

Environmental changes in man-made coastal dune pools since 1850 as indicated by sedimentary and epiphytic diatom assemblages (Belgium)

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ABSTRACT

1. Diatom assemblages of man-made coastal dune wetlands between Blankenberghe and Kist (Belgium), dating from 1850 to 1979 and sampled from herbarium specimens of macrophyte, were compared with more recent samples collected in the remaining calcareous dune marshes and pools in this area.

2. Overall nutrient conditions inferred from the reference assemblages were fairly eutrophic for phosphorus. Only a minority of the historical assemblages pointed to presumably nitrogen-limited conditions.

3. Significant alterations in general assemblage composition were observed, including a marked decline of epiphytic species, and a decrease in the compositional variation in sediment diatom assemblage. These changes can be attributed mainly to an increased availability of nutrients and degradable organic matter since the mid 1970s. No changes in the salinity range were observed, suggesting fairly stable hydrological conditions.

4. Possible causes for eutrophication include increased atmospheric deposition or nutrients, but also more site-related phenomena such as groundwater table, angling and, perhaps, effects of nature management on soil nutrient cycling. Their relative importance needs to be established and further monitoring is necessary.

5. Measures are required to reduce nutrient levels of both permanently and periodically inundated sites and to promote small-scale habitat differentiation. Due to physical constraints, the latter will be possible only by mimicking the processes that act upon more natural dune systems in management practice.

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INTRODUCTION

Assessment of the environmental status of aquatic ecosystems, consideration of sustainable goals for mitigation or restoration, and selecting priorities for site conservation all require ecological reference data. These may pertain to condition attributes and functioning of the system, as well as to the structure and composition of its biotic communities. A biotic perspective may be particularly useful if it relates to an important habitat features, responds rapidly and with a low threshold to environmental changes, and integrates conditions at a time-scale relevant to management and monitoring. It also outlines primary target variables of biodiversity conservation (Flower *et al.* 1997). In many areas, human impacts preclude obtaining a regional perspective of the characteristic communities and conditions in unimpacted water bodies from current observations. Hence, a 'state-changed' principle (Moss *et al.*, 1996, 1997; Lassi re and Duncan, 1997) is often preferred in setting goals for recovery and conservation (Moss *et al.*, 1997). Rapid detection of continuing environmental changes significantly improves possibilities for counteraction and such 'early warning' may also benefit from retrospective information (Smol, 1992). Palaeolimnological data are highly valued to document former biotic composition and trophic structure, to allow hindcasting of water quality variables, and to assess responses to perturbation or degree of naturalness (e.g. Smol, 1995; Hiltmorth *et al.*, 1996; Butterbee, 1997, 1999; Bennion and Applby, 1999; Jepsen *et al.*, 2001). However, for small, shallow or even intermittent waters, analysis of sediment cores may be less straightforward and, in general, possibilities to address former site condition change may remain limited. Such variation may be prominent among small lakes and ponds, compromising generalizations from single-site data. For practical applications also, ecological references for smaller, more dynamic waters should account for their potential range in successional and spatial variation. Standing waters in coastal dune areas are exemplary in this respect, as sea spray, soil development, hydrology and ageing can result in a wide range of limnological conditions and community composition within a comparatively small area (Leentvaar, 1981; van Dijk and Meltzer, 1981).

Fresh dune waters along the Atlantic Channel and North Sea coasts are typically small, shallow and often temporary. Due to intensive coastal development and lowered groundwater tables many are threatened or have disappeared. Moreover, their characteristic communities are sensitive to pollution and eutrophication. Consequently, aquatic and semi-terrestrial dune habitats of the Atlantic coast are in need of protection, as reflected for instance by the Natura 2000 list (Rom o, 1996). As elsewhere in Europe, strong concerns exist on the future of the coastal dunes in Belgium (De Raeve, 1989; Baeteman, 1995; Krier and Thomas, 1995), leading to legislative protection, initiation of monitoring, and active restoration (Herrier and Killemaes, 1998; Provoost, 1999, 2001). Hence, the need for reference data on aquatic conditions in the area is growing, especially as these are scantily documented.

Freshwater diatoms (Bacillariophyceae) are increasingly used to monitor trends in habitat quality of inland waters and wetlands (John, 1993; Dixit and Smol, 1994; Lancaster *et al.*, 1996; Mayer and Galois, 1999; Slooten and Smol, 1999). Diatoms also have identifiable siliceous remains which can be used for inferring past conditions, a feature highly exploited in sediment-core based palaeolimnology. In addition, their assemblages can be studied from old limnological samples (van Dam and Kooyman-van Blokkland, 1978; Butterbee, 1981, van Dam *et al.*, 1981; Flower, 1986; H rthmann *et al.*, 2001). Material obtained from herbarium exsiccata of aquatic macrophytes is used less frequently, although this probably represents a far more extensive historical archive for certain regions and habitats (van Dam and Beldjaars, 1984; van Dam and Mertens, 1993; Deryn, 1997a, 2000; Sayer *et al.*, 1999).

This paper examines habitat conditions in man-made depressions at the margin of the Belgian coastal dunes. The present-day variation in biotic and inferred environmental characteristics is related to that of similar habitats in the area between ca. 1850 and 1930 by comparing diatom assemblages from recent samples to historical counterparts obtained from herbarium specimens of macrophytes. Local records from the late 19th to the early 20th century indicate an exceptional botanical diversity and include a number of

sensitive plants from calcareous dune valleys (Vanhecke, 1993) suggesting that the beginning or the 20th century represents an appropriate ecological reference period. In a broader sense, Moss *et al.* (1996, 1997) argue in favour of the period of more sustainable land-use preceding the Second World War for such purposes. If present conditions deviate with respect to this period, future management may be adjusted in accordance. The European Water Framework Directive (WFD, 2000/60/EC) also requires a water-type specific, reference-based assessment of phytobenthic communities in standing waters. Although permanent dune waters in Belgium are quite small and man-made throughout, they will need attention in its implementation, as the dune area is largely 'protected' according to Annex IV of the Directive. By providing historical diatom data, the basis for assessing such waters following WFD specifications is extended. The time perspective also allows an appreciation of the effectiveness of reserve policy in the conservation of the site and an appreciation of the extent to which the present-day pools reflect former habitat variation. In order to plan future actions, it is important to know whether the reduction in the number of water bodies in the area resulted in a general loss of habitat differentiation.

STUDY SITE

The pools surveyed in this study, numbered A to G in Figure 1, are situated in the so-called 'Fonteintjes' (translated 'mountains' 51°19'30" N 3°10' E). This area consists of a nearly 2 km long but less than 100 m wide stretch of dunes and associated habitats extending from the village of Blankenberge towards the harbour of Zeebrugge. The main feature is a series of elongate depressions representing the last of the so-called 'inlagen' (German: 'Einlagen') along the Belgian coast. Vanhecke (1993) studied the history, hydrology and vegetation of the Fonteintjes in detail. Their origin goes back to the early 15th century with dike construction at the polder border for which the dunes were excavated. This left a series of depressions

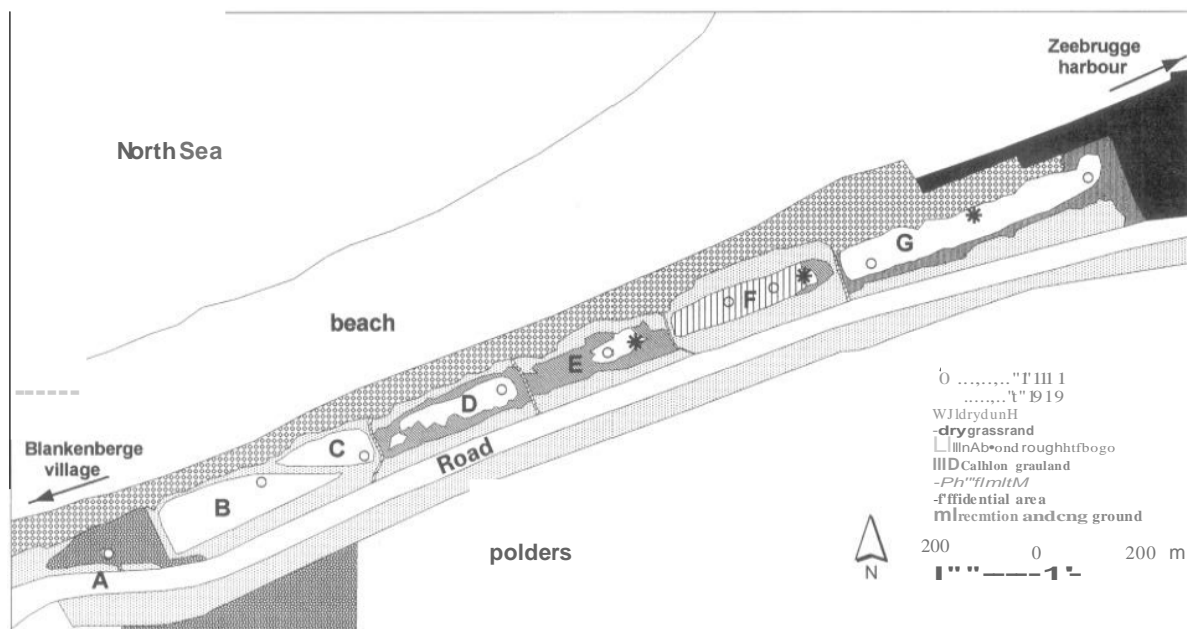


Figure 1. General map of the study area with indication of depressions A-G and sites where samples were taken in 1996 and 1999. Open circles indicate 1996 and asterisks 1999 sample sites.

over a length of ca. 5.7 km in which pools and dune marshes developed. Their configuration repeatedly changed due to infilling and dune migration as well as further engineering works and excavation. Several depressions northeast of the present Fonteintjes were obliterated, leaving only six larger ones and a small puddle. Notable activities in more recent times include construction of a railway around 1865, of an adjacent road at the beginning of the 20th century, and of coastal defences during both World Wars. Depressions B and C, and D and I, respectively, were separated more recently: the former by the now abandoned railway, the latter by a passage way during World War II. The small puddle A is not part of the historical 'inlagen' but the remains of a larger pond dating from about 1900 and largely filled up in the early 1960s. After the Second World War most defence works were dismantled, but a large bunker in depression I was demolished as late as the early 1970s. During these works, the level of almost a quarter of the depression was raised. Access to depressions D, I, and 1- was restricted from 1973 onwards and these became officially protected as a nature reserve in 1978. Recently, the reserve was extended to the largest pool, G.

The depressions show marked differences in environmental conditions and vegetation. Although the toponymy refers to the seepage-fed character, this phenomenon largely remains limited to periods following heavier rainfall. Intensity of mineral-rich seepage and infiltration of saline water also varies locally. Overall, this results in a gradient of decreasing ionic concentration of the surface

water from W to I. (Vanhecke, 1993). Recent data on water chemistry are limited and summarized in

Table 1 together with some vegetation characteristics. They illustrate the alkaline, calcium-rich nature of the water and reflect the ionic gradient, with poly-ionic conditions (Olsen, 1950) in most pools, but conductivity in the C'-meso-ionic range in pool G. The puddle at the south-western end, A, is used as a water hole for ponies. No data on nutrients are available, but their levels are probably even higher than in the other pools. The ponds B, C' and G are permanent with up to 2 m of water, steep banks and a bottom of marine sand with abundant shells. B and C' are turbid, had submerged vegetation and are used for angling. Measured total phosphorus (TP) concentrations are far into the hypereutrophic range and organic content of the water is high. Depressions D and E are shallow and marshy, with some permanent water of usually less than 0.5 m deep on a more clayey substrate. Reed predominates in D, while E is partly overgrown with willow scrub. The highest TP levels occur in pool D, whereas concentrations in F are more comparable to those in the fishing ponds. Depression F has a topsoil of dune sand and inundation is

temporarily during late autumn and winter. It is largely flooded and water levels reach up to 1 m, or the most part, it supports dune slack and Calthus-like grassland vegetation. Up to 1966, it was cropped for hay yearly but this continued on a much less regular basis until 1978. At this time an effective mowing regime started, resulting in a fairly rapid decline of the reed and sedge stands that had developed. In I, a small bomb-hole and a puddle dug in 1997 have permanent water and abundant aquatic vegetation. The largest pool, G, was used for boating and supports only sparse vegetation. Segers (1998) reports a species-poor tolerant rotifer community and a bloom of *Anabaena* from this pond. Still, nutrient concentration- and organic loading in this larger and well-oxygenated pool are far compared with the other sites.

The area is considered of considerable importance because of its vegetation, bird and invertebrate life and is protected under the EC Birds and Habitats Directives (Council Directives 79/409/EEC and 92/43/EEC). In terms of Annex 1 of the Habitats Directive, types 16.31, 16.34 and 16.35 are present in the wetter parts, with physical conditions in depressions D, E and F being most similar to those expected in natural dune pools. The population dynamics of *Actinopterygii* and the occurrence of *Potamogeton* in depressions F and D were considered especially important (Vanhecke, 1985, 1988, 1993, 1994). Hydrobiological data are few however. A recent reduction in the abundance of aquatic macrophytes,

including several *Chara* species, triggered concern over possible changes in overall water quality, but this

was not corroborated by substantial baseline evidence. Obviously, eutrophication would affect the conservation status of the reserve and compromise the survival of *Potamogeton coloratus*. As elsewhere in

Table 1. **Rult** of \\ater an.il} frontic' \ to G and prominent \cgctation char.icteri,lle'

Site (ycara)	,\(:!)	B (1 2)	<i>C m</i>	D (1 2 3)	EC 1 21	F. puddc (31)	G (1-1-3)
pH	8.1	9.2 9.6	9.0 9.6	8.0 8 X	8.8-	7.8 8.1	S.O 9.0
TP(mg L ⁻¹)		0.46	0.52	1.05 2.81	9.6	0.26-2.66	0.07 () 15
KJ-N(mg L ⁻¹)		7.1	5.8	2.3 5 5	0.38	1.4-12.6	IA 2.5
COD(mg L ⁻¹)		125	108	68 102	46	54- 73	23 64
SO ₄ (mg L ⁻¹)		25	15	9 12	91	2-8	16 31
Cl(mg L ⁻¹)		278	259	191 299	11	168 178	99 128
Na(mg L ⁻¹)		170	167	119 176	276	100 107	65 73
Ca(mg L ⁻¹)		54	45	66 85	148	73 78	40 52
K(mg L ⁻¹)		15	16	14 21	20	11 18	11 14
Mg(mg L ⁻¹)		18	17	17 21	19	16-17	12 14
l:C(1Scm ■)	4640	1200-1326	1098 1 190	1100 1770	1200 1531	945-1 161	638 758
Predominant cmrgcnt<111Û banl.: \Cgctation	<i>Alimw plc111r ag11-aq11aica</i>	<i>Phragmite\T_1plw cmgmtif1/iu</i>			<i>'aln. Phragmites. Cala1lwgrostis cp1gt'jos</i>	<i>Drepai11clad11.1 /luitans. Care. riparia. J111c11s s11h1od11/o1m. Ly.>inwchia rnS?ari1. Phragmite.1 Clwra rn/S?aris". C. maior".</i>	<i>Plirag111itc1</i>
Submerged and floating vegetation	<i>lc11111a 111111r</i>	<i>Jlyriophyllum .picat11111b</i>				<i>Polal1logel011 colorwus. mfr{ari 1. Iippuris Callitriche</i>	<i>.Itriophr/11111 , .1p1c1 1111111• Pol<1111pict1111 P. p66ri11ar111. Pllyg11111111 a111phih11111</i>

(1) 1995. (2) 1996.(3) 1999
No longer ob-cnced in must re<:enl years.

Europe (e. g. Korneck *et al.* 1996; van der Meijden *et al.* 2000), this species is highly endangered in Flanders and merits consideration as a conservation priority at national level.

MATERIAL AND METHODS

Table 2 lists the 56 samples used in this study. Herbarium specimens were selected by scrutinizing accompanying data on date of collection and origin, as well as condition and mounting of the material. A small amount of non-senescent plant material (roughly corresponding to 1 cm) or some sediment from close to the root base was used. Recent samples of surface sediment and epiphytes on aquatic plants or the submerged parts of helophytes were collected in 1996 (all depressions) and 1999 (depressions D. 1- and G only). Samples were cleaned using concentrated hydrogen peroxide. Permanent slides were prepared with Naphrax and examined with a Leitz Orthoplan microscope using interference contrast optics. Counts of 500 valves were made along random transects at 1200 \times magnification. Slides were scanned thoroughly, partly at lower magnification, for any further taxa. Identifications are based mainly on the works of Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Krammer (1992), Lange-Bertalot (1993) and Reidrardt (1997).

Sediment and epiphyton samples were considered separately in view of their different habitat characteristics and species composition. Mean ecological indicator scores were calculated as abundance-weighted averages of indicator values given by van Dam *et al.* (1994) for taxa within the counts. These indicator values included ordinal classifications for pH (R), salinity (S), organic nitrogen availability (N), oxygen saturation (O), saprobity (S), trophic status (T) and moisture (M) derived from extensive literature and personal data on diatoms reported from Dutch fresh waters. Marine littoral taxa are excluded from calculations. The number of taxa within the count, the total number of taxa recorded in a sample, and the dominance (highest relative abundance) are used as diversity measures (van Dam, 1982). Three sampling periods are considered: prior to 1930 (period 1), 1966-1988 (period 2), and 1996-1999 (period 3). Changes in assemblage composition and indicator values between periods were tested using Mann-Whitney *U* tests (one-tailed, considered significant at $p < 0.05$; STATISTICAL 5.1) and examined further by ordinations carried out with the CANOCO 4.1 package (ter Braak and Smilauer, 1998). Ordinations were performed on log(x+1) transformed relative abundance data of 148 taxa attaining 1% or more at least one sample.

Preliminary detrended correspondence analysis (DCA) of all samples indicated gradient lengths of 3.22 and 3.45 standard deviations, respectively, for the first two axes, and correspondence analysis (CA) was therefore preferred to methods assuming a linear species-response model (Jongman *et al.*, 1987). Abundances of rare species were downweighted in CA. Compositional turnover was estimated as the gradient length of the first DCA axis (Okland, 1986).

RESULTS

In the 19 recent samples, 313 taxa (including morphotypes and complexes) were observed. The 12 samples from 1966-1988 accounted for 260 taxa, and the 25 oldest samples included 339 taxa, giving a total of 476 (list available on request). Periods 1 and 3 had 206 taxa in common. Although 134 taxa were lost from the original inventory (40%), 107 (32%) were gained, for the most part these were common diatoms from fresh and slightly brackish waters, mixed with some displaced marine littoral taxa. Nearly all of the more abundant taxa develop optimally in more nutrient-rich waters. A number of newly reported diatoms,

including *Caloneis* *1110/aris*, *Cilloneis* *1111/aris*, *peiw111is*, *Denticula* *1111/aris*, *Gompl1011e111a* *gm.1m11c*, *Nmicula* *mwa111oger111anica*, *Nit-1-chiadesertor11111*, *Nit=schiai11cog11w*, *Pi111111laria1wlophila*, *Pi111111laria/wet=ingii* and *Surirella* *1venusta*, confer a certain distinctiveness to the flora. Their presence relates to the high mineral

Table 2. List of all >amplc>. Period 1 (1852-1929): nrs 1-25; period 2 (1966-1988): nrs 26-37; period 3 (1996-1999): nrs 38-56

Nr	Dale	Sample Lype	Epiphytes	Sediment	Site spccifications
1	8-1852	<i>Potamogeton pectinatus</i>	X		Blankenberge, 'mare derrière la <ligue'
2	6-1864	<i>Potamogeton pectinatus</i>	X		Blankenberge
3	8-1864	<i>Utricularia pectinatus</i>	X		Between Heist and Blankenberge
4	9-1865	<i>Ilippuris pectinatus</i>	X		Near Blankenberge
5	8-1867	<i>Cladophora hederacea</i>	X		Heist
6	7-1868	<i>Chara pectinatus</i>	X		Lissewege, 'mares'
7	1873	<i>Potamogeton pectinatus</i>	X		Lissewege
8	1873	<i>Potamogeton pectinatus</i>		X	Lissewege
9	8-1873	<i>Ceratophyllum demersum</i>	X		Lissewege
10	20-6-1881	<i>Hippuris vulgaris</i>	X		Blankenberge
11	7-1886		<i>Ceratophyllum major</i>		X Lissewege, 'marécages maritimes'
12	25-7-1887	<i>Ulricularia pectinatus</i>	X		Heist, 'mare'
13	24-8-1888	<i>Drepanocladus adpressus</i>		X	Near Heist, 'marais'
14	14-7-1889	<i>Myriophyllum spicatum</i>	X		Lissewege, 'mares maritimes'
15	14-7-1889	<i>Utricularia pectinatus</i>	X		Lissewege, 'mares maritimes'
16	14-7-1889	<i>Nymphoides peltata</i>	X		Lissewege, 'mares maritimes'
17	23-7-1890	<i>Scirpus tabernaemontani</i>		X	Lissewege, 'marécages maritimes'
18	9-1906	<i>Hydrocharis maritima</i>		X	Between Blankenberge and Zeebrugge
19	9-1906	<i>Baldellia ranunculoides</i>		X	Blankenberge, 'marais'
20	9-1906	<i>Potamogeton coloratus</i>	X		Blankenberge, 'bas-fond'
21	5-8-1923	<i>Potamogeton pectinatus</i>	X		Heist, 'mare dans une panne humide'
22	3-9-1923	<i>Zostera noltii</i> subsp. <i>pedicellata</i>	X		Heist, 'mare derrière les dunes'
23	3-9-1923	<i>Polygonum amphibium</i>	X		Heist aan Zee, 'mare'
24	17-8-1924	<i>Potamogeton pectinatus</i>	X		Zeebrugge, 'prairies derrière l'église, mares et fossés'
25	28-7-1929	<i>Ceratophyllum demersum</i>	X		Between Blankenberge and Zeebrugge, 'mare'
26	22-2-1966	<i>Drepanocladus adpressus</i>		X	Depression F
27	23-6-1970	<i>Polygonum amphibium</i>	X		Depression F, on moist sand
28	29-6-1973	<i>Potamogeton pectinatus</i>	X		Depression E
29	27-5-1973	<i>Potamogeton crispus</i>	X		Depression G, southern bank of pond
30	27-5-1973	<i>Polygonum amphibium</i>	X		Depression G, southern bank of pond
31	27-5-1973	<i>Elodea canadensis</i>	X		Depression G, southern bank of pond
32	22-4-1974	<i>Ranunculus repens</i>	X		Depression G, pond
33	30-9-1975	<i>Ceratophyllum demersum</i>	X		Depression E, shallow water
34	16-6-1982	<i>Chara pectinatus</i>	X		Depression D
35	16-6-1982	<i>Fotia antipyrretica</i>	X		Depression D, bomb hole
36	20-6-1985	<i>Chara globularis</i> var. <i>virgata</i>	X		Depression F
37	14-9-1988	<i>Chara globularis</i> var. <i>virgata</i>		X	Depression F
38	4-7-1996	Surface sediment		X	Depression G, pond
39	4-7-1996	<i>Potamogeton pectinatus</i>	X		Depression G, pond
40	4-7-1996	<i>Drepanocladus adpressus</i>		X	Depression F, marsh
41	4-7-1996	<i>Drepanocladus adpressus</i>		X	Depression F, marsh
42	4-7-1996	Surface sediment		X	Depression E, pool
43	4-7-1996	Surface sediment		X	Depression D, pool
44	4-7-1996	<i>Phragmites australis</i>	X		Depression D, pool
45	4-7-1996	Surface sediment		X	Depression C, pond
46	4-7-1996	<i>Tritium flavescens</i>	X		Depression C, pond

Table 3. Average (with standard deviation), median, minimum and maximum abundance of taxa reaching an abundance level of 5% in at least one sample, and diversity measures for each of the three periods with indication of significant differences (U test, one-tailed; $p < 0.05$; $p < 0.1$)

Epiphyton samples (select at least one)	Period 1: 1852-1929, 18 samples					Period 2: 1970-1982, 9 samples					Period 3: 1996-1999, 8 samples					Significant differences		
	Average	St dev.	Median	Min.	Max.	Average	St dev.	Median	Min.	Max.	Average	St dev.	Median	Min.	Max.	1vs.2	2vs.3	1vs.3
<i>Achnanthes minutissimum</i>	53	4.5	47		148	71	9.1	16		21.8	4.6	5.7	2.2		17.0			
<i>Ampelora coffeaeformis</i>	08	2.3			8.4													
<i>Ampelora pediculus</i>	1.4	2.8			10.0	35	6.0	0.8		17.8	2.2	3.3	1.4		10.2			
<i>Amphora veneta</i>	0.5	1.3			5.6		0.1			0.2	0.2	0.4		1.2				
<i>Cocconeis placentula</i> var. <i>euglypta</i>	363	31.8	302		97.2	9.3	14.2	40		44.4	3.8	9.0	0.1	25.8	+		***	
<i>Cocconeis placentula</i> var. <i>lineata</i>	2.1	5.5	0.2		21.8	0.8	10	0.4		3.2	2.5	6.6		18.8				
<i>Cratichneumon halophila</i>	38	9.3			320	0.3	0.6			1.8	0.2	0.3		0.6				
<i>Cyclotella atomus</i>						1.6	4.8			14		0.1		0.2				
<i>Cyclotella meneghiniana</i>	11	2.9			12.2	0.2	0.3	0.2		0.8	0.2	0.4		1.0				
<i>Diatoma tenuis</i>	0.2	0.4			1.5	36	10.4			38	2.2	4.6		13.0				
<i>Encyonopsis microcephala</i>	11	2.9			10.4													
<i>Eolimnion mirmma</i>	0.2	0.4			1.4	1.9	35	0.6		11.0	2.9	3.1	2.0	9.0			++	
<i>Epithemia adnata</i>	7.9	15.2	0.8		60.6	5.6	4.9	4.0		135	1.3	3.1		8.8	+		+	
<i>Epithemia somx</i>	80	12.3	2.0		366	15.7	24.1	0.4		61.0	5.4	12.5		35.6				
<i>Epithemia rurgida</i>	0.2	0.4			0	1.6	2.6	0.8		8.0	3.7	10.5		29.8				
<i>Fragilaria capucina</i> var. <i>vaucheriae</i>		0.1			0.4	0.2	0.5			1.2	2.0	3.4	0.4	9.6				
<i>Fragilaria constans</i> L. ventricosa						0.3	0.8			2.4	3.8	7.9		22.2				
<i>Fragilaria tumida</i> J. Grunwaldt					0.2	2.7	3.2	1.0		8.2	0.7	1.3		3.4				
<i>Fragilaria lascajalensis</i>	1.0	2.5	0.2		10.2	2.1	4.5	0.1		13.4	6.8	11.5	0.7	26.0				
<i>Fragilaria pupillata</i>	20	6.8	0.1		29.2	3.5	9.9			29.8	0	0.4		1.0				
<i>Fragilaria uva</i>		0.1			0.4	0.1	0.2			0.7	0.9	2.3		6.6				
<i>Gomphonema clavatum</i> Grunwaldt	0.1	0.2			1.0	0.1	0.2			0.6	2.3	5.4	0.3	15.6				
<i>Gomphonema punctatum</i>					0.2	1.4	3.8			11.6	2.0	5.4		15.2				
<i>Gomphonema muscicidum</i>										0.6	1.6			5.0				
<i>Gomphonema parvulum</i>	13	4.6	0.1		19.6	0.7	0.6	0.8		1.6	7.1	8.5	3.9	25.0	+			
<i>Gomphonema pumilum</i> var. <i>euglypta</i>										0.7	1.8			5.2		+		
<i>Navicula pusilla</i>	1.0	3.0			12.6													
<i>Mastogonia smithii</i>	2.3	6.0			22.4													
<i>Navicula capitata</i>											1.7	3.5		9.8				
<i>Navicula ayyptotenella</i>	3.0	7.6	0.1		32.4	5.2	4.3	4.0	0.4	11.6	2.6	2.7	2.3	7.4				
<i>Navicula veneta</i>	0.7	1.3			5.0	1.7	2.3	0		7.0	1.5	1.7	0.8	4.8				
<i>Nitzschia amphibia</i>	0.6	1.1	0.1		4.4	1.8	1.9	1.8		4.6	3.1	5.1	0.3	11.6				
<i>Nitzschia archibaldii</i>					0.2						5.6	15.7		44.4				
<i>Nitzschia dissipata</i> var. <i>medii</i>											1.5	3.5		10.2				
<i>Nitzschia elegantula</i>	0.4	1.9			8.0													
<i>Nitzschia frustulum</i>	1.6	1.9	0.6		6.2	4.9	6.2	2.2		18.6	8.8	10.5	4.1	31.6			***	
<i>Nitzschia hantzschiana</i>	0.1	0.3			0.8	1.7	4.9			14.8								
<i>Nitzschia microcephala</i>	0.4	0.9			2.6	0.8	2.4			7.2	0.1	0.1		0.4				
<i>Nitzschia palea</i> var. <i>debilis</i>	1.6	4.4			18.4	0.2	0.3			0.6	0.2	0.6		1.6				
<i>Nitzschia paleacea</i>	2.8	6.6	0.5		23.2	4.4	6.6	1.8		18.0	5.1	5.7	2.8	15.6				
<i>Nitzschia perniwata</i>	2.1	5.4			20.0	0.4	0.8			2.4	0.3	0.6		1.8				
<i>Rhodospira abbreviata</i>	0.6	1.4	0.1		6.2	2.6	4.5	0.2		12.8	1.2	1.0	0.8	2.8			++	
<i>Rhopalodia gibbata</i>	1.8	3.1			9.2	0.8	1.0			2.4	0.2	0.5		1.4				
Number of taxa > 500 valves	5.1	2.6	4.8	1.6	11.8	7.6	3.1	7.4	4.2	14.8	6.8	2.5	5.8	40	11.8			
Number of autochthonous taxa > 500 valves	5.0	2.5	4.8	1.6	11.6	7.3	2.7	7.2	4.2	13.6	6.8	2.5	5.8	40	11.8			
Number of taxa > 500 valves per sample	10.1	4.5	10.0	3.4	20.8	14.3	5.1	13.6	7.4	24.4	11.6	4.0	10.4	84	21.0			
Number of autochthonous taxa > 500 valves per sample	9.4	4.1	9.4	3.2	19.2	12.7	3.8	11.8	7.4	19.8	11.2	3.6	10.4	82	19.4			
Abundance < 10% (%)	9.4	4.7	8.2	2.8	19.4	6.1	3.4	4.4	2.3	12.2	5.6	1.8	5.2	30	8.9		+	

regression of the epiphyte *C. placei* var. *elliptica* since the first period. As in the epiphyte *F. pulchella* and *Epithemia adnata* lost ground in the course of time. *M. smithii* also seems to have become less abundant. Simultaneously, a rise of *Aliphora copilata*, *A. pedunculata*, *F. costata*, *Hippodonia lillipodonia* and the planktonic *Cyclotella meneghiniana* occurred, while *Eolimna millii*, *D. linnii*, *Fragilaria hirtella*, *Hippodonia capitata*, *Naipicula gregaria*, *N. veneta* and *Platoloidia frequentissima* became more prolific than ever. *A. hemicycla*, *Asterionella armosa*, *Cyclotella atomus*, *N. rhipidaria* and *Stenodiscus lenticularis* only show up in some numbers in the most recent samples. Although changes in species composition largely mirror those of the epiphyte, diversity measures remain unchanged.

Of the mean indicator values, significant changes were noted for the median values of R (pH), N (organic nitrogen), O (oxygen saturation), S (saprobity), T (trophic status) and M (moisture) (Table 5). R values remained slightly lower on average in the recent epiphyte samples. Although this could reflect slightly less carbonate-rich conditions, the difference remains too small for such a conclusion, especially as the sediment assemblages do not react similarly. Values for organic nitrogen availability and saprobity show a more consistent increase in time for both sample types. For the epiphyte, recent M values were higher than for historical samples, but for sediment assemblages rather lower (indicating 'wetter' conditions) values were obtained.

Table 6 gives the main characteristics of the CA ordination, while Figures 2 and 3 show the ordination plot for samples and the more abundant taxa for the two principal axes. These axes jointly capture almost 20% of the total variation in species composition. In the sample plot, sediment and epiphytic assemblages are differentiated. Polygons, demarcated by the most peripheral samples in each group, show the range in assemblage composition for each of the three periods. Larger polygons indicate stronger between-sample differences within a period for a particular sample type, while the overlap of polygons reflects similarity of diatom assemblages between periods and sample types. A clear shift is observed to lower axis 1 scores with

Table 6. Average (with standard deviation), median, minimum and maximum of mean ecological indicator values for pH (R), availability of organic nitrogen (N), saprobity (S), trophic status (T) and moisture (M) for the three periods. The implication of significant difference: (t, test, one-tailed, p < 0.05; + p < 0.01)

Epiphyte samples	Period 1: 1852-1929			Period 2: 1970-1982			Period 3: 1996-1999			Significant differences	
	Average	Stdev.	Median	Average	Stdev.	Median	Average	Stdev.	Median	2 vs. 3	1 vs. 3
R	4.1	0.2	4.0	4.1	0.4	4.0	3.9	0.4	3.8		+
H	2.3	0.4	2.1	2.2	0.4	2.0	2.2	0.2	2.1		
N	1.9	0.3	2.0	2.0	0.6	2.0	2.2	0.5	2.2		+
O	2.5	0.4	2.6	2.3	0.4	2.2	2.5	0.4	2.4		
S	2.2	0.3	2.1	2.3	0.4	2.1	2.4	0.3	2.5		+
T	4.6	0.4	4.8	4.6	0.3	4.7	4.6	0.2	4.6		
M	2.3	0.2	2.3	2.4	0.2	2.3	2.5	0.2	2.4		++

Sediment samples	Period 1: 1864-1906			Period 2: 1966-1988			Period 3: 1996-1999			Significant differences	
	Average	Stdev.	Median	Average	Stdev.	Median	Average	Stdev.	Median	2 vs. 3	1 vs. 3
R	3.9	0.3	4.0	3.8	0.2	3.8	4.0	0.1	4.0		
H	2.2	0.4	2.2	2.3	0.2	2.4	2.3	0.2	2.3		
N	2.0	0.6	2.0	1.9	0.2	1.8	2.2	0.2	2.1	-	+
O	2.4	0.6	2.5	1.7	0.3	1.6	2.5	0.6	2.6	-	
S	2.3	0.2	2.3	2.0	0.4	1.8	2.6	0.3	2.5		+
T	4.5	0.6	4.6	4.0	0.4	4.1	4.7	0.2	4.7	++	
M	2.6	0.3	2.5	2.5	0.5	2.8	2.3	0.5	2.3		

oldest samples. Here, major changes appear to have occurred as late as the 1990s, but this may result from the limited number of samples in period 2. Sediment assemblages from older samples all score negatively on the second axis. This is the case for only some of the recent ones, which show a larger range in scores along axis 2. Figure 3 illustrates which taxa are primarily responsible for these differences. Positive scores along the first axis are related to higher abundances of species such as *C. p. aculeata* var. *euglypta*, *L. litorea* spp., *R. topalodia*, *G. lwn-11/11111*, *E. minor* and *H. smitii*. Negative scores coincide with taxa such as *Fragilaria hrelistriata*, *G. lwn-11/11111*, *U. rnpwrn*, *V. mirna antonii*, *A. rhylichweta* and *N. reichardtiana*. This represents a shift from epiphyte-dominated assemblages towards a greater importance of less habitat-specific and epipelic species.

Species grouped at the right side of the diagram are also generally considered to be less tolerant to organic pollution and high organic nitrogen availability than those on the left-hand side. Those at the left are most abundant in nutrient-enriched conditions. If the abundance-weighted indicator values are added as passive variables to the analysis, the change towards a more pollution-indicative assemblage is highlighted further. The vectors indicate the direction and relative importance of environmental variation in each of these mean indicator values. Those for organic nitrogen availability (N) and saprobity (S) are directed similarly and correlate negatively with both axes, whereas those for high pH (R) and trophic status (T) show a positive correlation with the second axis and a negative correlation with the first. Axis 2 also differentiates between assemblages from more permanent/inundated, low-salinity habitats and high abundance of taxa associated with less nutrient-rich, sub-aerial conditions (M) and higher salinities (S). Scores for R, N, S and T clearly outweigh the other passive variables in their range of structured variation. Characteristic species for temporary inundation include *P. arw*, *A. litorea*, *Fragilaria litorea*, *F. fasciculata*, *N. cincta*, *Nit. chia acidochloa* and *E. lotia*. Among others, the planktonic *S. lwn-11/11111*, *A. fir1110.1a* and *Cyclo. tep1110.1* cf. *tn/for1111s*, as well as the epipelic *N. rnpitoradiuta*, *Parlihe/1111 prolacta*, *A. p/wra 01/1111s*, *A. hemicycla*, and the epiphytic *G. lwn-11/11111* var. *elegans* are associated with highly eutrophic but permanent water.

Figure 4 shows CA time trajectories for assemblage composition of samples from individual depressions. Samples collected in the same year from depressions G (1971), D (1982) and 1 (1996) are nested according to their sample location and considerably closer to each other than samples taken from these sites in different years. Even though the samples were derived from a single spot within each pool, they appear to be representative of the overall character of the pool at a given time. Substrate-related differences are not substantial either. Important changes in assemblage composition occurred abruptly in depression G in the early 1970s, as shown by the trajectory for epiphyte assemblages. This represents a replacement of *E. snrex* and *C. placeata* var. *elgata* by *D. tenuis*, *F. p/chel/a* and *F. fasciculata* as the most prominent taxa, corresponding to an increase in the mean indicator value H from 2 to 3.2, suggesting a slight rise in salinity. Trajectories for epiphytes from pools F and D are also quite long, with marked changes after 1970 in F and 1982 in D. There is a slight deviation towards lower axis 1 scores for sediment assemblages from F after 1988. In depressions 1 and G, a trend towards the left of the diagram seems to persist for the sediment assemblages even from 1996 to 1999.

Ecological distance between the samples from each period, as measured by compositional turnover, reflects the degree of habitat heterogeneity. Turnover values are very similar for epiphytic assemblages from the earliest and the most recent period (ca 4.3 SD), but slightly higher for the second period (ca 4.8 SD), suggesting somewhat stronger differentiation of epiphytic communities during the 1970s. For the sediment assemblages, a lower habitat heterogeneity was recorded for the recent samples (12 SD) and those of period 2 (3.1 SD) than for the oldest ones (5.2 SD), corresponding to a decrease in gradient length of almost 40%. This indicates increased uniformity of conditions at the sediment-water interface.

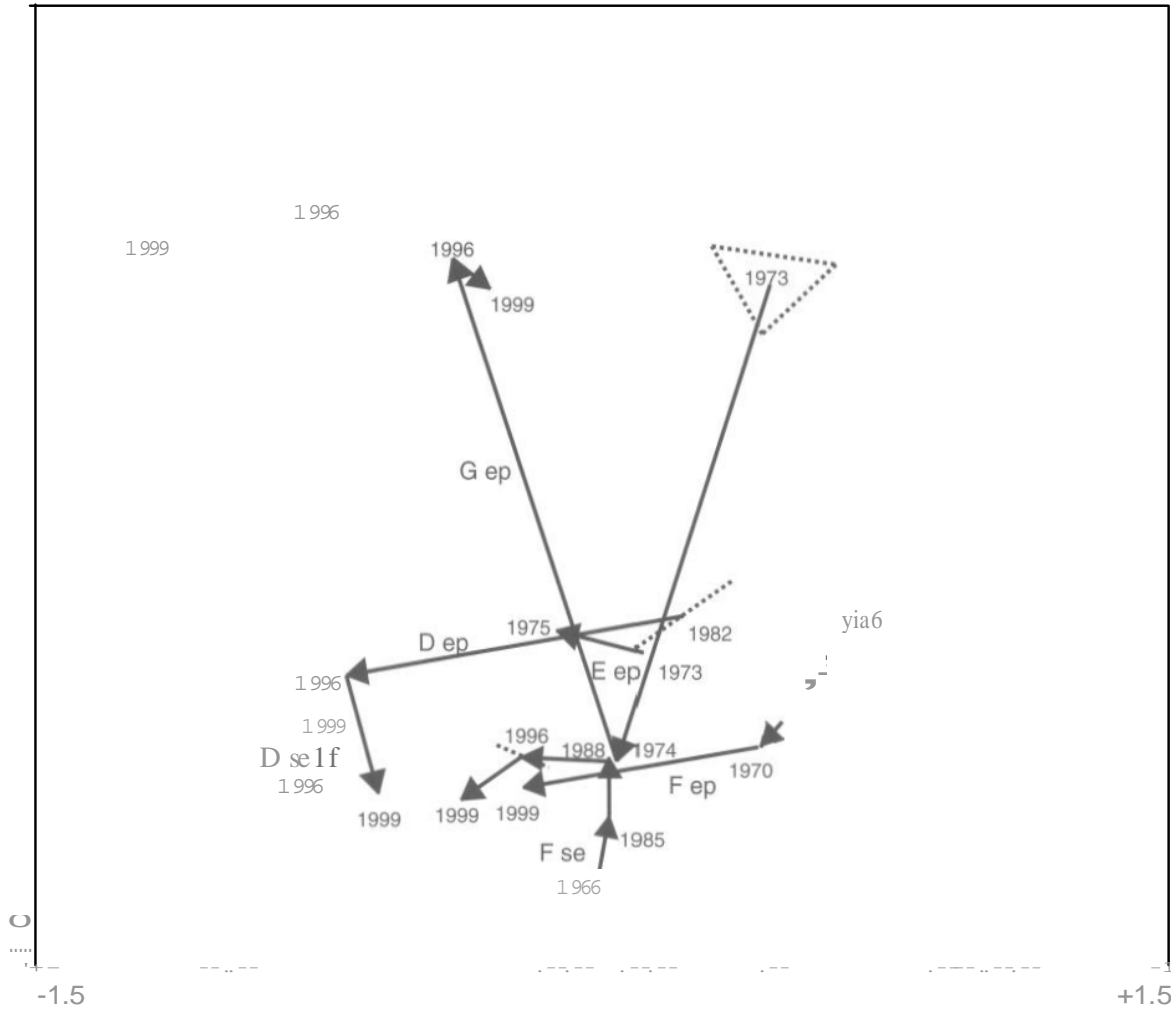


Figure 4. Ordination plot of diatom assemblages from sites D, E, and G (epiphytes) and F (free-living) in the CA ordination. Dotted lines connect samples from same site in different years. Dashed line indicates presumed correspondence between samples.

DISCUSSION

A comparison of present-day diatom assemblages from the modern 'inlagen' with their historical counterparts from the area points to significant changes. Contemporary diatom assemblages show little similarity to those of the mid-1800s up to the first decades of the 20th century. Diatoms from the latter period commonly occur in more calcareous dune slabs and lakes (e.g. Round, 1957, 1978a, b; Londo, 1967). Among them are several *Fragilariopsis* species. These are known to carry nitrogen-fixing endosymbionts and may be particularly indicative of nitrogen-limited yet phosphorus-rich conditions (Fairchild and Londo, 1984; Fairchild *et al.*, 1985; DeYoe *et al.*, 1992; Hofmann, 1994) or are considered sensitive to N enrichment (van Dam *et al.*, 1994; Schönfelder, 1997). Most abundant, however, was *Cocconeis plibbeiana* var. *equilata*, a common epiphyte proliferating in eutrophic conditions under a wide range of ionic

concentrations, but which seems to be limited by nitrogen (e.g. Hofmann, 1994). Conversely, most of the taxa showing an increase towards recent times have their optimum in hypereutrophic and organically polluted conditions. To some extent, these changes are reflected by abundance-weighted indicator values, in particular those relating to organic load. The representation of epiphytic species in sediment assemblages decreased markedly. In shallow lakes, this is usually related to the availability of hard substrates (e.g. Garrison and Wakeman, 2000) and represents a well-known signal of eutrophication-induced degradation of aquatic macrophyte vegetation (Moss, 1978, 1979, 1980). This is also likely to have taken place in the Fonteintjes, particularly in the permanent pools. Increased grazing by waterfowl may have also contributed to less submerged vegetation, while at sites with periodic inundation such as Fonteinljes intensification of mowing after 1978 caused hay production to drop rapidly, thus affecting substrate availability for epiphytes. Ordination shows that epiphytic assemblages differ most strongly from their reference composition. This may be due to a higher sensitivity of epiphytic taxa to the environmental changes that occurred, differences in time averaging between epiphyte and sediment assemblages, or additional variation caused by substrate bias (mostly *Platagium* or *Typha* for recent samples, vs. various hydrophytes for older ones). Although taxonomic richness, as such, does not appear to have changed, sediment assemblages are now more homogeneous indicating decreased habitat diversity. The protection offered to some of the pools by the establishment of the reserve and the management carried out so far have not prevented deterioration of habitat quality. In areas this size and with aquatic systems in particular, forest conservation is quite likely to meet with frustration (Moss, 2000).

As coastal dunes are particularly sensitive in their hydrology, this presents a first point of concern. Elsewhere, afforestation and shrinking of the dune surface, extraction of drinking water or increased drainage of adjacent polders has resulted in serious lowering of dune water tables (van Oijck and Grootjans, 1993). In the case of the Fonteintjes, the surrounding infiltration area is small and water levels respond strongly to variations in annual precipitation (Vanhecke, 1988, 1993), suggesting vulnerability to groundwater lowering. Depletion of the freshwater supply would lead to a stronger relative influence of salt water in the depressions. In spite of the sensitivity of diatoms as salinity indicators, no noticeable change in the salinity range of these coastal pools was detected, and marked hydrological changes seem unlikely. This agrees well with observations on the flooding frequency since 1966 (L. Vanhecke, personal communication). Some effects might also be expected from short-term variations in flooding and salinity due to variations in precipitation. Local conditions were particularly dry from 1970 to 1973, and the groundwater table only returned to a permanently high level in October 1974 (Vanhecke, 1993, 1994). Shifts in epiphytic assemblages at site G from 1973 to 1974 probably reflect this drier period.

The observed changes in epiphytic and sediment-associated communities are related to an increase of trophic status and enhanced availability of degradable organic matter. Although affecting epiphytic diatom communities at least since the mid-1970s, the onset of this process cannot be dated accurately for any of the depressions separately owing to the variation in local conditions and limited availability of samples. In some cases a rather later start seems likely. So far, it remains unclear whether changes in the vegetation of the depressions respond to alterations in external nutrient inputs, to natural processes, or to the management regime. This study indicates that the first of these should not be neglected. Whereas local impacts, such as coarse fish angling in pools B and C and partial infilling in depression E, are likely sources of enrichment for some pools, these do not account for the observed level of eutrophication. Among others, increased atmospheric nitrogen deposition and eutrophication are commonly recognized causes of eutrophication in coastal dunes (e.g. van Dijk, 1989; Koerselman, 1992; van Dijk and Grootjans, 1993). Yearly nitrogen deposition in the coastal area is estimated at no less than 20 to 26 kg ha⁻¹ (Van Gijsegem *et al.* 2000). With regard to the pools within the reserve, eutrophication may be particularly important as well. Due to a reduction in disturbance after fencing, the number of roosting ducks increased considerably in recent decades (J. Van Gompel, personal communication), showing peaks of up to 700 individuals in late summer and averages of 200-300 mallards during winter months since the 1980s. In

depression. Regular mowing resulted in reduced reed cover and more open water, also increasing attraction to water birds. Finally, internal nutrient sources need consideration, especially in the shallower depressions. As organic soil matter accumulates, the influence of the calcareous substrate is reduced and nutrient availability increases (Lammerts *et al.*, 1999). In ageing dune valleys some natural eutrophication therefore occurs. Vegetation changes induced by mowing since the late 1970s probably enhanced nutrient cycling further, i.e. through replacement of *Phragmites* by species with less persistent litter. Indications that eutrophication is still continuing make further study of its causes and installation of a proper monitoring programme essential. In view of the availability of historical data, inclusion of diatoms in such a programme would be appropriate.

The diatom evidence indicates a prevalence of rather nutrient-rich conditions for a considerable time in these pools. Although phosphorus was probably more often the (co-)limiting nutrient up to c. 1930, in view of the preponderance of *Cocconeis placentula* var. *euglypta* over *L. pithemia* spp., overall conditions were fairly P-eutrophic. Nowadays, phytoplanktonic assemblages with more than 50% *Cocconeis placentula* var. *euglypta* occur in Flemish standing waters generally at median TP concentrations of c. 70–200 µg L⁻¹ and Kjeldahl nitrogen values of 0.6–2 mg L⁻¹ (unpublished observations). Bennion (1994) calculated an annual mean TP optimum of 90 µg L⁻¹ for *Cocconeis placentula* in ponds in south-east England. Concentrations appear to have been similar to this in most coastal pools of the study area at the dawn of the 20th century. Availability of phosphorus in dune valleys decreases with the lime content of the soil or in the case of carbonate-rich seepage as more P is absorbed to calcium hydroxide compounds. In the case of the hrteintjes, however, phosphorus trapping by this mechanism may have been very efficient because of a high abundance of monovalent ions, reducing soil absorption capacity (Beltman *et al.*, 1992). The diatom assemblage of a single old *Orepa11ocfad11s* sample indicates that more nutrient-poor conditions were limited to less alkaline sub-aerial situations. The fairly high former nutrient status sets less severe overall standards for restoration initiatives than considered appropriate for meso-oligotrophic dune ponds and wet slacks (cf. Verdonchot and Janssen, 2000). To allow recovery of former diatom assemblages and maintenance of a diverse submerged vegetation, target levels slightly below 100 µg L⁻¹ TP and 1 mg L⁻¹ Kjeldahl N appear sufficient. These levels are markedly exceeded in all pools, except G.

In order to improve opportunities for formerly characteristic sensitive species, management should aim at restoring moderately eutrophic conditions in general, and intensifying processes that lead to small-scale habitat diversification by reducing local nutrient availability (see e.g. Jones and Therington, 1992; Lammerts *et al.*, 1992, 1999). Clearly, this cannot be left to naturally occurring dune processes for which this is fixed and spatially constrained setting leaves very little opportunity. Measures are needed to reduce external inputs, including deposition from nearby agricultural sources, as well as to remove excessive nutrients available for internal cycling. Obviously, ground-baiting for angling and bird feeding in the permanent pools open to the public should be stopped, while fish populations need to be managed accordingly. In the periodically inundated parts of the depressions, removing organic deposits is likely to be the most effective measure. Mowing, carried out in parts of the depressions D, F, and I, is not very effective in removing nitrogen and has been unable to stop the advance of nutrient enrichment. Vanhecke (1994) proposed less frequent mowing, allowing denser reed growth, as a measure to safeguard *Potamogeton amplifolius* from drought stress and bird grazing. In view of the eutrophication process, a more differentiated management strategy is warranted, including local removal of topsoil down to the substrate. If carried out on a rotational basis, habitat differentiation can be maximised and viable populations of species benefiting from earlier succession stages, e.g. *Potamogeton amplifolius* (Bruin, 1997) and charophytes, maintained. The relative importance of the water-bird population to the nutrient balance of the ponds needs further examination. If necessary, a more balanced situation might be sought by improving alternative roosting possibilities.

The results further illustrate the usefulness of collection material as a valid and easily accessible source of historical information. Compared with sediment core-based studies, such an approach suffers much less of

the claimed disadvantage presented by ... the time and expense that is required for the taking, processing, dating, analysis and interpretation ... necessary for such a study' (Moss *et al.* 1996, p. 308). Diatoms on herbarium macrophytes provide a means of obtaining information on an array of sites within a region, albeit perhaps with a smaller time window than from sediment cores. Moreover, the technique allows a dating precision matched only by varved sediments and can be applied to any water body, regardless of the quality of its depositional record. Studies carried out so far do not suggest that potential substrate specificity of epiphytic communities significantly hinders environmental inferences, although it may be prudent to focus on sediment assemblages in view of their more integrative nature.

ACKNOWLEDGEMENTS

Most of the data used in this paper were obtained in the course of the studies K/IN/95 DP195.02 commissioned by the Institute of Nature Conservation to the Biology Department of the University of Antwerpen, RUCA, and VLINA C97/02, grant-aided by the Flemish Community to this department, UIA and RUCA. The National Botanic Garden (Meise) and the Laboratory of Gent are acknowledged for allowing the use of their collections. The Vlaamse Milieumaatschappij provided the water chemistry data. F. Oesehemaeker provided bird census reports. Thanks are due as well to 1. Vanhecke, J. Van Gompel, P. Gohlgebeur, P. Compère, H. Stieperaere, P. Bogaert, D. Van Pelt, J. Rommcs, P. Van Avermaet and K. Devos, for various contributions. Technical assistance by J. Packet was greatly appreciated. The paper benefited considerably from comments of L. Vanhede, S. Provoost and two anonymous referees.

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