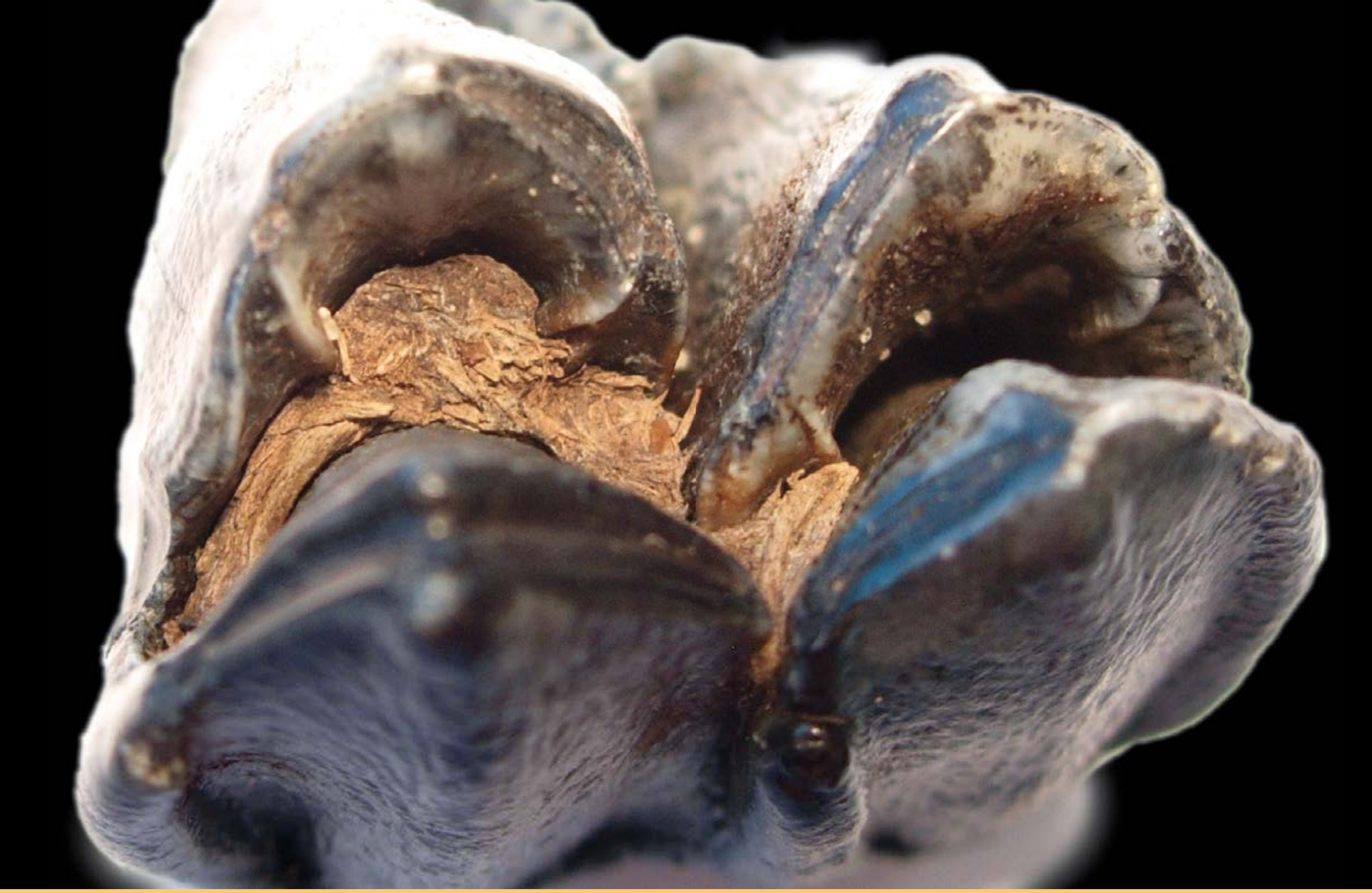

Weichselian and Holocene lake sediments, peat deposits and molar folds as environmental archives in the North Sea area

U vindt een Nederlandse samenvatting aan het eind van de tekst.

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Abstract | During the Weichselian the sea level was much lower than today because enormous quantities of water were stored as ice caps on land. In western Europe the southern limit of the ice cap connected northern Britain with southern Scandinavia. The present day North Sea mainly

FIGURE LEFT PAGE. | *Molar of* Megaloceros giganteus *(occlusal view) from Zandmotor, showing light-brown plant remains in infundibulum. Photo: Jan van Arkel (IBED-UvA).*

consisted of dry land. During the coldest periods the landscape was a polar desert without vegetation and therefore without fauna. Sandy deposits were mainly prone to aeolian transport. During periods of less extreme climatic conditions, vegetation could develop and thus the landscape became a habitat for a variety of mammal species. Soils were dry in upland areas, but lakes and peatlands could develop on top of permafrost in depressions in the landscape. Wind erosion and sand deposition played a minor role during periods with a relatively mild climate, because soils were covered with vegetation.

In areas with dry sandy soils, plant remains completely decomposed, but in peat deposits and lake sediments pollen grains, fruits, seeds, vegetative plant remains and fungal spores were fossilized (Plates I, II). These fossils formed archives of the former vegetation and landscape development.

In addition, molar embedded pollen grains represent habitats and diets of large herbivore species (Van Geel *et al.*, 2018, 2019).

Zoological and botanical fossils

There are two human activities that bring old organic deposits to the present North Sea surface. Firstly, sand extraction for the reinforcement of the present Dutch coast, and secondly, trawl fishing. Trawl fishing especially played a role in areas where sand has been removed to create continuous access for large ships to the harbour of Rotterdam. Deposits of pure sand (without organic remains) are not good archives of former vegetation because wet sand does not keep its compact structure; it falls apart in separate grains when lifted from the sea floor. Unfortunately, we did not find sediments in direct contact with dredged mammal bones, because any sediment or peat originally in contact with bones is washed from the bone surface during trawling. However, during a 2002 fishing tour fifty lumps of lake sediment and peat were sampled. At the laboratory in Amsterdam small sub-samples (c. 1 cc each) were taken from inside these lumps. The samples were used for the analysis of microfossils; sub-samples of c. 20 cc each were studied for macrofossils, such as fruits, seeds, leaves and mosses.

In 2017 a new sample type was explored: herbivore molars. The molars were collected by members of the working group Pleistocene mammals (WPZ) and successfully sampled for compacted plant remains from inside molar folds (Van Geel *et al.*, 2018, 2019).

Aspects of Weichselian and early Holocene vegetation history in the Netherlands

Supposedly the changes of Weichselian and early Holocene vegetation composition in the present North Sea area did not differ from the results of palaeoecological studies in The Netherlands. Different periods are characterized by specific pollen spectra and therefore palynological dating, linked to the radiocarbon-dated biostratigraphy of earlier studies, can be applied. The Weichselian pollen data from the North Sea area were compared with radiocarbon-dated pollen sequences from sediments in the central and eastern Netherlands (Kolstrup 1980; Ran, 1990; Van Huissteden, 1990; Brinkkemper *et al.*, 1987; Van Geel *et al.*, 2010). Lateglacial pollen spectra were compared with the detailed study of the Lateglacial Usselo site (Van Geel *et al.*, 1989) and with the compilation of Lateglacial pollen diagrams by Hoek (1997).

After the start of the Holocene tree species immigrated from their refugia in southern Europe. Those trees arrived in a characteristic sequence, their arrival was well-dated with radiocarbon. (Van Geel *et al.*, 1981).

Combining microfossil and macrofossil analysis with the known ecological requirements of recorded taxa allows reconstruction of various environmental aspects. The paleoecological records reflect climatic conditions and climate change, soil development, and competition between species. An important indicator for mild climates is the presence of thermophilous tree species in the landcape. Treeless landscapes often indicate relatively cold conditions (mean summer temperature below 10 °C). However, time lags between climate warming and the migration of tree species do occur (see, e.g., Van Geel *et al.*, 1984, 1989 and Bazelmans *et al.*, 2021).

Overview of successive landscapes and vegetation history in the Netherlands

Figure 1 shows a simplified scheme of mean summer temperature fluctuations and landscape development (vegetation and geological aspects) for the last c. 65000 years. Geological information (Kasse, 2002) is especially important for polar desert periods during the Lower-Pleniglacial and Upper-Pleniglacial because those periods were generally too cold for plants and animals (no fossils; no radiocarbon dating).

During the Middle-Pleniglacial (from c. 57,000 BP – c. 26,000 BP) the landscape (vegetation, geology) probably was quite similar to the area of the Dinkel Valley as reconstructed by Ran (1990) and Van Huissteden (1990). Based on archaeological data we know that people lived in north-west Europe, including the North Sea area (Roebroeks, 2014; Armkreutz and Van der Vaart-Verschoof, 2021). There were several Mid-Pleniglacial interstadials characterized by relatively mild climatic conditions when mean summer temperatures were between 5 and 10 °C. Sandy soils became partly covered with pioneer vegetation and lakes and mires existed in the landscape. Herbaceous vegetation allowed herbivores and their predators to live in north-west Europe during interstadials. The landscapes during the Middle Pleniglacial interstadials were treeless due to the mean summer temperature being below 10 °C. The initial lack of humic substances in sandy soils, related vulnerability for desiccation and the low level of nutrients (nitrogen and phosphorous components) will also have hampered the immigration of tree species (Van Geel *et al.*, 1989).

The Upper-Pleniglacial (c. 26,000 – c. 13,000 BP) was extremely cold. The landscape was a polar desert without vegetation and therefore

without herbivores. From this period only coversand deposits, gravel beds and periglacial frost phenomena are known. Mean summer temperature was probably below 5 °C.
After the transition (about 13,000 BP) from the Upper Pleniglacial to the warm Bølling-Allerød interstadial various herbaceous species with a pioneer strategy (like Artemisia) could immigrate and settle. Soon also the pioneers Juniper, Birch, and later Pine arrived.

The Younger Dryas (c. 11,000 – c. 10,200 BP) was a last, relatively cold period, almost without trees, but there was vegetation and thus herbivore mammals and their predators were present.

PLATE I. | *Selection of pollen grains:*
1: Quercus; 2: Alnus; 3: Tilia; 4: Ulmus; 5: Betula; 6: Salix; 7: Pinus; 8: Hedera; 9: Viscum; 10: Ericaceae; *11: Artemisia; 12:* Asteraceae tubuliflorae; *13:* Chenopodiaceae; *14: Plantago; 15:* Poaceae; *16:* Dipsacaceae; *17:* Armeria; *18:* Thalictrum; *19:* Apiaceae; *20:* Potentilla; *21:* Cyperaceae; *22: Mentha; 23: Iris pseudacorus; 24:* Typha latifolia; *25:* Typha angustifolia; *26:* Sparganium; *27:* Nymphaea; *28:* Nuphar.
Photo: Jan van Arkel (IBED-UvA).

The Holocene started started with a steep temperature rise c. 10,200 BP. Again light-demanding Juniper, Birch and Pine expanded. Hazel, Elm, Oak, Lime and Alder arrived later (Van Geel *et al.*, 1981). Diminishing light in the forests was not problematic for later arriving shade-tolerant species, but light-demanding species declined because of the competition with shade-tolerant tree species.

After the start of the Holoceen, sea levels quickly rose worldwide. Within a few thousand years an increasing part of the present North Sea area became inundated. In elevated areas inundation was relatively late, so the upland forest succession lasted longer

Plate II. | *Selection of microfossils and macroremains:*
29: Ceratophyllum, *hair; 30:* Selaginella selaginoides*; 31:* Equisetum*; 32 and 33: fern spores; 34: charred epidermis* Poaceae*; 35-37:* Spirogyra*, spores; 38-40:* Mougeotia*, spores,* operculum*; 41-43: spores of* coprophilous fungi*; 44:* Pediastrum*; 45:* Botryococcus*; 46:* Psammodiscus nitidus*; 47:* Hystrichosphaeridae*; 48 and 49:* Alisma*, seed; 50:* Mentha*, seed; 51:* Typha*, seed; 52:* Bryozoa*, statoblast; 53:* Ostracoda*; 54: Bithynia,* operculum.
Photo: Jan van Arkel (IBED-UvA).

than in depressions in the landscape. Overall, we assume that the chronology of the changing forest composition was similar to what we know from studies in the present area of The Netherlands.

During the Preboreal (c. 10,200 to c. 9150 BP) England was still connected with the European continent. Groundwater tables rose in areas that were still outside the direct influence of the North Sea and thus lakes and peatlands could develop, and lake sediments and peat deposits were formed. During the Boreal (c. 9150 to c. 7900 BP) major parts of the southern North Sea area were already inundated by the sea. Around 8000 BP the English Channel became connected with the North Sea. At the beginning of the Atlantic period (c. 7900 BP) the North Sea almost had its present extension and marine sediments covered the whole area.

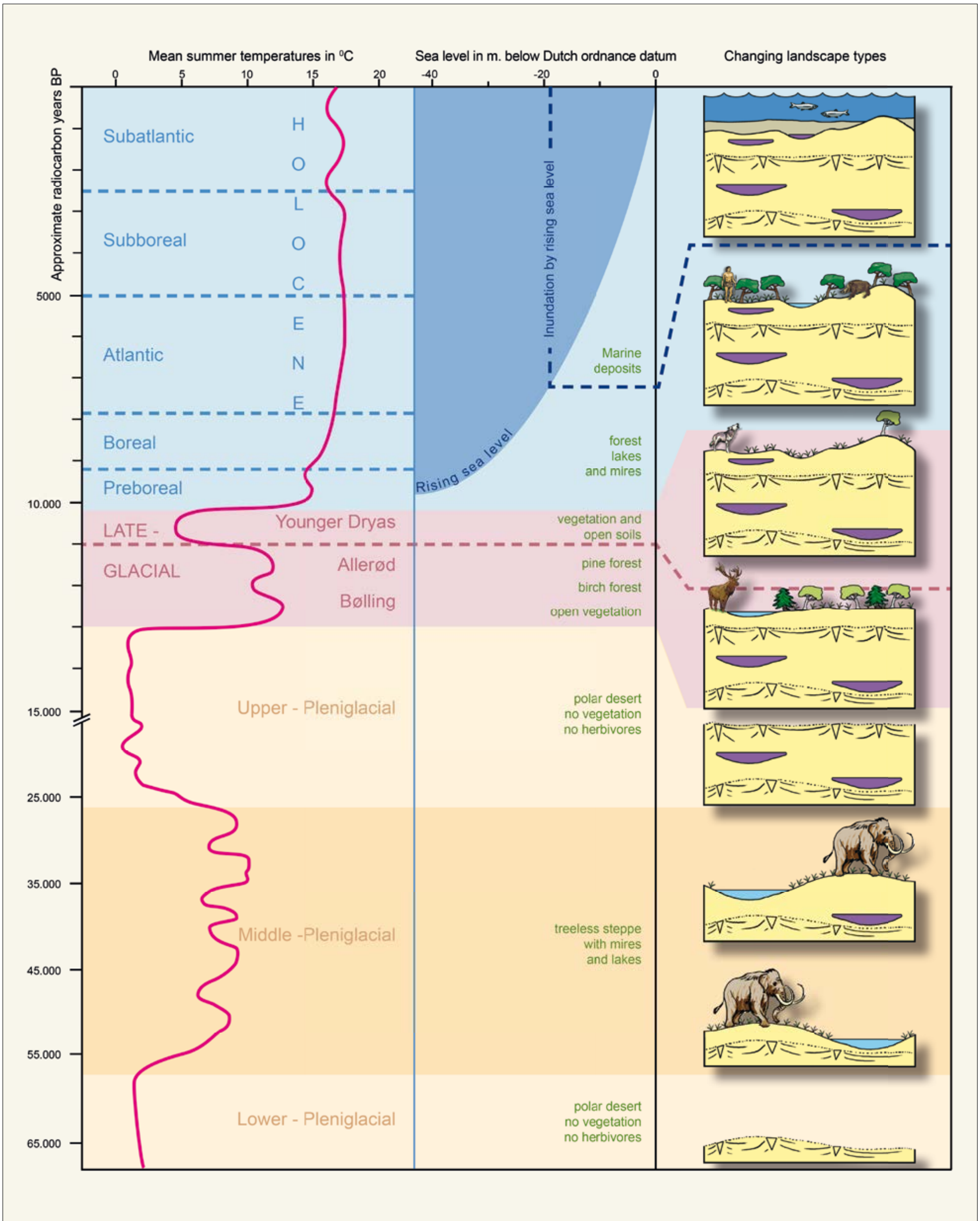

Figure 1. | *Cartoon showing the development of climate and landscape during the last c. 65,000 years in the present North Sea area.*

Taxa/samples	NRZ-1	NRZ-2	NRZ-12
**Alnus* - Alder	-	0.8	21.9
**Betula* - Birch	-	3.0	4.3
**Corylus* - Hazel	-	38.8	40.4
**Pinus* - Pine	0.5	24.2	5.6
**Picea* - Spruce	0.5	0.4	-
**Quercus* - Oak	-	10.4	15.6
**Salix* - Willow	1.0	1.9	5.0
**Tilia* - Lime	-	1.5	+
**Ulmus* - Elm	-	3.0	7.3
*Apiaceae - Parsley family	-	1.5	0.3
**Artemisia* - Mugwort	+	+	-
Armeria maritima - Sea pink	-	-	+
Asteraceae - Aster family	-	-	0.7
Ceratophyllum - Hornwort	-	-	+
Chenopodiaceae - Goosefoot fam.	-	-	1.7
*Cyperaceae - Sedge family	90.1	7.3	6.0
Dipsacaceae (C3) - Teasel family	+	-	-
*Ericales - Heath/Crowberry fam.	0.5	-	-
Fabaceae - Pea family	+	-	-
**Humulus* - Hop	-	0.4	-
Iris pseudacorus - Yellow flag iris	-	0.4	-
Myriophyllum - Watermilfoil	-	-	0.3
Nymphaeaceae - Water lilies	-	-	+
Nuphar - Yellow water lily	-	-	+
*Poaceae - Grass family	5.4	6.5	28.8
charred grass cuticles	-	+	+
Potentilla type - Cinquefoil type	+	-	-
*Ranunculaceae - Buttercup family	-	0.4	0.7
Rumex - Dock	-	+	-
Sparganium - Bur-reed	-	5.4	0.3
**Thalictrum* - Meadow-rue	1.0	-	0.3
Typha angustifolia - Cattail	-	0.8	5.6
Typha latifolia - Cattail	-	-	0.3
Viburnum - Guelder-rose	-	+	-
Viscum album - Mistletoe	-	+	-
Monolete verrucate fern spores	0.5	1.8	0.3
Monolete psilate fern spores	-	0.8	3.6
Selaginella selaginoides-Spike moss	+	-	-
Equisetum - Horsetail	-	238.2	-
Pediastrum (green algae)	10.3	0.4	0.7
Botryococcus (green algae)	3.2	-	-
Mougeotia laetevirens type (gr. alg)	-	0.4	-
Mougeotia spec. (green algae)	-	-	0.3
Spirogyra (green algae)	1.6	0.4	0.7
Type 128A algal spore	6.5	2.7	0.7
Type 128B algal spore	0.5	0.8	-
Rivularia type (Cyanobacteria)	-	0.4	-
Clasterosporium caricinum (fungus)	2.2	-	-
Kretzschmaria deusta (fungus)	-	0.8	-
Charred plant remains	-	++	-
Diatoms (brackish and salt)	-	-	+
Foraminiferae (brackish water)	-	-	0.3
Hystrichosphaeridae (salt w.)	-	-	+

TABLE 1. | *Percentages of microfossils in three sediment samples from the Eurogeul area. Taxa included in the pollen sum have been indicated with a star. For sample NRZ-12 only tree pollen (Alnus to Ulmus) was included in the pollen sum.*

Results: samples from the bottom of the North Sea in the Eurogeul area

Microfossils and macroremains in fifty samples lifted from the bottom of the North Sea by trawling were studied. They were indirectly dated, based on the known radiocarbon dated biostratigraphy of the Netherlands. Different periods appeared to be represented. Tables 1 and 2 show the microfossil and macrofossil spectra of three representative samples indicated as NRZ-1, NRZ-2 and NRZ-12, and in plates I and II a selection of microfossils and macroremains is illustrated.

NRZ-1: an example of Weichselian interstadial conditions

Sample NRZ-1 consists of peat that was formed by aquatic mosses. The pollen spectrum is completely dominated by Cyperaceae (sedges). Lumps of cyperaceous pollen point to a strictly local occurrence. Local presence is supported by the record of the parasitic fungus *Clasterosporium caricinum* (Van Geel and Aptroot, 2006) and by seeds of *Carex* species that grow in wet habitats. The ecological niches of the bryophytes point to direct contact with alkaline groundwater. Various green algae indicate stagnant, shallow freshwater. Tree pollen is low frequent, indicating a treeless landscape. Herbaceous taxa of dry soils are of limited occurrence and the species diversity is very low. Referring to the detailed study by Ran (1990) for comparison, sample NRZ-1 reflects interstadial conditions preceding the Upper Pleniglacial: the sample is probably younger than 57,000 BP and older than 26,000 BP.

NRZ-2: an early Holocene forest

Sample NRZ-2 consisted of peaty clay. Trees like hazel, pine and oak dominate the pollen spectrum. Lime and elm had already immigrated. Comparison with the Borchert pollen record (Van Geel *et al.*, 1981) points to a Boreal age (between 9150 en 7900 BP) because hazel dominated, and alder was still absent. Remains of plants and invertebrates point to shallow freshwater (Cladocera, Porifera, Algae) and nearby terrestrialisation to a mire with *Alisma, Eupatorium, Iris, Mentha* and *Phragmites*. The pollen slide of this sample and the macrofossil sample showed small charcoal particles, some of which had the characteristic cell pattern of grass epidermis. We cannot exclude natural fires, but people may also actively have burned regional vegetation to create attractive fresh, green hunting areas.

NRZ-12: at the boundary between freshwater and marine conditions

Sample NRZ-12 was a clayey lake deposit. *Alnus* pollen is common and therefore the sample is younger than 7900 BP (Van Geel *et al.*, 1981). Various microfossils point to freshwater: *Nymphaea, Lythrum* and freshwater algae, but the presence of salt-tolerant taxa (Chenopodiaceae and *Armeria maritima*) indicate a nearby presence of the seashore. Foraminiferae and Hystrichosphaeridae that occur in brackish and marine conditions even point to temporary marine inundations and the diatom species *Psammodiscus nitidus* indicates a sandy substrate in a tidal environment.

Fourty-nine samples (out of fifty) could be roughly dated based on characteristics of the pollen spectra. Two samples showed a Middle Pleniglacial spectrum of pollen taxa. Both samples were built up of compacted peat consisting of aquatic mosses (sample NRZ-1 is an example; see Tables 1 and 2). One sample appeared to be of Lateglacial or Preboreal age. Thirty samples were of Boreal age (NRZ-2 is an example). Most of these Boreal samples consisted of peaty clay or peat. Sixteen, mostly clayey samples showed a pollen spectrum pointing to the Atlantic period (compare NRZ-12). The relatively low representation of Middle Pleniglacial samples and the dominance of Holocene samples may have to do with the depth to which deposits were collected.

Taxa/samples	NRZ-1	NRZ-2	NRZ-12
Alisma plantago-aquatica - Water plantain	-	+	-
Carex pseudocyperus - Cyperus sedge	-	+	-
Carex rostrata/vesicaria - Beaked/Blister sedge	-	+	-
Carex vesicaria - Blister sedge	-	+	-
Carex sect. *Acutae* - various sedge species	+	-	-
Eupatorium cannabinum - Hemp-agrimony	-	+	-
Mentha aquatica - Watermint	-	+	-
Myrica gale - Sweetgale	-	+	-
Phragmites australis - Common reed	-	+	-
Ranunculus flammula - Lesser spearwort	-	+	-
Typha - Cattail	-	+	+
Equisetum - Horsetail (vegetative plant remains)	-	+	-
Calliergonella cuspidata - moss	++	-	-
Scorpidium scorpioides - moss	++	-	-
Scorpidium revolvens - moss	+	-	-
Drepanocladus sp. - moss	+	-	-
Acari - Mites	+	-	-
Bryozoa - Moss animals	-	+	+
Bithynia - Mud bithynia	-	+	-
Cladocera - Water fleas	-	+	-
Freshwater sponges (gemmulae)	-	+	+
Ostracoda - Seed shrimps	-	-	+

Table 2. | *Botanical and zoological macrofossils (presence/absence) in three sediment samples from the Eurogeul area.*

The observed sedimentological differences between early Holocene and later samples fit with the trends of the sequence of sediments in the western Netherlands. Basal peat was formed on top of Pleistocene cover sands. This basal peat already reflected rising ground water tables (post-glacial sea level rise). Clays were deposited in the Atlantic period on top of Boreal peat. The early Holocene sedimentation sequence apparently shows the same characteristics as the sequence that we know from the western Netherlands. But there is a fundamental difference: during the second half of the Holocene, and thus after marine inundation, only marine sedimentation occurred in the low-lying North Sea area.

The botanical contents of molar folds: an additional source of information

Deep folds in molars of various large herbivore species from North Sea deposits were screened for compacted plant remains. In many cases pollen grains appeared to be well-preserved in such fold-infills. First results were based on plant remains obtained from the molar of a giant deer of Mid-Weichselian age (Van Geel *et al.*, 2018). The pollen spectrum from this molar was dominated by *Artemisia* and other Asteraceae, with a limited number of other steppe taxa, like *Plantago, Helianthemum* and Plumbaginaceae. The pollen grains indicate that the giant deer foraged in a steppe environment and may have preferred to eat *Artemisia* which contains a high level of nutrients, especially calcium and phosphorous which are used for antler growth. Van Geel *et al.* (2018) even hypothesized about possible links between the disappearance of giant deer at the onset of the Holocene in northwest Europe and the transition to a less dynamic landscape with acidifying soils and a decline of *Artemisia* and other calciphilous plant species.

A second study (Van Geel *et al.*, 2019) on pollen and spore records from molar folds of eight large herbivore species (*Megaloceros giganteus, Cervus elaphus, Rangifer tarandus, Alces alces, Bison priscus, Ovibos moschatus, Coelodonta antiquitatis and Stephanorhinus kirchbergensis*) was used to reconstruct food preferences. Pollen spectra showed valuable aspects of vegetation composition, food choice, and landscapes, from sub-arctic open areas to interglacial forest.

	Tundra	Steppe
1.	Climate humid (thick snow cover during winter)	Climate dry (food available also during winter)
2.	Late start of plant growth in spring (melting of thick snow cover takes time)	Early start of the growing season (snow absent, or only a thin snow cover; so sunshine melts the snow quickly)
3.	Thick (isolating) layer of plant remains on top of soil	Not much accumulation of organic material (grazing!)
4.	Slow recycling of nutrients	Fast recycling of nutrients (a lot of dung produced by grazing animals)
5.	Unfrozen part of soil during summer quite thin, therefore availability of nutrients for plants quite low	Thicker unfrozen part of soil during summer, therefore availability of nutrients higher
6.	Many tundra plant species are not palatable, their growing points are at the end of the stems (vulnerable to grazing)	Dominance of grasses (excellent food for grazing animals). The growing point of grasses is just near their roots, so grazing does not do any harm to grasses (grazing stimulates growth).

TABLE 3. | *Tundra versus steppe.*

STEPPE AND TUNDRA

The tundras in the northern parts of Eurasia and North America nowadays are among the coldest areas with vegetation cover. However, such areas are not the appropriate reference areas when we study the environments of Pleistocene glacial periods. Guthrie (1990) stated that the carrying capacity of tundras and steppe areas were quite different (Table 3). A major difference is the relatively high level of precipitation in the present-day tundras, while cold steppes were dry. Moist tundra soils with a developed moss layer are not what large herbivores need or prefer. In cold dry steppe areas, grasses (Poaceae) are a dominant component of the vegetation and grazing (compare mowing of lawns by people) does not harm them, because their growing point is situated directly above the top of the soil. Grazing even stimulates vegetative growth of grasses, which is a positive factor in the competition with other plants.

Winter is a critical period for large herbivores. Collecting food in a dry steppe (low amounts of snow) is possible but grazing in tundras with a thick snow cover is difficult. According to F. Vera (pers. comm.) a fast transition to cold conditions in autumn is important because in that way grasses become freeze-dried and thus leaves and stems still contain many nutrients for the herbivores. Grazing and trampling in steppe areas will have had a positive influence on steppe plants in their competition with tundra plants, because grasses are 'adapted' to grazing and steppe plants like *Artemisias* prefer open soils. In other words: large herbivores may partly have been responsible for the existence and species composition of steppe areas. Grazing will also have hampered the migration of tree species from their southern refugia. Only after the climate shift – from cold and dry, to warmer and moist – at the transition from Lateglacial to the Holocene the fast migration of tree species to the north re-started. Increased precipitation at the beginning of the Holocene caused moist soils and a decline of steppe species even may have been a factor in the extinction of some large herbivores. Decreased grazing pressure will have contributed to the success of arboreal germlings (Zimov, 2005) and thus may have been a factor in the decline of steppe vegetation. According to Zimov even the more sophisticated hunting methods of Cro Magnon people may have caused a decrease of the population density of large herbivores and thus may have stimulated the development of tundra vegetation in northern areas.

Samenvatting

Meersedimenten, veen en kiesplooien uit het Weichselien en Holoceen als archief voor het milieu en het klimaat in het huidige Noordzeegebied.

Voor een reconstructie van de ontwikkeling van de vegetatie en het klimaat van het huidige zuidelijke Noordzeegebied zijn monsters bewerkt op hun inhoud aan microfossielen, met name stuifmeel, en macroresten. Uit geologisch en paleo-ecologisch onderzoek in Nederland – vrijwel zeker ook representatief voor het Noordzeegebied – weten we dat gedurende de koudste fasen een poolwoestijn aanwezig was, zonder planten en dus ook zonder dieren. Maar er waren gedurende het Weichselien ook perioden met een wat milder klimaat dat wel geschikt was voor vegetatie en fauna.
Bij de zandwinning in de Noordzee en bij de visserij zijn kluiten klei en veen opgevist die dateren uit het Weichselien en de eerste helft van het Holoceen. Uit dat materiaal zijn monsters bewerkt om milieureconstructies te maken en om die reconstructies te vergelijken met de kennis die we hebben van de ontwikkelingen van de vegetatie in Nederland. Daarbij zijn met name stuifmeelkorrels, zaden en vegetatieve plantenresten gedetermineerd en geïnterpreteerd. Bovendien zijn monsters bewerkt van materiaal uit kiesplooien van acht soorten grote grazers (reuzenhert, edelhert, rendier, eland, steppewisent, muskusos, wolharige neushoorn en bosneushoorn).
Een beknopt overzicht van de vegetatiegeschiedenis is gegeven, ervan uitgaande dat de ontwikkelingen in het Noordzeegebied niet wezenlijk verschilden van de ontwikkelingen binnen de grenzen van Nederland.
Via biostratigrafische correlatie kon ruwweg de ouderdom van de bestudeerde monsters worden bepaald en gebruikmakend van de bekende ecologische eisen van gevonden planten, konden aspecten van het klimaat en de vegetatie worden beschreven.

In twee tabellen worden van drie monsters (representatief voor de overige monsters) de analyseresultaten betreffende microfossielen en macroresten getoond en in een cartoon wordt een overzicht gegeven van de opeenvolgende landschappen in relatie tot veranderingen in het klimaat, de vegetatie en de zeespiegelstijging. Er kunnen drie categorieën monsters worden onderscheiden: Midden-Pleniglaciaal, Vroeg-Holoceen (nog geen mariene taxa) en Midden-Holocene monsters met mariene taxa die wijzen op een naderende Noordzee.
De monsters uit kiesplooien geven informatie over het dieet en de datering van grote herbivoren.