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Relation of abundance-weighted averages of diatom indicator values to measured environmental conditions in standing freshwaters

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Abstract

Abundance-weighted averages of diatom indicator values for pH, salinity, organic nitrogen availability, oxygen saturation, saprobity and trophic status according to van Dam et al. [Neth. J. Aquat. Ecol. 28 (1994) 117] were calculated for surface sediment and epiphytic diatom assemblages in 186 standing waters distributed throughout Flanders, Belgium, and tested against environmental variables measured in the water column, covering water chemistry, trophic status and organic load. With exception of the pH indication, most scores related rather poorly to variables which they are assumed to reflect and correlated even more strongly to non-target variables. For instance, the trophic indication provided a measure of pH and base status rather than of nutrient levels or phytoplankton productivity. Relations to measured variables differed according to the pH regime. Correction for uneven distribution of indicator values in the species pool usually yielded little improvement and was detrimental in some cases. Compared to epiphyton, weighted averages of species indicator values derived from sediment assemblages tended to be higher in water bodies yielding the most elevated indication scores. Except for the pH and salinity indication, differences between weighted averages pertaining to these different habitats were often considerable. Limitations to the use of abundance-weighted averages of diatom indicator values for environmental monitoring and assessment of lentic waters are discussed.

Keywords: Indicator values; Bacillariophyceae; Water quality; Phytobenthos; Standing waters; Belgium

1. Introduction

Ecological indicator values are a simple and robust tool for environmental calibration (ter Braak and Barendregt, 1986; ter Braak and Gremmen, 1987; ter Braak and Prentice, 1988; ter Braak, 1995). They are most widely applied in the vegetation ecology of vascular plants and bryophytes, where the so-called Ellenberg numbers are most renowned (cf. Ellenberg et al., 1992). Since early classifications for salinity and pH (Kolbe, 1932; Hustedt, 1939), indicator characteristics have been attributed to numerous diatom taxa (Bacillariophyceae) for a range of environmental variables (e.g. Cholnoky, 1968; Lowe, 1974; Salden,

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Table 1
Indicator values for diatoms according to van Dam et al. (1994)

pH (R)[a]		Salinity (H)	
R = 1	pH optimum < 5.5	H = 1	<100 Cl^- (mg L^{-1}); salinity <0.2‰
R = 2	Mainly at pH < 7	H = 2	<500 Cl^- (mg L^{-1}); salinity <0.9‰
R = 3	Mainly at pH ca. 7	H = 3	500–1000 Cl^- (mg L^{-1}); salinity 0.9–1.8‰
R = 4	Mainly at pH > 7	H = 4	1000–5000 Cl^- (mg L^{-1}); salinity 1.8–9.0‰
R = 5	Only at pH > 7		
Nitrogen uptake metabolism		Oxygen saturation (O)	
N = 1	Nitrogen autotrophic, tolerating very low concentrations of organically bound nitrogen	O = 1	ca. 100% O_2
N = 2	Nitrogen autotrophic, tolerating elevated concentrations of organically bound nitrogen	O = 2	>75% O_2
N = 3	Facultative nitrogen heterotrophic, needing periodically elevated concentrations of organically bound nitrogen	O = 3	>50% O_2
N = 4	Obligate nitrogen heterotrophic, needing continuously elevated concentrations of organically bound nitrogen	O = 4	>30% O_2
		O = 5	ca. 10% O_2
Trophic status (T)[a]		Saprobity (S)	
T = 1	Oligotraphentic	S = 1	Oligosaprobic; >85% O_2, BOD_5 < 2 mg L^{-1}
T = 2	Oligo-mesotraphentic	S = 2	β-Mesosaprobic; 70–85% O_2, BOD_5 2–4 mg L^{-1}
T = 3	Mesotraphentic	S = 3	α-Mesosaprobic; 25–70% O_2, BOD_5 4–13 mg L^{-1}
T = 4	Meso-eutraphentic	S = 4	α-Mesosaprobic/polysaprobic; 10–25% O_2, BOD_5 13–22 mg L^{-1}
T = 5	Eutraphentic	S = 5	Polysaprobic; <10% O_2, BOD_5 > 22 mg L^{-1}
T = 6	Hypereutraphentic		

[a] Indifferent class not shown.

1978; Beaver, 1981; de Wolf, 1982; Sládeček, 1986; Denys, 1991; Hofmann, 1993). Using ordinal classifications, van Dam et al. (1994) proposed indicator values for pH, salinity, organic nitrogen availability, oxygen saturation, saprobity and trophic status (Table 1) for 948 diatom taxa observed in fresh and brackish waters of the Netherlands (their 'moisture' classification is beyond the scope of this paper). These represent the majority of taxa commonly recognized in standard floras for such waters throughout Western Europe and even elsewhere. Often, comparison of the relative representation of taxa with similar indicator values is used to infer conditions in fresh waters (e.g. Haworth et al., 1996; Prygiel and Coste, 1996; Eloranta and Kwandrans, 2000), but abundance-weighted averages of the species indicator values provide a more integrated basis for site comparisons, condition estimates and trend monitoring of water quality. This paper addresses the reliability of such indication scores for water quality assessment.

Weighted averaging using indicator values presents a more general alternative to the use of transfer functions and is particularly valued where a statistically based calibration of response characteristics is lacking (van Dam et al., 1994; Stevenson and Pan, 1999). Applications include, for instance, the assessment of surface-water quality and its deviation from historical reference conditions (Rott et al., 1998; Denys, 2001, 2003; Newall and Bate, 2002; van der Molen et al., 2002), the monitoring of habitat-restoration efforts (van Ee, 2000), and paleoecological inferences (Baier et al., 2004). Moreover, these indices may be considered in the development of multimetric tools to assess ecological status of freshwaters from phytobenthic assemblages (e.g. Hill et al., 2003). Development of such methods presently receives strong impetus in Europe from the EU's Water Framework Directive.

In support of their approach, van Dam et al. (1994) refer to a number of Dutch case studies, usually involving a pollution gradient within a single watercourse, where a satisfactory agreement was found between the abundance-weighted averages of indicator values for organic nitrogen, nutrient status, saprobity, or oxygen saturation and corresponding water-quality variables measured in the field. However, the method has so far not been tested over a wide range of surface waters differing considerably in physical and chemical conditions. Whether it can be used confidently in the presence of multiple gradients therefore remains unclear. Furthermore, it has been applied to diatom assemblages collected from living and dead hard substrates, both natural and artificial, as well as from surface sediments. Such assemblages usually differ considerably in species composition and diversity, as well as in their ontogeny and microhabitat. Consequently, a different sensitivity and response to conditions measured in situ can be expected. In an Australian study, Newall and Bate (2002) found only poor correspondence between abundance-weighted species indicator values calculated according to van Dam et al. (1994) and measured water chemistry. Differences in autecological characteristics between morphologically identical diatom strains in different continents were considered as a possible cause by these authors. Investigation of such hypotheses also requires additional information on the reliability of these indication scores.

In order to test the usefulness of abundance-weighted averages of the indicator values provided by van Dam et al. (1994) for estimating environmental conditions in standing freshwaters, their correspondence to measured variables was examined over a wide range of water bodies in Flanders, Belgium. By using data from a region adjacent to the Netherlands, presenting similar geographic characteristics and an identical diatom flora, biogeographic complications were ruled out. A comparison was also made between scores calculated from sympatric epiphytic and sediment-derived diatom assemblages to investigate their respective sensitivities to variables measured in the water column.

2. Material and methods

Flanders, the low-lying (largely <150 m.a.s.l.) northern part of Belgium, is characterized by a temperate oceanic climate and a highly diverse soilscape, including mineral (ranging from heavy clays and calcareous loess to leached sands) as well as peaty top soils, developed in predominantly Quaternary surface deposits of marine, fluvial and niveo-eolian origin. One hundred and eighty six standing water bodies were selected throughout the region, covering the range of permanent freshwater conditions, exclusive of canals and ditches. Most of these waters were man-made, small, shallow, and well mixed. Surrounding land use varied and included semi-natural heaths, shrubs and woodlands, as well as tree plantations (mostly conifers or poplar), lawns, pastures and agricultural fields. In general, anthropogenic pressures (eutrophication, fish stocking, acidification) are strong in the region, but care was taken to include the full spectrum from highly impaired to not markedly impacted sites. General characteristics of the sampled waters are given in Table 2.

Some 32 variables, covering different aspects of water chemistry, trophic status, and organic load, were measured during the growing season (May–November), either in 1998 or 1999. Water samples were taken with a horizontal 2.2 L Van Dorn sampler at a depth of 0.5 m, or halfway the water column in case maximum depth was less than 1 m, and at the same site where diatoms were sampled. Samples were taken preferably near the outflow, if present, or at a well-mixed site as far from the bank as could be reached in waders or from a jetty. Oxygen saturation (O_2%), pH and specific conductivity (EC) were measured 5–6 times in the field with portable meters (WTW Multiline P4) fitted with CellOx 325, TetraCon 325 and SenTix 97/T electrodes. Water samples for laboratory analysis were kept cool during transport, stored at 4 °C and analysed as rapidly as possible, no later than the next day. On three occasions, water samples were analysed by a certified laboratory for major ions (Ca^{2+}, Na^+, K^+, Mg^{2+}, $Fe^{2+/3+}$, Cl^-, SO_4^{2-}), silica, inorganic nitrogen and phosphorus compounds (total phosphorus, TP, and soluble reactive phosphorus, SRP), Kjeldahl nitrogen (KjN) and dissolved inorganic carbon (DIC), using a segmented flow analyser (SAN^{plus}, SKALAR) or inductively coupled plasma mass spectrometry (ICP IRIS/CID, Thermo Jarrell Ash) after filtering through a 0.45 μm Millipore polycarbonate membrane. Total inorganic nitrogen (TIN) was calculated as the sum of nitrate, nitrite and ammonium nitrogen, and total organic nitrogen (TON) as the difference between Kjeldahl and ammonium nitrogen. Variables reflecting biochemical and metabolic status or phytoplankton development were usually measured 4–5 times. Chemical oxygen demand (COD) was analysed following NBN (1974). The COD of dissolved substances (COD_f) and particulate matter (COD_p) was determined by analysing the filtrate through

Table 2
Range and median value of selected environmental variables (site medians, except for dimensions) for all sampled water bodies and for subsets according to pH

	Entire dataset (no. of sites: 186)	Median pH ≤ 7 (no. of sites: 45)	Median pH > 7 (no. of sites: 141)
Dimensions			
$Z_{max.}$ (m)	1.5–3 (<1 to ca. 18)	1.5–3 (<1 to ca. 12)	1.5–3 (<1 to ca. 18)
Surface (m^2)	13×10^3 ($211–740 \times 10^3$)	9.8×10^3 ($272–111 \times 10^3$)	15.8×10^3 ($211–740 \times 10^3$)
Turbidity			
A440 (m^{-1})	4.1 (0.3–24.4)	6.1 (0.3–24.4)	3.9 (0.5–23.5)
pH, inorganic			
pH	7.7 (3.4–9.4)	6.5 (3.4–7)	7.9 (7.1–9.4)
DIC (mg C L^{-1})	15.3 (<1.6–62.6)	5.7 (<1.6–35.7)	17.7 (<1.6–62.6)
Major ions			
EC (mS m^{-1})	460 (24–3520)	131 (24–1216)	548 (146–3520)
Na^+ (mg L^{-1})	21 (1.9–571)	8.4 (1.9–156)	24 (7–571)
K^+ (mg L^{-1})	6.5 (0.4–39.1)	6.5 (0.4–17.9)	7.7 (1.2–39.1)
Ca^{2+} (mg L^{-1})	61.3 (1.4–307)	61.3 (1.4–133)	75.4 (10–307)
Mg^{2+} (mg L^{-1})	6.8 (0.6–65.8)	6.8 (0.6–32.1)	8.6 (2.2–65.8)
SiO_2 (mg L^{-1})	4 (0.06–30.3)	1.3 (0.06–22.1)	5 (0.1–30.3)
SO_4^{2-} (mg L^{-1})	38 (<4–390)	20 (<4–390)	46 (<4–374)
Cl^- (mg L^{-1})	37 (3–921)	14 (3–220)	40 (9–921)
Total P, inorganic P, inorganic N			
TP (mg P L^{-1})	0.13 (<0.07–2.89)	<0.07 (<0.07–2.89)	0.15 (<0.07–2.62)
SRP (mg P L^{-1})	0.04 (<0.02–1.92)	<0.02 (<0.02–0.93)	0.06 (<0.02–1.92)
TIN (mg P L^{-1})	0.24 (0.07–8)	0.27 (0.07–4.3)	0.2 (0.07–8)
NO_3^- (mg N L^{-1})	<0.05 (<0.05–6.6)	<0.05 (<0.05–2.5)	<0.05 (<0.05–6.6)
NH_4^+ (mg N L^{-1})	0.08 (<0.08–6.4)	0.08 (<0.08–4.3)	0.08 (<0.08–6.4)
Organic N, organic matter			
KjN (mg N L^{-1})	1.5 (0.3–10)	1.4 (0.3–10)	1.7 (0.5–8)
TON (mg N L^{-1})	1.3 (0.3–7.4)	1.07 (0.3–7.4)	1.3 (0.3–3.6)
COD (mg O_2 L^{-1})	37.4 (<1.5–309)	38.6 (<1.5–309)	37.3 (9.3–108.1)
$A254_f$ (m^{-1})	25.4 (2.9–225.4)	31.3 (2.9–143.2)	23.9 (3.4–225.4)
$A440_f$ (m^{-1})	1.2 (<0.1–19.9)	2.3 (<0.1–13.0)	1.1 (0.1–19.9)
Productivity, phytoplankton, metabolism			
O_2 (%)	92 (12–206)	87 (12–109)	93 (15–206)
Chlorophyll *a* (μg L^{-1})	20.6 (<3–310)	19.5 (<3–257)	20.8 (<3–310)
Phaeo (μg L^{-1})	2.0 (<3–102)	1.4 (<3 -102)	2.2 (<3–42.8)
BOD_1 (mg O_2 L^{-1})	1.7 (0.2–8.8)	1.4 (0.4–8.8)	1.9 (0.2–8.5)
pGOP (mg O_2 L^{-1})	3.3 (−1–41.8)	2.5 (0.2–11.7)	3.9 (−1–41.8)
pNOP (mg O_2 L^{-1})	1.9 (−2–42.5)	1.3 (−1.4–8.5)	2.6 (−2–42.5)

Whatman GF/C and subtraction from COD. Biochemical oxygen demand (BOD_1), potential gross oxygen production (pGOP) and potential net oxygen production (pNOP) were measured by dark and light bottle incubation for 24 h at 20 °C in controlled light conditions (Einheitsverfahren, 1971). Chlorophyll *a* (chl *a*) and phaeopigments (phaeo) were analysed following Golterman et al. (1978); extraction in 90% acetone). Absorbance of unfiltered and filtered water (Whatman GF/C) at 440 nm (A440, $A440_f$) were determined, using a Beckman DB-GT spectrophotometer and 2 cm glass cuvettes, as measures of turbidity and humic substances ('Gelbstoff' or 'gilvin'), respectively. Absorbance at 254 nm after filtration (1 cm quartz cuvette; $A254_f$) was used as a further indication of organic matter. In the analyses, site medians of water chemistry data, as well as maximum values for N- and P-fractions and chlorophyll *a*, were considered. Levels below detection thresholds were set at 50% of the latter for all calculations.

Diatom assemblages were sampled once at a single site in each water body during the summer. Superficial sediment was sampled at the maximum water depth that could be reached in waders (at most ca. 1.2 m) and always where water was permanent. A plexi 3.4 cm diameter hand-held coring tube was used to retrieve the sediment/water interface, from which the upper 2–3 mm of sediment were collected by suctioning. Epiphytic diatom assemblages were sampled from hand-collected site-representative plant substrates, either permanently submerged macrophytes (preferably hydrophytes or, if none were present, helophytes). In case the water body did not support any aquatic plant growth, permanently submerged parts of overhanging vegetation were sampled. Diatom samples were fixed immediately with dilute formaldehyde. Small aliquots of sediment or a small amount of non-senescent plant material were treated with concentrated hydrogen peroxide, potassium permanganate and dilute hydrochloric acid to decompose organic material and dissolve carbonates. After repeated addition of demineralised water and settling in test tubes for at least 48 h, the sludge was used to prepare permanent slides with the highly refractive resin Naphrax. Slides were examined with Leitz Orthoplan and Olympus BX 50 microscopes equipped with differential interference optics. Diatoms were identified using standard floras and extensive additional literature (mainly Krammer, 1992, 1997a, 1997b; Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b; Lange-Bertalot, 1993; Lange-Bertalot and Moser, 1994; Reichardt, 1997). From each sample, 500 valves were counted at high magnification to calculate percentage abundance of individual taxa.

Abundance-weighted averages of species indicator values ($\mathrm{mI} = (\sum a_j I_j)/\sum a_j$, with a_j the abundance of taxon j and I_j its indicator value in the classifications for R, H, N, O, S or T as in Table 1) were calculated using the list presented by van Dam et al. (1994), complemented with some additional values, partly provided by H. van Dam and A. Mertens (personal communication, 1999). In deviation from the original list, *Eunotia bilunaris* was considered acidophilous instead of pH-indifferent, while *Achnanthidium minutissimum* was entered as meso- to eutrophic, not oligo- to hypertrophic, as this reflected the observed distribution of these abundant species better. In addition, abundance-weighted averages of species indicator values were calculated with a correction for the frequency of particular indicator values in the regional diatom flora, using the formula given by Schaffers and Sýkora (2000): $\mathrm{mI_f} = (\sum a_j I_j/f_j)/\sum a_j/f_j$, with a_j the abundance of taxon j, I_j its indicator value, and f_j the total frequency of I_j. This correction was considered potentially useful to compensate for the very uneven frequency distributions of most indicator values (Fig. 1) and to lessen so-called boundary effects. Such effects result from the fact that at sites with extreme conditions, corresponding to a lowest or a highest category in a classification, species with less extreme indicator values may still be present, while incidence of even more extreme values is excluded.

Where appropriate, environmental variables were log-transformed (optionally adding a constant to obtain positive values) to attain a more normal distribution. Proportional agreement between measured variables and scores obtained by weighted averaging of indicator values was investigated by Pearson correlation coefficients. In the absence of prior knowledge on possible relations, linear regression or multiple linear regression (MLR) was used to investigate the amount of variation in diatom scores accounted for by (groups of) a priori selected variables. The relation between environmental variables and indication scores was examined by stepwise MLR with forward selection (F-to-include = 1.0, F-to-remove = 0.0; $P \leq 0.01$; tolerance > 0.1). Standardized regression (β) and partial correlation coefficients (R_p) were considered to assess the relative contribution of selected variables. Since pH prominently influenced diatom distribution in this dataset and the response to other environmental variables may change along its gradient, stepwise MLR was also carried out with data subsets grouping waters with median pH ≤ 7 or >7 (Table 2). Statistical analyses were performed with the Statistica 6.1 package.

3. Results

3.1. Relation to target variables

Pearson correlation coefficients between weighted indicator values and selected environmental variables

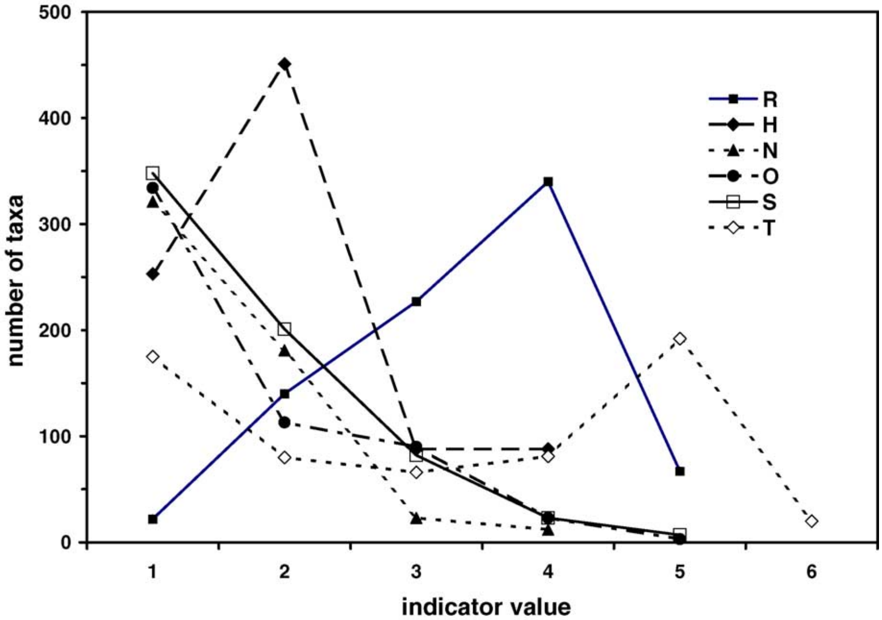

Fig. 1. Frequency distribution of indicator values in the regional diatom species pool (legend see Table 1).

(i.e. those retained in subsequent MLR analyses, complemented by some of general interest) are given in Tables 3 and 4. With relatively few exceptions, correlations were weak. All indication scores correlated significantly to a wide array of variables. The highest correlations were noted with pH, DIC, conductivity and calcium, and slightly less prominent, magnesium and chloride. These variables, associated primarily with buffering conditions and mineral content, correlated particularly strong with mR and mT, less markedly also with mH. The lowest correlations were found with iron, inorganic nitrogen compounds, absorbance measures, chlorophyll *a* and oxygen saturation. Most other variables were moderately correlated with the complete set of diatom scores. It is noteworthy that mN, mO and mS, or their frequency-adjusted variants, all showed a comparable degree of correlation to variables reflecting nutrient levels, organic load and biological conditions. Correlation coefficients of sediment-assemblage derived or epiphyte-derived values with corresponding variables were generally quite similar. Scores calculated from sediment assemblages, nevertheless, appeared to relate slightly more strongly with chlorophyll *a*, pGOP and phaeopigments than their epiphyte-derived counterparts. The effect of correcting for the frequency distribution of indicator values differed according to the indication score. For example, most variables correlated slightly better with mH_f than with mH, both for sediment assemblages and epiphytes. Particularly with sediment assemblages, the correlation of mN_f to Kjeldahl nitrogen or TP was lower than that of mN; similarly, mS_f related less well to most measures of organic load, COD excepted, than mS in this case. Overall, differences remained very limited in spite of the very skewed distribution of most indicator values (Fig. 1).

Each indication score can be assumed to relate to a particular (set of) target variable(s) reflecting the corresponding gradient at the water-chemistry level. Such variables were selected by referring to the original indications of van Dam et al. (1994) (Table 1) or general considerations. Results of linear regression or MLR with these variables are shown in Table 5 and scatter plots in Figs. 2 and 3 (in the latter, BOD_1 and chlorophyll *a* were chosen to reflect saprobity or trophic status). Regression against pH indicated that this variable always explained at least 3/4 of the variance in mR, except at pH values above 7, where the $R^2_{\mathrm{adj.}}$ dropped below 10%. The relation to the frequency-corrected scores, mR_f, was generally slightly poorer. Both chloride and conductivity were

Table 3
Pearson correlation coefficients for selected environmental variables and sediment-derived scores (all samples; $P \leq 0.05$; ns not significant)

	pH		Salinity		Organic N		Oxygen		Saprobity		Trophic status	
	mR	mR_f	mH	mH_f	mN	mN_f	mO	mO_f	mS	mS_f	mT	mT_f
pH	0.88	0.84	0.57	0.63	0.38	0.53	0.35	0.46	0.23	0.37	0.78	0.75
DIC[a]	0.80	0.84	0.69	0.76	0.56	0.60	0.58	0.56	0.52	0.53	0.84	0.81
EC[a]	0.73	0.76	0.66	0.72	0.53	0.60	0.52	0.56	0.45	0.50	0.77	0.74
Ca^{2+}[a]	0.82	0.83	0.62	0.69	0.51	0.59	0.50	0.53	0.43	0.51	0.83	0.81
K^{+}[a]	0.54	0.53	0.51	0.54	0.44	0.51	0.45	0.55	0.35	0.42	0.55	0.55
Mg^{2+}[a]	0.66	0.69	0.60	0.66	0.48	0.56	0.47	0.54	0.37	0.45	0.69	0.64
$Fe^{2+/3+}$[a]	−0.19	−0.22	−0.15	−0.19	ns	ns	ns	ns	ns	ns	ns	ns
Cl^{-}[a]	0.64	0.63	0.56	0.61	0.42	0.51	0.41	0.51	0.29	0.36	0.63	0.60
SiO_2[a]	0.35	0.36	0.27	0.32	0.33	0.30	0.42	0.39	0.35	0.34	0.42	0.42
TP[a]	0.35	0.36	0.39	0.45	0.50	0.44	0.55	0.52	0.50	0.46	0.44	0.45
$TP_{max.}$[a]	0.32	0.33	0.41	0.46	0.52	0.46	0.55	0.51	0.52	0.48	0.43	0.44
SRP[a]	0.29	0.30	0.33	0.37	0.40	0.35	0.46	0.41	0.41	0.37	0.35	0.36
TIN[a]	ns	ns	ns	ns	ns	ns	ns	0.15	ns	ns	0.15	0.17
NO_3[a]	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
$NO_{3\ max.}$[a]	0.17	0.18	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.15
NO_2[a]	0.19	0.21	0.22	0.21	0.19	0.16	0.17	0.21	0.19	0.16	0.24	0.25
NH_4[a]	ns	ns	ns	ns	0.19	0.16	0.25	0.23	0.27	0.26	ns	ns
$NH_{4\ max.}$[a]	ns	ns	ns	0.17	0.30	0.23	0.37	0.33	0.37	0.33	0.20	0.20
TON[a]	0.39	0.39	0.41	0.45	0.48	0.45	0.48	0.56	0.44	0.40	0.44	0.49
KjN[a]	0.33	0.32	0.35	0.39	0.50	0.44	0.52	0.56	0.49	0.45	0.43	0.46
A440	ns	ns	ns	ns	0.29	0.21	0.29	0.35	0.26	0.20	0.16	0.21
$A440_f$	ns	−0.15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
COD_f[a]	0.32	0.25	0.24	0.28	0.27	0.36	0.27	0.37	0.17	0.25	0.27	0.29
Chlorophyll *a*[a]	0.20	0.21	0.22	0.21	0.31	0.18	0.30	0.32	0.34	0.21	0.26	0.31
O_2%	ns	ns	ns	ns	−0.16	−0.15	−0.23	−0.18	−0.20	−0.22	ns	ns
pGOP[a]	0.36	0.37	0.30	0.29	0.31	0.22	0.30	0.39	0.34	0.23	0.37	0.43
phaeo[a]	0.27	0.27	0.28	0.35	0.38	0.27	0.38	0.40	0.38	0.29	0.33	0.38
BOD_1[a]	0.40	0.40	0.35	0.38	0.37	0.35	0.39	0.47	0.37	0.31	0.43	0.47

[a] Transformed.

considered as primary target variables for mH, the former relating more particularly to the influence of sea salt, the latter reflecting total ionic strength. Conductivity provided the nearest proxy. The highest coefficients of determination were obtained with the entire dataset, where hardly any differences emerged between sediment and epiphyte assemblages. At pH $\leq$ 7 explained variance was very low. Above pH 7, epiphyte-derived scores were most effectively predicted, with an $R^2_{adj.}$ of 0.34 for conductivity and mH. Frequency correction slightly improved correlations with sediment-derived indication scores as well as with epiphyton for the complete pH gradient. A larger range of values and some improvement in linearity accompanied the gain in slope (Figs. 2 and 3). Total organic nitrogen, as such, explained only 1/4 to 1/3 of the variation in the corresponding mN values for the complete dataset, with epiphytic assemblages again showing the strongest response. Calculated from sediment assemblages, this indication score was hardly associated with TON at lower pH, whereas the $R^2_{adj.}$ amounted to a mere 0.22 with epiphytes. Correcting for frequencies somewhat improved the correlation for sediment assemblages in this case, but also introduced more scatter (Figs. 2 and 3). Results were particularly poor for the oxygen scores and oxygen saturation. At lower pH, frequency correction gave some improvement. Agreement of mO_f values of at least ca. 3.5 to an oxygen saturation below 50% was the only noteworthy feature (Figs. 2 and 3). However, values close to 4 occurred commonly at saturations up to 150%. The saprobity metric also corresponded rather poorly to the combination of low oxygen saturation and high BOD_1. The strongest association ($R^2_{adj.}$ 0.28) occurred with uncorrected values for sediment assemblages at pH > 7. Effects of frequency

Table 4
Pearson correlation coefficients for selected environmental variables and epiphyton-derived indication scores (all samples; $P \leq 0.05$; ns not significant)

	pH		Salinity		Organic N		Oxygen		Saprobity		Trophic status	
	mR	mR_f	mH	mH_f	mN	mN_f	mO	mO_f	mS	mS_f	mT	mT_f
pH	0.87	0.85	0.53	0.55	0.38	0.49	0.33	0.40	ns	0.22	0.78	0.75
DIC[a]	0.76	0.79	0.67	0.71	0.45	0.53	0.47	0.47	0.31	0.33	0.77	0.74
EC[a]	0.70	0.73	0.67	0.70	0.45	0.50	0.42	0.41	0.30	0.30	0.74	0.70
Ca^{2+}[a]	0.78	0.79	0.61	0.63	0.43	0.50	0.40	0.44	0.27	0.31	0.79	0.75
K^{+}[a]	0.55	0.57	0.48	0.50	0.49	0.51	0.47	0.45	0.33	0.34	0.60	0.58
$Fe^{2+/3+}$[a]	−0.17	−0.22	−0.15	−0.19	ns	ns	ns	ns	ns	ns	ns	ns
Mg^{2+}[a]	0.64	0.65	0.58	0.62	0.43	0.47	0.36	0.37	0.24	0.24	0.67	0.63
Cl^{-}[a]	0.64	0.64	0.53	0.58	0.40	0.44	0.36	0.36	0.20	0.21	0.63	0.59
SiO_2[a]	0.34	0.35	0.27	0.29	0.24	0.26	0.29	0.30	0.28	0.29	0.39	0.39
TP[a]	0.36	0.38	0.42	0.48	0.52	0.51	0.58	0.52	0.54	0.51	0.49	0.50
$TP_{max.}$[a]	0.33	0.35	0.43	0.50	0.54	0.53	0.57	0.51	0.53	0.52	0.46	0.48
SRP[a]	0.32	0.34	0.38	0.44	0.41	0.41	0.50	0.43	0.44	0.42	0.40	0.41
TIN[a]	ns	ns	ns	ns	ns	ns	ns	ns	0.16	ns	ns	ns
NO_3^{-}[a]	ns	ns	ns	ns	ns	ns	ns	ns	ns	−0.17	ns	ns
$NO_{3\ max.}$[a]	0.17	0.18	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.15
NO_2^{2-}[a]	0.18	0.19	0.20	0.20	ns	ns	ns	ns	ns	ns	0.20	0.21
$NH4+$[a]	ns	ns	ns	ns	0.19	ns	0.22	0.18	0.32	0.23	ns	ns
$NH4max.+$[a]	ns	ns	0.18	0.18	0.24	0.20	0.27	0.26	0.37	0.30	0.18	0.18
TON[a]	0.37	0.37	0.31	0.40	0.54	0.56	0.48	0.50	0.44	0.48	0.45	0.49
KjN[a]	0.30	0.30	0.32	0.37	0.52	0.49	0.49	0.49	0.50	0.48	0.41	0.44
A440	ns	ns	ns	ns	0.27	0.28	0.20	0.23	0.20	0.25	ns	0.16
$A440_f$	ns	ns	ns	ns	ns	ns	0.15	0.16	ns	0.19	ns	ns
COD_f[a]	0.36	0.32	ns	0.20	0.32	0.38	0.33	0.36	0.20	0.30	0.33	0.34
chl *a*[a]	ns	ns	0.15	0.17	0.27	0.31	0.18	0.27	0.26	0.30	0.17	0.20
O_2%	ns	ns	ns	ns	ns	ns	−0.21	−0.24	−0.20	−0.24	ns	ns
pGOP[a]	0.27	0.28	0.21	0.25	0.30	0.36	0.20	0.31	0.22	0.29	0.28	0.32
phaeo[a]	0.24	0.25	0.20	0.27	0.32	0.36	0.27	0.27	0.24	0.27	0.28	0.31
BOD_1[a]	0.35	0.37	0.25	0.29	0.41	0.45	0.38	0.42	0.34	0.38	0.40	0.43

[a] Transformed.

correction varied, from slight improvement at lower pH and with epiphytes and all samples, to degradation with sediment assemblages at higher pH. The relation to BOD_1, as such, became noisier (Figs. 2 and 3). A combination of chlorophyll *a*, total phosphorus (TP) and nitrogen levels (TIN, TON) was used to approximate trophic status. Although yielding significant regressions for mT, the $R^2_{adj.}$ usually amounted to only ca. 0.30 or less. With sediment assemblages, frequency correction slightly increased values (up to 0.36 at pH > 7). As shown for chlorophyll *a*, this improvement was realized mainly at the high end of the trophic gradient (Fig. 2). In general, correlations between the selected target variables associated to either organic nitrogen availability, oxygen saturation, saprobity or nutrient status were low to moderate (Table 6). It is therefore unlikely that poor performance of the indication scores for these characteristics resulted merely from particularities of the data distribution, as corroborated further by Figs. 2 and 3.

The pH and salinity indication scores could be fitted reasonably well to respective target variables by simple linear regression. With sediment assemblages the best results were obtained using the expressions pH = 1.1776 mR + 3.2559 (R^2 0.77, S.E. 0.54) and $\log_{10}$ EC = 0.4703 mH_f + 1.5368 (R^2 0.51, S.E. 0.24), whereas for epiphyton pH = 1.2459 mR + 3.2736 (R^2 0.76, S.E. 0.56) and $\log_{10}$ EC = 0.6031 mH_f + 1.3602 (R^2 0.49, S.E. 0.24) were the best-fitting models.

3.2. Confounding factors

Since frequency correction did not yield a considerable improvement of performance in most

Table 5
Results of linear or multiple linear regression with selected target variables for sediment and epiphyton-derived indication scores using the entire dataset and subsets according to pH

Dependent variable	Independent variable(s)		Sediment			Epiphytes		
			All	pH ≤ 7	pH > 7	All	pH ≤ 7	pH > 7
mR	pH	$R^2_{adj.}$	0.77^{****}	0.80^{****}	0.07^{***}	0.76^{****}	0.83^{****}	0.08^{***}
			$F_{1,184} = 627.7$	$F_{1,43} = 176.3$	$F_{1,139} = 11.8$	$F_{1,184} = 581.8$	$F_{1,43} = 212.7$	$F_{1,139} = 14.0$
mR_f	pH	$R^2_{adj.}$	0.71^{****}	0.64^{****}	0.08^{***}	0.73^{****}	0.75^{****}	0.09^{***}
			$F_{1,184} = 458.2$	$F_{1,43} = 78.3$	$F_{1,139} = 12.5$	$F_{1,184} = 493.7$	$F_{1,43} = 134.2$	$F_{1,139} = 14.4$
mH	Cl^{-} [a]	$R^2_{adj.}$	0.30^{****}	0.06^{ns}	0.16^{****}	0.28^{****}	0.01^{ns}	0.29^{****}
			$F_{1,184} = 82.0$	$F_{1,43} = 3.6$	$F_{1,139} = 28.6$	$F_{1,184} = 72.6$	$F_{1,43} = 1.2$	$F_{1,139} = 58.0$
mH_f	Cl^{-} [a]	$R^2_{adj.}$	0.37^{****}	0.15^{**}	0.19^{****}	0.33^{****}	0.01^{ns}	0.26^{****}
			$F_{1,184} = 109.3$	$F_{1,43} = 8.9$	$F_{1,139} = 34.3$	$F_{1,184} = 92.2$	$F_{1,43} = 1.2$	$F_{1,139} = 50.8$
mH	EC[a]	$R^2_{adj.}$	0.43^{****}	0.14^{**}	0.17^{****}	0.45^{****}	0.09^{*}	0.34^{****}
			$F_{1,184} = 143.4$	$F_{1,43} = 8.3$	$F_{1,139} = 29.4$	$F_{1,184} = 151.7$	$F_{1,43} = 5.5$	$F_{1,139} = 73.2$
mH_f	EC[a]	$R^2_{adj.}$	0.51^{****}	0.21^{***}	0.22^{****}	0.49^{****}	0.10^{*}	0.31^{****}
			$F_{1,184} = 193.0$	$F_{1,43} = 12.9$	$F_{1,139} = 40.2$	$F_{1,184} = 176.9$	$F_{1,43} = 5.9$	$F_{1,139} = 63.3$
mN	TON[a]	$R^2_{adj.}$	0.23^{****}	0.08^{*}	0.25^{****}	0.29^{****}	0.22^{***}	0.29^{****}
			$F_{1,184} = 55.5$	$F_{1,43} = 4.7$	$F_{1,139} = 47.3$	$F_{1,184} = 77.3$	$F_{1,43} = 13{,}1$	$F_{1,139} = 58{,}2$
mN_f	TON[a]	$R^2_{adj.}$	0.20^{****}	0.15^{**}	0.17^{****}	0.31^{****}	0.22^{***}	0.31^{****}
			$F_{1,184} = 46.3$	$F_{1,43} = 8.9$	$F_{1,139} = 29.9$	$F_{1,184} = 83.5$	$F_{1,43} = 13{,}6$	$F_{1,139} = 62{,}9$
mO	O_2%	$R^2_{adj.}$	0.05^{**}	0.02^{ns}	0.12^{****}	0.04^{**}	0.03^{ns}	0.08^{***}
			$F_{1,184} = 10.3$	$F_{1,43} = 1.9$	$F_{1,139} = 20.3$	$F_{1,184} = 8.6$	$F_{1,43} = 2{,}6$	$F_{1,139} = 13{,}3$
mO_f	O_2%	$R^2_{adj.}$	0.03^{*}	0.13^{**}	0.06^{**}	0.05^{**}	0.11^{*}	0.09^{***}
			$F_{1,184} = 6.5$	$F_{1,43} = 7.3$	$F_{1,139} = 9.9$	$F_{1,184} = 11.0$	$F_{1,43} = 6{,}4$	$F_{1,139} = 15{,}0$
mS	O_2%, BOD_1[a]	$R^2_{adj.}$	0.17^{****}	0.00^{ns}	0.28^{****}	0.15^{****}	0.03^{ns}	0.21^{****}
			$F_{2,183} = 20.1$	$F_{2,42} = 0.3$	$F_{2,138} = 28.0$	$F_{2,183} = 17.3$	$F_{2,42} = 1.6$	$F_{2,138} = 19.9$
mS_f	O_2%, BOD_1[a]	$R^2_{adj.}$	0.14^{****}	0.14^{*}	0.17^{****}	0.20^{****}	0.15^{*}	0.21^{****}
			$F_{2,183} = 16.3$	$F_{2,42} = 4.4$	$F_{2,138} = 15.5$	$F_{2,183} = 23.6$	$F_{2,42} = 5.0$	$F_{2,138} = 19.3$
mT	chl *a*[a], TP[a], TON[a], TIN[a]	$R^2_{adj.}$	0.23^{****}	0.22^{**}	0.31^{****}	0.26^{****}	0.26^{**}	0.29^{****}
			$F_{4,181} = 15.2$	$F_{4,40} = 4.1$	$F_{4,136} = 17.0$	$F_{4,181} = 17.1$	$F_{4,40} = 4.9$	$F_{4,136} = 15.0$
mT_f	chl *a*[a], TP[a], TON[a], TIN[a]	$R^2_{adj.}$	0.28^{****}	0.29^{**}	0.36^{****}	0.29^{****}	0.28^{**}	0.30^{****}
			$F_{4,181} = 18.8$	$F_{4,40} = 5.4$	$F_{4,136} = 21.0$	$F_{4,181} = 19.8$	$F_{4,40} = 5.2$	$F_{4,136} = 15.9$

[a] Transformed.
* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.
**** $P \leq 0.0001$.

cases, analyses of confounding factors were restricted to uncorrected weighted averages of indicator values. The results of MLR with stepwise selection of variables for indication scores from sediment assemblages are shown in Table 7. The strongest models were obtained for mR and mT with either all sites or those of pH ≤ 7 ($R^2_{adj.}$ resp. 0.85 for mR and 0.78 or 0.77 for mT). In most other cases about 40–55% of the variance in weighted indicator values could be explained by the selected variables. For mR, pH was by far the most influential variable with all waters included and in the model for those of lower pH. The positive relation deteriorated strongly at pH > 7, where pGOP and DIC (+) became the primary variables. DIC (+) had most leverage on mH when the entire pH gradient was considered. At lower pH, DIC (+) and nitrate (−) were equally important. Within the more alkaline pH range, EC and TON (+) were significant. Although Kjeldahl nitrogen was retained for mN with all sites included, it was preceded here by DIC (+). This score was most strongly related to conductivity (+) if only the lower

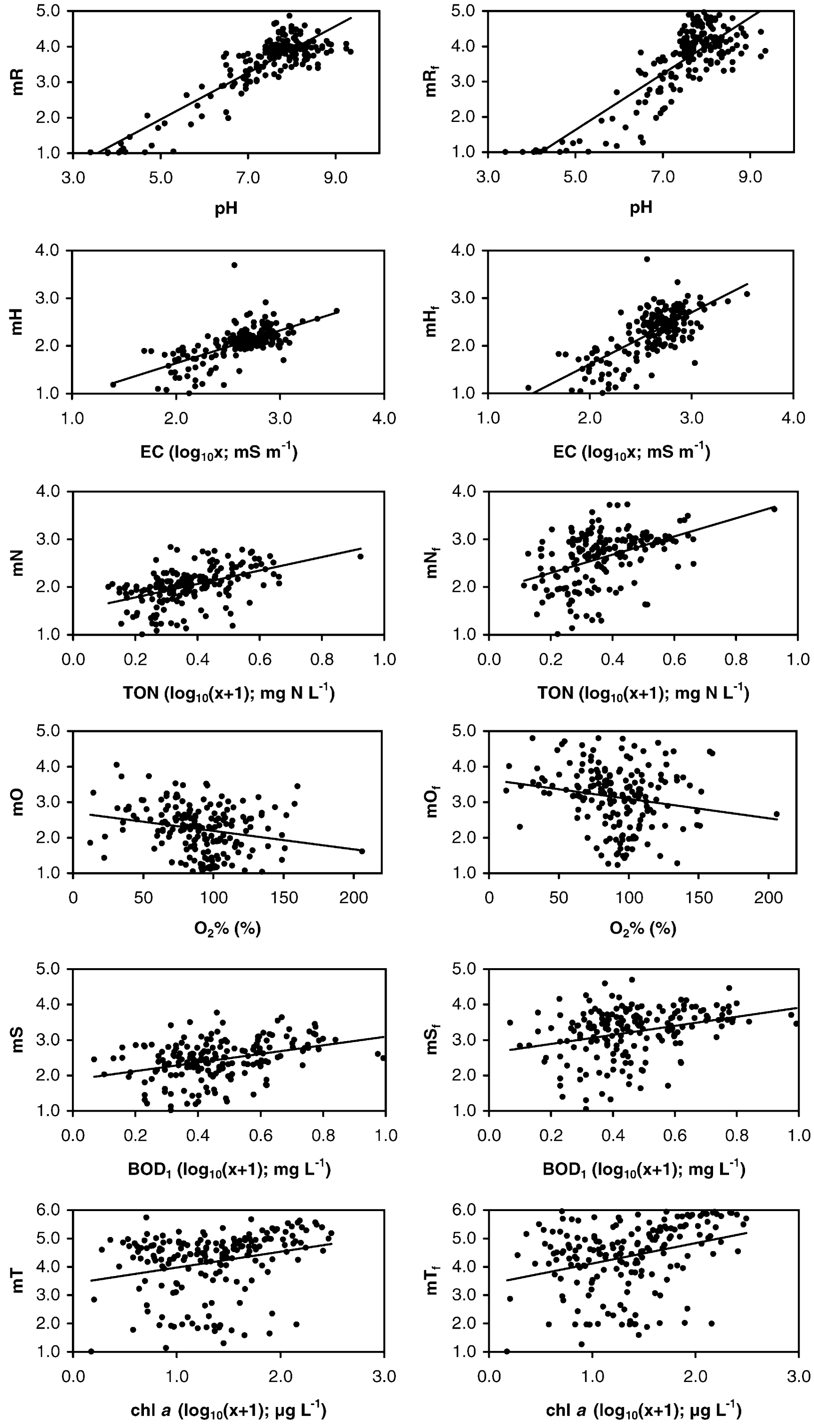

Fig. 2. Abundance-weighted averages of species indicator values from sediment assemblages against selected target variables with linear fit.

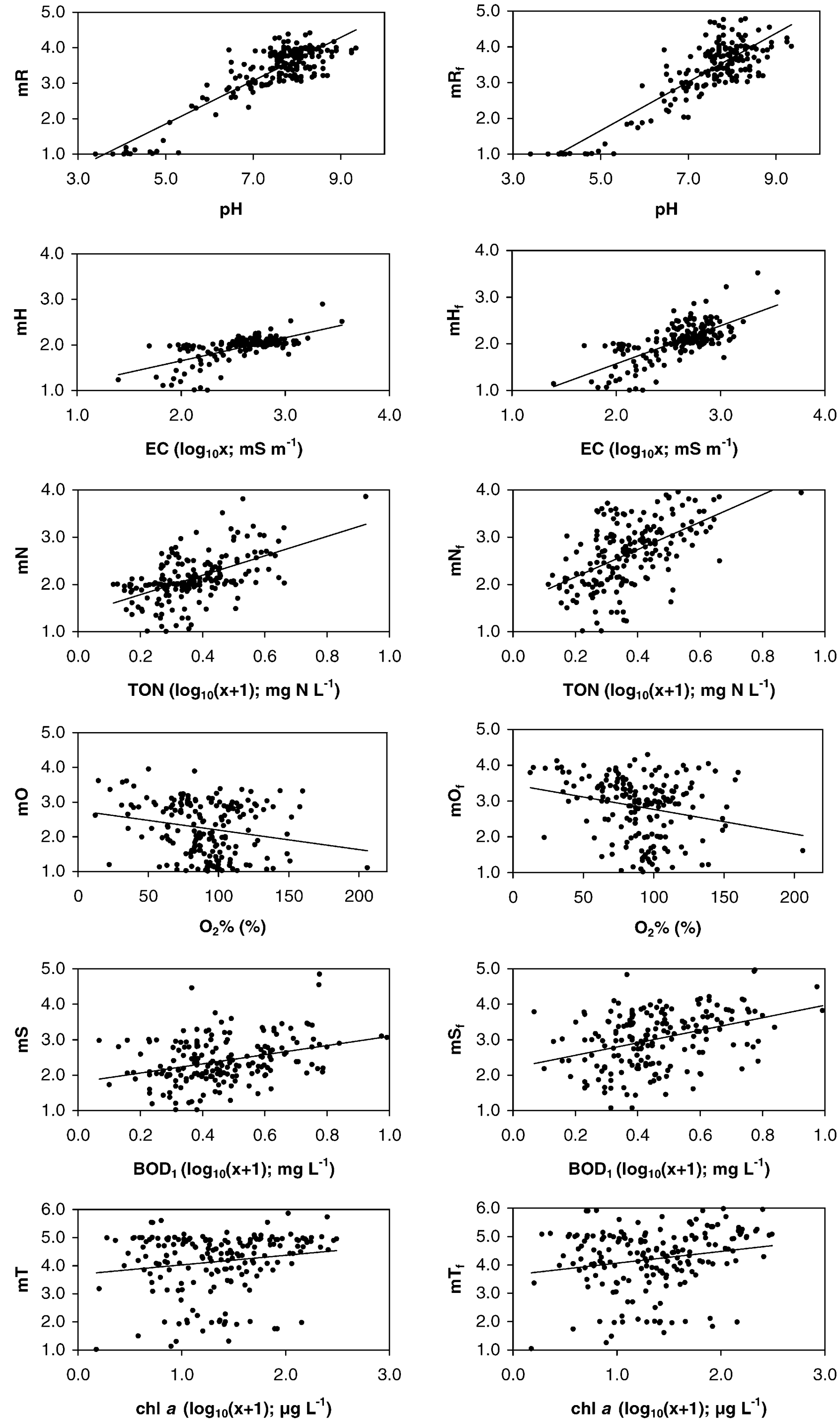

Fig. 3. Abundance-weighted averages of species indicator values from epiphytic assemblages against selected target variables with linear fit.

Table 6
Pearson correlation coefficients between targeted environmental variables for the three datasets

	pH			EC[a]			Cl^{-}[a]			TP[a]			TIN[a]			TON[a]			O_2%			BOD_1[a]		
	All	pH ≤ 7	pH > 7	All	pH ≤ 7	pH > 7	All	pH ≤ 7	pH > 7	All	pH ≤ 7	pH > 7	All	pH ≤ 7	pH > 7	All	pH ≤ 7	pH > 7	All	pH ≤ 7	pH > 7	All	pH ≤ 7	pH > 7
EC[a]	0.69	0.40	0.26																					
Cl^{-}[a]	0.63	0.64	0.31	0.86	0.85	0.82																		
TP[a]	0.26	ns	ns	0.49	0.48	0.49	0.48	0.54	0.41															
TIN[a]	ns	ns	ns	0.26	0.34	0.29	0.19	0.31	ns	ns	0.30	ns												
TON[a]	0.32	0.53	ns	0.37	ns	0.39	0.45	0.45	0.41	0.62	0.76	0.58	ns	ns	ns									
O_2%	0.22	−0.45	0.56	ns	−0.40	ns	ns	−0.39	ns	−0.25	−0.31	−0.29	ns	ns	ns	ns	ns	ns						
BOD_1[a]	0.30	0.52	ns	0.28	0.36	ns	0.31	0.50	ns	0.29	0.50	0.20	ns	ns	ns	0.61	0.55	0.61	ns	ns	ns			
pGOP[a]	0.23	0.38	ns	0.21	ns	ns	0.20	ns	ns	ns	ns	ns	ns	ns	ns	0.53	ns	0.59	ns	ns	ns	0.70	0.46	0.74

[a] Transformed; $P \leq 0.05$; ns: not significant.

Table 7
Results of stepwise multiple linear regression for sediment-derived indication scores (significance levels see Table 5)

		Dependent variable																	
		mR			mH			mN			mO			mS			mT		
		All	≤7.0	>7.0	All	≤7.0	>7.0	All	≤7.0	>7.0	All	≤7.0	>7.0	All	≤7.0	>7.0	All	≤7.0	>7.0
		0.85****; 4, 181; 273.7[a]	0.85****; 3, 41; 84.4	0.35****; 3, 137; 25.6	0.51****; 2, 183; 93.4	0.42****; 2, 42; 16.8	0.25****; 2, 138; 24.1	0.40****; 2, 183; 62.2	0.56****; 4, 40; 15.0	0.36****; 4, 136; 20.5	0.51****; 6, 179; 33.2	0.49****; 3, 41; 14.9	0.37****; 3, 137; 27.9	0.44****; 5, 18; 29.9	0.55****; 4, 4; 14.3	0.40****; 3, 137; 32.1	0.78****; 4, 181; 168.6	0.77****; 4, 40; 38.2	0.44****; 3, 137; 37.5
pH	β	0.69****	0.75****	0.20**	–	–	–	–	–	–	–	–	–	−0.25***	−0.56***	–	0.45****	–	–
	R_p	0.74	0.84	0.24	–	–	–	–	–	–	–	–	–	−0.20	−0.54	–	0.50	–	–
DIC[b]	β	–	–	0.34****	0.60****	0.47***	–	0.43****	–	–	0.40****	–	–	0.55****	0.47**	–	0.46****	–	0.41****
	R_p	–	–	0.38	0.58	0.53	–	0.45	–	–	0.44	–	–	0.38	0.46	–	0.52	–	0.46
EC[b]	β	–	–	–	–	–	0.30***	–	0.74***	–	–	–	–	–	–	–	–	–	–
	R_p	–	–	–	–	–	0.30	–	0.52	–	–	–	–	–	–	–	–	–	–
Ca^{2+}[b]	β	0.24****	0.26**	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.69****	–
	R_p	0.35	0.46	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.81	–
K^{+}[b]	β	–	–	–	0.18**	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	R_p	–	–	–	0.21	–	–	–	–	–	–	–	–	–	–	–	–	–	–
$Fe^{2+/3+}$[b]	β	–	–	–	–	–	–	–	–	0.14*	–	–	–	–	–	–	–	–	–
	R_p	–	–	–	–	–	–	–	–	0.17	–	–	–	–	–	–	–	–	–

Cl^{-b}	β	–	–	–	–	–	–	–	-0.53^{**}	–	–	–	–	–	–	–	–	–	–
	R_p	–	–	–	–	–	–	–	−0.38	–	–	–	–	–	–	–	–	–	–
$TP_{max.}^{b}$	β	–	–	–	–	–	–	–	0.42^{***}	0.23^{**}	0.21^{**}	0.66^{***}	0.27^{**}	0.23^{****}	–	0.25^{**}	–	–	–
	R_p	–	–	–	–	–	–	–	0.49	0.22	0.21	0.52	0.26	0.24	–	0.25	–	–	–
TIN^{b}	β	–	–	–	–	–	–	–	–	–	–	–	–	–	-0.50^{***}	–	–	–	–
	R_p	–	–	–	–	–	–	–	–	–	–	–	–	–	−0.51	–	–	–	–
NO_3^{-b}	β	–	–	–	–	-0.46^{***}	–	–	-0.44^{****}		-0.34^{****}	–	–	–	–	–	–	-0.33^{****}	–
	R_p	–	–	–	–	−0.52	–	–	−0.56		−0.30	–	–	–	–	–	–	−0.58	–
$NO_3^{-}{}_{max.}^{b}$	β	–	-0.15^{**}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	R_p	–	−0.37	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
NO_2^{2-b}	β	–	–	–	–	–	–	–	–	–	0.24^{**}	–	–	–	–	–	–	–	–
	R_p	–	–	–	–	–	–	–	–	–	0.21	–	–	–	–	–	–	–	–
NH_4^{+b}	β	–	–	–	–	–	–	–	–	–	–	–	–	0.13^{*}	–	–	–	–	–
	R_p	–	–	–	–	–	–	–	–	–	–	–	–	0.16	–	–	–	–	–
$NH^{+}_{4\,max.}{}^{b}$	β	–	–	–	–	–	–	–	–	–	–	0.36^{**}	–	–	0.67^{****}	–	–	–	–
	R_p	–	–	–	–	–	–	–	–	–	–	0.39	–	–	0.60	–	–	–	–
TON^{b}	β	–	–	–	–	–	0.31^{***}	–	–	–	–	–	–	–	–	–	–	–	–
	R_p	–	–	–	–	–	0.32	–	–	–	–	–	–	–	–	–	–	–	–
KjN^{b}	β	–	–	–	–	–	–	0.33^{****}	–	0.21^{*}	0.30^{***}	–	0.27^{**}	–	–	0.30^{**}	–	0.44^{****}	–
	R_p	–	–	–	–	–	–	0.37	–	0.19	0.27	–	0.24	–	–	0.27	–	0.58	–
A440	β	–	–	–	–	–	–	–	–	0.23^{**}	–	–	0.22^{**}	–	–	0.24^{**}	–	–	–
	R_p	–	–	–	–	–	–	–	–	0.24	–	–	0.23	–	–	0.26	–	–	–
COD_f^{b}	β	–	–	–	–	–	–	–	–	–	-0.18^{**}	–	–	–	–	–	–	–	–
	R_p	–	–	–	–	–	–	–	–	–	−0.20	–	–	–	–	–	–	–	–
chl a^{b}	β	–	–	–	–	–	–	–	–	–	–	–	–	0.22^{***}	–	–	0.17^{****}	–	–
	R_p	–	–	–	–	–	–	–	–	–	–	–	–	0.28	–	–	0.34	–	–
O_2%	β	-0.16^{****}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	-0.16^{****}	–	–
	R_p	−0.36	–	–	–	–	–	–	–	–	–	–	–	–	–	–	−0.30	–	–
$pGOP^{b}$	β	0.15^{****}	–	0.35^{****}	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	R_p	0.36	–	0.39	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
$phaeo^{b}$	β	–	–	–	–	–	–	–	–	–	–	-0.39^{**}	–	–	–	–	–	-0.28^{**}	0.25^{***}
	R_p	–	–	–	–	–	–	–	–	–	–	−0.37	–	–	–	–	–	−0.43	0.29
BOD_1^{b}	β	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.23^{**}
	R_p	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.27

[a] $R^2_{adj.}$; d.f.; F.
[b] Transformed.
* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.
**** $P \leq 0.0001$.

pH samples were included; $TP_{max.}$ (+), chloride (−) and nitrate (−) also joined in here. At higher pH values, the total $R^2_{adj.}$ dropped to 0.36, and although Kjeldahl nitrogen reappeared after A440 and $TP_{max.}$ (+), expectations for a meaningful relation with organic nitrogen were hardly met. No direct link is suggested between mO and oxygen saturation. Conversely, variables such as DIC (+), $TP_{max.}$ (+) and nitrogen compounds showed significant relations. Any reflection of the oxygen regime was limited to a positive relation to nitrite in the analysis covering all sites, or to $NH^+_{4\,max.}$ at pH $\leq$ 7. The saprobity indication, mS, was most strongly related to DIC (+) in the model for all samples. Ammonium was relatively unimportant. At pH $\leq$ 7, $NH^+_{4\,max.}$ (+) became the most influential variable, but pH (−) followed rather closely. At higher pH, Kjeldahl nitrogen, $TP_{max.}$ and A440 gave similar positive contributions. DIC and pH explained most of the variance in mT throughout the entire pH range. At pH $\leq$ 7, the effect of calcium was most prominent, with smaller contributions by Kjeldahl nitrogen (+) and nitrate (−). At pH > 7, the trophic score was associated primarily with higher DIC values, but in this case the $R^2_{adj.}$ amounted to no more than 0.44.

In general, results were rather similar for epiphyte-derived scores (Table 8). Very comparable multiple determination coefficients were generated for mR. With all samples included, pH again predominated quite strongly. At pH $\leq$ 7, calcium was nearly as important. For mH, the poorest model now resulted at pH $\leq$ 7 from conductivity (+), $NH_{4\,max.}$ (+), TIN (−) and chloride (−). Using the other datasets, the $R^2_{adj.}$ increased to ca. 0.5, with particularly conductivity (+) and, at pH above 7, also gilvin (+) among the more powerful variables. As with sediment assemblages, mN was fitted best at pH $\leq$ 7, but in this case only by SRP (+). The $R^2_{adj.}$ values were slightly lower for the other pH ranges, but some relation to total phosphorus and organic nitrogen was substantiated here as well. For mO, selected variables gave a slightly better approximation at pH below or above 7 than with sediment assemblages, but less determination for the full dataset ($R^2_{adj.}$ 0.40). Here, oxygen saturation (−) was selected at pH above 7, but TP was at least as important. Relations of mS values from epiphytes to measured conditions were never stronger than with sediment assemblages. With all samples or at pH > 7

Table 8
Results of stepwise multiple linear regression for epiphyton-derived indication scores (significance levels see Table 5)

		Dependent variable																	
		mR			mH			mN			mO			mS			mT		
		All	≤7.0	>7.0	All	≤7.0	>7.0	All	≤7.0	>7.0	All	≤7.0	>7.0	All	≤7.0	>>7.0	All	≤7.0	>7.0
		0.83****; 3, 182; 298.3[a]	0.90****; 3, 41; 132.3	0.32****; 4, 136; 17.8	0.50****; 4, 181; 48.1	0.35***; 4, 40; 7.0	0.55****; 4, 136; 43.7	0.40****; 4, 181; 32.0	0.44****; 1, 43; 35.7	0.32****; 2, 138; 34.6	0.40****; 3, 182; 42.8	0.54****; 3, 41; 18.5	0.42****; 4, 136; 26.1	0.33****; 3, 182; 31.9	0.55****; 4, 40; 14.5	0.37****; 2, 138; 41.4	0.75****; 4, 181; 142.8	0.64****; 2, 42; 40.5	0.41****; 4, 136; 25.1
pH	β	0.79****	0.72****	0.45****	–	–	0.25****	–	–	–	–	–	0.32****	–	–	–	0.54****	–	0.36****
	R_p	0.75	0.87	−0.4	–	–	0.34	–	–	–	–	–	0.32	–	–	–	0.55	–	0.39
DIC[b]	β	–	–	0.60***	0.36**	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	R_p	–	–	0.32	0.23	–	–	–	–	–	–	–	–	–	–	–	–	–	–
EC[b]	β	–	–	–	0.38***	0.73**	0.37****	0.21**	–	–	–	–	–	–	–	–	–	–	–
	R_p	–	–	–	0.25	0.44	0.44	0.24	–	–	–	–	–	–	–	–	–	–	–
Ca^{2+}[b]	β	0.17***	0.64****	−0.41**	–	–	–	–	–	–	–	–	–	–	–	–	0.29****	0.66****	–
	R_p	0.24	0.66	−0.23	–	–	–	–	–	–	–	–	–	–	–	–	0.33	0.72	–
K^+[b]	β	–	–	–	–	–	–	–	–	–	0.20**	–	–	–	–	–	–	–	–
	R_p	–	–	–	–	–	–	–	–	–	0.22	–	–	–	–	–	–	–	–
Mg^{2+}[b]	β	–	−0.41***	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	R_p	–	−0.53	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cl^-[b]	β	–	–	–	–	−0.50*	–	–	–	–	–	–	–	–	–	–	–	–	–

	R_p	–	–	–	–	−0.31	–	–	–	–	–	–	–	–	–	–	–	–	–
SiO_2[b]	β	–	–	–	−0.20**	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	R_p	–	–	–	−0.22	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TP[b]	β	–	–	–	–	–	–	–	–	–	0.43****	–	0.37****	0.45****	–	0.48****	0.18****	–	0.36****
	R_p	–	–	–	–	–	–	–	–	–	0.43	–	0.41	0.46	–	0.51	0.31	–	0.32
$TP_{max.}$[b]	β	–	–	–	0.17**	–	–	0.27***	–	0.24**	–	–	–	–	–	–	–	–	–
	R_p	–	–	–	0.20	–	–	0.25	–	0.23	–	–	–	–	–	–	–	–	–
SRP[b]	β	–	–	–	–	–	–	–	0.67****	–	–	0.75****	–	–	0.71****	–	–	–	–
	R_p	–	–	–	–	–	–	–	0.67	–	–	0.66	–	–	0.60	–	–	–	–
TIN[b]	β	–	–	–	–	−0.49**	–	–	–	–	–	–	–	–	−0.43**	–	–	–	–
	R_p	–	–	–	–	−0.43	–	–	–	–	–	–	–	–	−0.45	–	–	–	–
NH_4^+[b]	β	–	–	–	–	–	–	–	–	–	–	–	–	0.20**	–	–	–	–	–
	R_p	–	–	–	–	–	–	–	–	–	–	–	–	0.23	–	–	–	–	–
$NH^+_{4\,max.}$[b]	β	–	–	–	–	0.65***	–	–	–	–	–	0.31**	–	–	0.56***	–	–	–	–
	R_p	–	–	–	–	0.54	–	–	–	–	–	0.39	–	–	0.53	–	–	–	–
TON[b]	β	–	–	–	–	–	–	0.21*	–	0.40****	–	–	–	–	–	–	–	–	–
	R_p	–	–	–	–	–	–	0.17	–	0.37	–	–	–	–	–	–	–	–	–
KjN[b]	β	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.28***	–
	R_p	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.41	–
A440	β	–	–	–	–	–	–	–	–	–	–	–	–	–	−0.40**	–	–	–	–
	R_p	–	–	–	–	–	–	–	–	–	–	–	–	–	−0.42	–	–	–	–
$A440_f$	β	–	–	–	–	–	0.40****	–	–	–	–	–	–	–	–	–	–	–	–
	R_p	–	–	–	–	–	0.50	–	–	–	–	–	–	–	–	–	–	–	–
O_2%	β	−0.22****	–	−0.37***	–	–	–	–	–	–	–	–	−0.36****	–	–	–	−0.17****	–	−0.32***
	R_p	−0.45	–	−0.33	–	–	–	–	–	–	–	–	−0.35	–	–	–	−0.29	–	−0.31
pGOP[b]	β	–	–	–	–	–	–	–	–	–	–	–	–	0.19**	–	–	–	–	–
	R_p	–	–	–	–	–	–	–	–	–	–	–	–	0.22	–	–	–	–	–
phaeo[b]	β	–	–	–	–	–	0.19***	–	–	–	–	−0.40**	–	–	–	–	–	–	–
	R_p	–	–	–	–	–	0.27	–	–	–	–	−0.43	–	–	–	–	–	–	–
BOD_1[b]	β	–	–	–	–	–	–	0.15*	–	–	0.19**	–	0.23***	–	–	0.29****	–	–	0.24***
	R_p	–	–	–	–	–	–	0.15	–	–	0.22	–	0.29	–	–	0.34	–	–	0.30

[a] $R^2_{adj.}$; d.f.; F.
[b] Transformed.
* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.
**** $P \leq 0.0001$.

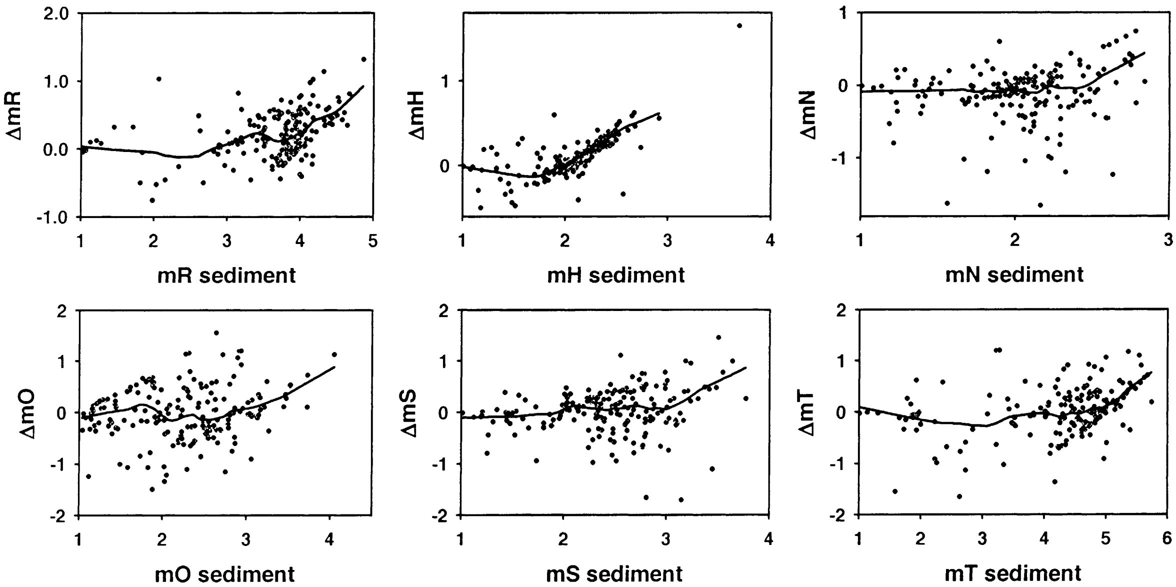

Fig. 4. Residuals of sediment-derived to epiphyton-derived indication scores (ΔmI) against sediment-derived abundance-weighted averages of species indicator values. Trend lines are a LOWESS smooth (stiffness 0.25).

the influence of total phosphorus (+) was more straightforward. At lower pH, SRP (+) was most influential, while a link to ammonium ($NH^{+}_{4\,max.}$) remained present. Effects of variables reflecting saprobity levels were always subordinate. When all samples were included, a strong regression was obtained for mT ($R^2_{adj.}$ 0.75) from pH (+) and calcium (+) mainly, with only minor contributions of total phosphorus (+) and oxygen saturation (−). At lower pH, a model with calcium (+) and Kjeldahl nitrogen (+) performed only slightly poorer. With pH restricted to the range > 7, the $R^2_{adj.}$ was nearly half that of the full model, while pH (+), total phosphorus (+) and oxygen saturation (−) remained the most important contributors. Overall, regressions for this score were slightly less effective with epiphytes than with sediment assemblages.

3.3. Correspondence of sediment-assemblage and epiphyton-derived values

The difference between scores derived from the sediment-assemblages and those obtained from the epiphyton in the same water body (ΔmI) is plotted against the former in Fig. 4. Both values often diverged considerably, even up to almost two units in the case of mO, mS and mT. Deviations were the smallest, usually within one unit, for mR and mH. Generally, sediment-derived scores tended to be higher than their epiphyton-derived counterparts at the higher end of the ordinal spectrum, leading to a relative over-estimation. Such a trend was absent at lower values.

4. Discussion

4.1. Reliability

These analyses showed that the use of weighted indicator values for diatoms in their present form is not without difficulties when applied to standing waters. Using linear models, 64–90% of the variation in mR and mT could be explained by measured variables if sites were not limited to those of pH > 7. However, with other indication scores this level of determination was never approached. Frequently, predominant relations to environmental variables were not in line with the assumed character of the indicator values. This was most apparent in the case of mT, which reflected pH and calcium rather than trophic status.

In its present form, mR was the most reliable indication score over a wide range of lentic conditions. However, in more base-rich conditions, as well as in pronounced acid circumstances, its linear relation to pH levelled-off to a plateau. This was expected to occur, as few species characterize these areas of extreme pH and some basic conditions for weighted averaging (i.e. equally spaced species optima and equal maximum values) were more strongly violated (ter Braak and Barendregt, 1986; ter Braak and Prentice, 1988). The linear fit of mR values to pH found in this study for the entire gradient and sites with pH $\leq$ 7 compared rather well with the accuracy of more sophisticated pH-calibration models for diatoms. Nevertheless, even lower prediction errors can be attained with more precise estimation of species parameters (e.g. ter Braak and Juggins, 1993; Korsman and Birks, 1996; Racca et al., 2001; Enache and Prairie, 2002). A good correlation was also found between conductivity and the salinity indication, particularly if frequency correction was applied. Other indication scores, however, related only vaguely, if at all, to assumed principal proxy variables measured in the water column and showed strong interference from non-target variables.

Secondary effects are a classic caveat associated with the use of indicator values in terrestrial vegetation (Melman et al., 1988; Thompson et al., 1993; ter Braak and Gremmen, 1987; Dierschke, 1994; Schaffers and Sýkora, 2000), and this holds for there use with aquatic diatoms also. Here as well, it remains difficult to discriminate between interacting variables and to filter out secondary from overriding structuring gradients. Particularly pH, DIC and calcium were identified as important confounding factors. Consequently, interpretations should only refer to limited pH ranges or similar buffering conditions. With fossil assemblages, diatom-inferred pH, or eventually the mR indication score, should be used to ascertain comparability. The overriding influence of pH and strongly related variables also needs to be considered in view of the observation that relations of scores to particular variables varied considerably according to the pH regime.

While most indications showed only a limited response to water-chemistry variables such as organic nitrogen load, oxygen saturation or nutrient levels, mN, mO and mS still reflected overall water quality to some extent. However, this occurred rather at the more compound level of simultaneous nutrient and organic enrichment and even in such a perspective interpretations should be made with considerable restraint. At least in standing waters, the use of separate indication scores for organic nitrogen availability, breakdown of organic matter, oxygen levels and trophic status seems overoptimistic.

A perfect fit of biotic indications to measured environmental conditions is never to be expected. For instance, 'lack of fit' with target variables may be explained partly by their unsuccessful appreciation, due to high temporal variation and too limited sampling. Also, conditions fluctuating more strongly on the short term will favour euryecious taxa and are less likely to be reflected accurately by species composition. Nevertheless, certain diatom scores effectively tracked pH in spite of its often pronounced short-term variation. In this study, a high analysis detection limit for total phosphorous may also have restricted the significance of this variable, as part of the species turnover along the trophic gradient will have occurred at lower values. Temporal response characteristics of biological communities and time integration at the assemblage level are also likely to affect the outcome of such comparisons. For woodland plants, Dzwonko (2001) demonstrated that adjustment of species composition to prevailing conditions affects prediction of environmental conditions by weighted averaging of indicator values. Ertsen and Alkemade (1998) also consider time lags as a potential source of variation. Yet, for diatoms with cell cycles in the order of days and rapid dispersion, this is a less likely explanation. Moreover, the total amount of variation accounted for by measured variables was not markedly different for epiphytic and sediment assemblages, even though their accumulation history, weeks to months versus several months or possibly even years, differed considerably.

4.2. Sediment assemblages versus epiphytes

Assemblage type affected the indication scores considerably. Except at the coarsest level, comparisons based on samples from different microhabitats are inappropriate. In Austrian lakes with low total phosphorous levels, Poulíčová et al. (2004) also report a markedly different trophic indication by diatoms from different substrates. The present study supports their appeal for standardized sampling in monitoring. This observation is of importance for paleoecological applications also, particularly in shallow lakes, since the contribution of epiphytic habitats to the core material can vary considerably in the course of a lake's history. Only mR and mH were relatively uncompromised by the nature of the source assemblage. For indications aimed at organic loading or trophic status and particularly oxygenation, large differences were common. For all scores, a tendency existed for sediment assemblages to yield higher values than ephiphytes towards the upper classes of the ordinal classifications. Taxa attributed to the highest categories of these schemes were clearly more abundant in sediment assemblages. Epiphyte-derived scores therefore pictured a less 'impaired' situation than those calculated from the sediment assemblage in extreme cases. This may well have resulted from different microhabitat conditions, as for instance pH, osmotic conditions, the concentration of organic substances and the availability of nutrients will differ considerably at the surface of physiologically active macrophytes, from that at the sediment–water interface, or in the top layer of the sediment. In a comparison with pollution indices in Finnish streams, Eloranta and Andersson (1998) observed higher values (indicating less pollution) for epiphytic samples than for bottom samples, which they related to the higher organic content of the sediment. Winter and Duthie (2000a), however, found no marked differences between the epipelon and epiphyton of low order streams. They suggested that the chemical environment would be crucial in this and that differences might be greater in larger rivers. The trend for higher abundance-weighted averages of diatom indicator values from sediment assemblages arising in more enriched lentic conditions is consistent with such a hypothesis. Kitner and Poulíčová (2003) found similar values for the trophic indication score from epilithon, epipelon and epiphyton in eutrophic to heavily hypertrophic fishponds, but their values for mT did not extend into the range where a differential pattern emerged in the present study.

Poulíčová et al. (2004) consider epiphytes on reed better indicators of eutrophication than littoral mud assemblages. Phosphorous compounds usually ranked higher among significant variables for scores calculated from epiphytes than for those from sediment assemblages in this study as well. Responses to other variables linked to eutrophication less consistently favoured a particular substrate, however. Overall, apparent differences in sensitivity were subordinate to unexplained variation. Whether sediment assemblages or epiphytes provided a better assessment of general water quality in combination with weighted-averaging of indicator values largely remained undetermined. It may be good practice to consider indications from both habitats complementary or to make choices depending on the response time frame envisaged by the monitoring programme.

4.3. Possible improvements and further application

Even though uneven frequency distributions in indicator values and boundary effects are considered among the basic problems associated with the use of indicator values (Böcker et al., 1983; ter Braak and Barendregt, 1986; ter Braak, 1995; Schaffers and Sýkora, 2000), the effects of adjusting for their frequencies were small. Less drift towards intermediate values was usually obtained, but relations to target variables did not always improve. The indication scores for salinity and—using epiphytes—organic nitrogen availability, benefited from the correction procedure. The lack of success with other scores casts further doubt on the effective representation of species optima in this dataset by their present classification with regard to oxygen saturation, saprobity and trophic status.

For a number of reasons—inconsistencies in taxonomy or chemical measurements, differences in sampling, geographic variation in environmental interactions, dataset characteristics—compilation of apparent environmental requirements of diatoms from different sources is hazardous. Although van Dam et al. (1994) accounted for such problems where possible and critically examined a vast amount of literature data against personal observations, it is clear that indicator values were still compromised by inadequate information for a number of taxa. van Dam et al. (1994) particularly acknowledged that assignation of trophic indication values was often difficult. As already pointed out by ter Braak and van Dam (1989), regional calibration sets are to be preferred. Besides adjusting for 'local' and more precise optima, the most obvious prospect for improving the reliability of weighted-averaging using indicator values would be to include an extra weighting for the indicative strength or tolerance of each taxon, as applied also in the classic saprobity calculation (Kolkwitz and Marsson, 1908) and a score of other diatom-based indices of water quality (e.g. Descy, 1979; Sládeček, 1986; Hofmann, 1993; Kelly and Whitton, 1995). Particularly with assemblages showing strong dominance of only a few eurytopic taxa, tolerance weighting may still yield little improvement. Another drawback remains the fact that certain indicator values have not yet been attributed to a considerable number of taxa, sometimes decreasing the proportion of the assemblage that is given consideration.

In conclusion, it is suggested that—with exception of mR—abundance-weighted averaging of diatom indicator values provided by van Dam et al. (1994) should be used cautiously in standing freshwaters and preferably only in conditions where expected sensitivities have been affirmatively tested. The usefulness of these scores for developing indices of ecological status or integrity appears limited, even when working within a framework of water types reflecting essential community-structuring gradients, such as pH. As highlighted on several occasions (Cox, 1991, 1993, 1994; Steinberg and Trumpp, 1993; Medley and Clements, 1998; Ivorra, 2000; Winter and Duthie, 2000b), most applied diatom ecology rests purely on empirical observations, while experimental validation of species responses to particular stressors is still scanty. Field testing and critical evaluation of assessment tools based on such data within the specific context of each application remains essential (Jackson et al., 2000; Downes et al., 2002).

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