mm) is slightly dorso-ventrally flattened with a very wide distal end, which characterises it as a Gaviidae. The Did: 15.5 mm is clearly above the range for *Gavia stellata* (Pontoppidan, 1763) (Table 2). Based on the measurements of Fitzgerald (1980), who had more specimens of *G. arctica* at his disposal, the specimen can be assigned to *G. arctica*.

***Gavia immer* (Brünnich, 1764)**

Material – Zandmotor: coll. WW, 1 proximal fragment of a carpometacarpus (Pl. 1, fig. 7).

This proximal fragment (Bp: 16.5 mm) of a flattened carpometacarpus with an extended and flattened process of metacarpal I (Olsen, 1979) clearly matches the carpometacarpi of Gaviidae. Its size identifies it as *Gavia immer* (Table 2 and Fitzgerald, 1980).

***Gavia stellata* (Pontoppidan, 1763)**

Material – Zandmotor: coll. DD, 1 distal fragment of a humerus; coll. WW, 1 distal fragment of a humerus.

	Carpometacarpus GL	Carpometacarpus Bp	Ulna Did	Humerus Bd	Femur Bd
Gavia immer, n=7					
Range	85.0-100.6	15.8-18.6	18.1-20.2	18.1-20.5	17.6-19.0
Mean	95.0	16.9	19.0	19.3	18.6
SD	5.4	0.9	0.7	0.8	0.5
Gavia stellata, n=15					
Range	71.4-81.6	10.9-13.1	11.9-13.4	13.5-15.5	13.9-15.9
Mean	75.3	12.1	12.6	14.7	15.0
SD	3.7	0.7	0.4	0.5	0.6
Gavia arctica, n=2					
NMR9989-2513	80.8	13.3	13.0	15.5	15.8
NMR9989-4522	74.3	12.7	14.4	15.2	14.9

Table 2. Selected measurements in mm of the carpometacarpus, ulna, humerus and femur of *Gavia* in the Natural History Museum Rotterdam (NMR). GL: greatest length of the bone, Bp: width at proximal end, Did: diagonal of the distal end, Bd: width at distal end.

Although not very well preserved, the specimens (max. dimension: 22.2 mm and 61.2 mm) retain enough diagnostic characters for attribution to Gaviidae. Based on their small size and the slenderness of the small part of the diaphysis that is preserved in both specimens, they are assigned to *G. stellata*.

***Gavia arctica* (Linnaeus, 1758) / *G. immer* (Brünnich, 1764)**

Material – De Banjaard: coll. NMR998900155749, 1 fragment of a skull including os frontale, os parietale and os nasale (Pl. 1, fig. 8).

This is one of the very few fossil bird skull fragments from the North Sea. It is well preserved and shows many characteristics, including the presence of a depressio frontalis, clear crista temporalis, well-defined crista nuchalis sagittalis and deep fossae glandulae nasalis. In all these and other characteristics (such as presence of numerous small perforations in the fossae glandulae nasalis; Olsen, 1979) it proved indistinguishable from *Gavia* Forster, 1788. Based on its size (SBO: 15.5 mm) it can be assigned to either *G. arctica* or *G. immer* (SBO in present-day *G. arctica*: 10.5-14.5 mm, n=2; *G. immer*: 13.6-21.8 mm, n=6; *G. stellata*: 9.4-13.5 mm, n=13; coll. NMR).

***Gavia arctica* (Linnaeus, 1758) / *G. stellata* (Pontoppidan, 1763)**

Material – Zandmotor: coll. NMR998900153396, 1 distal fragment of a femur (Pl. 1, fig. 9); coll. RB, 1 carpometacarpus; coll. WW, 2 distal fragments of humeri; Hoek van Holland: coll. NMR998900159703, 1 carpometacarpus.

The distal femur fragment exhibits the groove typical for birds in the lateral trochlea (Cohen & Serjeantson, 1996). The preserved part of the diaphysis is noticeably curved in a caudal direction. The medial trochlea is much reduced and both trochleae barely protrude in cranial direction. A pronounced deepening is present on the cranial side just above the distal end of the bone. These characteristics allow identification as Gaviidae. Its Bd: 15.4 mm falls in the zone of overlap between *G. arctica* and *G. stellata* (Table 2). In the distal humerus fragments (Bd: 15.5 mm and *ca*. 15 mm), the well-defined processus flexorius and the shape and depth of the fossa m. brachialis combined with the size point to the Gaviidae. The Bd falls in the zone of overlap between the two species (Table 2 and Fitzgerald, 1980). Both carpometacarpi are quite well preserved. They are very flattened with an extended process of metacarpal I (Olsen, 1979), clearly matching the carpometacarpi of Gaviidae. Their GL (76.2 and 80.2 mm respectively) falls in the zone of overlap between the species (Table 2 and Fitzgerald, 1980).

Family Procellariidae

***Calonectris* sp. / *Pterodroma* sp.**

Material – Zandmotor: coll. RB, 1 distal fragment of a humerus (Pl. 1, fig. 10).

This distal fragment (max. dimension: 31.0 mm) is well preserved, but slight damage to the distal end prevents any standard measurements. Its Bd can however be estimated at *ca*. 13 mm. The shaft of the bone is typically flattened, which together with the presence, size and shape of a processus supracondylaris dorsalis points to the Procellariidae. The fossa m. brachialis is extremely deep and rounded, reaching till the proximal margin of the processus supracondylaris dorsalis. It is a very conspicuous characteristic that was observed to this extent

only in *Calonectris* Mathews & Iredale, 1915, *Procellaria* Linnaeus, 1758 and *Pterodroma* Bonaparte, 1856. This state of the fossa m. brachialis is much less developed in *Fulmarus* Stephens, 1826 and not at all in the other genera in the family. The attachment of the processus supracondylaris dorsalis to the bone is clearly wider than in *Fulmarus*. *Procellaria* is confined to the Southern and Pacific oceans (Del Hoyo *et al*., 1992), has no fossil record in Europe (Tyrberg 1998, 2008a) and would thus be a very unlikely identification. The specimen's small size matches with *Calonectris edwardsii* (Oustalet, 1883). Damage to the specimen and limited comparative material do not allow exclusion of *Pterodroma*, which today occurs in the Atlantic Ocean (Del Hoyo *et al*., 1992).

***Puffinus* sp.**

Material – Zandmotor: coll. HM, 1 damaged proximal fragment of a humerus.

The specimen (max. dimension: 61.1 mm) is too damaged to take any standard measurements, but can still be compared with complete comparative material. Its craniocaudally flattened but not triangular cross-section and the non-pneumatised proximal end point to the Procellariidae and its size corresponds well to *Puffinus puffinus* (Brünnich, 1764), but the specimen is not diagnostic at species level (Wragg, 1985).

Family Podicipedidae

***Podiceps* sp.**

Material – Zandmotor: coll. WW, 1 damaged coracoid.

The specimen (max. dimension: 35.4 mm) is damaged and worn. The broad and angular facies articularis humeralis and the very broad facies articularis on both sides of the end of the blade of the coracoid are typical for the Podicipedidae; the size suggests *Podiceps* Latham, 1787.

Family Ciconiidae

***Ciconia nigra* (Linnaeus, 1758)**

Material – Zandmotor: coll. DD, 1 distal fragment of a tibiotarsus (Pl. 1, fig. 11).

The specimen is a well-preserved distal fragment (Bd: 12.8 mm) of a tibiotarsus. The pronounced papilla just lateral of the short and broad pons supratendineus, the narrow build and the low condyli protruding both anteriorly and posteriorly characterise it as a Ciconiidae (Boles, 2005). Based on Gruber (1990), its small size, the narrow sulcus extensorius, the condylis medialis that barely extends laterally and the narrow trochleae all point to *Ciconia nigra*.

Family Sulidae

***Morus bassanus* (Linnaeus, 1758)**

Material – Zandmotor: coll. HM, 1 rostrum maxillare with os nasale (Pl. 1, fig. 12); Maasvlakte 2: coll. NJ, 1 distal fragment of a humerus.

The well-preserved rostrum maxillare with os nasale with LI: 101.4 mm is characterised by its massive build and very little curvature at the tip only; combined with the large size, this allows identification. The distal humerus fragment (Bd: 24.4 mm) preserves many morphological details, including the sharp condylus dorsalis, pronounced tuberculum supracondylare ventrale, deep fossa m. brachialis and fossa olecrani which all proved indistinguishable from comparative material of *Morus bassanus*.

Family Phalacrocoracidae

***Phalacrocorax carbo* (Linnaeus, 1758)**

Material – Zandmotor: coll. DD, 1 tarsometatarsus (Pl. 1, fig. 13); coll. RB, 1 distal fragment of a tibiotarsus (Pl. 1, fig. 14); Maasvlakte 2: coll. FB, 1 distal fragment of an ulna.

The slightly worn tarsometatarsus (GL: 67.5 mm) shows a remnant of the typically pronounced crista medialis hypotarsi, while the deep sulcus extensorius also matches *Phalacrocorax* Brisson, 1760. The size identifies it as *P. carbo*. The articular end of the distal fragment of the ulna (max. dimension: 39.9 mm) is damaged to some degree, but the pronounced condylus ventralis ulnae projecting far distally and the clear incisura tuberculi carpalis are still visible and identify the specimen as *Phalacrocorax*; the size allows identification to *P. carbo*. The distal tibiotarsus fragment (max. dimension: 29.5 mm) is worn but shows the position and size of the pons supratendineus and fibular remnant near the distal end. Especially the presence of this last characteristic allows identification as *Phalacrocorax* (Cohen & Serjeantson, 1996); the size matches *P. carbo*.

Family Pandionidae

***Pandion haliaetus* (Linnaeus, 1758)**

Material – Maasvlakte 2: coll. HS, 1 tarsometatarsus fragment (Pl. 1, fig. 15).

This specimen is damaged on the proximal and distal ends, allowing only one standard measurement: SC: 9.4 mm. However, from the preserved bases of the trochleae as well as the distal part of the tuberositas muscularis tibialis cranialis, it is clear that the specimen is of a remarkably short and stout build. The trochleae do curve

outward, but not as much as in Accipitridae. This characteristic, combined with the compressed build, the deep sulcus flexorius, the pronounced tuberositas muscularis tibialis cranialis and the large canalis interosseus distalis just distal to the pronounced foramen vasculare distale allowed identification in comparison with Olsen (1979), Aves 3D (2020) and McNall (2020).

Family Accipitridae

***Accipiter gentilis* (Linnaeus, 1758)**

Material – Zandmotor: coll. WW, 1 distal fragment of a tarsometatarsus (Pl. 1, fig. 16).

This fragment (max. dimension: 23.6 mm) comprises the slightly worn distal portion of an accipitrid tarsometatarsus. It can be assigned to this family based on the large trochleae and their wide arrangement as well as the location and size of the foramen vasculare distale, which is very pronounced. The trochlea metatarsi II is damaged, which hampers the accurate measurement of the Bd; the Td following Schmidt-Burger (1982) can however be measured: 7.3 mm. This falls in the known range of *Accipiter gentilis* (Schmidt-Burger, 1982). The flattened plantar surface of the specimen and its pronounced vasculare distale are characteristic for *Accipiter gentilis* (Schmidt-Burger, 1982).

***Haliaeetus albicilla* (Linnaeus, 1758)**

Material – Zandmotor: coll. WW, 1 distal fragment of an ulna (Pl. 1, fig. 17).

This fragment of a large specimen (Did: 19.9 mm) matched well in both size and morphology to specimens of *Haliaeetus albicilla* in the comparative coll. GIA (Did: Va. 4891: 20.4 mm; RW68 560/5651: 18.2 mm).

Accipitridae indet.

Material – Zandmotor: coll. DD, 1 distal fragment of a tibiotarsus (Pl. 1, fig. 19); coll. HM, 1 distal fragment of a tibiotarsus (Pl. 1, fig. 20); coll. WW, 2 distal fragments of tarsometatarsi (Pl. 1, figs 21-22); Westkapelle: coll. NMR998900005882, 1 distal fragment of an ulna (Pl. 1, fig. 18).

The small ulna fragment of a large specimen (Did: 16.8 mm) could not be identified to species. However, the triangular shape of the well-preserved distal end clearly points to a large bird of prey. The tibiotarsus fragments with their typically angled pons supratendineus (Cohen & Serjeantson, 1996) have Bd: 17.5 mm and 19.2 mm, which points to large birds of prey. The tarsometatarsus fragments (max. dimensions: 25.9 mm and 29.6 mm) are heavily built. Their large trochleae and their wide arrangement as well as the location and size of the foramen vasculare distale allow attribution to Accipitridae, their fragmentary state however obscures further identification.

Family Scolopacidae

Scolopacidae indet.

Material – Zandmotor: coll. NMR998900153392, 1 humerus (Pl. 1, fig. 24); coll. HKV 00286ZM, 1 humerus; coll. RB, 1 humerus (Pl. 1, fig. 23).

These rather well-preserved specimens could be assigned to the Scolopacidae based on presence of a canalis n. coracobrachialis cranialis and a processus supracondylaris dorsalis and the proximal location of the attachment of the m. supracoracoideus on the humerus (Ballmann, 2004). Their size (GL: 29.6 mm, 50.5 mm and 37.2 mm, respectively) is not diagnostic at the species level and slight damage to both the proximal and distal ends hampers detailed comparison with reference collections.

Family Laridae

Laridae indet.

Material – Zandmotor: coll. HM, 2 coracoid fragments (Pl. 1, fig. 25).

In both specimens the blade of the coracoid has broken off and only the proximal part of the bone is present, but well preserved. The presence of the narrow foramen n. supracoracoidei, wide sulcus m. supracoracoidei and wide impressio lig. acrocoracohumeralis point to the Laridae. The specimens were compared to various medium sized gulls, but it was impossible to assign them to a species. Size matched with a.o. *Larus argentatus* Pontoppidan, 1763 and *L. fuscus* Linnaeus, 1758, thus they can be assigned to an unidentified Laridae (medium sized species).

Family Stercorariidae

***Stercorarius pomarinus* (Temminck, 1815)**

Material – Zandmotor: coll. NMR998900153395, 1 coracoid (Pl. 1, fig. 26).

The coracoid shows close affinities to Laridae, but it is more robust and the shaft of the bone is more rounded. The impressio lig. acrocoracohumeralis on the processus acrocoracoideus is much narrower and better defined in the specimen than in Laridae. Also, the facies articulares clavicularis is located at a smaller angle to the length axis of the coracoid than in Laridae. These characteristics allow identification as Stercorariidae. Two measurements on the fossil could be taken: the Lm following Von den

	Lm	MWpa
Stercorarius skua, n=12		
Range	47.3-55.4	14.2-16.3
Mean	50.7	15.3
SD	2.5	0.7
Stercorarius pomarinus, n=4		
Range	40.5-43.3	11.8-12.7
Mean	41.6	12.2
SD	1.2	0.4
Stercorarius parasiticus, n=2		
NMR9989-4863	31.5	9.3
NMR9989-4860	33.5	10.2

Table 3. Selected measurements in mm of the coracoid of *Stercorarius* in the Natural History Museum Rotterdam (NMR). Lm: medial length of the bone, MWpa: maximum width of the processus acrocoracoideus.

Driesch (1976): 44.1 mm and the maximum width of the processus acrocoracoideus: 13.3 mm. Table 3 shows that the fossil has a relatively wide processus acrocoracoideus but is closest in dimensions to *Stercorarius pomarinus*.

Family Alcidae

***Alca torda* Linnaeus, 1758**

Material – Zandmotor: coll. NMR998900154430, 1 coracoid (Pl. 1, fig. 27); coll. NMR998900154431, 1 proximal fragment of an ulna; coll. HM, 1 distal fragment of a humerus; coll. JD, 1 humerus; Hoek van Holland: coll. NMR998900006151, 1 distal fragment of a humerus; Cadzand: coll. NMR998900154385, 1 distal fragment of a humerus (Pl. 1, fig. 28).

The shafts of the distal humerus fragments are characteristically flattened with a rounded triangular cross-section which allows attribution to Alcidae (*e.g.* Cohen & Serjeantson, 1996). Their Bd cannot be measured exactly due to slight damage, but must have been between 10.0 and 10.5 mm; SC: 6.8 mm, 6.7 mm and 6.7 mm, respectively. The complete humerus has SC: 6.8 mm. These measurements allow identification as *Alca torda* (Table 4). The coracoid is more or less completely preserved but rather worn, hampering accurate measurements. Its size and morphology however match *Alca torda*, while it can be distinguished from roughly similarly sized *Fratercula arctica* (Linnaeus, 1758) by the latter species' much more compressed and triangular sternal facet and from *Cepphus grylle* (Linnaeus, 1758) by the latter species' much smaller foramen n. supracoracoidei much closer to the edge of the bone. The ulna has a characteristic dorso-ventrally flattened triangular cross-section. Direct comparison of the worn specimen allowed attribution to *Alca torda* based on its size.

***Pinguinus impennis*, n Bp=18, n SC=27, n Bd=15, n GL=12**				
	Bp	SC	Bd	GL
Range	22.3-26.8	9.0-11.6	14.0-16.9	99-113
Mean	25.0	10.2	15.4	104.4
SD	1.3	0.7	0.8	4.7
***Uria aalge*, n=13**				
	Bp	SC	Bd	GL
Range	17.3-18.7	7.3-8.0	11.8-12.3	82-90
Mean	18.1	7.8	11.9	85.5
SD	0.3	0.2	0.2	2.3
***Alca torda*, n=11**				
	Bp	SC	Bd	GL
Range	15.3-17.1	6.5-7.0	10.2-11.2	69.2-76.3
Mean	16.2	6.8	10.6	73.2
SD	0.5	0.2	0.3	2.1
***Uria lomvia*, n=3**				
	Bp	SC	Bd	GL
Range	17.3-18.0	7.0-7.5	11.8-12.0	86-88
Mean	17.6	7.2	11.9	87.0
SD	0.4	0.3	0.1	1.0
***Cepphus grylle*, n=3**				
	Bp	SC	Bd	GL
Range	14.4-15.4	4.7-5.0	8.9-9.3	59.4-63.4
Mean	14.9	4.8	9.1	61.5
SD	0.5	0.2	0.2	2.0
***Fratercula arctica*, n=4**				
	Bp	SC	Bd	GL
Range	14.4-14.9	5.1-5.2	9.8-10.1	62.6-66.8
Mean	14.7	5.2	9.9	64.8
SD	0.2	0.1	0.1	2.1

Table 4. Selected measurements in mm of the humerus of Alcidae based on material in the Natural History Museum Rotterdam and the Groningen Institute of Archaeology (University of Groningen). Bp: width at proximal end, SC: smallest width of the shaft, Bd: width at distal end, GL: greatest length of the bone.

***Alle alle* (Linnaeus, 1758)**

Material – Zandmotor: coll. HM, 2 damaged proximal fragments of ulnae.

Both specimens are proximal fragments (max. dimension: 32.0 mm and 25.8 mm respectively) from which no standard measurements could be taken due to damage on both ends of the bones. However, their small size, slenderness and characteristically dorso-ventrally flattened triangular cross-section allowed them to be identified as *Alle alle* beyond any doubt.

***Uria aalge* (Pontoppidan, 1763)**

Material – Yerseke: coll. HS, 1 distal fragment of a humerus

(Pl. 1, fig. 29); Zoutelande: coll. NMR998900153398, 1 humerus.

Both specimens exhibit the typical flattening with a rounded triangular cross-section, which allows attribution to Alcidae (*e.g.* Cohen & Serjeantson, 1996). The complete specimen has GL: 81.4, SC: 7.5 and Bd: 11.7 mm; the distal fragment has SC: 8.0 mm. These dimensions allow attribution to *Uria aalge* (Table 4).

Family Strigidae

***Bubo scandiacus* (Linnaeus, 1758)**

Material – Zandmotor: coll. HZ 547-ZM-17, 1 tarsometatarsus (Pl. 1, fig. 30); Hoek van Holland: coll. HKV 00702HvH, 1 tarsometatarsus.

Both specimens are well preserved. The presence of an arcus extensorius identifies them as strigid (Baumel & Witmer, 1993; Cohen & Serjeantson, 1996). Most measurements could be accurately taken (specimen 547-ZM-17: GL: 58.3, DW: 19.2, DD: 13.6, WS: 10.7, DS: 6.9, LPF: 42.5, LTD: 31.3 mm; specimen 00702HvH: GL: 54.2, PW: 16.5, DW: 18.5 mm). These all fall within the range of *Bubo scandiacus* reported by Meijer *et al*. (2017) except for WS and DS of 547-ZM-17, which are bigger in the current specimen. These larger sizes however do occur in Pleistocene populations of *B.scandiacus* (Potapova, 2001).

***Bubo scandiacus* (Linnaeus, 1758) / *Strix nebulosa* Forster, 1772 / *Strix uralensis* Pallas, 1771**

Material – Zandmotor: coll. DD, 2 distal fragments of tibiotarsi (Pl. 1, fig. 31).

The larger fragment (max. dimension: 49.7 mm) is damaged at the condyles so its Bd could not be accurately measured but it is at least 15 mm. The smaller fragment is well preserved and has Bd: 14.8 mm. The lack of a pons supratendineus allows attribution to Strigidae. The strigid tibiotarsus is a poor bone to identify to species level; size is its main characteristic. The present specimens fall in the range of *Bubo scandiacus*, *Strix nebulosa* and *S. uralensis* (Kessler, 2017).

Discussion

Significance of the specimens

As the specimens have been collected *ex situ,* geological information such as depositional environment, geological age and faunal association of the studied material has been lost. However, that does not justify simply dismissing this material, as it is the only direct evidence available for Pleistocene and Holocene bird communities of former ecosystems of what is now the North Sea. Besides, the organic preservation of fossils recovered from the North Sea is often very good and may surpass that of contemporaneous deposits on land (Peeters & Amkreutz, 2020). Furthermore, geological evidence suggests that already in the North Sea areas from which the sand for beach nourishments is sourced, the majority of the Pleistocene fossils are not preserved *in situ*, but have been reworked by fluvial processes in the geological past (Hijma *et al*., 2012). Hence the information loss through *ex situ* collecting of this material is limited. In the North Sea sand source areas the Holocene material may be preserved in its highly detailed original context (Missiaen *et al*., 2020).

Age of the specimens

Radiocarbon dating may provide valuable insight into the geological age of the specimens and thus help in interpretation (Reumer *et al*., 2003), but it is costly and not always successful: three attempts at radiocarbon dating remains of cf. *Anas* sp. and *Lagopus lagopus* failed to yield results due to insufficient collagen preservation (Langeveld *et al*., 2017). Radiocarbon dating of eight bones of *Pinguinus impennis* (Linnaeus, 1758) yielded only four dates, ranging from 1425-1300 BC until beyond 48,000 cal BP (Langeveld, 2020). This suggests that the bird bones studied have a broad temporal range, overlapping with that of the mammalian remains from the same area (Mol *et al*., 2006, 2008, 2013, 2020; Langeveld *et al*., 2018).

Many bird species in the study area have long temporal ranges, extending from today at least back into the Pleistocene (Tyrberg, 1998). These long ranges in combination with the *ex situ* collecting of the material and lack of absolute dates create a methodological problem: how does one age the specimens under study? In a previous study it turned out to be possible to separate present-day specimens (*i.e.* less than *ca.* 1,000 years old) from fossil (older than *ca*. 1,000 years) specimens; present-day bones can be separated from older material based on their state of diagenesis and colour (Langeveld *et al*., 2017).

Truly fresh bones are white and are easily excluded from the study material. Bones of domestic species, *Gallus gallus domesticus* and *Meleagris gallopavo*, have maximum potential ages of 2,000 and 400 years respectively, due to these species not having been imported into the study area earlier (Prummel, 1987; Serjeantson, 2009). The domestic species' bones from the study area generally are rather light in colour, with white tones and they have a smudged appearance including dark green colours. Bones of wild species with similar preservation were excluded from the study material under the assumption that they too would not hold significant geological age. Bones of *Lagopus lagopus*, which based on the species' ecology (Kuz'mina, 1992; Potapov *et al*., 2003) and known fossil record (Tyrberg, 1991, 1998, 2008a) must date from the Pleistocene, have a smooth light to dark brown colour, comparable with well dated mammal remains from the North Sea in general and the Eurogeul area in particu-

lar (*e.g.* Mol *et al*., 2008; pers. obs.) suggesting a similar depositional environment and taphonomical history (Dupras & Schultz, 2013) and hence a similar age (Langeveld *et al*., 2017). The same holds true for the remains of *Bubo scandiacus* reported here (Mourer-Chauviré, 1993; Potapova, 2001; Potapov & Sale, 2013).

Hence, it is clear that all specimens reported here are not present-day. They are all at least *ca.* 1,000 years of age and most likely significantly older: many of them were probably contemporaneous with the terrestrial mammals from the North Sea that have well established radiocarbon dates (Mol *et al*., 2006, 2008, 2013, 2020; Langeveld *et al*., 2018) of more than 50,000 years until inundation of the North Sea at *ca.* 8,000 BP (Beets & Van der Spek, 2000). The carpometacarpus of *Tetrao praeurogallus* recovered from Maasvlakte 2 must be of Early or Middle Pleistocene age, based on its known *in situ* records elsewhere in Europe (Tyrberg, 1998). Strikingly, the specimen is more strongly mineralised than any of the other material, except for the tarsometarsus of *Pandion haliaetus* (also from Maasvlakte 2) that is similarly preserved. When this state of diagenesis with strong mineralisation is compared to other fossils from Maasvlakte 2, it matches Early or early Middle Pleistocene mammalian taxa and differs from Late Pleistocene ones, which are not mineralised (Mol & Langeveld, in press), as has also been observed for mammalian fossils from other parts of the North Sea (Drees, 1986; Van Kolfschoten & Laban, 1995; Mol *et al*., 2003).

Faunal composition

It is worth noting that the faunal list (Table 1) is skewed to bird families with odd morphologies or sizes or families that are poor in species, since specimens from these families can be identified with greater certainty than specimens from specious families with conserved skeletal morphology, in which species differ very little from each other in their skeletal characteristics, such as Laridae and Anatidae (Stewart, 2004, 2010). Hence, the data presented here should not be interpreted in any quantitative way. From studying the various private collections, it is clear that Anatidae, especially ducks, are the most common bird fossils from the North Sea. Molecular methods, such as aDNA analysis or Zooarchaeology by Mass Spectrometry (ZooMS), described by Dalén *et al*. (2017), Buckley (2018) and Horn *et al*. (2019) could be used in the future to gain more insight into the North Sea fossil record (of fragmentary remains) of Anatidae and other families which pose similar problems. For example, the common Accipitridae indet. material may be partially attributable to *Haliaeetus albicilla*, which is commonly identified by zooarchaeologists from Holocene sediments in The Netherlands (Amkreutz & Corbey, 2008; Zeiler, 2019). However, the fragmentary state of the remains and incompleteness of reference collections in this taxonomic group (*e.g.* lacking large vultures) prevent positive identifications through morphology alone.

The non-overlapping modern habitat preferences of some identified species (Table 5: *e.g.* open ocean for *Puffinus* sp. versus rocky country with cliffs and patches of woodland for *Bubo bubo*, or woods, both coniferous, deciduous and mixed, preferably near forest edge for *Accipiter gentilis* versus open tundra, marshes, fields and dunes for *Bubo scandiacus*) suggest that various palaeoenvironments are represented and that not all recovered taxa were contemporaneous, similar to what is observed with the mammalian remains from the study area (Mol *et al*., 2008). Given the lack of radiocarbon dates for the avian material, this is a valuable insight. It however hinders reaching palaeoecological conclusions based on the avian material without more radiocarbon dates. Mixing of faunas (time-averaging) from different palaeoenvironments however does not have to be the sole explanation for our results: Late Pleistocene bird communities were non-analogous with taxa co-occurring that today have diverging habitat preferences (*e.g.* Tyrberg, 1991; Stewart & Jacobi, 2015), as indeed were Late Pleistocene vegetation and mammal communities (Guthrie, 1990). The classification into marine, freshwater and land birds (Fig. 2) shows that land birds form a minority and taking into account the modern distributional and habitat data in Table 5, this suggests most of the recovered taxa lived in (possibly near-shore) wetland environments in temperate to subarctic climatic conditions. Burial and preservation of bird remains is more likely in such environments than in terrestrial environments (Serjeantson, 2009), thus this predominance of marine and freshwater birds may partially be a taphonomic artefact.

Only 3 out of 44 recovered species are extinct: *Anser* cf. *djuktaiensis* Zelenkov & Kurochkin, 2014, *Tetrao praeurogallus* and *Pinguinus impennis*. This low percentage of extinct species can be explained by the predominantly Late Pleistocene/Holocene age of the specimens, as significant avian extinctions did not occur in the study region at the Pleistocene-Holocene transition (Tyrberg, 2008b) or during the Holocene (Tyrberg, 2009). Although some consider *Tetrao praeurogallus* a junior synonym of the extant *Tetrao urogallus* (*e.g.* Mourer-Chauviré, 1975; Sánchez Marco, 2009), many others have retained

Figure 2. Ecological classification of extant taxa based on data in Table 5. Black: marine, dark grey: freshwater, light grey: land.

Taxon	Marine	Water	Land	Nesting habitat	Non-breeding habitat	Breeding range	Non-breeding range
Cygnus olor		X		near or on freshwater	freshwater, sometimes on estuaries or sheltered coasts	temperate to boreal	temperate
Anas sp. indet.		X		near water	near water	boreal to arctic	temperate to boreal
Anas querquedula/A. crecca		X		shallow freshwater with abundant vegetation	shallow freshwater, occasionally near coast or on sea	temperate to arctic	subtropical to boreal
Bucephala clangula	X	X		small freshwater bodies with coniferous trees	coastal lagoons, estuaries, inshore marine waters	temperate to arctic	temperate to boreal
Clangula hyemalis	X	X		small freshwater bodies, also on coast	sea, occasionally inland on large freshwater bodies	subarctic to arctic	temperate to arctic
Melanitta nigra	X	X		small freshwater bodies, sometimes with scaterred trees	sea, preferentially shallow water near coasts	subarctic to arctic	temperate to subarctic
Anser spp.		X		near water	near water	boreal to arctic	temperate to boreal
Anser/Branta spp.		X		near water	near water	boreal to arctic	temperate to boreal
Lagopus lagopus			X	prefers low vegetation on arctic tundra with willow or dwarf birch	prefers riparian thickets of willows, often in forest glades	boreal to arctic	boreal to arctic
Gavia arctica	X	X		near large deep lakes of freshwater	coasts	boreal to subarctic	temperate
Gavia immer	X	X		near large deep lakes of freshwater	coasts	boreal to subarctic	temperate
Gavia stellata	X	X		near any body of still freshwater	coasts	boreal to subarctic	temperate
Calonectris sp./*Pterodroma* sp.	X			near ocean/sea, in colonies	open ocean/sea	tropical to arctic	tropical to arctic
Puffinus sp.	X			near ocean/sea, in colonies	open ocean/sea	tropical to arctic	tropical to arctic
Podiceps cf. *cristatus*	X	X		small freshwater bodies with emergent vegetation and stretches of open water	coasts, estuaries and large exposed bodies of water	temperate to boreal	temperate
Ciconia nigra		X		usually in trees in open woodland with small bodies of water	open woodland with small bodies of water; avoids closed forest and large waterbodies	temperate to boreal	tropical to subtropical
Ardea sp.		X		usually in trees, in colonies	near any body of water	tropical to arctic	tropical to boreal
Morus bassanus	X			cliffs, preferably on islands	open ocean/sea	boreal to arctic	tropical to arctic
Phalacrocorax carbo	X	X		often in trees (or ledges)	open water, fresh or near-coastal sheltered areas	tropical to arctic	tropical to boreal
Phalacrocorax carbo cf. *carbo*	X	X		often in trees (or ledges)	often marine, near-coastal sheltered areas	tropical to arctic	tropical to boreal
Pandion haliaetus	X	X		shallow waters	shallow waters	tropical to subarctic	tropical to subtropical
Accipiter gentilis			X	woods, both coniferous, deciduous and mixed, preferably near forest edge	woods, both coniferous, deciduous and mixed, preferably near forest edge	temperate to subarctic	subtropical to subarctic

Haliaeetus albicilla	X	X	X	prefers high trees near significant waterbodies	prefers near significant waterbodies; but may also be in steppe or desert far from water	temperate to arctic	subtropical to subarctic
Fulica atra	X	X		still or slow-moving fairly shallow waters with rich vegetation	open water, fresh or near-coastal sheltered areas	tropical to boreal	tropical to boreal
Grus grus		X	X	shallow wetlands	shallow wetlands, open landscapes	temperate to boreal	tropical to temperate
Haematopus ostralegus	X	X		salt-marshes, sandy beaches, sometimes inland along water bodies	prefers estuarine mudflats, but also sandy/rocky shores and salt-marshes	temperate to arctic	tropical to boreal
Calidris canutus	X			tundra, upland gravel, marshes, usually near coast	strictly coastal, prefers tidal mud-/sandflats	arctic	tropical to boreal
Gallinago gallinago		X	X	open fresh or brackish marshland with rich vegetation and other areas providing grassy cover	open fresh or brackish marshland with rich vegetation and other areas providing grassy cover	temperate to arctic	tropical to boreal
Lymnocryptes minimus	X	X		open marshes, floodplains in forest tundra and northern taiga	brackish and freshwater mudflats with vegetation	subarctic	tropical to boreal
Numenius arquata	X	X	X	moist grasslands, bogs, swampy and dry heathland, coastal marshes	muddy coasts and muddy shores of lakes and rivers	boreal to subarctic	tropical to boreal
Chroicocephalus cf. *ridibundus*	X	X		moors, sand dunes and beaches, mostly near freshwater	calm, shallow, coastal or inland waters	temperate to boreal	tropical to boreal
Larus marinus	X			vegetated islands, dunes	rocky or sandy coasts, estuaries and open sea	boreal to arctic	temperate to subarctic
Stercorarius pomarinus	X			tundra, preferably with pools and hummocky areas in moist bogs	marine, somewhat coastal	arctic	tropical to subtropical
Alca torda	X			rocky coastal regions on steep cliffs and offshore islands	marine, not much further than edge of continental shelf	boreal to arctic	temperate to arctic
Alle alle	X			on sea coasts, usually in crevices in rock scree	open ocean and sea	arctic	boreal to arctic
Uria aalge	X			on sea coasts with steep cliffs or on low flat islands	marine, not much further than edge of continental shelf	temperate to arctic	subtropical to arctic
Bubo bubo			X	rocky country with cliffs and patches of woodland	rocky country with cliffs and patches of woodland	temperate to subarctic	temperate to subarctic
Bubo scandiacus			X	open tundra	open tundra, marshes, fields and dunes	subarctic to arctic	subarctic to arctic

Table 5. Ecological characteristics (based on literature) of extant bird taxa identified from Quaternary bones from the southern North Sea.

the species and reported it from Early and Middle Pleistocene sites from Hungary, Poland, Romania, Slovakia, Austria, Germany and the Czech Republic (*e.g.* Jánossy, 1976; Bocheński, 1997; Tyrberg, 1998, 2008b; Boev, 2002; Bocheński *et al*., 2012; Kessler, 2014, 2019). The present record extends the distribution area of this species westwards.

Conclusion

Quaternary (predominantly Late Pleistocene/Holocene) fossils of at least 44 bird species are now known from the southern North Sea (Table 1). Compared to the mammal record, the avifauna remains relatively poorly known, due to scarcity of material and comparatively low research effort. Lack of dating also poses a problem when interpreting the record. The fossil bird record does however contain taxa that do not currently occur in the study area (*e.g. Calonectris* sp./*Pterodroma* sp.) and specimens that must date from the Pleistocene (*e.g.* remains of *Lagopus lagopus*, *Tetrao praeurogallus*, *Bubo scandiacus*) and therefore adds to our understanding of the past ecosystems of the North Sea area. More specimens need to be collected, studied and dated in order to gain more insight into the Quaternary avifauna of what is now the southern part of the North Sea.

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Plate 1

1. Anatidae indet., coracoid, Zandmotor, coll. NMR998900156723.
2. *Anas crecca* Linnaeus, 1758/*Anas querquedula* Linnaeus, 1758, humerus, Zandmotor, coll. NMR998900154389.
3. *Lagopus lagopus* (Linnaeus, 1758), humerus, Zandmotor, coll. NMR998900006029, cranial (left) and caudal views.
4. *Lagopus lagopus* (Linnaeus, 1758), humerus, Zandmotor, coll. RB, cranial (left) and caudal views.
5. *Lagopus lagopus* (Linnaeus, 1758), ulna, Zandmotor, coll. HM.
6. *Tetrao praeurogallus* Jánossy, 1969, carpometacarpus, Maasvlakte 2, coll. KT 4364, dorsal (left) and ventral views.
7. *Gavia immer* (Brünnich, 1764), carpometacarpus, Zandmotor, coll. WW.
8. *Gavia arctica* (Linnaeus, 1758)/*Gavia immer* (Brünnich, 1764), skull fragment, De Banjaard, coll. NMR998900155749.
9. *Gavia arctica* (Linnaeus, 1758)/*Gavia stellata* (Pontoppidan, 1763), femur, Zandmotor, coll. NMR998900153396.
10. *Calonectris* sp./*Pterodroma* sp., humerus, Zandmotor, coll. RB.
11. *Ciconia nigra* (Linnaeus, 1758), tibiotarsus, Zandmotor, coll. DD, cranial (left), caudal (centre) and lateral views.
12. *Morus bassanus* (Linnaeus, 1758), rostrum maxillare with os nasale, Zandmotor, coll. HM.
13. *Phalacrocorax carbo* (Linnaeus, 1758), tarsometatarsus, Zandmotor, coll. DD.
14. *Phalacrocorax carbo* (Linnaeus, 1758), tibiotarsus, Zandmotor, coll. RB.
15. *Pandion haliaetus* (Linnaeus, 1758), tarsometatarsus, Maasvlakte 2, coll. HS, plantar (left) and dorsal views.
16. *Accipiter gentilis* (Linnaeus, 1758), tarsometatarsus, Zandmotor, coll. WW, dorsal (left) and plantar views.
17. *Haliaeetus albicilla* (Linnaeus, 1758), ulna, Zandmotor, coll. WW.
18. Accipitridae indet., ulna, Westkapelle, coll. NMR998900005882.
19. Accipitridae indet., tibiotarsus, Zandmotor, coll. DD.
20. Accipitridae indet., tibiotarsus, Zandmotor, coll. HM.
21. Accipitridae indet., tarsometatarsus, Zandmotor, coll. WW.
22. Accipitridae indet., tarsometatarsus, Zandmotor, coll. WW.
23. Scolopacidae indet., humerus, Zandmotor, coll. RB.
24. Scolopacidae indet., humerus, Zandmotor, coll. NMR998900153392.
25. Laridae indet., coracoid, Zandmotor, coll. HM.
26. *Stercorarius pomarinus* (Temminck, 1815), coracoid, Zandmotor, coll. NMR998900153395, lateral (above) and dorsal views.
27. *Alca torda* Linnaeus, 1758, coracoid, Zandmotor, coll. NMR998900154430.
28. *Alca torda* Linnaeus, 1758, humerus, Cadzand, coll. NMR998900154385.
29. *Uria aalge* (Pontoppidan, 1763), humerus, Yerseke, coll. HS.
30. *Bubo scandiacus* (Linnaeus, 1758), tarsometatarsus, Zandmotor, coll. HZ 547-ZM-17, dorsal (left) and plantar views.
31. *Bubo scandiacus* (Linnaeus, 1758)/*Strix nebulosa* Forster, 1772/*Strix uralensis* Pallas, 1771, tibiotarsus, Zandmotor, coll. DD.


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