Palaeolimnology without a core: 153 years of diatoms and cultural environmental change in a shallow lowland lake (Belgium)

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Abstract: Time series of diatom assemblage composition can be obtained from samples of various collection materials. This allows assessment of 'more natural' conditions and their temporal variability in shallow lakes and ponds, similar to traditional core–based palaeolimnology. Such information is useful to underpin restoration targets that are ecologically relevant and that conform to legal requirements posed by the European Water Framework Directive. Using sediment samples from herbarium macrophytes and other sources, historical conditions are documented for a shallow man-made soft–water lake in lower Belgium (Kraenepoel, Aalter). Both assemblage composition and diatom-inferred water chemistry varied considerably from 1853 to the first half of the 20th c. The lake was used for pisciculture during this time. From this situation, two alternatives are envisaged to determine the lake's ecological potential, depending on whether it is kept hydrologically isolated or reconnected to the brook that supplied its water originally. Later in the 20th c., inflow of polluted water and altered management caused considerable eutrophication up to the time when restoration measures were undertaken (1999–2002). Since then both diatom-inferred and measured physical-chemical conditions have improved considerably, even to the point of approaching those in the early 20th c. Post-restoration sediment assemblages reflect some functional and structural rehabilitation of the lake ecosystem, but return to a former species composition was limited. The most recent observations (2006) suggest a possible reversal of the recovery process warranting further vigilance. The potential of using sediment assemblages for monitoring lentic water bodies is highlighted.

Key words: Bacillariophyta, Water Framework Directive, ecological potential, soft water, restoration, phytobenthos, sediment assemblages, eutrophication

Introduction

In the agro–industrial landscape of today's Europe, shallow lowland lakes and ponds are among the ecosystems posing the most considerable challenges to sustaining a variety of societal services. During the second half of the 20th c., widespread ecological decline of such water bodies became obvious, giving rise to an equally general interest in their rehabilitation. Nowadays, this is embodied by the European Water Framework Directive (CEC 2000; WFD), which sets near-natural conditions as the benchmark for safeguarding biodiversity values and human amenities. According to the WFD, basic restoration targets – defined as 'good status' – should deviate only slightly from such 'reference conditions' which encompass certain aspects of selected biota, including the phytobenthos, and their supporting physical-chemical and hydromorphological conditions. Reference conditions are determined at the level of water types for natural water bodies from spatial networks, retrospective data, models or expert opinion. However, shallow water bodies excel in concealing their natural background. The prime reason for this is the sheer absence of reliable references sites in large parts of Europe, but properties inherent to their very nature are also at the heart of the problem. Shallowness, a large catchment to surface ratio, small–scale variation in geohydrology and strong interactions between limnological and biological conditions all result in a high degree of spatial variation, complex temporal dynamics and individuality in pressure–response relations (cf. Moss et al. 1996, Cremer et al. 2004). Moreover, succession can be swift and overall lifespan fairly short due to infilling and other geomorphological processes. Although there are notable exceptions (e.g. Moss 1979, Haworth et al. 1996, Sayer &

ROBERTS 2001), possibilities for sediment–based palaeolimnology may be restrained by poor stratigraphic resolution due to sediment mixing or traditional management regimes that impede the formation of a continuous, undisturbed sediment record. Artificial and hydromorphologically modified shallow lakes perhaps present an even greater challenge, as conditions often intentionally differ from a pristine situation throughout their history and the required base line is a water-body specific 'ecological potential' that accounts for some disturbances ensuing from the specific hydromorphology imposed by priority uses. As such, their restoration target may correspond to the good status required for the most pertinent natural lake-water type or deviate ± considerably due to societal restraints. So far, reference conditions for natural, often stratified lakes have drawn most attention (BENNION et al. 2003, 2004, LYCHE SOLHEIM 2005, LEIRA et al. 2006, CARDOSO et al. 2007) and ecological potential was addressed more sparingly (e.g. LAMMENS et al. 2008), even though it probably pertains to a majority of lowland water bodies.

Pragmatically, diatoms can be considered to represent the quality element phytobenthos as required by the WFD (KELLY et al. 2008) and as such they are singled out in the majority of member states. Consequently, data on former species composition and structure of benthic diatom assemblages can be used to underpin phytobenthos assessment and basic restoration goals. Various collection materials can serve to obtain such information (e.g. VAN DAM & KOOYMAN–VAN BLOKLAND 1978, BATTARBEE 1981, VAN DAM & MERTENS 1993, SAYER et al. 1999, DENYS 2000, 2003, SHIREY et al. 2008). Moreover, application of appropriate diatom–inference models allows estimation of accompanying values of several key limnological variables (TER BRAAK & VAN DAM 1989, DENYS 2006, 2007). As most collection materials date from the last two centuries, they will not necessarily reveal true 'natural' background (ANDERSON et al. 1995, TAYLOR et al. 2006, HÜBENER et al. 2009), but nevertheless this time perspective may suffice to improve knowledge on suitable restoration targets, i.e. at least good ecological potential, for many artificial and heavily modified shallow lakes and ponds.

Within this framework, I use a time series of sediment diatom assemblages obtained from herbarium macrophytes as well as other types of samples, to document biological and environmental changes from 1853 to 2006 in a small artificial lake (or large pond) that was recently subjected to restoration measures.

Materials and Methods

The study site, 'Lake Kraenepoel' (51°07'64" N, 3°48'04" E; altitude 10.8 m TAW), is a very shallow (max. 1.5 m) c 22 ha large basin near the town of Aalter in the province of Eastern Flanders (Belgium; Fig. 1). It was probably created in the 16th c. and originally used for fish farming. To allow this, water was provided by a small diverted brook entering the lake from the south. Fish farming was not practiced with the same endeavor throughout its history, and after being interrupted for an unknown length of time it was resumed near the beginning of the 19th c. when the water level was raised. Due to its situation in an area of shallow sandy soils with little agriculture and mainly heath and woodland, it possessed a rich soft–water vegetation at this time (incl. e.g. *Deschampsia setacea*, *Lobelia dortmanna*, *Luronium natans*, *Littorella uniflora*, *Myriophyllum alterniflorum*; VAN WICHELEN et al. 2007). Not unlikely, this vegetation initially benefited to some extent from drawdown events effected as part of traditional

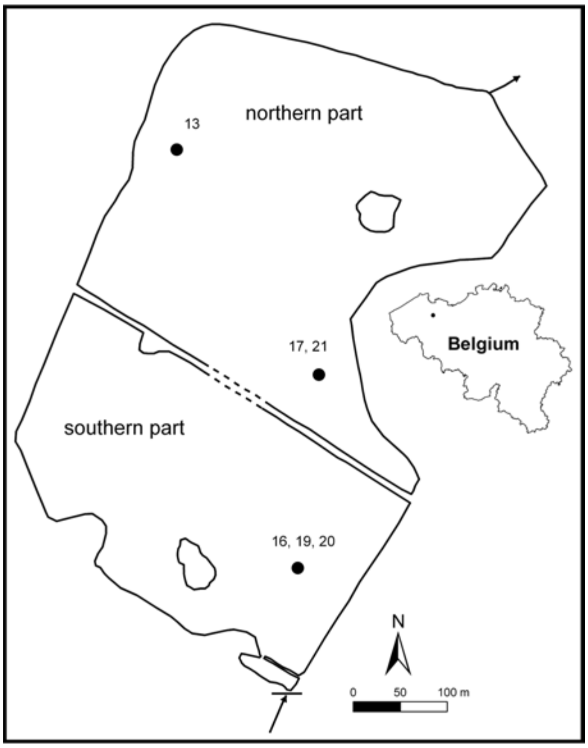


Fig. 1. Sketch of the Kraenepoel with sampling sites in 1970 (nr 13), 1999 (nr 19), 2003 (nrs 16, 17) and 2006 (nrs 20, 21). Arrows indicate inlet (now blocked) and plugged outlet used to adjust the water level. Dashed lines mark part of the dam presently flooding in winter.

pisciculture. The presence of many species which were by then lacking elsewhere in Eastern Flanders due to lack of suitable habitat, turned the Kraenepoel into a popular excursion and collecting site for naturalists (Vander Meersch 1874, Mac Leod 1894, Van Oye 1941). Gradually, recreation (bathing, angling, hunting) also stepped up. Decreased abundance of *Lobelia* in the 1920s signaled the onset of deterioration, possibly in line with gradually intensified fish farming, which at least later on included substantial feeding. Pisciculture was halted altogether in the mid fifties and the water level was now kept permanently as high as possible. A dam was constructed in 1957 which divided the lake into a southern and a northern part but still allowed water to flow through in case of excess. Initially, large stands of reeds (*Phragmites*, *Scirpus*) and nymphaeids developed in the southern part, whereas the northern part remained more open. The latter part was drained for local maintenance in 1969 and again in the winter of 1984/1985. By the nineties, all of the more demanding soft–water macrophytes had disappeared. The southern part, heavily stocked with coarse fish for angling, had become turbid and almost devoid of aquatic vegetation, whereas nymphaeids and narrow–leaved potamids were still present in the northern basin. By now, biodiversity conservation was the key issue and restoration started in 2000. Measures were carried out in two phases. At first, the inflow of water from the brook was terminated, restricting water supply to ground water and precipitation. The entire lake was drained, benthivorous fish were removed and the northern part largely dredged. In 2002, the southern part was drained and most of the organic sediments were removed here as well, as were some remaining benthivorous fish. On both occasions the lake was allowed to refill spontaneously and stocked with juvenile pike. These measures resulted in considerable water-quality changes, most importantly much reduced turbidity in the southern part and generally lower conductivity (c 120 µS cm^{-1}) and phosphorus levels (SRP c 20 µg l^{-1}). An initial drop in pH followed refilling (Van Wichelen et al. 2007). A marked expansion of submerged vegetation occurred, including e.g. *Elatine hexandra*, *Eleocharis acicularis, Pilularia globulifera* and charophytes (Denys 2008; Van Wichelen et al. 2008) and zooplankton composition and biomass changed concomitantly (Louette et al. 2008).

Sediment samples were obtained from 15 dried herbarium specimens of macrophytes collected from the lake between 1853 and 1983 (Table 1). More recent surface sediment samples were collected at one site in the southern part on 16/7/1999 (nr 19) and at two sites, one in each part, on 3/9/2003 and 5/9/2006 (Fig. 1, nrs 16–17 and 20–21). A plexiglass coring tube (internal diameter 3.4 cm) was used to retrieve the sediment/water interface and some of the surface material (c. 2 mm) was collected by siphoning. These samples were preserved with dilute formaldehyde. An additional sample (nr 15) was prepared by combining subsamples from two formalin-preserved zooplankton samples with some sediment collected on 19/7/1999 and 24/8/1999 in the northern part. These were taken with a Lund tube at multiple sites and had been filtered with a 30 µm mesh plankton net.

All samples were treated with HCl (0.1 N) and oxidized with 30% H_2O_2 at 80 °C, followed by repeated settling and rinsing with demineralized water to remove solutes. Diatom slides (40 x 22 mm cover glasses) were prepared using Naphrax®. Counts of 500 valves were made along randomly chosen transects at 1000 times magnification using Olympus BX50 and BX51 microscopes with DIC. Presence of additional taxa was noted by scanning the slides at 1000 and 400 times magnification using a stopping rule. All of these were counted as 0.1 valve.

Identifications mainly followed standard reference works (Krammer 1992, 1997a, b, Lange–Bertalot & Moser 1994, Lange–Bertalot & Metzeltin 1996, Krammer & Lange–Bertalot 1999–2004). Phenodemes of the *Sellaphora pupula* complex were only minor constituents and not discriminated consistently, with exception of a few attributed to species rank.

Planktonic taxa and indicators of nutrient-poor conditions were selected mainly according to van Dam et al. (1994), Lange–Bertalot & Steindorf (1996) and above-mentioned floras. Taxa were attributed to Red List (RL) categories according to Lange–Bertalot & Steindorf (1996). Categories 2, 3 and G were combined as ‘endangered’, very rare and expected taxa were grouped as ‘rare’.

Ordinations were performed using CANOCO 4.5 (ter Braak & Šmilauer 2002). As the species gradient length in a detrended correspondence analysis (DCA, detrending by segments) was fairly large (3.2 SD), CA of square–root–transformed relative abundance data of all taxa (rare taxa down–weighted), was used to summarize major differences in assemblage composition between samples. Bray–Curtis distances (Sd) between samples were calculated with the PC-ORD 5.0 package (McCune & Mefford 1999) using all taxa with an abundance > 0.2 % in at least one sample.

I applied diatom inference models developed for littoral sediment assemblages of ponds and lakes in lower Belgium (Denys 2006) to estimate former pH, dissolved organic carbon (DIC), alkalinity and sodium to all samples, and models for calcium, silicate, chemical oxygen demand (COD) and potential gross oxygen production (pGOP) to samples with diatom-inferred pH > 6.5. All reconstructions are for median values of the vegetation period (May – November) and inferred values are reported with back–transformed sample–specific bootstrap errors. The C^2 1.3 program (Juggins 2003) was used to implement these models.

Table 1. Specifications of herbarium specimens from the Kraenepoel that provided sediment samples.

	Date	Plant species	Collection	Part of pool	Specifications
1	8/1853	*Scirpus fluitans* L.	BR nr 1036985, Coll. Coemans	-	'β *terrestris'*, 'bords du Kraenpoel'
2	27/8/1863	*Lobelia dortmanna* L.	BR nr 1029946, Herb. J.E. Bommer	-	'Etang d'Aeltre'
3	15/7/1872	*Lobelia dortmanna* L.	BR nr 1029977, Herb. L. et V. Coomans	-	'Aeltre – Etang'
4	7/1873	*Lobelia dortmanna* L.	BR nr 1029932 Herb. E. Vandermeersch	-	'Etangs de Bellem'
5	20/6/1881	*Littorella uniflora* (L.) ASCHERS.	BR nr 1036401 Herb. Wodon-Rousseau	-	'Kraenpoel'
6	8/1882	*Littorella uniflora* (L.) ASCHERS.	BR nr 1036309 Herb. Jules Henry	-	'Kranenpoel'
7	19/7/1883	*Hypericum elodes* L.	BR nr 1036212 Herb. Louis Magnel	-	' Bords du Kranepoel Aeltre'
8	7/1893	*Lobelia dortmanna* L.	BR nr 1029975, Herb. M. Stuyvaert	-	'bords de l'étang Kraenepoel, Bellem près Aeltre'
9	15/7/1901	*Lobelia dortmanna* L.	BR nr 1029957, Coll. M. Goetghebuer	-	'Kraenpoel à Bellem'
10	21/7/1923	*Hypericum elodes* L.	BR nr 1036245, Herb. Isaacson	-	'étang Kraenpoel'
11	14/7/1924	*Eleocharis multicaulis* (SMITH) DESV.	BR nr 1036112, Herb. Isaacson	-	'bords du Kraenpoel Bellem'
12	11/10/1969	*Eleocharis acicularis* (L.) ROEM. ET SCHULT.	GENT, Herb. H. Stieperaere	northern part	' Kranepoel, Bellem', deepest part of drained pond
13	19/9/1970	*Elatine hexandra* (LAPIERRE) DC	GENT Herb. H. Stieperaere	northern part	'Kranepoel, Aalter, zwembad'
14	11/8/1983	*Elatine hexandra* (LAPIERRE) DC	GENT Verz. Pierre Van Vooren	northern part	'de Kraenepoel, Aalter', drying shore
18	26/7/1969	*Hypericum elodes* L.	BR nr 1036255, Herb. Jan Van Den Haute	southern part	'Kranepoel, Bellem'

Results

All 461 taxa observed in the 21 samples are listed in Table S1 (http://fottea.czechphycology.cz). Fig. 2 shows some of the more noteworthy ones. Many of them are nowadays uncommon in lower Belgium and according to the RL, 47 (10.2%) are rare, 98 (21.3%) could be endangered and 51 (11.1 %) appear to be decreasing; two are listed as almost extinct in the region. *Eunotia* (37 entities), *Navicula* (31), *Nitzschia* (59) and *Pinnularia* (66) were the genera represented by the highest number of morphotaxa, with *Achnanthidium* (3.3%), *Fragilariforma* (2.7%), *Encyonopsis* (1.8 %) and *Staurosira* (1.7%) reaching the highest average abundance. Based on differences in management, water quality and morphology (division of the lake into two parts), which were also manifest from changes in overall assemblage composition (Fig. 3), two periods separated by a sampling hiatus of more than 40 years were distinguished: 1. from 1853 to 1924 and 2. from 1969 to 2006.

1853 to 1924

All samples from this period presented very similar positive scores on CA axis 1 (Fig. 3). Overall, *Achnanthidium minutissimum*, *Brachysira microcephala*, *Encyonopsis subminuta* and *Fragilariaforma exiguiformis* were well represented (Fig. 4), with *Brachysira garrensis*, *Eunotia implicata*, *Navicula radiosa* and *Tabellaria flocculosa* as minor but regular

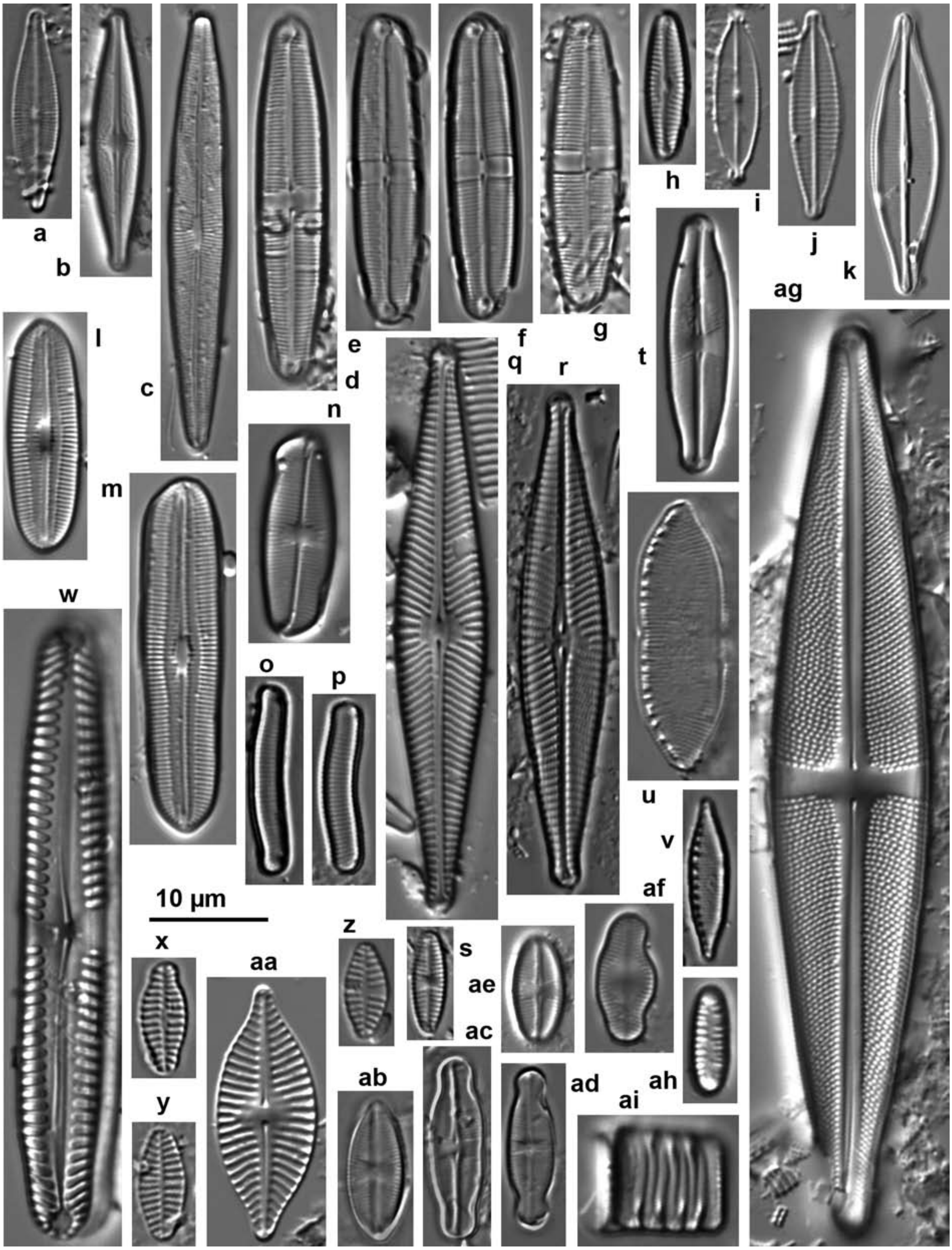


Fig. 2. Selection of notable diatom taxa from the Kraenepoel: (a) *Brachysira garrensis*; (b) *B. microcephala*, (c) B. procera; (d–g) *Caloneis borealis*; (h) *Chamaepinnularia* sp. nr. 11; (i) *Craticula dissociata*; (j) *C. submolesta*; (k) *C. vixnegligenda*; (l–m) *Diploneis petersenii*; (n) *Eucocconeis alpestris*; (o) *Eunotia compacta* (narrow form); (p) *Eunotia kruegeri*; (q–r) *Navicula radiosiola*; (s) *Navicula obsoleta*; (t) *Naviculadicta stauroneoides*; (u) *Nitzschia aerophila*; (v) *Nitzschia* cf. *bryophila*; (w) *Pinnularia tirolensis*; (x–y) *Planothidium granum*; (z) *P. minutissimum*; (aa) *P. schwabei*; (ab) *Psammothidium altaicum*; (ac–ad) *P. perpusillum*; (ae) *P. scoticum*; (af) *P. ventralis*; (ag) *Stauroneis angustilancea*; (ah–ai) *Tabellaria binalis* var. *elliptica*.

assemblage constituents. Several taxa were observed almost exclusively in samples from this period, e.g. the capitate phenodeme of *Achnanthidium minutissimum*, *Caloneis undulata*, *Diploneis petersenii*, *Eucocconeis alpestris*, *Navicula radiosiola*, *Psammothidium perpussilum* and *Stauroneis angustilancea*. Throughout, 50 % or more of all valves belonged to taxa considered typical of ± oligotrophic conditions and RL taxa (mostly considered endangered) easily attained a relative abundance of 20%.

Assemblage composition was, however, not entirely homogeneous. The two oldest samples were set apart by an abundant occurrence of either *Eunotia exigua*, *Fallacia vitrea*, and *Staurosira venter* (in 1853) or *Eunotia incisa* (80.2%) and *Tabellaria binalis* var. *elliptica* (in 1863); *Frustulia crassinervia* was slightly more abundant in both of these samples, as well. Due to its very deviating composition, the 1863 sample represented an outlier with an extremely high CA axis 2 score. All aforementioned taxa were virtually absent in samples collected 10 years later, which presented a high proportion of *Nitzschia fonticola*, as well as some *Navicula radiosa* and capitate *Achnanthidium minutissimum*. Another 10 years later, these taxa had dwindled again and *Achnanthidium minutissimum* predominated. A very narrow phenodeme of the latter, usually assumed to occur at lower nutrient levels, characterized the sample from 1893. In the early 1920s *Encyonopsis subminuta* had almost disappeared and *Eunotia implicata*, *E. naegelii*, *Nitzschia gracilis* and *Tabellaria flocculosa* attained their highest abundance. Table 3 illustrates well that more important changes in relative assemblage composition occurred at a decadal scale; samples from consecutive years were rather similar (Sd 26–39%).

These compositional changes are particularly well reflected by the values for inferred pH and DIC, or its substitute alkalinity (Fig. 5). Altogether, slightly to distinctly acid, poorly buffered water is indicated at the beginning as well as at the end of this period, in contrast to circumneutral conditions somewhat richer in bicarbonate (alkalinity up to c 0.2 mmol l^{-1}) from 1872 to 1901. Diatom-inferred pH reached a minimum of 4.9 in 1863. The reconstructions also hint at some variation in calcium, and especially a decline in silicate after 1873 and a rise in COD to close to 100 mg l^{-1} in the 1920s, but these possible trends remained within the range of sample-specific errors. According to the low values inferred for pGOP, phytoplankton productivity was always quite limited.

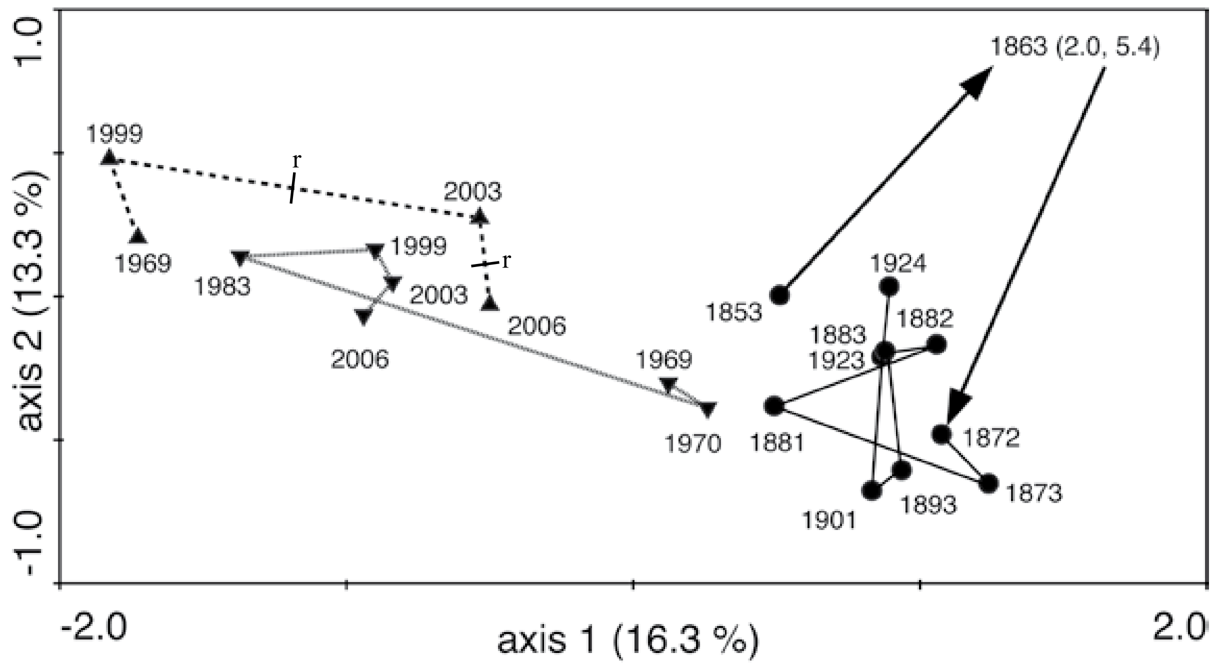


Fig. 3. CA ordination plot of all samples (axes 1 and 2), with indication of the year of sampling and time trajectories. Circles, full line: 1853–1924; downward triangles, dotted line, N: 1969–2006 northern part; upward triangles, dashed line, S: 1969–2006 southern part. Completion of restoration measures is indicated by perpendicular line segments marked r.

Table 2. Bray-Curtis percentage distance (Sd; 0% identical composition, 100% no agreement) between all sediment assemblages (see text and Table 1 for sample numbers; -N northern part, -S southern part).

Nr.		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	Date	1853	1863	1872	1873	1881	1882	1883	1893	1901	1923	1924	1969–N	1970–N	1983–N	1999–N	2003–N	2006–N	1969–S	1999–S	2003–S
2	1863	94	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	1872	66	98	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	1873	72	99	26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	1881	59	98	48	62	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	1882	59	94	44	56	29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	1883	58	97	57	70	29	26	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	1893	68	99	51	61	42	40	47	-	-	-	-	-	-	-	-	-	-	-	-	-
9	1901	66	100	37	48	31	28	38	38	-	-	-	-	-	-	-	-	-	-	-	-
10	1923	66	97	75	81	73	64	59	74	76	-	-	-	-	-	-	-	-	-	-	-
11	1924	63	96	68	78	55	44	45	52	55	39	-	-	-	-	-	-	-	-	-	-
12	1969-N	56	99	54	55	53	59	63	60	52	70	75	-	-	-	-	-	-	-	-	-
13	1970-N	60	99	65	77	50	51	48	56	56	66	51	57	-	-	-	-	-	-	-	-
14	1983-N	76	99	86	86	82	86	84	85	85	88	86	65	79	-	-	-	-	-	-	-
15	1999-N	64	98	79	82	70	81	81	83	80	86	83	52	75	47	-	-	-	-	-	-
16	2003-N	58	99	71	76	61	73	71	76	72	79	79	47	65	51	40	-	-	-	-	-
17	2006-N	76	99	76	85	51	57	51	66	55	83	66	71	59	69	76	62	-	-	-	-
18	1969-S	73	99	89	90	78	91	89	93	89	95	92	68	80	58	57	58	76	-	-	-
19	1999-S	87	99	94	94	92	94	94	95	94	93	94	78	89	75	71	73	83	77	-	-
20	2003-S	62	97	81	84	79	83	82	85	82	85	84	75	72	80	75	66	81	83	85	-
21	2006-S	66	99	67	78	43	53	52	62	51	79	61	66	52	77	71	52	42	77	87	61

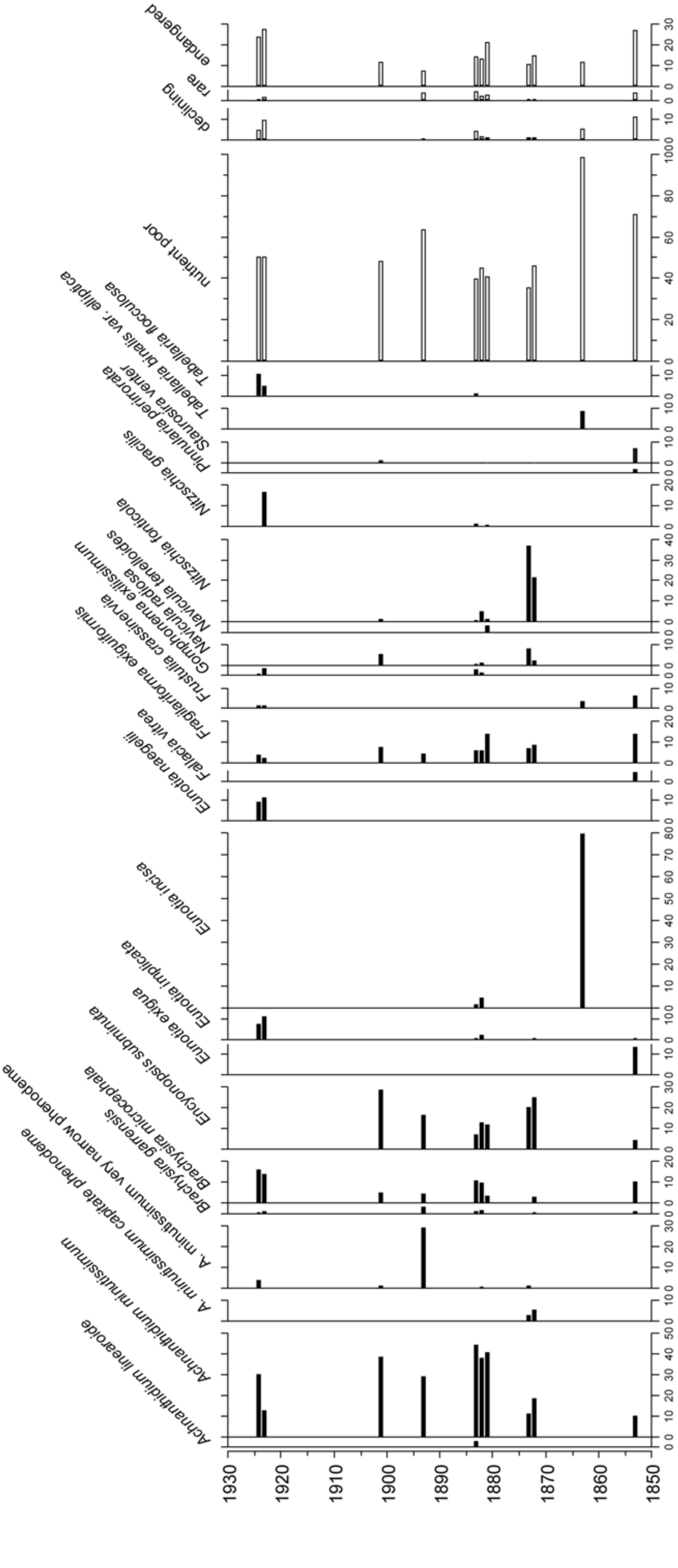


Fig. 4. Relative abundance of taxa with at least 3% in a sample and total relative abundance of taxa indicating nutrient-poor conditions and RL categories from 1853 to 1924.

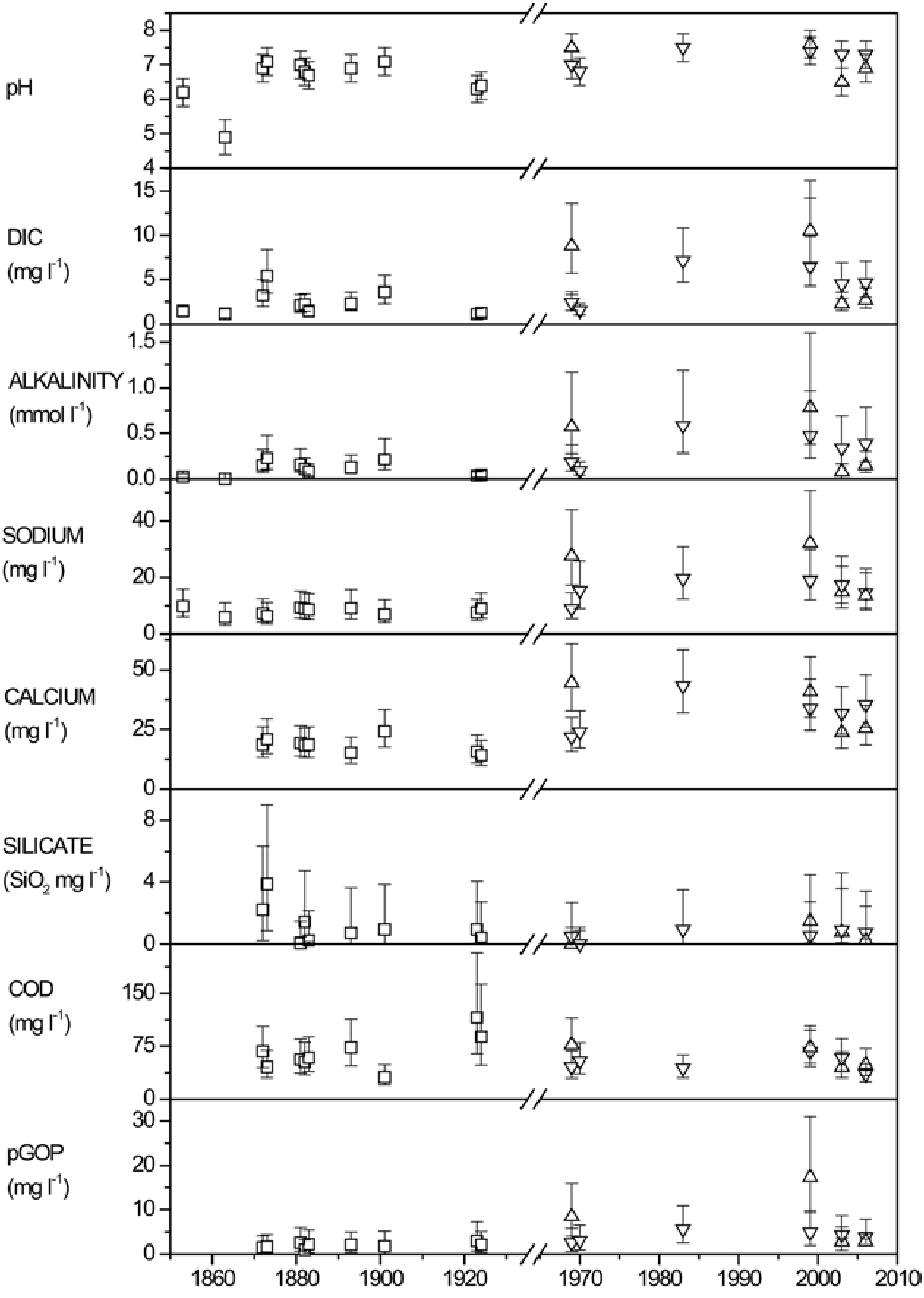
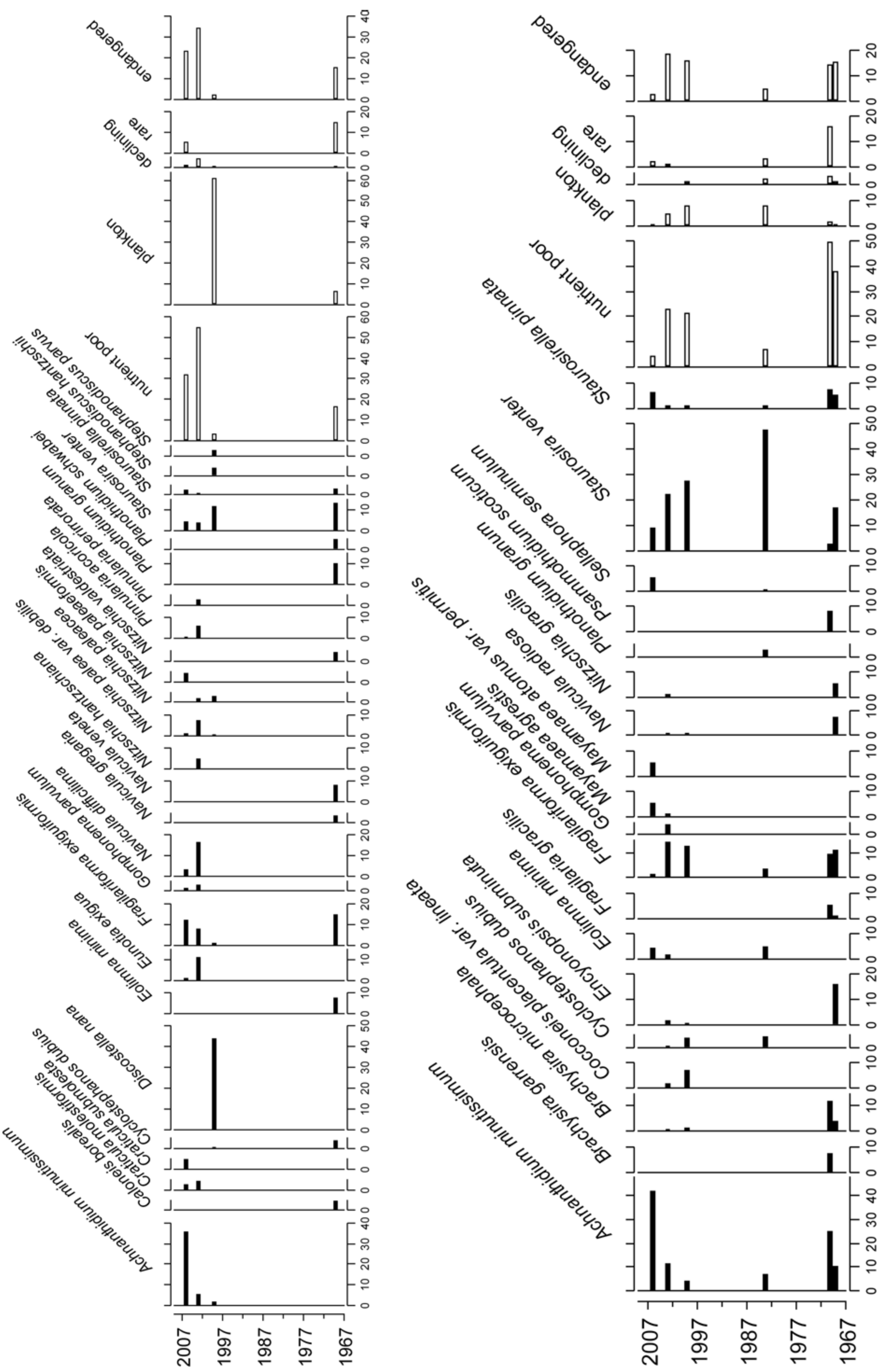


Fig. 5. Diatom-inferred values for pH, DIC, alkalinity, sodium, calcium, silicate, COD and pGOP with their sample-specific errors. Squares: 1853–1924; downward triangles: 1969–2006 northern part; upward triangles: 1969–2006 southern part.


endangered
rare
declining
plankton
nutrient poor
Staurosirella pinnata
Staurosira venter
Sellaphora seminulum
Psammothidium scoticum
Planothidium granum
Nitzschia radiosa
Navicula atomus var. permitis
Mayamaea agrestis
Eolimna minima
Encyonopsis subminuta
Cyclostephanos dubius
Cocconeis placentula var. lineata
Brachysira garrensis
Achnanthidium minutissimum
Discostella nana
Eunotia exigua
2007
1997
1987
1977
1967

1969 to 2006

For this period, the diatom record of the northern part was somewhat more extensive (Fig. 6). Compared to the older samples, *Staurosira venter* became more abundant prior to the restoration measures. Initially, *Achnanthidium minutissimum*, *Brachysira* spp., *Encyonopsis subminuta*, *Fragilariforma exiguiformis*, *Navicula radiosa* and *Psammothidium scoticum* also occurred with notable abundances, but they all had declined by the 1980s. *Cocconeis placentula* var. *lineata*, the centric *Cyclostephanos dubius, Eolimna minima* and *Planothidium granum* modestly marked the samples from 1983 and 1999. The total percentage of ± oligotraphentic taxa dropped noticeably, from values which were initially similar to those in the preceding period to only slightly more than 20% before restoration. The proportion of planktonic taxa increased to almost 10%. Very little happened shortly after measures were taken, but by 2006 *Achnanthidium minutissimum* showed a strong expansion, whereas *Fragilariforma exiguiformis* and *Staurosira venter* had declined. Several small naviculoid taxa (*Eolimna minima*, *Mayamaea* spp., *Sellaphora seminulum*), reputed to indicate organic pollution, increased alongside and a more catholic assemblage with poor representation of RL taxa arose. The CA time trajectory depicts the progressive deviation from the previous period, followed by very limited recovery following restoration (Fig. 3). In general, dissimilarity to samples from 1881 to 1924 was higher in 2003 (Sd usually > 70%) than in 2006, when Sd was only 51% in some cases. The discrepancy with the assemblage from 1853 was somewhat less in 2003 (Sd 58%) but no resemblance at all was attained compared to 1863 (Table 2).

Estimates of DIC, alkalinity, sodium and calcium from the 1980s to late 1990s were at least double those for earlier times (Fig. 5), whereas pGOP may also have increased slightly. Values for all reconstructed variables did not change markedly in the years following restoration, although a slight decrease of DIC, alkalinity, COD and perhaps sodium might be suggested.

Only one sediment sample from the southern part could be retrieved from herbarium material for this period. This sample from 1969 showed a diverse assemblage with *Fragilariaforma exiguiformis* and *Staurosira venter* as the most prominent taxa, but *Planothidium granum*, *Navicula veneta* and *Eolimna minima* were also quite well represented (Fig. 7). Notable as well were *Cyclostephanos dubius*, *Navicula gregaria*, *Nitzschia valdestriata*, *Planothidium schwabei* (usually reported as *P. delicatulum* (Kütz.) Round et Bukht.) and the 'forgotten' species *Caloneis borealis*. Except for the latter, these are eutraphentic taxa which are absent from the older samples, whilst less abundant in the corresponding sample from the northern basin. Compared to this sample, the proportion of taxa from nutrient–poor conditions was only half as high (17%). Also, the percentage of planktonic taxa, although still a modest 7%, was higher. By 1999 the picture had become quite different again. The thinly silicified *Discostella nana* (previously often reported incorrectly as the brackish–marine species *Thalassiosira pseudonana* Hasle et Heimdal, Chang & Chang–Schneider 2008, Chang 2009) now attained almost 50 %. Associated with it were mainly *Staurosira venter*, *Stephanodiscus hantzschii* and *S. parvus* which are also planktonic, and some *Nitzschia paleacea*. Overall, 61% of all valves belon+ged to planktonic taxa and more oligotraphentic or RL taxa were hardly present. The consequences of the restoration measures were much more striking than in the northern part. *Discostella parva* and the *Stephanodiscus* spp. disappeared entirely and the abundance of *Cyclostephanos dubius* and *Staurosira venter* also dropped considerably. *Eunotia exigua*, *Gomphonema parvulum*, *Navicula difficilima*, *Nitzschia hantzschiana*, *N. palea* var. *debilis* and some small *Pinnularia* species made a short–lived appearance, reflecting the transient occurrence of acid as well as more subaerial conditions. *Achnanthidium minutissimum*, *Fragilariforma exiguiformis* and *Craticula molestiformis* also expanded at the expense of the plankton, but their increase continued up to 2006. *Achnanthidium minutissimum* predominated in the most recent sample. Two species from more acid waters, *Nitzschia paleaeformis* and *Craticula submolesta*, were recent additions. By 2006, the recovery of taxa from nutrient–poor conditions was not

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Fig. 6. Relative abundance of taxa with at least 3% in a sample and total relative abundance of taxa indicating nutrient-poor conditions and RL categories for the northern part from 1969 to 2006. *(left column)*

Fig. 7. Relative abundance of taxa with at least 3% in a sample and total relative abundance of taxa indicating nutrient-poor conditions and RL categories for the southern part from 1969 to 2006. *(right column)*

as evident anymore as in 2003. Similar to the increase in the proportion of endangered taxa, it resulted mainly from taxa associated with an acid-subaerial situation.

Fig. 3 shows that assemblage composition in both basins was quite distinct in 1969 and that the most extreme departure from former conditions evolved in the southern part. Nevertheless, return to a former assemblage composition after completion of the restoration efforts was also more distinct in this part, albeit far from complete. As in the northern part, Sd values were substantial and did not decrease relative to the earliest period from 2003 to 2006, but similarity to samples from 1881 to 1924 did increase with 6 to 36% resulting in a minimum Sd of 43%. (Table 2).

Diatom-inferred values for 1969 of DIC, alkalinity, sodium, calcium and possibly also pGOP were higher in the southern part than in the northern half (Fig. 4). A very high phytoplankton productivity was especially evident in 1999, in line with the predominance of this group in the sediment assemblage. Immediately after restoration, all variables related to buffering status showed a notable decrease; inferred pH dropped by almost a unit to 6.5 and alkalinity was reduced to c 0.1 mmol l^{-1}. The demise of the phytoplankton was highlighted by a tenfold reduction of pGOP. Values inferred for the other variables tended to decline slightly as well, and by 2006 all appeared to be at a level similar to the late 19th – early 20th C, perhaps with calcium and sodium still somewhat in excess.

Discussion

Some of the variation in diatom assemblage composition between the different samples undoubtedly can be attributed to very local conditions. Further analysis of 'replicate' samples could to some extent help to address issues of intra–annual variation and adequate representation. To examine spatial variability, samples should preferably be from different plant species or made by different collectors to reduce the risk of resampling the same spot. Nevertheless, the patterns observed through time appear consistent enough to outline the general course of recent events in the Kraenepoel. Prior to the second World War, sediment diatom assemblages evidenced considerable and rapid environmental shifts spanning the range from dilute, acid (pH 5–6) and bicarbonate–poor, ± oligotrophic water with prevalence of *Eunotia*, *Frustulia* and *Tabellaria* spp. at about 1850 to circumneutral and slightly buffered (estimated alkalinity 0.1–0.2 mmol l^{-1}), oligo-mesotrophic conditions characterized mainly by the small–sized epiphytes *Achnanthidium* and *Encyonopsis* in the late 19th and early 20th c. Throughout, the representation of species of *Brachysira* and *Fragilariforma* remained fairly constant. A transient increase of alkaliphilous and more eutraphentic diatoms, i.c. *Nitzschia fonticola* and *Navicula radiosa*, occurred in the early 1870s, as the acid conditions passed into a phase of higher alkalinity, but otherwise diatom assemblages evidence no significant nutrient-enrichment. This agrees well with the macrophyte composition reported from the lake for this period. Considering that the hydrology of the lake was actively controlled, a lesser or stronger input of minerals as indicated by these assemblage shifts is plausibly explained by a change in the relative input of brook water. However, other activities carried out as part of fishpond exploitation may also have played a role. Cyclic drawdown and refilling, as well as feeding and mowing of reeds are known to have occurred in the Kraenepoel at least from the 1900s. Elsewhere in Flanders and well before this time, fishponds were usually emptied every 5 years or so, and a harvest of oat was made before refilling. Such practices are not documented for the Kraenepoel, however, and it appears that the lake was allowed to fill again immediately after all fish had been collected in autumn. Environmental consequences of such events may have been rather limited and too long time periods between diatom samples could also conceal such detail. Yet, some of the variation in species composition and inferred variables, especially the salient rise in alkalinity at about 1880 and the very high COD at c 1924 may indeed be related to stronger disturbances resulting from fish-pond management. However, the major differences in ionic composition were more enduring and agree rather well with different regimes in hydrological connectance: 1. a situation with only limited inflow of water from the brook represented by the more acid conditions of 1853–1863, and 2. a period with more regular inflow of still unpolluted and nutrient–poor brook water between 1881 and 1901. The physical–chemical characteristics going along with these two settings match with different types of unstratified lakes according to the Flemish WFD typology, respectively moderately acid and circumneutral weakly buffered. The corresponding diatom assemblages in the Kraenepoel also agree reasonably well with phytobenthos expectations for these types. Depending on management options, both water types present alternatives to establish the lake's ecological potential. Considering that no significant additional effects are expected from compulsory hydromorphological features of the water body, restoration goals should at least equal their respective expectations for good status. Biodiversity concerns, such as obligations regarding the Natura 2000 Habitat Directive and areas requiring special protection, may even imply committing to more stringent restoration ambitions (Van Looy et al. 2008).

Due to the lack of suitable samples from the 1930s up to late sixties, developments in this period could not be documented. In the southern part, taxa from nutrient–rich water with a higher mineral content (*Navicula gregaria*, *N. veneta*, *Planothidium granum*, *P. schwabei*, *Nitzschia valdestriata*) had entered the picture by 1969. An increased representation of plocon (unattached semi–planktonic diatoms), especially *Staurosira venter* and plankton signaled the decline in submerged vegetation. Conditions became alkaline and levels of calcium and sodium rose. Later on, a hypertrophic turbid system with high plankton productivity developed here. In the northern part, development of centric plankton remained more limited, although it could be that a tiny species like *Discostella nana*, which prevailed elsewhere, was underestimated here in 1999 because of the way that the zooplankton sample was prepared. Although the better light climate had allowed at least some submerged vegetation to remain present, the high abundance of chain–forming semi–plankton nevertheless illustrates that vegetation structure changed here as well. Phytoplankton, macrophyte and chemical data from 1976 and 1983 indicated a further deterioration of the water quality in this period, with onset of cyanobacterial blooms. Whereas the diatom–inferred data suggest that concentrations of major ions still differed in both basins in the late 1960s, monthly measurements of electric conductivity and alkalinity demonstrate that this was no longer the case between August 1983 and March 1984 (Van Vooren & Coppejans 1986, Van Wichelen et al. 2008). The inflow of brook water, by then polluted with household sewage and runoff from agricultural fields and a major highway, was an obvious cause for the observed eutrophication and increased concentration of solutes. Especially in the southern basin, internal processes may also have contributed to increased nutrient availability and turbidity.

The comparison of diatom-inferred and measured values for several variables (Van Wichelen et al. 2007, 2008) shows that composition of the sediment assemblages tracked the post-restoration changes in water chemistry rather accurately. Perhaps the most significant change was a strong drop in phytoplankton representation and productivity (as pGOP), corresponding to a marked increase in transparency and lower concentrations of suspended matter in the southern part. Diversion of the brook and less *in situ* alkalinity production through break down of organic matter after sediment removal also lowered ionic concentrations and alkalinity to levels approaching those of the early 1900s. Decrease of soluble reactive phosphorus to concentrations less than 40 µg l^{-1} was mirrored by the return of oligotraphentic taxa. Interestingly, oxidation of sulfide and organic sediments during the first drawdown produced very low pH and extreme ammonium concentrations in the southern part after refilling during 2001–2003 (median pH 5.3 and 2.7 mg l^{-1} NH_4^+ in 2002). This coincided with a strong representation of *Eunotia exigua* and *Navicula difficilima* in the sediment in 2003 (at the same site *E. exigua* attained 55 % in the epiphyton). Proliferation of *E. exigua* is a well–known phenomenon when sulphate is released into the water column as dried acidified moorland pools refill (e.g. van Dam 1988), whereas *N. difficilima* occurs in abundance in acid pools undergoing eutrophication by cattle or birds (personal obs.). Developments hereafter provide a better picture of the consequences of restoration. *Achnanthidium minutissimum*, a fairly tolerant and opportunistic epiphyte showed the most consistent increase, which reflects improved water quality and better growth of submerged macrophytes, and thus a more acceptable state of overall ecosystem functioning. On the other hand, the gain in taxa more characteristic of less impacted acid or circumneutral water − whether the same as present in the past, or different ones with similar ecological traits − has remained rather limited. This is accentuated even more if the present hydrological isolation of the lake is considered. Moreover, it appears that the abundance of a number of taxa usually associated with organic pollution in soft waters (*Craticula molestiformis*, *Eolimna minima*, *Gomphonema parvulum, Mayamaea* spp., *Nitzschia paleaeformis, Sellaphora seminulum*) could be increasing. Alongside, higher concentrations of nitrate and suspended matter are measured. These changes could be caused by the rapid accumulation of leaf litter and organic sludge and the large numbers of geese that started to flock at the lake. Trends are still tentative, but should become more apparent in the forthcoming years.

This study shows that historical diatom data can help to establish the ecological potential of man–made or hydromorphologically heavily modified water bodies to meet WFD objectives. It illustrates the importance of water type attribution and hydrological management alternatives to the establishment of possible restoration goals. The historical observations may help in deciding which hydrological option is most promising in order to reach required restoration goals, given present conditions. Former assemblage composition and inferred water quality can be used in monitoring to assess distance to target, to guide managers in planning measures and to help determine the necessity for undertaking supplementary actions. Whereas phytobenthos assessment of lakes for the WFD now focuses entirely on epiphytic and epilithic communities, sediment diatom assemblages may provide additional information on the ecological status of this quality element as such, as well as on the structure and functioning of the lake ecosystem as a whole. Both the temporal and spatial resolution of environmental signals provided by sediment assemblages are apt to the monitoring programs imposed for lentic water bodies by this directive and their contemporary composition can be related more easily to available palaeolimnological data.

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Supplementary material

the following supplementary material is available for this article:

Table S1. Diatom taxa observed in sediments from the Kraenepoel and their occurrence in different periods.

This material is available as part of the online article (http://fottea.czechphycology.cz)

Table S1. Diatom taxa observed in sediments from the Kraenepoel and their occurrence in different periods.

Period	1853–1924	1853–1863	1881–1901	1969–1999	2003–2006
Achnanthes coarctata (Bréb.) Grun.	+	-	+	-	-
Achnanthidium caledonicum (L.-B.) L.-B.	+	+	+	-	+
Achnanthidium linearoide (L.-B.) L.-B.	+	-	+	+	+
Achnanthidium minutissimum (Kütz.) Czarn.	+	+	+	+	+
Achnanthidium minutissimum var. K.& L.-B. pl. 32, 48-52	+	+	+	-	-
Achnanthidium minutissimum very narrow phenodeme K.& L.-B. pl. 32, 27-30	+	+	+	+	-
Achnanthidium pyrenaicum (Hust.) Kobayasi	-	-	-	+	-
Achnanthidium saprophilum (Kobayasi & Mayama) Round & Bukht.	-	-	-	-	+
Actinocyclus normanii (Greg.) Hust.	-	-	-	+	-
Actinoptychus senarius (Ehr.) Ehr.	+	-	+	-	-
Adlafia bryophila (Petersen) L.-B.	-	-	-	+	-
Adlafia minuscula (Grun.) L.-B.	-	-	-	-	+
Amphora copulata (Kütz.) Schoeman & Archibald	+	+	+	+	+
Amphora montana Krasske	-	-	-	+	-
Amphora ovalis (Kütz.) Kütz.	+	-	+	+	-
Amphora pediculus (Kütz.) Grun.	-	-	-	+	-
Anomoeoneis sphaerophora (Ehr.) Pfitzer	-	-	-	+	-
Asterionella formosa Hassall	-	-	-	+	-
Aulacoseira ambigua (Grun.) Simonsen	-	-	-	+	+
Aulacoseira crenulata (Ehr.) Thwaites	-	-	-	-	+
Aulacoseira granulata (Ehr.) Simonsen	-	-	-	+	+
Aulacoseira granulata var. *angustissima* (O. Müller) Simonsen	-	-	-	+	+
Aulacoseira muzzazensis (Meister) Krammer	-	-	-	+	+
Aulacoseira pusilla (Meister) Tuji & Houki	-	-	-	+	-
Brachysira brebissonii Ross	+	+	-	-	-
Brachysira garrensis (L.-B. & Krammer) L.-B.	+	+	+	+	-
Brachysira microcephala (Grunow) Compère	+	+	+	+	+
Brachysira procera L.-B. & Moser	+	-	+	+	-
Brachysira serians (Breb.) Round & Mann	+	+	-	-	-
Caloneis aerophila Bock	+	-	+	-	-
Caloneis bacillum (Grun.) Cl.	+	-	+	-	+
Caloneis borealis Carter	+	+	+	+	-
Caloneis lancettula (Schulz) L.-B. & Witkowski	-	-	-	-	+
Caloneis schumanniana (Grun.) Cl.	-	-	-	-	+
Caloneis silicula (Ehr.) Cl.	-	-	-	+	+
Caloneis sp. K. & L.-B. pl. 173, 5	+	+	-	-	-
Caloneis undulata (Greg.) Krammer	+	+	+	+	-
Cavinula cocconeiformis (Greg.) Mann & Stickle	+	-	-	+	-
Cavinula pseudoscutiformis (Hust.) Mann & Stickle	+	+	+	+	+
Cavinula variostriata (Krasske) Mann & Stickle	+	-	-	-	-
Chamaepinnularia evanida (Hust.) L.-B.	+	-	+	+	-
Chamaepinnularia mediocris (Krasske) L.-B.	+	+	-	+	-
Chamaepinnularia soehrensis (Krasske) L.-B. & Krammer var. *hassiaca* (Krasske) L.-B.	+	-	+	-	-
Chamaepinnularia soehrensis var. *muscicola* (Petersen) L.-B. & Krammer	+	+	-	-	-
Chamaepinnularia sp. nr. 11 (aff. C. sp. Nr. 1 Julma Ölkky L.-B. & Metzeltin & *C. bremoides* Flower)	+	-	+	-	-
Cocconeis pediculus Ehr.	-	-	-	+	-

Cocconeis placentula Ehr.	+	-	+	+	+
Cocconeis placentula var. *euglypta* (Ehr.) Grun.	+	-	-	+	-
Cocconeis placentula var. *lineata* (Ehr.) V.H.	+	-	+	+	+
Cocconeis placentula var. *tenuistriata* Geitler	-	-	-	-	+
Craticula accomoda (Hust.) D.G. Mann	-	-	-	+	-
Craticula accomodiformis L.-B.	-	-	-	-	+
Craticula ambigua (Ehr.) D.G. Mann	-	-	-	+	-
Craticula cf. *subhalophila* (Hust.) L.-B.	-	-	-	+	-
Craticula cuspidata (Kütz.) D.G. Mann.	-	-	-	+	+
Craticula disscociata (Reichardt) Reichardt	-	-	-	-	+
*Craticula molestiformis (*Hust.) L.-B.	-	-	-	+	+
Craticula riparia (Hust.) L.-B.	-	-	-	-	+
Craticula riparia (Hust.) L.-B.var. *mollenhaueri* L.B.	-	-	-	-	+
Craticula submolesta (Hust.) L.-B.	+	+	-	-	+
Craticula vixnegligenda L.-B.	-	-	-	-	+
Ctenophora pulchella (Ralfs) Williams et Round	-	-	-	+	+
Cyclostephanos dubius (Fricke) Round	-	-	-	+	+
Cyclotella atomus Hust.	-	-	-	+	-
Cyclotella meneghiniana Kütz.	-	-	-	+	+
Cymatopleura solea (Bréb.) W. Sm.	-	-	-	+	-
Cymatopleura solea var. *apiculata* (W. Sm.) Ralfs	-	-	-	+	-
Cymbella aspera (Ehr.) Cl.	-	-	-	+	-
Cymbella cymbiformis Ag.	-	-	-	+	-
Cymbella neocistula (Ehr.) Kirchner	-	-	-	+	-
Cymbella proxima Reimer	-	-	-	+	-
Cymbopleura amphicephala (Naegeli) Krammer	+	+	-	-	-
Cymbopleura anglica (Lagerstedt) Krammer	-	-	-	-	+
Cymbopleura hercynica (A. Schmidt) Krammer	-	-	-	-	+
Cymbopleura naviculiformis (Auerswald) Cl.	+	+	+	+	+
Diadesmis biceps Arnott	-	-	-	+	-
Diadesmis brekkaensis (Petersen) D.G. Mann	+	-	+	-	-
Diatoma tenuis Ag.	-	-	-	+	-
Diploneis fontanella L.-B.	-	-	-	+	+
Diploneis petersenii Hust.	+	-	+	-	-
Discostella nana (Hust.) Chang	-	-	-	+	+
Discostella pseudostelligera (Hust.) Houk & Klee	+	-	-	+	+
Encyonema bipartitum (A. Mayer) Krammer	+	+	-	-	-
Encyonema elginense (Krammer) D.G. Mann phenodeme 2	-	-	-	+	-
Encyonema hebridicum Grun.	+	+	+	-	+
Encyonema lange-bertalotii Krammer phenodeme 1	-	-	-	+	-
Encyonema lange-bertalotii Krammer phenodeme 2	-	-	-	+	-
Encyonema minutum (Hilse) D.G. Mann	+	+	+	+	+
Encyonema neogracile Krammer phenodeme I	+	+	+	+	+
Encyonema neogracile Krammer phenodeme 2	-	-	-	-	+
Encyonema pergracile Krammer	-	-	-	+	-
Encyonema perpusillum (A. Cl.) D.G. Mann	+	+	-	-	+
Encyonema silesiacum (Bleisch) D.G. Mann aggr.	-	-	-	+	+
Encyonema silesiacum (Bleisch) D.G. Mann var. *distinctepunctatum* Krammer	-	-	-	-	+
Encyonema ventricosum (Ag.) Grun. phenodeme 1	-	-	-	+	-

Encyonema vulgare Krammer aggr.	+	-	-	+	+
Encyonopsis cesatii (Rabenh.) Krammer	-	-	-	+	+
Encyonopsis falaisensis (Grun.) Krammer	+	+	-	-	-
Encyonopsis microcephala (Grun.) Krammer	-	-	-	+	+
Encyonopsis subminuta Krammer & Reichardt	+	+	+	+	+
Entomoneis ornata (Bailey) Reimer	-	-	-	-	+
Eolimna minima (Grun.) L.-B.	+	+	+	+	+
Epithemia adnata (Kütz.) Bréb.	-	-	-	+	-
Epithemia turgida (Ehr.) Kütz.	+	+	-	+	-
Eucocconeis alpestris (Brun) L.-B.	+	-	+	-	-
Eucocconeis laevis (Østrup) L.-B.	-	-	-	-	+
Eunotia arculus (Grun.) L.-B. & Nörpell	+	+	+	-	-
Eunotia arcus Ehr.	+	-	+	+	+
Eunotia biceps Ehr.	+	+	-	-	-
Eunotia bidens Ehr.	+	+	+	-	+
Eunotia bilunaris (Ehr.) Souza	+	+	+	+	+
Eunotia bilunaris var. *mucophila* L.-B. & Nörpel	+	+	-	-	-
Eunotia bilunaris ‚subarcuata‘ phenodeme	-	-	-	+	-
Eunotia botuliformis Wild, Nörpel & L.-B.	+	+	+	+	-
Eunotia compacta (Hust.) Mayama	+	+	-	-	-
Eunotia curtagrunowii Nörpel-Schempp & L.B.	+	-	+	+	-
Eunotia diodon Ehr.	+	+	-	+	+
Eunotia exigua (Bréb.) Rabenh.	+	+	-	+	+
Eunotia glacialifalsa L.-B.	+	+	-	+	+
Eunotia implicata Nörpel, L.-B. & Alles	+	+	+	+	+
Eunotia incisa Greg.	+	+	+	+	+
Eunotia islandica Østrup	-	-	-	-	+
Eunotia jemtlandica (Fontell) Berg	+	+	+	+	+
Eunotia kruegeri L.-B.	+	+	-	+	-
Eunotia meisteri Hust.	+	+	-	-	-
Eunotia minor (Kütz.) Grun.	+	+	+	+	+
Eunotia muscicola Krasske var. tridentula (Grun.) Nörpel-Schempp & L.-B.	+	+	-	-	-
Eunotia naegelii Migula	+	+	-	+	-
Eunotia neofallax Nörpel-Schempp	+	+	-	-	-
Eunotia paludosa Grun.	+	+	-	+	+
Eunotia parallela Ehr.	+	-	+	-	-
Eunotia pectinalis (Dillwyn) Rabenh.	+	+	-	-	+
Eunotia pectinalis (Dillwyn) Rabenh.var. *undulata* (Ralfs) Rabenh.	-	-	-	+	+
Eunotia pectinalis (Dillwyn) Rabenh.var. *ventralis* (Ehr.) Hust.	+	+	+	+	-
Eunotia praerupta Ehr.	+	-	-	-	-
Eunotia rhomboidea Hust.	+	+	-	+	+
Eunotia rhynchocephala Hust.	-	-	-	-	+
Eunotia septentrionalis Østrup	-	-	-	+	-
Eunotia soleirolii (Kütz.) Rabenh.	-	-	-	+	-
Eunotia sp. nr. 1	+	+	-	-	-
Eunotia subarcuatoides Alles, Nörpel & L.-B.	+	-	+	-	-
Eunotia tenella (Grun.) Hust.	+	+	-	-	-
Eunotia tetraodon Ehr.	+	+	+	+	+
Eunotia variundulata Nörpel-Schempp & L.B.	+	+	-	-	-

Fallacia vitrea (Østrup) D.G. Mann	+	+	-	+	-
Fragilaria acidoclinata L.-B. & Hofmann	-	-	-	+	-
Fragilaria bidens Heiberg	-	-	-	+	-
Fragilaria capucina '*Synedra rumpens* sensu Hust.' phenodeme	-	-	-	+	+
Fragilaria capucina Desmaz. var. *vaucheriae* (Kütz.) L.-B.	+	+	+	+	+
Fragilaria crotonensis Kitton	-	-	-	-	+
Fragilaria fasciculata (Ag.) L.-B.	+	-	-	+	+
Fragilaria gracilis Østrup	+	+	+	+	+
Fragilaria mesolepta Rabenh.	-	-	-	+	+
Fragilaria nanana L.-B.	+	+	+	+	-
Fragilaria parasitica (W. Sm.) Grun. var. *subconstricta* Grun.	-	-	-	+	-
Fragilaria radians (Kütz.) L.-B.	-	-	-	+	-
Fragilaria rumpens (Kütz.) Carlson	-	-	-	+	+
Fragilaria tenera (W. Sm.) L.-B.	-	-	-	+	+
Fragilariforma constricta Ehr.	-	-	-	+	+
Fragilariforma exiguiformis L.-B.	+	+	+	+	+
Fragilariforma virescens Ralfs	-	-	-	-	+
Frustulia crassinervia (Breb.) L.-B. & Krammer	+	+	+	+	+
Frustulia krammeri L.-B. & Metzeltin	+	+	-	-	-
Frustulia marginata Amossé	-	-	-	-	+
Frustulia saxonica Rabenh.	+	+	+	+	-
Frustulia vulgaris (Thwaites) De Toni	+	-	+	+	+
Gomphonema acuminatum Ehr.	+	-	+	+	+
Gomphonema acuminatum Ehr. var. *pusillum* Grun.	+	-	+	-	+
Gomphonema aff. *kaweckanum* Metzeltin, Reichardt & L.-B.	-	-	-	-	+
Gomphonema aff. *micropus* Kütz. var. *aequale* (Greg.) Reichardt	+	-	-	-	-
Gomphonema angustatum (Kütz.) Rabenh.	+	+	+	+	+
Gomphonema auritum A. Braun	+	-	+	+	+
Gomphonema brebissonii Kütz.	+	-	+	-	-
Gomphonema capitatum Ehr.	+	-	+	+	+
Gomphonema clavatulum Reichardt	-	-	-	+	-
Gomphonema clavatum Ehr.	+	-	+	+	+
Gomphonema coronatum Ehr.	+	+	+	-	+
Gomphonema cymbelliclinum Reichardt	+	+	-	-	+
Gomphonema drutelingense Reichardt	-	-	-	+	-
Gomphonema exilissimum (Grun.) L.-B. & Reichardt	+	+	+	+	+
Gomphonema gracile Ehr.	+	-	+	+	+
Gomphonema hebridense Greg.	+	+	+	+	+
Gomphonema lateripunctatum Reichardt & L.-B.	-	-	-	-	+
Gomphonema longiceps Ehr.	-	-	-	+	-
Gomphonema micropus Kütz.	-	-	-	-	+
Gomphonema parvulum Kütz.	+	-	+	+	+
Gomphonema pseudotenellum L.-B.	+	-	+	-	-
Gomphonema subclavatum V.H.	-	-	-	+	-
Gomphonema truncatum Ehr.	-	-	-	+	-
Gyrosigma acuminatum (Kütz.) Rabenh.	-	-	-	+	+
Hantzschia abundans L.-B.	-	-	-	+	-
Hantzschia amphioxys (Ehr.) Grun.	+	+	+	+	+
Hippodonta capitata (Ehr.) L.-B., Metzeltin & Witkowski	+	-	-	+	+

Hippodonta hungarica (Grun.) L.-B., Metzeltin & Witkowski	-	-	-	+	-
Kobayasiella micropunctata (Germain) L.-B.	+	+	-	+	-
Kobayasiella subtilissima (Cl.) L-B.	+	+	-	-	-
Luticola acidoclinata L.-B.	+	-	+	+	-
Luticola mutica (Kütz.) D.G. Mann	+	-	+	+	-
Luticola sp. nr. 10	+	-	-	-	-
Mayamaea agrestis (Hust.) L.-B.	-	-	-	+	+
Mayamaea atomus (Kütz.) L.-B. var. *alcimona* (Reichardt) Reichardt	-	-	-	-	+
Mayamaea atomus (Kütz.) L.-B. var. *permitis* (Hust.) L.-B.	+	-	-	-	+
Mayamaea fossalis (Krasske) L.-B.	-	-	-	+	-
Melosira varians Ag.	-	-	-	+	-
Microcostatus krasskei (Hust.) Johansen & Sray	+	-	+	-	-
Muelleria gibbula (Cl.) Spaulding & Stoermer	-	-	-	+	-
Navicula arvensis Hust. var. *major* L.-B.	-	-	-	-	+
Navicula capitatoradiata Germain	+	-	+	+	-
Navicula cf. *bourelliyivera* L.-B., Witkowski & Stachura	+	-	+	-	-
Navicula cincta (Ehr.) Ralfs	+	-	+	+	+
Navicula cryptocephala Kütz.	+	-	+	+	+
Navicula cryptofallax L.-B. & Hofmann	-	-	-	+	-
Navicula cryptotenella L.B.	-	-	-	+	+
Navicula difficilima Hust.	-	-	-	+	+
Navicula digitoconvergens L.-B.	-	-	-	+	-
Navicula geisslerae Jahn	-	-	-	+	-
Navicula gregaria Donkin	-	-	-	+	+
Navicula heimansioides L.-B.	+	+	+	+	+
Navicula indifferens Hust.	-	-	-	-	+
Navicula krammeriae L.-B.	-	-	-	-	+
Navicula laterostrata Hust.	-	-	-	+	-
Navicula leptostriata Jørgensen	-	-	-	+	-
Navicula libonensis Schoeman	-	-	-	+	-
Navicula longicephala Hust. var. *villaplanii* L.-B. & Sabater	+	-	+	-	-
Navicula oblonga Kütz.	-	-	-	+	-
Navicula obsoleta Hust.	+	-	+	-	-
Navicula pseudoventralis Hust.	-	-	-	+	-
Navicula radiosa Kütz.	+	+	+	+	+
Navicula radiosiola L.-B.	+	-	+	-	-
Navicula rhynchocephala Kütz.	+	-	+	+	+
Navicula rhynchotella L.-B.	-	-	-	+	+
Navicula rostellata Kütz.	-	-	-	+	-
Navicula slesvicensis Grun.	-	-	-	+	+
Navicula subrhynchocephala Hust.	-	-	-	+	-
Navicula tenelloides Hust.	+	-	+	+	+
Navicula tripunctata (O. Müller) Bory	-	-	-	+	-
Navicula trivialis L.-B.	-	-	-	+	-
Navicula trophicatrix L.-B.	+	+	+	-	-
Navicula veneta Kütz.	+	-	+	+	+
Naviculadicta stauroneoides L.-B.	+	-	+	-	-
Neidium affine (Ehr.) Pfitzer	+	+	-	-	-
Neidium affine var. *linearis* Foged	-	-	-	+	-

Neidium alpinum Hust.	+	+	-	-	-
Neidium ampliatum (Ehr.) Krammer	+	+	+	+	+
Neidium densestriatum (Østrup) Krammer	+	+	+	-	-
Neidium dubium (Ehr.) Cl.	-	-	-	+	-
Neidium hercynicum A. Mayer	+	+	-	-	-
Neidium iridis (Ehr.) Cl.	+	-	-	+	-
Neidium productum (W. Sm.) Cl.	-	-	-	+	+
Nitzschia acicularis (Kütz.) W.Sm.	-	-	-	+	-
Nitzschia acidoclinata L.-B.	+	+	+	+	+
Nitzschia aerophila Hust.	+	+	-	+	+
Nitzschia alpinobacillum L.-B.	+	+	+	-	+
Nitzschia amphibia Grun.	-	-	-	+	-
Nitzschia angustata Grun.	+	-	+	-	+
Nitzschia archibaldii L.-B.	+	-	+	+	-
Nitzschia bavarica Hust.	-	-	-	+	+
Nitzschia bremensis Hust.	-	-	-	-	+
Nitzschia calida Grun.	-	-	-	+	-
Nitzschia frequens Hust.	-	-	-	+	+
Nitzschia capitellata Hust.	-	-	-	+	+
Nitzschia cf. *bryophila* (Hust.) Hust.	+	+	+	-	-
Nitzschia commmunis Rabenh.	-	-	-	+	-
Nitzschia debilis Arnott	-	-	-	+	+
Nitzschia dissipata (Kütz.) Grun. var. *media* (Hantzsch) Grun.	-	-	-	+	-
Nitzschia dissipata (Kütz.) Grun. var. *oligotraphenta* L.-B.	-	-	-	+	-
Nitzschia draveillensis Coste & Ricard	-	-	-	+	-
Nitzschia filiformis (W. Sm.) V.H.	-	-	-	+	-
Nitzschia fonticola Grun.	+	+	+	-	-
Nitzschia frustulum (Kütz.) Grun.	+	-	+	+	+
Nitzschia fruticosa Hust.	-	-	-	-	+
Nitzschia gracilis Hantzsch	+	-	+	+	+
Nitzschia hantzschiana Rabenh.	-	-	-	-	+
Nitzschia hungarica Grun.	-	-	-	+	+
Nitzschia intermedia Hantzsch	-	-	-	+	-
Nitzschia lacuum L.-B.	+	-	+	+	-
Nitzschia levidensis (W. Sm.) Grun.	-	-	-	-	+
Nitzschia levidensis (W. Sm.) Grun. ‘salinarum phenodeme’	-	-	-	+	+
Nitzschia linearis (Ag.) W. Sm.	-	-	-	+	-
Nitzschia microcephala Grun.	-	-	-	+	+
Nitzschia nana Grun.	+	-	+	+	+
Nitzschia palea (Kütz.) W. Sm.	+	+	+	+	+
Nitzschia palea var. *debilis* (Kütz.) Grun.	+	-	+	+	+
Nitzschia palea var. *minuta* Bleisch	-	-	-	+	-
Nitzschia palea var. *tenuirostris* Grun.	-	-	-	+	+
Nitzschia paleacea Grun.	-	-	-	+	+
Nitzschia paleaeformis Hust.	-	-	-	-	+
Nitzschia parvula W. Sm.	-	-	-	+	-
Nitzschia perminuta (Grun.) M. Perag.	+	+	+	+	+
Nitzschia pseudofonticola Hust.	+	-	+	+	+
Nitzschia pumila Hust.	-	-	-	+	-

Nitzschia pura Hust.	-	-	-	+	+
Nitzschia pussila Grun.	-	-	-	+	-
Nitzschia recta Hantzsch	+	-	+	-	-
Nitzschia rectiformis Hust.	+	-	+	-	-
Nitzschia rectirobusta L.-B.	-	-	-	+	-
Nitzschia scalaris (Ehr.) W. Sm.	+	-	+	+	+
Nitzschia sigma (Kütz.) W. Sm.	-	-	-	+	+
Nitzschia sigmoidea (Nitzsch) W. Sm.	-	-	-	+	+
Nitzschia sinuata (Thwait.) Grun. var. *delognei* (Grun.) L.-B.	+	-	+	-	-
Nitzschia subacicularis Hust.	-	-	-	+	-
Nitzschia sublinearis Hust.	-	-	-	-	+
Nitzschia subtilis Grun.	-	-	-	+	+
Nitzschia supralitorea L.-B.	-	-	-	+	+
Nitzschia terrestris (Petersen) Hust.	+	-	+	-	-
Nitzschia tryblionella Hantzsch	-	-	-	+	+
Nitzschia umbonata (Ehr.) L.-B.	-	-	-	-	+
Nitzschia valdestriata Aleem & Hust.	-	-	-	+	+
Nitzschia vermicularis (Kütz.) Hantzsch	-	-	-	+	-
Nitzschia wuellerstorfii L.-B.	-	-	-	+	-
Opephora mutabilis (Grun.) Sabbe & Vyverman	-	-	-	+	-
Parlibellus protracta (Grun.) Witkowski, L.-B. & Metzeltin	-	-	-	+	-
Peronia fibula (Bréb) Ross	+	+	-	-	+
Pinnularia acoricola Hust.	+	+	-	+	+
Pinnularia acuminata W. Sm. phenodeme 1	+	+	-	+	+
Pinnularia acuminata W. Sm. phenodeme 2	+	+	-	-	-
Pinnularia anglica Krammer	+	+	-	-	-
Pinnularia angusta (Cl.) Krammer	-	-	-	+	-
Pinnularia biceps Greg.	+	+	+	+	+
Pinnularia borealis Ehr. var. *scalaris* (Ehr.) Rabenh.	+	-	+	+	-
Pinnularia borealis Ehr. var. *subislandica* Krammer	+	-	-	-	-
Pinnularia brauniana (Grun.) Mills	-	-	-	+	-
Pinnularia cardinalis (Ehr.) W. Sm.	+	+	+	+	+
Pinnularia decrescens (Grun.) Krammer	+	+	-	+	+
Pinnularia decrescens (Grun.) Krammer var. *ignorata* Krammer	-	-	-	+	-
Pinnularia divergens W. Sm. var. *media* Krammer	-	-	-	-	+
Pinnularia divergens W. Sm.	+	-	-	-	-
Pinnularia divergentissima (Grun.) Cl.	+	+	-	-	-
Pinnularia divergentissima (Grun.) Cl var. *minor* Krammer	-	-	-	+	+
Pinnularia esoxiformis Fusey	+	-	+	-	-
Pinnularia frequentis Krammer	+	+	+	+	+
Pinnularia gentilis (Donkin) Cl.	+	-	+	-	-
Pinnularia gigas Ehr.	+	+	+	+	-
Pinnularia grunowii Krammer	+	-	+	+	+
Pinnularia interruptiformis Krammer	-	-	-	-	+
Pinnularia islandica Østrup	-	-	-	+	-
Pinnularia lata (Bréb.) W. Sm.	+	+	+	-	-
Pinnularia legumiformis Krammer	-	-	-	+	-
Pinnularia macilenta Ehr.	-	-	-	+	-
Pinnularia mesogongyla Ehr.	-	-	-	+	+

Pinnularia microstauron (Ehr.) Cleve	+	+	+	+	+
Pinnularia microstauron (Ehr.) Cleve var. *nonfasciata* Krammer	+	+	+	-	-
Pinnularia microstauron (Ehr.) Cleve var. *rostrata* Krammer	-	-	-	+	+
Pinnularia neglectiformis Krammer	-	-	-	-	+
Pinnularia neomajor Krammer	+	+	+	+	+
Pinnularia neomajor Krammer var. *inflata* Krammer	+	-	-	+	+
Pinnularia nobilis (Ehr.) Ehr.	+	-	+	+	-
Pinnularia nobilis (Ehr.) Ehr. var. *regularis* Krammer	-	-	-	+	-
Pinnularia nodosa (Ehr.) W. Sm. phenodeme 1	-	-	-	-	+
Pinnularia nodosa (Ehr.) W. Sm. var. *pseudogracillima* A. Mayer	-	-	-	+	-
Pinnularia obscura Krasske	+	-	+	+	-
Pinnularia obscura Krasske phenodeme 3	+	+	-	-	-
Pinnularia oriunda Krammer	-	-	-	-	+
Pinnularia parvulissima Krammer	-	-	-	+	+
Pinnularia peracuminata Krammer	-	-	-	+	-
Pinnularia percuneata Krammer var. *minor* Krammer	-	-	-	+	+
Pinnularia perirrorata Krammer	+	+	+	+	+
Pinnularia pisciculus Ehr.	+	-	+	+	-
Pinnularia pseudogibba Krammer	+	+	+	-	-
Pinnularia rhombarea Krammer	-	-	-	+	-
Pinnularia rhomboelliptica Krammer var. *inflata* Krammer	-	-	-	-	+
Pinnularia schoenfelderi Krammer	+	-	-	+	+
Pinnularia schroeterae Krammer	-	-	-	+	+
Pinnularia schroeterae Krammer var. *elliptica* Krammer	-	-	-	-	+
Pinnularia similiformis Krammer	+	+	-	-	-
Pinnularia sinistra Krammer	+	-	+	-	-
Pinnularia stomatophora Grun.	+	+	+	+	+
Pinnularia subcapitata Greg.	+	+	+	+	+
Pinnularia subcapitata Greg. var. *elongata* Krammer	-	-	-	+	-
Pinnularia subcommutata Krammer var. *nonfasciata* Krammer	-	-	-	-	+
Pinnularia subfalaiseana Krammer	+	+	+	-	+
Pinnularia subgibba Krammer	+	+	+	+	+
Pinnularia subgibba Krammer var. *undulata* Krammer	-	-	-	-	+
Pinnularia subinterrupta Krammer & Schroeter	+	-	-	+	-
Pinnularia subrupestris Krammer	+	-	+	+	+
Pinnularia subrupestris Krammer var. *cuneata* Krammer	-	-	-	+	-
Pinnularia tirolensis (Mezeltin & Krammer) Krammer	+	+	-	-	-
Pinnularia transversa (A. Schmidt) Mayer	-	-	-	-	+
Pinnularia viridiformis Krammer phenodeme 1	+	+	+	+	+
Pinnularia viridiformis Krammer phenodeme 2	+	-	+	+	-
Pinnularia viridiformis Krammer var. *minor* Krammer	-	-	-	-	+
Pinnularia viridis (Nitzsch) Ehr. phenodeme 1	-	-	-	-	+
Placoneis amphibola Cl.	+	+	-	-	-
Placoneis anglica (Ralfs) E.J. Cox	-	-	-	+	+
Placoneis clementis (Grun.) Cox	-	-	-	+	+
Placoneis exigua (Greg.) Mereschk.	-	-	-	+	-
Placoneis hambergii (Hust.) L.-B.	+	-	+	-	-
Placoneis navicularis (Ehr.) E.J. Cox	-	-	-	-	+
Placoneis pseudanglica (L.-B.) E.J. Cox	-	-	-	+	-

Placoneis undulata (Østrup) L.-B.	-	-	-	+	+
Planothidium biporomum (Hohn & Hellerman) L.-B.	-	-	-	+	+
Planothidium frequentissimum (L.-B.) L.-B.	-	-	-	+	+
Planothidium granum (Hohn & Hellerman) L.-B.	-	-	-	+	+
Planothidium lanceolatum (Bréb.) L.-B.	+	-	+	+	-
Planothidium minutissimum (Krasske) Lange-Bertalot	-	-	-	+	-
Planothidium rostratum (Østrup) Round & Bukth.	-	-	-	-	+
Planothidium schwabei (Krasske) L.-B.	+	-	-	+	+
Platessa conspicua (A. Mayer) L.-B.	-	-	-	+	-
Psammothidium altaicum Bukht.	+	+	+	+	-
Psammothidium chlidanos (Hohn & Hellerman) L.-B.	+	-	+	-	-
Psammothidium daonense (L.-B.) L.-B.	+	-	+	-	-
Psammothidium grischunum (Wuthrich) Bukht. & Round	+	+	-	-	-
Psammothidium helveticum (Hust.) Bukht. & Round	+	+	+	+	+
Psammothidium marginulatum (Grun) Bukht. & Round	+	-	+	-	-
Psammothidium perpusillum (Østrup) L.-B.	+	-	+	-	-
Psammothidium rossii (Hust.) Bukht.& Round	+	-	+	+	+
Psammothidium scoticum (Flower & Jones) Bukht. & Round	+	+	+	+	+
Psammothidium sp. Nr. 3 Julma Ölkky cf. *marginulata* L.-B & Metzeltin	-	-	-	-	+
Psammothidium subatomoides (Hust.) Bukht. & Round	+	+	-	+	+
Psammothidium ventralis (Krasske) Bukht. & Round	+	+	+	+	-
Rhoicosphenia abbreviata (Ag.) L.-B.	-	-	-	+	+
Rossithidium pusillum (Grun.) Round & Bukth.	+	-	+	+	+
Sellaphora blackfordensis D.G. Mann & Droop	-	-	-	+	-
Sellaphora joubaudii (Germain) Aboal	+	-	+	-	-
Sellaphora laevissima (Kütz.) D.G. Mann	+	-	+	+	-
Sellaphora mutata (Krasske) L.-B.	+	-	+	-	-
Sellaphora parapupula L.-B./ *S. pupula* 'gross' sensu Mann, Thomas & Evans	-	-	-	-	+
Sellaphora pupula (Kütz.) Mereschk. aggr.	+	+	+	+	+
Sellaphora rectangularis (Greg.) L.-B. & Metzeltin / *S. pupula* 'cf. large' sensu Mann, Thomas & Evans	+	-	+	+	+
Sellaphora seminulum (Grun.) D.G. Mann	-	-	-	+	+
Sellaphora verecundiae L.-B.	-	-	-	+	-
Stauroneis neofossilis L.-B. & Metzeltin	-	-	-	+	-
Stauroneis angustilancea L.-B. & Metzeltin	+	+	+	-	-
Stauroneis gracilis Ehr.	+	-	+	+	+
Stauroneis gracillior (Rabenh.) Reichardt	-	-	-	+	+
Stauroneis kriegeri Patrick	-	-	-	+	+
Stauroneis leguminopsis L.-B. & Krammer	+	+	+	-	+
Stauroneis muriella Lund	-	-	-	+	-
Stauroneis phoenicenteron (Nitzsch) Ehr.	+	+	+	+	+
Stauroneis producta Grun. f. *minor* Foged	-	-	-	-	+
Stauroneis producta Grun.	+	-	-	-	-
Stauroneis reichardtii L.-B., Cavacini, Tagliaventi & Alfinito	+	+	+	+	-
Stauroneis smithii Grun.	-	-	-	+	+
Stauroneis subgracilis L.-B. & Krammer	-	-	-	-	+
Stauroneis thermicola (Petersen) Lund	+	-	-	+	+
Staurosira construens Ehr.	-	-	-	+	-
Staurosira construens Ehr. var. *binodis* (Ehr.) Hamilton	-	-	-	+	-
Staurosira elliptica Schumann	-	-	-	+	-

Staurosira subsalina (Hust.) L.-B.	-	-	-	+	+
Staurosira venter (Ehr.) Grun	+	+	+	+	+
Staurosirella berolinensis (Lemm.) Bukth.	-	-	-	+	-
Staurosirella pinnata (Ehr.) Williams & Round	+	+	+	+	+
Stephanodiscus hantzschii Grun.	-	-	-	+	+
Stephanodiscus minutulus (Kütz.) Cl. & Möller	-	-	-	+	-
Stephanodiscus parvus Stoermer & Håkansson	-	-	-	+	+
Surirella amphioxys W. Sm.	+	+	+	+	+
Surirella angusta Kütz.	-	-	-	+	+
Surirella biseriata Bréb.	-	-	-	+	-
Surirella linearis W. Sm.	+	-	+	+	-
Surirella minuta Bréb.	-	-	-	-	+
Surirella robusta Ehr.	-	-	-	+	-
Surirella splendida (Ehr.) Kütz.	-	-	-	-	+
Surirella terricola L.-B. & Alles	-	-	-	+	-
Surirella visurgis Hust.	-	-	-	+	+
Tabellaria binalis (Ehr.) Grun. var. *elliptica* Flower	+	+	-	-	-
Tabellaria flocculosa (Roth) Kütz.	+	+	+	+	+
Tabellaria quadriseptata Knudson	+	+	-	+	+
Ulnaria acus (Kütz.) Aboal	-	-	-	+	-
Ulnaria biceps (Kütz.) Compère	-	-	-	-	+
Ulnaria ulna (Nitzsch.) Compère	+	+	-	+	+
Ulnaria ulna var. *angustissima* (Grun.) Compère	-	-	-	+	-