Long-Term Changes in Wetland Area and Composition in the Netherlands Affecting the Carrying Capacity for Wintering Waterbirds

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Long-term changes in wetland area and composition in The Netherlands affecting the carrying capacity for wintering waterbirds

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In The Netherlands, arising in geological time as the delta of the rivers Rhine, Meuse and Scheldt, a considerable change in landscape occurred during the Holocene period due to sea level rise. In more recent times this change was dramatically enforced by human actions. This started with the opening up of the large woods on higher soils, some 4500 years BP. It is estimated that the country was only populated then by a few thousand people. During the next 2000 years, the extensive forest clearing continued, and up to approximately 60% of the upland area changed into grazed woodland. Over-exploitation during the Middle Ages resulted in extended heathlands, which covered up to 40% of the total area of upland sands by 1500 AD. Today woodlands cover only 1 promille of the surface area it covered 7000 years ago. Wetlands remained undisturbed for a long period, but they have become seriously affected since the late Middle Ages; the construction of dikes, embankments and drainage have caused the area of wetlands to shrink dramatically. Especially when in the 19th and 20th centuries, as a result of the introduction of steam and later diesel and electric engines, large-scale projects could be realised. This led to the disappearance of many freshwater lakes and the almost complete loss of the area of brackish water, the natural link between sea water and freshwater. Although the influence of Man upon the Dutch landscape commenced some 4500 years ago, it is only during the last 600 years that wetlands have been affected. Particularly the last 100 years have been crucial with respect to drainage and cultivation. By reconstructing ancient landscapes, an attempt has been made to describe the species composition and numerical abundance of waterbirds, starting 7000 years BP. Two species have become extinct in the territory, many others show changes in abundance. The start of agriculture has caused a major change in the food provisioning of many herbivorous waterbirds. Over the last 7000 years, a sevenfold increase of the number of herbivorous waterfowl is estimated. On the other hand the number of fish-eaters, benthos-eaters and planktivorous waterbirds has declined, their available habitat now having diminished by 45%, 36% and 55% respectively with respect to the Late Subatlantic period, c. 850–1350 AD.

Key words: carrying capacity, historical changes, landscape, cultivation

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As delta of the rivers Rhine, Meuse and Scheldt, The Netherlands has always been a territory where the link between water and land has been an important feature. Wetlands have presently changed compared to the situation of 7000 BP. In general, climatic changes after the last glaciation, which ended about 10,000 years ago, have caused the sea level to rise and have affected the shoreline and the course and water discharge of the large rivers, as well as the vegetation. Moreover, the human impact upon the landscape has greatly influenced the extent to which natural fluctuations of water tables occur.

This paper aims to describe the general change in landscape and habitat diversity that has occurred over the last 7000 years, in order to evaluate the present-day situation. Our approach was to combine information from palaeo-geographical, socio-economical and biological databases. The role of Man in changing the wetland communities will be emphasised, focusing upon the period from 850 AD until the present. The present situation will be evaluated with respect to habitat diversity, degree of natural processes and possible changes in carrying capacity for waterbirds.

Water birds (divers, grebes, cormorants, ducks, swans, geese and rails) were chosen as they constitute a well-documented element of the wetlands, and are often used to illustrate the importance of these areas. By their highly mobile life-style they are able to respond quickly to changes in habitat quality.

A better understanding of the situation in the past is important with respect to the goals for integrated water management (Ministry of Transport, Public Works & Water Management 1989), nature conservation and the possible line of development and/or the restoration of (parts of) the original situation (Ministry of Agriculture, Nature Management and Fisheries 1990). This knowledge is also useful in order to reconstruct possible ancient migration systems in waterbirds (Hale 1984, Piersma 1994).

METHODS

Palaeo-geographical maps

Basic information about landscape development was derived from the literature, supplemented by unpublished material for the IJsselmeer area. For this project, a new series of palaeo-geographical maps of The Netherlands has been compiled. The most important sources were the palaeo-geographic reconstructions of the prehistoric environment made by Zagwijn (1986, scale 1:1,500,000). This series of ten maps is based on data from published and sometimes unpublished material from the Geological Survey. Since then, as a result of the joint project 'Coastal Genesis' of the Geological Survey of The Netherlands and the Ministry of Transport, Public Works and Water Management, a large amount of new data has become available, especially for the coastal areas (van de Valk 1992, van der Spek 1994). In the intervening years, over twenty thousand cores, gathered since the early twenties on behalf of the Zuiderzee-project, have also been interpreted by Rijkswaterstaat Directorate Flevoland (and its successor Directorate IJsselmeergebied), which has resulted in revised landscape reconstructions for the IJsselmeer area. Together with the updated maps on coastal areas, they form the basis of a new series of six palaeo-geographical reconstructions for the IJsselmeer area, the province of Noord-Holland and a part of Zuid-Holland (Lenselink & Koopstra 1994, 1:250,000).

These three data sets together have been incorporated in the new series of six palaeo-geographical maps for the entire country. For this purpose Zagwijn's palaeo-geographical reconstructions, published at 1:1,500,000 , and the reconstructions of the prehistoric environment by Lenselink & Koopstra (1994), published at 1:250,000, were digitised in the Geographical Information System ARC/INFO and pragmatically linked (Table 1). No attempts have been made to make the polygons fit exactly, but the minor discrepancies apparent upon close examination of our images do not affect our areawise reconstructions. Both maps with their differences in scale and geographical imperfections were supposed to be best represented when still identifiable in the newly compiled series.

To tune the legend description of the different palaeo-geographical maps, generalisations have been made resulting in the following legend: open water, Pleistocene sand areas (originally afforested areas), tidal flats, salt marshes and mudflats, peat (divided into fen-peat and raised bogs), riverine deposits and dunes and beach barriers.

For the present situation the land use database of The Netherlands (LGN-2 database, Staring Centrum, 1994) has been used and modified into a map with a simplified legend. The land use map of the present situation, based at 1:50,000 was generalised to 1:250,000.

To show the degree of Man's influence on the landscape in more detail, for the IJsselmeer region during the last millenium a series of land use maps has been compiled. The maps focus on the degree in which landscape forming processes occur naturally.

Landscape units as habitat for waterbirds

For each map an estimate was made concerning water depth (0–2 m, 2–5 m and deeper) as well as salt content (fresh, brackish and saltwater), based on the course and extent of the river flow and the dimension and estimated depth of the ancient lagoons and lake systems. We used information from malaco-fauna remains in the soil layers and where no information was available, a crude estimate was made by judging the effluent of the streams and rivers as well as the distance and width of the connection (if present) to the sea. Sea water, important for seaducks and divers, was considered present in a stretch of c. 10 km outside the beach barrier in the

Early Atlantic. For ease of comparison, this boundary was kept constant during all later periods.

From data of land use in Louwe Kooijmans (1995), the following habitat types were added: afforested land, grassland and arable land. The latter, man-induced habitats were established primarily on the drier Pleistocene soils and riverine deposits according to Louwe Kooijmans (1995). The recently forwarded view by Vera (1997) that the primeval vegetation of the lowlands of western and central Europe was not a closed forest but a park-like landscape in which woodlots are interspersed with grasslands, does not affect our study on the effects on waterfowl. Neither pristine climax forests nor semi-open landscapes with tall grasses and herbs form an important habitat for this group. Only in historical times (after 1350 AD) became wetlands also drained and developed for agricultural purposes.

Based on soil characteristics, marshes were divided into sandy, peaty and clayey categories. To get a crude figure, we estimated that at least 5% of the area of dunes and beach barriers and 10% of the area of heathland consisted of this wet type (water at the surface in winter). Similarly, clay marshes were approximated as occupying 2% of the freshwater area (soil dependent) and 2% of the brackish waters.

In order to describe the animal abundance in the past, we used the partitioning in landscape types as a basic measure. Information about bird density was derived from recent inventories in comparable landscapes in The Netherlands (coastal area: Baptist & Wolf 1993, Camphuysen & Leopold 1994; estuarine and delta habitat: Meininger et al. 1984, 1985, 1994, Meininger & van Haperen 1988, Meire *et al.* 1989; Wadden Sea: Smit & Wolff 1981, Zegers & Kwint 1992, Meltofte *et al.* 1994; fresh-water wetlands (clayey and sandy soils: Lauwersmeer, Oostvaardersplassen, IJsselmeer, Markermeer, Flevoland): de Leeuw & van Eerden 1995, van Eerden 1985, van Eerden & bij de Vaate 1984, van Eerden & Zijlstra 1986, van Eerden *et al.* 1995, unpubl. data; riverine wetland habitat (Rhine, Waal, IJssel and Meuse): van den Bergh *et al.* 1979, (Meuse in Limburg): van Noorden 1992; fen-peats (NW Overijssel): SOVON, M. van Roomen pers. comm., MRE pers. obs.; raised bogs (Fochteloërveen, Bargerveen and adjacent areas in Niedersachsen): SOVON pers. comm., MRE pers. obs.). Additionally, literature data from neighbouring countries were used: coastal sites in Schleswig Holstein, Germany (Petersen 1987) and Denmark (Joensen 1974, Meltofte 1988, Laursen *et al.* 1997), raised bogs in Jutland (J. Gregersen, pers. comm.).

Two estimates of abundance of waterbirds were used to reconstruct a crude pattern of bird abundance in the past. Average winter (November–February) density was taken as to represent the significance of the Dutch territory as winter habitat. Also, the maximum numbers per habitat were used although they are difficult to extrapolate to the much larger areas of the past and may easily lead to over-estimation. Peak numbers can occur if other factors are not limiting bird numbers, such as capacity of the breeding areas or, more likely, the wintering areas. As agriculture played a far less prominent role in the past, it is likely that the winter food bottle-neck will have been set by the presence of natural foods (see discussion in van Eerden *et al.* 1996). Therefore, the use of natural habitats by (merely herbivorous) waterbirds at maximum density during the peak of exploitation (mainly in autumn) is only possible if elsewhere on the flyway enough winter capacity would exist. We assume here that this was the case further to the west and southwest to The Netherlands.

The GIS maps were used to calculate surface areas of the different landscapes. Subsequently, bird numbers

Table 1. Compilation of a new series of palaeo-geographical maps for The Netherlands derived from different sources (see Fig. 1). LGN = Landgebruik Nederland, database of land use in The Netherlands, Staring Centrum.

Source	Zagwijn (1986) (C^{14} years ago)	Lenselink & Koopstra (1994)	LGN-2 (1994)	This paper
2:	7000	7000 BP		A Early Atlantic, 7000 BP
3:	5300	5500 BP		B Late Atlantic, 5500 BP
5:	3700	3700 BP		C Middle Subboreal, 3700 BP
7:	2300–2100	2100 BP		D Early Subatlantic, 2100 BP
9:	500–700	850 AD		E Middle Subatlantic, 850 AD
10:	1000–1200	1350 AD		F Late Subatlantic, 1350 AD
	Recent	1993 AD	1993 AD	G Recent, 1993 AD

per landscape unit were calculated. The sum of the different habitat types gave an estimate for the average total population present.

In order to assign bird densities in the ancient landscape types as accurately as possible, we used a maximum estimate (100% of the area available to the birds) and a lower estimate (only a fraction of the habitat available). For example, fen-peats are partly afforested or covered with rough shrubs not suitable for waterbirds. The fractions applied to arrive at the lower estimate were: fen-peat (30%), raised bog (15%), river deposits (30%), salt marshes (60%), tidal flats (80%), grassland and arable land during the past (60%), idem recent (20%). The fractions differ according to estimated percentage of water on surface and the proportion of vegetation cover suitable for bird use. The latter 'best educated guesses' are based on today's knowledge of larger-scale habitats still present in Europe.

RESULTS

Palaeo-geographical reconstruction

The change in landscape and physio-geographical characteristics of The Netherlands has been depicted in six maps (Fig. 1). The different periods are briefly described below.

1. An impressive rise of sea level (10,000–7000 BP)
About ten thousand years ago, at the transition of the last Pleistocene glaciation to the Holocene period, the sea level was at least 45 m lower than today (Jelgersma 1980). The Dutch landscape in this period can be described as an undulating sandy landscape. By this time the climatic changes e.g. the temperature rise, took place very quickly, and within 2000 years enough ice had melted to let the sea level rise to about 25 m below Dutch Ordnance Level (NAP).The southern part of the North Sea area became flooded and the sea penetrated valleys in the western part and, at a smaller scale, in the northern part of The Netherlands. Water tables started to rise and the succession of the prevailing vegetation of pine forest into deciduous forests may have depressed evapo-transpiration (Zagwijn 1986, Pons 1992). The milder climate greatly stimulated the vegetation growth. Around 8000 BP peat developed in small brooklets and in the area between the salt marshes and the higher Pleistocene areas.

In the following millennium the sea level rose again by about 10 m, so that around 7000 BP the coastline was situated about 10 km outside the present Dutch coast line.

2. An extensive lagoon complex (7000 BP – 5500 BP)
Around 7000 years ago, the western part of The Netherlands was marked by an extensive lagoon as well as tidal flats and salt marshes that covered the oldest peatlands. This lagoon in 'Northern Holland' and its hinterland 'the IJsselmeer area' was situated in an abandoned Pleistocene valley of the river Rhine. Small rivers drained the fringing Pleistocene sand area over gently sloping surfaces to the west. Sediment supply was largely lacking and fresh water supply was limited to the discharge of superfluous rainfall. In a calm environment, sedimentation of brackish lagoon clays took place (with typical brackish water fauna). Outside the lagoon, due to the deterioration of natural drainage conditions as a consequence of sea level rise, peat developed at the lowest parts (up to 9 meter below NAP) of this afforested Pleistocene cover-sand area.

From 7000 to 5500 BP, the sea level rose further to 6 to 4 m below NAP. This caused an expansion of the lagoon to the east where it reached its greatest size about 5000 years ago. Marshes and mudflats developed and constituted an important part of the actual coastal area. Large forests in the Pleistocene areas were flooded and reduced the total surface covered with forest from 70% to a mere 50%. Fens spread and shifted progressively inland and upward both in the IJsselmeer area and the area around the Frisian Middelzee. At the end of this period the peatlands covered more than 10% of the total surface of The Netherlands.

The riverine area about 7000 years ago formed only a few percent of the total surface. Its extent was determined mainly by the discharge of the rivers Rhine and Meuse. At this period there was no significant sedimentation in the floodplain. With the increase of poor drainage conditions and the sea level rise, this floodplain area extended. Considerable clay deposits formed and peat growth started locally.

There is neither evidence nor suspicion of human influence on landscape development at that time. Only a few thousand people lived here, especially in the Pleistocene afforested areas, and they were hunters, fishermen and gatherers making use of the natural resources (van Es *et al.* 1988, Louwe Kooymans 1995). All habitats can still be considered natural.

3. Extended peatland formation (5500 BP – 3700 BP)
With the slowing down of the sea level rise to less than 2 mm per year, coastal barriers developed more strongly and closed off the coast almost completely. Due to strong protection by these barriers the former brackish lagoon became more fresh, which created optimal conditions for further peat growth. The 'IJsselmeer area'

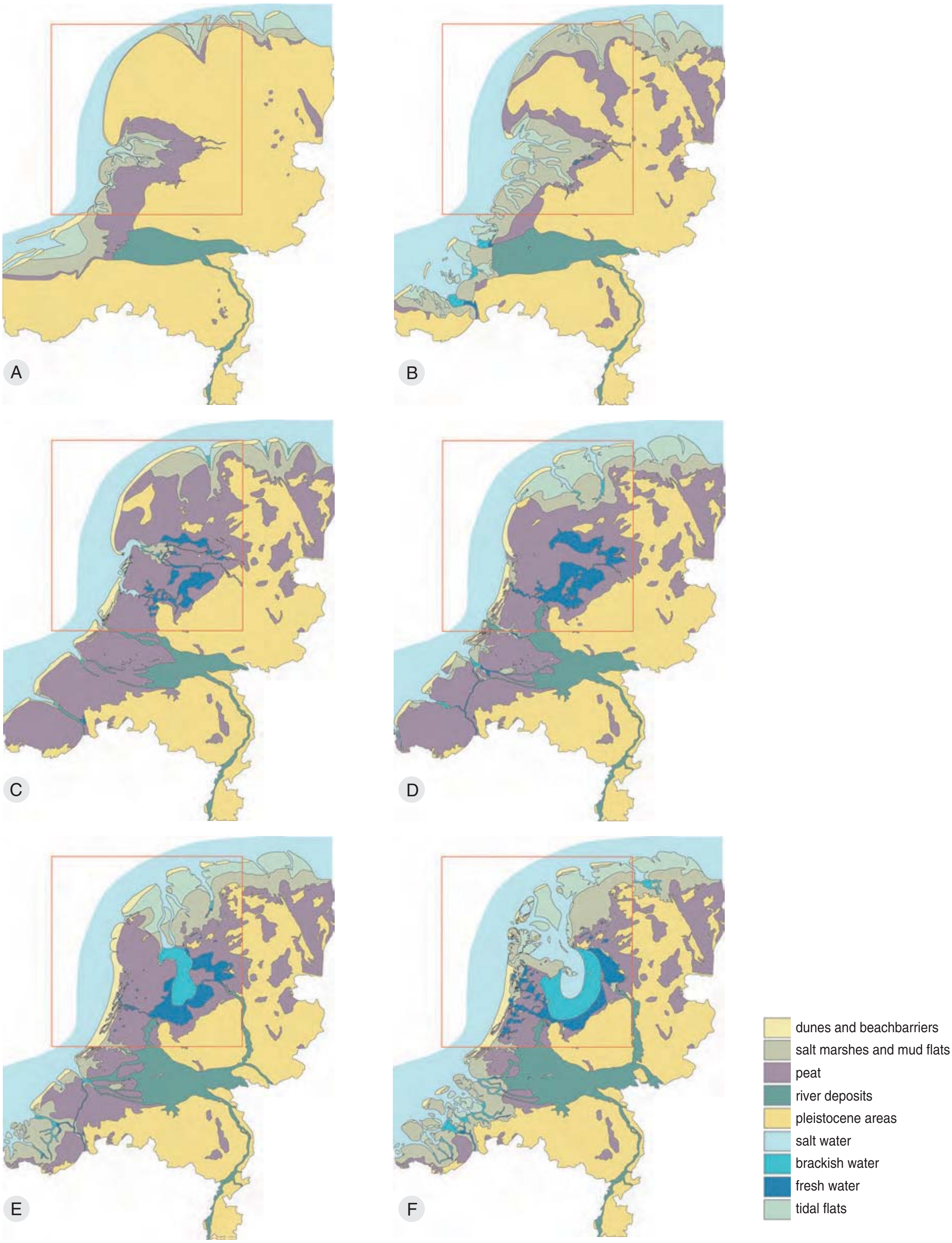

Figure 1. Compiled palaeo-geographical maps of The Netherlands for 6 periods: (A) the Early Atlantic (7000 BP), (B) the Late Atlantic (5500 BP), (C) the Mid Subboreal (3700 BP), (D) the Early Subatlantic (2100 BP), (E) the Early Middle Ages (Mid Subatlantic, 850 AD), (F) the Late Middle Ages (Late Subatlantic, 1350 AD).

and nearly the entire coastal plain, including the tidally influenced lower floodplain of the rivers Scheldt, Meuse and Rhine, were transformed in less than 2000 years into extensive peatlands which occupied more than one third of the total surface. Outside the areas under direct influence of the rivers and brooklets, reed marshes (or fens) may have turned into mesotrophic fens and carrs and developed into bogs and raised bog complexes. A mosaic of fens and raised bogs characterised the coastal zone (Pons 1992).

Small streams such as the river IJssel were not able to maintain their individual outlets to the sea. The courses in the coastal areas were closed off and the river IJssel started to discharge into a lake; one of the early stages of the lake Flevo.

Tidal flats and salt marshes only continued in the northern part of the country and at the outlets of the main rivers. Because of the formation of coastal barriers, the total area influenced by sea or brackish water was reduced from about 25% in 5500 BP to less than 6% in 3700 BP.

In this period, people still preferred the higher Pleistocene areas to live. The introduction of farming resulted in the opening up of the forest for settlements and arable land (shifting cultivation); cattle grazing must have taken place, but there are ample signs that it affected the natural vegetation composition. In general, the environmental impact was very limited (Louwe Kooymans 1995) and natural conditions prevailed.

4. Enlargement of open water area; first evidence of environmental impact by Man (3700 BP – 2100 BP)

The virtual closure of the coastline of northern Holland was a turning point in the history of the 'IJsselmeer area'. The freshwater discharge to the west had come to an end. In the former lagoon a further enlargement of the lakes took place at the cost of the surrounding peatlands. Besides, the loss of peatland was stimulated by wind erosion. So-called detritus-gyttja was deposited, a mixture of fine peat particles and fine sand. In this era, a small peat rivulet most probably started to drain the IJsselmeer area to the north.

Especially in the northern part of The Netherlands, saline to brackish conditions prevailed. The influence of the continual sea level rise is visible in the transformation of part of the former peatland area into mudflats and salt marshes. The total area covered by tidal flats, mudflats and salt marshes nearly doubled to 10%.

In the riverine area, the sedimentation, due to the rise of the sea level, resulted in an enlargement of the river floodplain. Locally clayey deposits were deposited in previous peatland areas.

Although the palaeo-geographical maps of 3700 BP and 2100 BP do not show many differences, an interesting development had started. From 2500 BP onwards, there is evidence in pollen diagrams for the opening up of the afforested area on the Pleistocene surface by Man. Louwe Kooymans (1995) states that the system of shifting cultivation with plough agriculture and integrated mixed farming resulted in soil degradation and woodlands changing into heathlands (Fig. 2).

The increasing human population also began to exploit the riverine areas. The favourable conditions in this area made a permanent occupation possible. From this time on, cattle grazing greatly affected the character of the landscape by setting back the vegetation succession (see Fig. 2). The dense forests transformed into a more open landscape, a mixture of woodland and grassland. At that time a few thousand people occupied the country and the environmental impact of Man increased. People not only settled in the afforested areas, but eventually also on the salt marshes in the northern part of The Netherlands (van Gijn & Waterbolk 1984) and even the margins of peatland were colonised (van Es *et al.* 1988). However, half of The Netherlands, coinciding with the peatland area in the west and the IJsselmeer area, was still not suitable for settlement and was therefore not affected by Man.

5. Formation of a new lagoon; some recovery of woodlands (2100 BP – 850 AD)

Although the sea level rise had slowed down, sea intrusions increased during the first 800 years of our era. It transformed peatlands into tidal flats and salt marshes, especially in the south-western part of The Netherlands. In the IJsselmeer area the peat cover vanished because of erosion. The initially small outlet in the north had become broader and acted as an inlet for marine clays. Also salt seawater penetrated in the area at a limited scale, creating a brackish environment.

Human occupation was still largely restricted to the higher Pleistocene areas, the riverine area and the salt marshes in the north. The decrease of the population after the Roman period resulted in a partial recovery of afforested areas (Louwe Kooijmans 1995).

6. Formation of an inland sea; the start of water management (850 AD – 1350 AD)

With the development of tidal gullies in the IJsselmeer area, the tidal influence in the new lagoon increased and started to drain the surrounding peatlands, which made these peatlands suitable for cultivation. So far these peatland areas could still be considered completely natural.

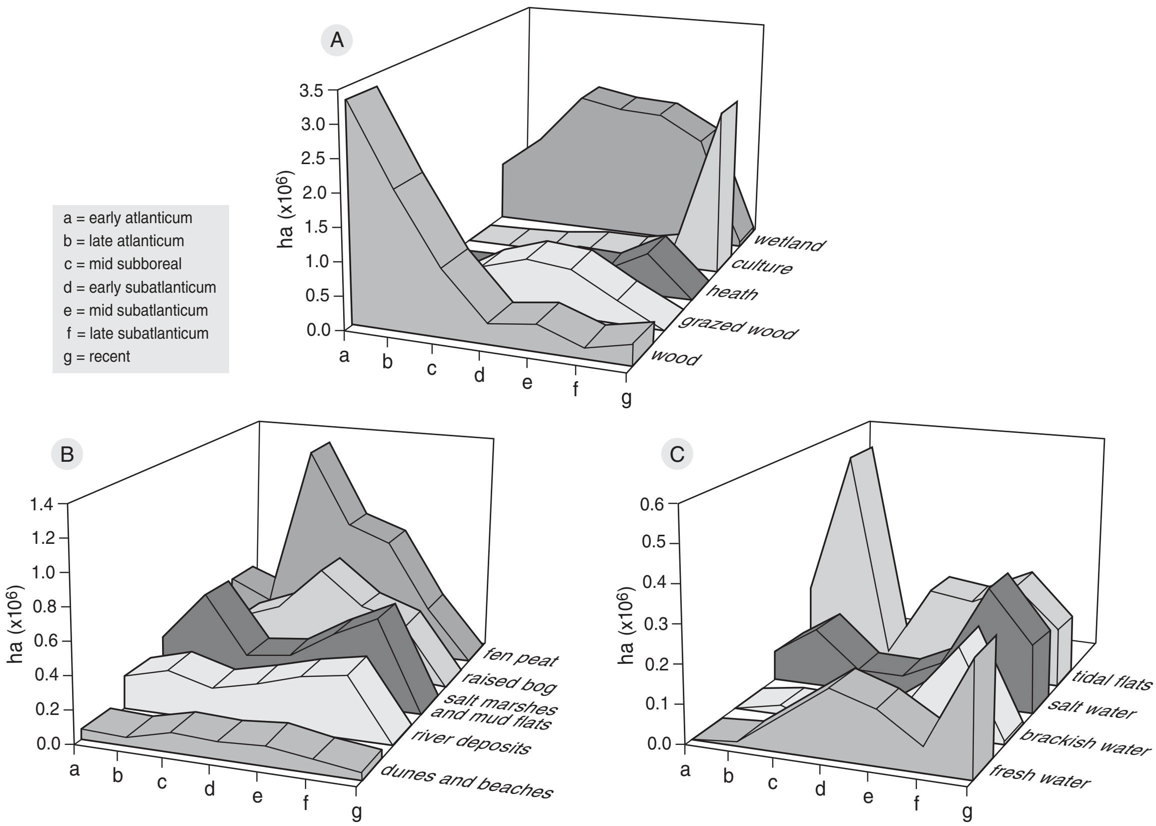

Figure 2. Changes in surface area of main habitat types in The Netherlands for seven periods, including the present situation (see Fig. 1). (A) Major terrestrial landscapes, (B) wetland ecotopes , (C) water.

From the eighth century onwards, exploitation of peatland took place, which resulted in subsidence and oxidation leading to a drop in the land surface. The human occupation of the peatland areas between Wieringen, West-Friesland and Gaasterland, and Northern Holland made the entire IJsselmeer area more vulnerable to sea influences. Small gullies widened and caused more and more erosion. Large areas of peatland transformed into salt marshes, tidal flats and shallow open salt to brackish waters. Large-scale freshwater was restricted to the south-eastern part of the IJsselmeer area. Similar processes took place in the southwestern part of The Netherlands with the transformation of extensive peatland areas into salt marshes. The total peatland area was reduced from 24% to 14%.

In the late Middle Ages Man started the battle against the water and tried to protect himself by dikes and dams. In the 12th and 13th century Man constructed dikes not only in the south-western Delta area, the northern salt marshes and along the Zuiderzee, but also in the riverine area dikes to prevent flooding by river water. This marked the end of free-flowing rivers. Although a large part of The Netherlands was protected by dikes, the situation was by no means under control. Dike breaches and floodings occurred very often and caused a set-back in the situation.

Figure 2 shows the estimated surface area of main landscape types, in a fixed geographical range of the territory now known as The Netherlands. From a diverse, multiple habitat environment it has become a man-made, agriculture-based landscape. Eye-catching for instance is the loss of mesotrophic fen-peats due to land reclamation and the reduction in surface area of raised bogs due to drainage and cutting.

Clearly the continual speeding up of the actions of Man has greatly altered the extent and composition of Dutch wetlands. Considering the water areas, a tremendous narrowing down of ecologically important transitional zones between water and land has taken place. Around 850 AD some 17% belonged to this category, in 1350 it rose to 33% because of the cultivation of natural areas, declining thereafter to 11% in 1650 and a mere 2% in 1993. Especially the loss of brackish intertidal water areas is obvious.

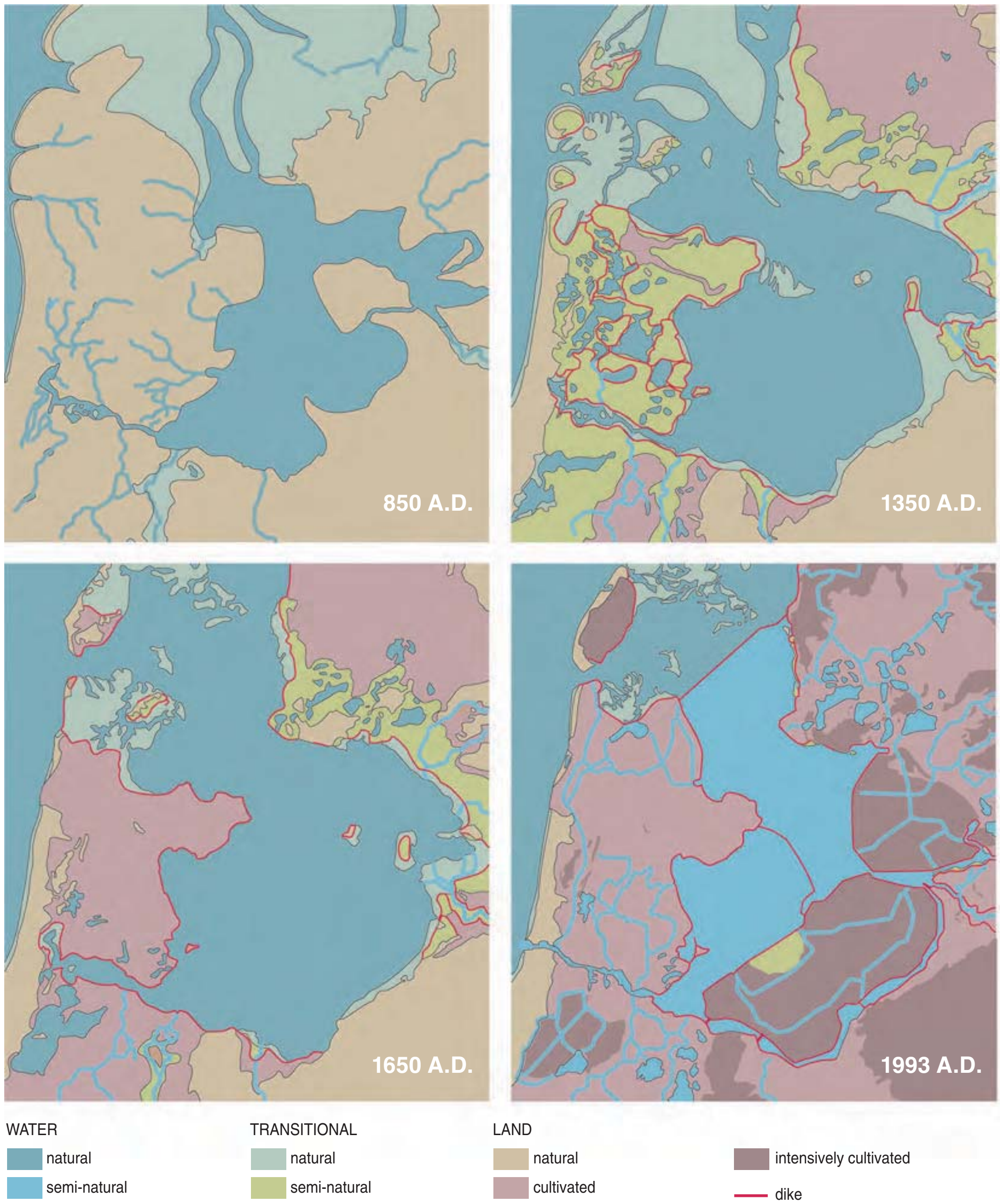

Figure 3. Human influence on the landscape in the IJsselmeer region by means of the construction of dikes, drainage of lakes and lowering of groundwater tables, for the periods 850 AD, 1350 AD, 1650 AD and at present (1993 AD).

Land use and historical changes in landscape

The period between 1350 and 1600 is characterised by changes caused by the permanent struggle of Man against the water (van de Ven 1993). The influence of the sea in the IJsselmeer area, the Dollard and in the Delta area caused further loss of land. In the riverine area the river courses were affected by the increasing sea influence. Beside protecting himself by raising the dikes, Man also found ways to reclaim land from the sea.

A new tidal gully between Bergen and Texel together with new reclamations resulted in further loss of peatland and increasing brackish to saline conditions. In 1340 for the first time the term *Sudersee* is used, but it took until 1600 AD for the eastern part of the former

Zuiderzee to become saline by a reduced discharge of the river IJssel. By this time the Zuiderzee reached its greatest size. Further deepening of tidal gullies in the Zuiderzee occurred and locally considerable layers of sand were deposited. Deeper inside the basin, clayey sediments with marine shells were deposited.

The human population rose from 750,000 in 1250 to 1,500,000 in 1600. This resulted in the expansion of agriculture, the creation of meadows and a further decline in the area of peatlands. Peat was dredged and dried for fuel on a large scale.

From the 17th century onwards, windmills and later on steam engines were used to drain lakes in order to reclaim new land. Figure 3 shows the extent of construction of dikes and polder making from lakes over the last centuries. As time proceeded, ever deeper and larger lakes could be dealt with (Schultz 1992). The damming up of estuaries also caused large changes in the wetland areas. Table 2 shows the embankments and closing off of estuaries which were realised in the 20th century. Also the lowering of the groundwater table caused great changes in the landscape as ever more terrestrial habitat was turned into agricultural land.

Not only did the total surface area of natural habitats decline, also the intensification of land use meant an enormous narrowing down of the variation in landscapes (Fig. 4). It is important to note that, with respect to wetland degradation, the greater part of this development has taken place within a period of no longer than 600 years. With respect to the impact on the vegetation, especially grassland communities were favoured (see van Eerden *et al.* 1996). The last 100 years were conclusive with respect to the capacity of Man to govern nature's forces.

A reconstruction of abundance of wetland birds

PREHISTORIC DATA

Data of avian finds in prehistoric human settlements in The Netherlands provide information about species composition in different eras. The first finds are available from the period 4000–2000 BC. Clason & Prummel (1979) present data about 33 species of waterbirds

Table 2. Large land reclamations and man-made changes of hydrological regime in waterbodies during the 20th century in The Netherlands. Enclosed water indicated separately.

Area	Year	Total area (ha)	Remaining water (ha)	Habitat
Carel Coenraadpolder	1927	650		Salt marsh
Wieringermeer[1]	1930	2000		Estuary
Zuiderzee	1932	365,000	365,000	Estuary
Linthorst Homanpolder	1941	1300		Salt marsh
Noordoostpolder[1]	1942	48,000		Lake
Emmapolder	1945	800		Salt marsh
Quarlespolder	1948	480	50	Salt marsh
Brielse Maas	1949	290		Salt marsh
Braakmanpolder	1952	1550	250	Salt marsh
Dijkwater	1954	170	25	Lake
Oost Flevoland[1]	1957	54,000		Lake
Veerse Meer	1961	4170	2125	Sea arm
Zuidersloe	1963	170		Sea arm
Plaat van Scheelhoek	1965	225		Salt marsh
Zuiderdieppolder	1966	180		Sea arm
Zuid Flevoland[1]	1968	43,000	1000	Lake
Lauwerszee	1969	9100	2000	Estuary
Haringvliet	1971	9850	7700	Estuary
Grevelingen	1971	1390	10,800	Sea arm
Markiezaat	1983	2130	1000	Salt marsh
Volkerak Zoommeer	1987	8250	6250	Sea arm
Oosterschelde[2]	1987	36,900	25,200	Sea arm

[1] Polders in the former Zuiderzee area.
[2] Enclosed by storm-surge barrier with reduced tides.

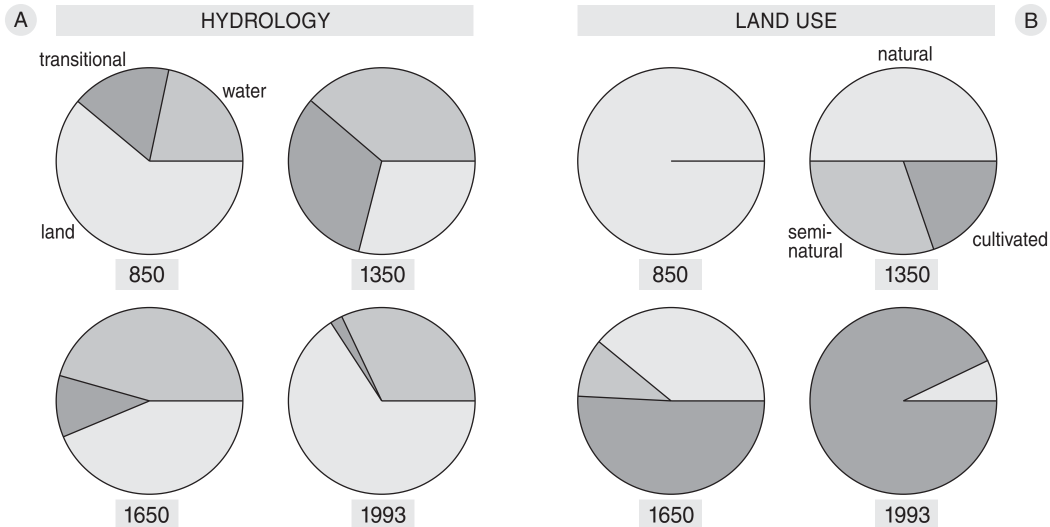

Figure 4. Development of habitat composition in historical time (A) in terms of major landscape types, and (B) scaled by degree of 'naturalness' in the same area and for the same time series as depicted in Figure 3.

identified in human settlements. Except for the seaducks *Melanitta nigra* and *M. fusca*, the Gadwall *Anas strepera*, the Eurasian Coot *Fulica atra* and the Purple Heron *Ardea purpurea* which are lacking from this list, virtually all species described are still present in considerable numbers today. The only two species which were present in prehistoric times, but became extinct later on, are, according to the finds, a pelican (probably Dalmatian Pelican *Pelecanus crispus*) and the Great Egret *Casmerodius albus*, both species of large-scale fresh and brackish water marshes. Also Squacco Heron *Ardeola ralloides* and possibly Little Egret *Egretta garzetta* have become extinct as breeding birds (Vera 1988).

On the basis of the general description of changes in landscape caused by sea level rise and human impact we have attempted to explore the possible effects of these prehistoric habitat shifts on the long-term presence and composition of the waterbird assembly. As an example, Figure 5 depicts the estimated annual peak and average winter numbers (October–March) for 16 selected species belonging to different ecological groups, showing the most important trends.

In the group of herbivores Brent Goose *Branta bernicla*, Garganey, Common Teal *Anas crecca* and Eurasian Wigeon *Anas penelope* have always been abundant. Especially the peak numbers during migration are estimated to have been considerably higher than nowadays, e.g. about two to three times around 1350 (Fig. 5). These species feed on salt marshes, seagrasses *Zostera* spp. in tidal bays and pioneer vegetations under freshwater conditions. In some species like Eurasian Wigeon, as well as in Greylag Goose *Anser anser* and White-fronted Goose *Anser albifrons*, numbers during mid-winter have strongly increased in recent times, coinciding with the extension of grassland, which forms their major food source nowadays. Other species, more dependent upon natural food, have declined during mid-winter compared to the situation around 1350.

Also benthos-feeding ducks like Eiders *Somateria mollissima*, a marine species, had fluctuating numbers lately peaking during the Late Subatlantic period around 1350. Also Common Scoter *Melanitta nigra*, Velvet Scoter *M. fusca* and Common Goldeneye *Bucephala clangula* were abundant earlier on with the highest numbers in the period around 1350. A gradual increase over time is apparent in Scaup *Aythya marila* and Tufted Duck *A. fuligula* with the highest numbers in recent years. This trend is based on the great extension of shallow freshwater habitat, which for these species is important habitat as well. Unlike the herbivores, the benthos-feeders do not show large differences between average winter numbers and peak numbers during migration. The trends follow the same pattern for most species.

The third group, that of the fish-eaters generally shows the highest numbers from 850–1350 while in recent times a decline is apparent due to the lower capacity of freshwater as wintering area. This decline is less marked or absent in Great Crested Grebe *Podiceps cristatus* and Goosander *Mergus merganser*. In Red-breasted Merganser *M. serrator* the pattern is comparable to that for the *Melanitta* seaducks, being related to

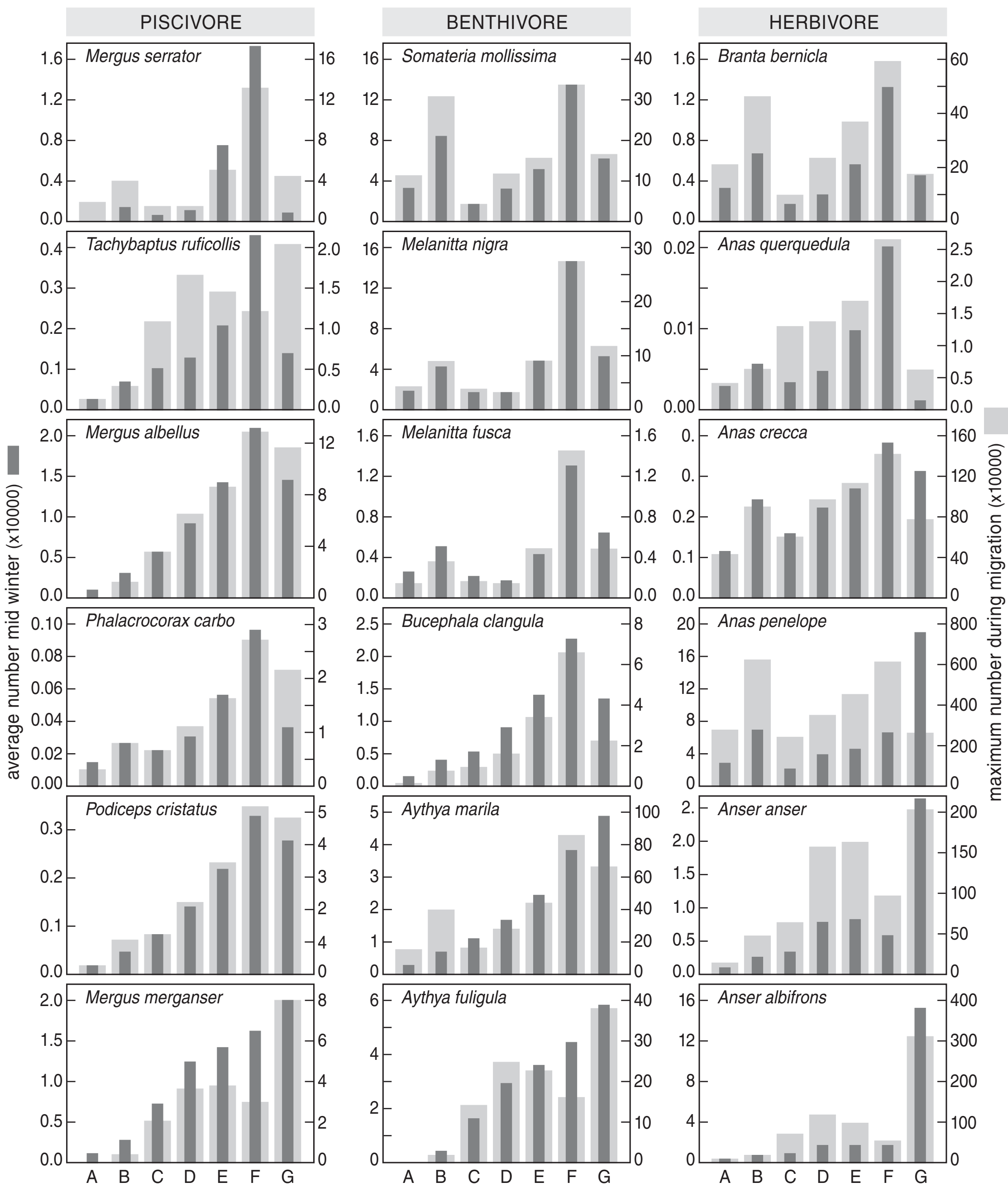

Figure 5. Estimated average population of 16 bird species in The Netherlands, representing three main ecological groups. For seven periods, including the present situation, see Fig. 2. Two estimates have been calculated being the peak number during migration and the average mid-winter number which is less, especially in herbivorous waterbirds. Calculated numbers are considered indicative as peak numbers can only occur if other factors are not limiting.

the presence of brackish water. High numbers of these species occurred in the period of the Late Subatlantic around 1350.

We estimate that, based on 36 species, the total number of waterbirds present in winter gradually increased from the Early Atlantic (7000 years BP) until the Late Subatlantic (1350 AD) (Fig. 6). In the latter period several habitat types reached their greatest range: freshwater marshes (390,000 ha), salt marshes (560,000 ha), mudflats (262,000 ha) and brackish

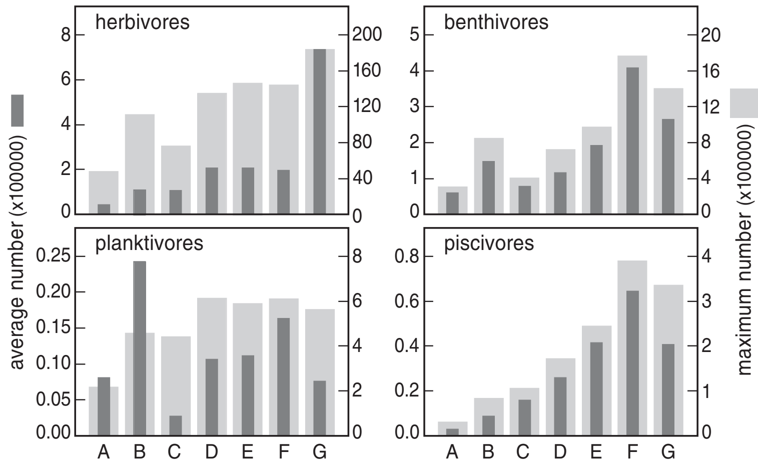

Figure 6. Estimated composition of the avian fauna for seven periods (including present, G) and four different groups of waterbirds. Calculated total for The Netherlands has been based on peak and average winter numbers cumulative over all habitats.

shallow water (111,000 ha), while still considerable areas of fen-peats (332,000 ha) and raised bogs (357,000 ha) existed. All categories of waterbirds peaked in this period, still little influenced by Man (Fig. 6). Thereafter, the extension of grasslands and arable land was enormous, mainly at the cost of peatland, heather and salt marshes. This led to an explosive, almost seven-fold increase in the number of wintering herbivorous waterbirds compared to 850–1350 AD, despite the loss of salt marshes and riverine marshes which form an important habitat for this group. The capacity for migratory herbivorous waterbirds did not show such a strong increase in recent times (Fig. 6). Concerning the waters, the category shallow open freshwater (<10 m deep, 294,000 ha) which exists nowadays has never been precedented. However, calculated numbers of wintering benthos-eaters (36% reduction) and fish-eaters (45%) have sharply declined, due to the flagrant decrease in brackish and marine shallow waters. Also the planktivorous waterbirds like Northern Shoveler *Anas clypeata* are estimated to have declined with some 55% since 1350 AD.

Although the total number of wintering waterbirds is estimated to be higher today than at any time before in the period of study (until 7000 years BP), 17 species of the non-herbivorous waterbirds have strongly declined during the late Middle Ages due to the land use activities of Man, whilst 15 herbivorous species have increased.

Historical data

Historical data provide especially detailed information about colonial birds, mainly fish-eaters, and the following is illustrative for the role of Man in exploiting and repressing colonially breeding waterbirds. From sales accounts (1359–1361) it is known that colonial birds such as Grey Herons *Ardea cinerea*, Eurasian Spoonbills *Platalea leucorodia* and Black-crowned Night Herons *Nycticorax nycticorax* and "White Herons and other white birds" (van Pelt Lechner 1919 in Brouwer 1954) lived in the Goudsche Bosch, near Gouda. Other sources tell that in 1357 no less than 564 herons and 2000 Black-crowned Night Herons were sold. From the 16th century more historical data are known. Regulations, so-called "Plakkaten", tried to regulate the hunting and catching of birds of importance such as "Perdrysen (*Perdix*), Fesanen (*Phasianus*), Putoren (*Botaurus*), Moerhoenderen (*Tetrao tetrix*), Cranen (*Grus*), Trap-ganzen (*Otis*), Swanen (*Cygnus*), Reijgeren (*Ardea*), Quacken (*Nycticorax*), Schollevaers (*Phalacrocorax*), Lepelaers (*Platalea*) en Berch Eenden (*Tadorna*)", most of which are nowadays important wetland species. Regulations to protect the rights of landowners were also necessary as populations of some species like Swans were known to become exterminated rather easily: "*binnen korten tijdt ... merckelick vergaen ende gedepeupleert is*". In former times The Netherlands harboured internationally well-known important breeding places for birds such as "Het Zevenhuizensche bosch, Schollevaerseiland, Eyerland". All of them, being hot-spots for the species at the time, were successively destroyed by cultivation measures of the landscape or peat-digging. The habitat changed in such a way that it was no longer suitable for colonial birds such Great Cormorants *Phalacrocorax carbo*, Eurasian Spoonbills and herons. 'Het Zevenhuizensche Bosch' (near Gouda, about 26 ha) harboured a heronry as early as the 14th century. Around the end of the 17th century the area had been almost completely cultivated "*weggeraeckt en de grond sedert genoegzaem geheel en al weggeveent*". About the fate of the remainder of the colonially breeding birds it is reported that large quantities of young herons, Black-crowned Night Herons, Eurasian Spoonbills and (most) Great Cormorants were shaken out of their breeding trees and were transported by barge to the markets in the cities of Holland : "*seer groote quantiteyt van reygers, quacken, lepelaers... ende meest van alle noch schollevaers ... die dan ... uyt haere nesten van de bomen geschudt, ende nedervallende worden alsoo gevangen ende met geheele schuyten seffens in alle steden van Hollandt vervoert ende verkoght....*". In 1668 400–500 young were collected twice a week in this way; some 10 years before, this had been about 800. Around 1760 the colonies of these bird species were found once more at 'Schollevaerseiland' near Nieuwerkerk (C. Nozeman), where they remained until the second part of the 19th century. Again, numbers were reported as "countless": "*De hoeveelheid van op den naeckten grond aengelegde en bezette nesten, van Scholvers en Reigeren dooreen, was onnoemlyk, en zelfs niet by gissing te begrooten... De Lepelaers, welken ik hier mede broedende vond, maekten verre weg den kleinsten hoop uyt*". This colony was also heavily exploited and was already greatly diminished in 1864. The birds had moved to lake Horstermeer near Vreeland along the river Vecht. In 1851 there were about 1000 pairs of Great Cormorants, 700 pairs of Grey and Purple Herons and 1000 pairs of Eurasian Spoonbills. Egg-culling remained important with maximum numbers collected per week being 800 heron, 1100 Great Cormorant and 1600 Eurasian Spoonbill eggs (Brouwer 1954). In 1865 this breeding colony was almost completely exterminated and the lake was subsequently reclaimed in 1883 (620 ha).

We may conclude that with respect to the species composition, the avian fauna of wetlands in The Netherlands has not changed dramatically in the last 7000 years. However, the exploitation of birds used to be common practice and this had a reinforcing effect upon habitat loss from the 17th century on, especially on the disappearance of many breeding colonies of fish-eating birds.

DISCUSSION

From a natural towards a man-made delta

The enormous impact of Man on the continually changing outlook of The Netherlands has been emphasised. Especially the short period of time during which these changes occurred was unequalled in the past. Many land reclamation projects were realised, most of them not or only marginally documented with respect to their biological significance.

As an example we will briefly discuss the Zuiderzee project in this context. The construction of the Barrier Dam (1932) heralded a new period of dominance of freshwater lakes. Within 5 years the brackish Zuiderzee changed into the largest freshwater lake in western Europe with a surface area of 3650 km^2 (lake IJsselmeer). Beside a reduced risk of floods, the length of the coastline had been shortened to improve the water control in and outside the IJsselmeer area. Later on, reclamation of parts of the lake bottom resulted in a major decline of the lake area in favour of a considerable enlargement of the agricultural area. Successively, the Noordoostpolder (1942), Oostelijk Flevoland (1957) and Zuidelijk Flevoland (1968) were constructed; a total of 1650 km^2. Further compartmentalisation of the lake was caused by the dike Enkhuizen–Lelystad (1976).

What was the effect on the natural values in the area? The sudden transition of an open, gradient-rich water system into a closed, more uniform water body brought about the greatest changes for the plankton, benthos, fish and mammal communities (De Beaufort 1954). For example, before the closure 52 species of fish were known to inhabit the area, some of which were anadromous migrants (Havinga 1954). In the IJsselmeer the species composition was greatly reduced as 26 species became extinct (Fig. 7). The extinction of local races of Anchovy *Engraulis encrasicholus* and Herring *Clupea harengus* was not only a dramatic biological event but also negatively affected the position of the local fishermen. Also mammals such as Harbour Porpoises *Phocoena phocoena* and Common Seals *Phoca vitulina* disappeared completely. Although the bird community changed in numbers, no major loss of species occurred. On the other hand, many of the remaining freshwater fish and benthic species could expand enormously. For instance, newly established populations of Zebra Mussels *Dreissena polymorpha* since 1934 have expanded greatly in the lake (van Benthem Jutting 1954), as did the salmonid Smelt *Osmerus eperlanus* (Havinga 1954). The latter managed to increase spectacularly in biomass and to shorten its life cycle; from an anadromous spawner in its third season, Smelt became mature within one year as non-migrants in the stagnant freshwater situation. Both *Dreissena* and *Osmerus* play a very important role e.g. as food organisms in the system nowadays (see van Eerden 1998). The human fisheries shifted target and concentrate on the freshwater species Eel *Anguilla anguilla*, Perch *Perca fluviatilis* and Pikeperch *Stizostedion lucioperca* (Buijse 1992, Buijse *et al.* 1993, Dekker 1997).

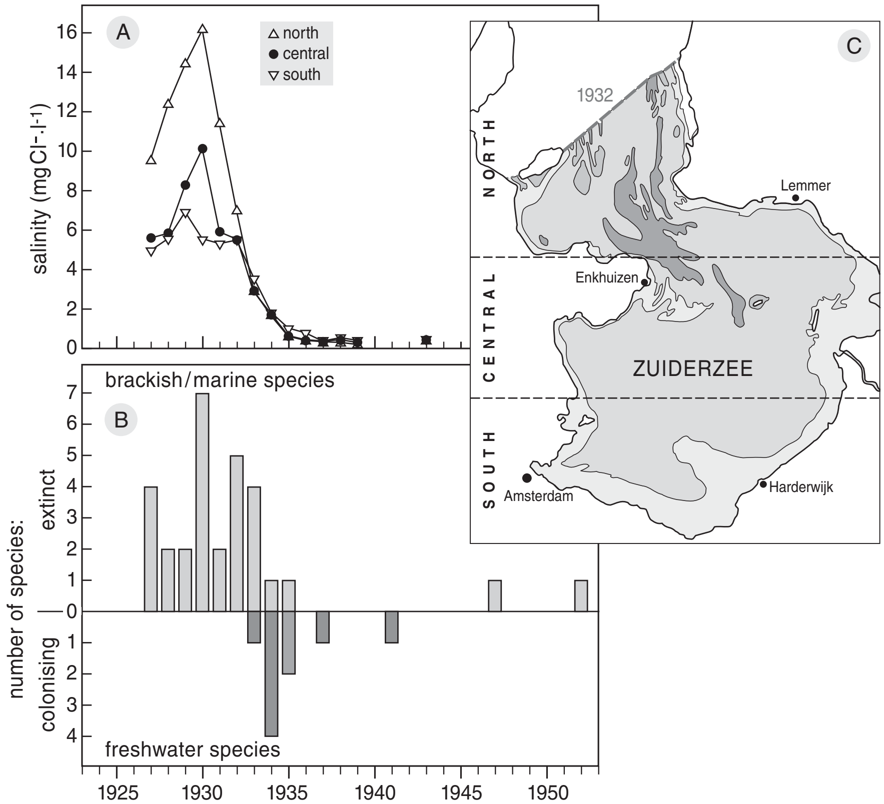

Figure 7. The effect of closing off the Zuiderzee on salt content at three sites in the area (notice gradient!) and the recordings of either extinction or major expansion of fish species. Data compiled after Havinga (1954). Contrasting to birds, system-bound species like fish incurred severe losses at the level of species occurrence.

We consider the example of the transformation of the Zuiderzee into the freshwater lake IJsselmeer and the subsequent large-scale land reclamation illustrative for the recent changes that have occurred in many Dutch water systems. It shows how specialist organisms which depend tightly on a particular type of landscape react very sharply. This will also have been the case in natural changes as, for example, from fresh to marine conditions and from oligotrophic fen-peats to estuarine clay marshes as happened many times in prehistory. Many of the effects on species of invertebrates and fishes that were involved remain unknown and undoubtedly this is also true for many species of mammals, amphibians, insects, higher plants, mosses and lichens. Birds, which are less strictly confined to one system (they operate on a mega-scale because they can fly), can respond with a change in numbers over a much vaster area. Although this change can be dramatic, a complete extinction is rare. If a suitable habitat reappears, however, birds may colonise these areas again. This happened with the nature development project in the Oostvaardersplassen where in 1978 Great Egrets recolonised The Netherlands as a breeding bird after a period of absence of c. 600 years (Poorter 1980, see also Voslamber *et al.* 2010).

During this century also the within-habitat degradation has levied its toll. The examples of water pollution (eutrophication, contamination), disturbance by fishing, hunting and recreation as well as the deteriorating effects of habitat shrinkage are well-described, and a general policy to counteract these effects has been approved (Ministry of Transport, Public Works and Water Management 1989, Ministry of Agriculture, Nature Management and Fisheries 1990). Less known are the effects of the levelling down of oscillation of natural processes which cause a set-back of succession (e.g. erosion, sedimentation, water level fluctuation and fire). Proposals to eliminate or reduce these effects are now being discussed (Rhine–Meuse delta: Smit *et al.* 1994, large lakes in IJsselmeer area: Iedema 1996, larger freshwater marshes (Oostvaardersplassen: van Eerden *et al.* 1995).

Long-term effects upon carrying capacity for wetland birds

Because they can fly, birds are able to reach isolated patches of wetland. Compared to mammals and some plant and insect groups, birds respond faster to changes in habitat availability. Due to this highly versatile behaviour, only two species of waterbirds have become (locally) extinct in the last 7000 years according to archaeological finds: (Dalmatian) Pelican, and/or historical data: Great Egret (14th century, Vera 1988) and Squacco Heron (c. 1860, Vera 1988). Many other populations of herons have become extremely scarce such as Black-crowned Night Heron *Nycticorax nycticorax*, Little Bittern *Ixobrychus minutus* and White Stork *Ciconia ciconia* or they have an unfavourable status (Great Bittern *Botaurus stellaris*). This group of breeding birds, amplified by Garganey *Anas querquedula*, has both the loss of feeding territory in The Netherlands as well as a deteriorating wintering situation in Africa (drought, drainage and transformation of wetlands) in common. Most of the anatid waterbirds, however, still have their breeding grounds intact in the remote areas of Iceland, Scandinavia and Russia. Although their wintering area has greatly changed, no species seems to have become (locally) extinct yet. However, as we showed, their population size must have changed considerably.

By his tremendous impact on the landscape, Man has had an enormous effect on the carrying capacity for waterbirds. Not only in The Netherlands, but also along the coasts of the Baltic many archaeological finds of waterbirds are known from early human settlements. For example, in Sweden Great Cormorants have extensively bred in ancient times and the oldest records date back to 9000 years BP (Ericson & Hernández Carrasquilla 1997). After severe persecution the species became extinct here as a breeding bird in 1909. In Denmark Dalmatian Pelican was described as breeding in the period 6000–4000 BP (Løppenthin 1967). Eurasian Spoonbills were considered to have colonised Denmark first in the 14th century. A severe storm in 1362 had been the cause of many new wetland areas which were formerly not available. Later on, like in The Netherlands, cultivation measures caused the disappearance of many wetlands, and Eurasian Spoonbills and Great Cormorants became completely extinct in this country during the 20th century (Gregersen 1982).

The most important effects of Man's actions include (1) habitat loss by the transformation of nature into grassland and arable land, (with a reduced flux in groundwater levels) (2) a reduction in surface area of shallow brackish and marine waters and (3) banning the effect of the tides by construction of large infrastructural works, which causes the disappearance of transitional zones. The avian fauna of the group of waterbirds has shifted from a pluriform assembly to one dominated by herbivorous birds. The carrying capacity for fish-eaters (45% less), benthos-eaters (36% less) and plankton-eaters (55% less) has declined enormously. The only natural large-scale habitat still present is that of the Wadden Sea. As a sign of remnant of past glory, this area is subject of much concern in relation to questions about nature management and the desirability of joint use, putting this area under greater pressure. This concern is justified given the relatively small change in surface area of this habitat over the different periods (Fig. 2).

How reliable are the calculations of our reconstruction? Data about bird density per habitat type necessarily come from recent investigations. We can, however, not completely oversee all effects of landscape diversity and species composition on bird use. Also the availability of aquatic communities of the past may have been different from the situation we know today. Moreover, the effect of scale on total numbers can only provisionally be extrapolated from our present-day experience. The historic densities may therefore have differed from the actual ones. A clear example of our incomplete knowledge is the effect of eutrophication which could not be taken into account. It is well-known that waterbirds respond to enriched food situations (e.g. herbivores see van Eerden *et al.* 1996; benthos-eaters van Eerden *et al.* 2010, fish-eaters van Eerden *et al.* 1995). By using recent data for extrapolation into the past, this effect will lead to over-estimation of bird abundance in ancient times. On the other hand, food availability may have been greater because of unknown resources and the previously mentioned effect of scale of habitat. The conclusion from this is that the effects described before can either have been greater or smaller. The data are therefore to be considered with caution, but, as we see it, they do show the likely trends. The prehistoric phase was by no means more rich in numbers of waterbirds than today, at least not in winter. This is largely due to the estimated small number of herbivorous waterbirds that can be taken up during midwinter in areas as fen-peats, wet heathland and the afforested parts which have dominated the landscape for a long time. Only on passage in autumn and spring do these areas provide more food, and this may have attracted more birds on passage, given the presence of enough winter habitat elsewhere. Because we know little of the primeval situation further to the south (e.g. the British Isles, the French west coast and the Iberian Peninsula) as a winter habitat, the comparison of our estimated peak and mid-winter numbers remains tentative. However, at least in the case of the herbivores the effect of shortstopping, that is shortening the migratory flyway and wintering further north, is suggested by Figure 6.

Evaluation of the occurrence and functioning of Dutch wetlands

At present, natural landscapes contribute no more than 30% of the total surface of the Dutch territory (excluding deeper coastal sea water). Most of this consists of water, tidal flats and coastal habitats (salt marshes, dunes). Maybe as a consequence of the long-lasting transformation of wetlands into agricultural land, the public consciousness about nature and natural values rose steadily. Hunting legislation, the creation of 'nature reserves' since 1905 and educational programmes have been important steps to preserve the remaining natural values. So much was lost recently that even studies abroad in so-called reference areas (relatively undisturbed areas, comparable to the Dutch situation in the past) were undertaken, in order to find out what should be aimed at. Even now, the question as to what extent bird numbers are regulated by available food stocks in natural and man-made habitats remains largely unanswered. This is the more oppressing as questions about the effect of large-scale habitat changes are still going on (cf. discussions about the effects of a second national airport, the seaward extension of industrial areas and the continual urbanisation in The Netherlands).

Effects of habitat deterioration caused by acid rain, fragmentation and disturbance are beyond the scope of this paper. What has been elucidated here is the dramatic turnover of habitats by the increasing banning of natural dynamic processes. Sedimentation, erosion, the changing coastlines and the course of rivers and streams as well as the gradient situations brought about by tidal forces are largely diminished. As a consequence of closing off the sea-arms the polluted sediments affected the food chain in the newly created water bodies (e.g. Bijlsma & Kuipers 1989). Active management as to replace these natural processes by mowing, cutting and grazing (Bakker 1989) preceded measures like the reintroduction of species and proposals about the rehabilitation of natural processes by the restoration of the former super-abundant connections between rivers and the sea (e.g. Smit *et al.* 1994).

Early successional stages in wetlands have become extremely scarce. The importance of this originally super-abundant facet (see Fig. 1) is one of the missing links in our thinking about the functioning and maintenance of present-day wetlands. This point has been emphasised elsewhere (e.g. van Eerden 1990). As to the newly created land areas, the embankments are often followed by a pioneer stage of marshland and/or extensive agriculture. This phase is attractive to many bird species as it is a highly productive period (seeds, insects, young fish and small mammals; cf. Dijkstra *et al.* 1995, Dijkstra & Zijlstra 1997). By a continual process of developing new areas by draining of wetlands, the loss of wetlands was flanked by the occurrence of man-induced pioneer phases at the transition of water and land during a period of several hundreds of years. This has unintentionally toned down the effects of loss of area and will have had a temporary, positive effect on those species groups which use multiple habitats, such as waterbirds. Especially now, when these pioneer effects have faded and the last large-scale waterworks have been carried out, we are at the onset of a new phase in history. Before we can judge this effect we have to consider the present functioning of natural and man-made wetlands in more detail.

The present biological significance of Dutch wetlands may seem of modest interest if compared to the situation of the past. Many nature reserves preserve fragments of habitat that was much more extensive earlier on. Many of them have a regulated water level and strongly depend on Man's management of the landscape. A great many have even been derived from cultivation measures (e.g. peat cutting activities) and there is a general lack of transitionary zones. However, on an international scale, the Dutch environment still functions as a major haunt for millions of migratory waterbirds (Wolff 1988). Many birds still profit from the remaining wetlands and agricultural areas on their biannual journey to and from the breeding grounds. It is this international responsibility to preserve these populations on a mega scale, being the flyway of the species, which makes the effort for an adequate wetland management worthwhile. The question of the 'restoration of naturalness' (a hot topic in Dutch nature conservation) should be considered also in relation to this goal. Any endeavour towards a more natural situation, based on a reference from the past, could easily lead to a deterioration of the carrying capacity for migratory waterbirds. This group of organisms, which has been able to withstand changes over a long period of time, still depends for part of the year on purely natural and unspoiled ecosystems in northern Europe. Only by preservation of their stopover and wintering habitats, necessary as stepping stones along the flyway, their role in these ecosystems can be safeguarded. As the wintering areas have diminished so strongly in size, this requires a fair knowledge of the carrying capacity of these habitats.

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SAMENVATTING

Er is een palaeo-geografische reconstructie gemaakt van de avifauna in verschillende perioden, tot c. 7000 jaar geleden. Als basis diende een landschapsbeschrijving uit iedere periode, die werd gekoppeld aan schattingen van de vogeldichtheid op grond van de huidige vogelaantallen in vergelijkbare habitats. Het blijkt dat de omvang van de wetlands enorm is geslonken en dat in het bijzonder brakwatergebieden nagenoeg zijn verdwenen. Als gevolg daarvan is de opvangcapaciteit voor visetende en bodemfauna-etende watervogels sterk afgenomen.