



Natural variation of macrophyte vegetation of lowland streams at the regional level



Gerhard Wiegleb^{a,*}, Wolfgang Herr^b, Bärbel Zander^c, Udo Bröring^a, Holger Brux^b, Klaus van de Weyer^d

^a General Ecology, Faculty of Environmental Sciences and Process Engineering, Brandenburg University of Technology Cottbus-Senftenberg, Platz der Deutschen Einheit 1, 03046 Cottbus, Germany

^b IBL Umweltplanung GmbH, Bahnhofstraße 14a, 26122 Oldenburg, Germany

^c Landscape Architecture, Geoinformatics, Geodesy and Civil Engineering, University of Applied Sciences Neubrandenburg, Brodaer Straße 2–4, 17033 Neubrandenburg, Germany

^d Lanaplan GbR, Lobbericher Straße 5, 41334 Nettetal, Germany

ARTICLE INFO

Article history:

Received 8 April 2014

Received in revised form

16 December 2014

Accepted 20 December 2014

Available online 27 December 2014

Keywords:

Biogeography

Frequency variation

Ordination

Physiographic units

Spatial dependence

Spatial gradients

ABSTRACT

In the present study, we present a synopsis of two macrophyte surveys of physiographic units in north-west Germany carried out over one decade. Data were used to test a set of hypotheses on macrophyte distribution at the regional level. Rank–frequency curves resembled the broken stick model. Twenty-one species of the 59 most frequent species occurred at high frequencies above 15%. Helophytes made up a high percentage (12 of 21) of the frequent species. *Phalaris arundinacea* was the most frequent species in both sampling periods. Most species showed no considerable change in frequency over time, among them the core hydrophytes. Spatial variation of species frequencies among physiographical units showed a unimodal distribution in relation to frequency. Spatial variation of frequencies of functional groups was significantly lower. Most uneven distribution among physiographical units was found in cryptogams. DCA ordinations of physiographical units showed a spatial gradient from alluvial plains to higher grounds units, which remained constant over time. CCA ordination of physiographical units in relation to environmental parameters identified two main axes, an altitudinal gradient and an alkalinity gradient. Species composition of units corresponded to the main landscape pattern of alluvial plains, glacial lowlands, and higher grounds on Mesozoic rock. Species diversity showed a complex behavior. Diverse units were found both in alluvial plains and glacial lowlands of intermediate elevation. The study may help defining regionally differentiated reference states for stream management, benchmarking indicator scores of species and avoiding application of assessment methods outside their range of applicability.

© 2014 The Authors. Published by Elsevier GmbH. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Introduction

Since the implementation of the Water Framework Directive of the EU (WFD, 2000) major progress has been made both on consolidating river typology in Central Europe (Schaumburg et al., 2004; Van de Weyer, 2008b; Szoszkiewicz et al., 2010) and identifying reference states for ‘good ecological conditions’ of water courses (Baattrup-Pedersen et al., 2006; Birk and Willby, 2010). Observed variation of macrophyte species composition at the reach level was directly related to anthropogenically induced factors such as

trophic state, morphological degradation or mechanical disturbance (O’Hare et al., 2006; Szoszkiewicz et al., 2010). Or macrophyte assemblages were classified into types or clusters, for which differentiating environmental parameters were sought (Paal et al., 2007; Grinberga, 2011). Both approaches did not take into account the spatial context of river vegetation.

Well before the Water Framework Directive was implemented, a complementary approach was proposed in Germany analyzing vegetation differences of rivers among physiographic units (Wiegleb, 1988; Herr et al., 1989). Differences between river vegetation of adjacent physiographic units had already been described by Steusloff (1939) and Weber-Oldecop (1969) in northern Germany and by Decornet (1979) (under the term ‘symphytosociology’) in France. Physiographic units represent the ‘regional conditions’ in which the river is embedded (Barendregt and Bio, 2003). ‘Physiographic units’ are spatial units characterized by common physical

* Corresponding author. Tel.: +49 331 692201; fax: +49 331 692225.

E-mail addresses: wiegleb@b-tu.de (G. Wiegleb), herr@ibl-umweltplanung.de (W. Herr), zander@hs-nb.de (B. Zander), brux@ibl-umweltplanung.de (H. Brux), klaus.vdweyer@lanaplan.de (K. van de Weyer).

and geographical characters such as geomorphology, geology, hydrology, and geochemistry (see Wiegleb, 1988; using the term 'physiographical regions'; Granke et al., 2004). Similarities among reaches within physiographic units can neither be explained by short-range spatial processes such as colonization producing 'river zonation' (Demars and Harper, 2005; Van de Weyer, 2008a; Tremp, 2009), nor by change of local habitat conditions. Either medium- to long-range dispersal or long-lasting selective forces must be involved. For lake macrophytes, Beck et al. (2013) introduced so-called 'ecoregions', which are similar to the physiographic units used in this paper, but different from 'ecoregions' in the sense of European Environment Agency (2014).

Exhaustive macrophyte surveys have been published for Great Britain (Haslam, 1978; Holmes, 1983), Denmark (Riis et al., 2000; Baatrup-Pedersen et al., 2003), Poland (Szozkiewicz et al., 2002, 2010) and Estonia (Paal and Trei, 2004; Paal et al., 2007). Still, only a few papers presented their results differentiated by physiographic units (e.g. Riis et al., 2000, as 'geographical regions'; Steffen et al., 2013, as 'regions'). However, in these papers physiographic units were not used as units of data analysis, but as a tool for summarizing and displaying reach-based results.

Recently, Birk et al. (2012) and Thorp (2013) emphasized the urgent need for large-scale surveys. Thorp (2013) regarded the basic sample unit (the reach) as imbedded into a nested hierarchy of hydrogeomorphic patches. All levels of the hierarchy require specially adapted methods. It cannot be expected that simple upscaling of variables may work. At the reach level macrophyte growth can be quantified using a variety of metrics such as cover, abundance, richness, diversity or evenness of taxa, growth forms, or attribute types (Willby et al., 2000; Birk and Willby, 2010; Wiegleb et al., 2014a). Along a river course or in the course of time turnover and autocorrelation measures can be related either to hydrochemical, morphological, sedimentological, hydrological and spatial variables, or discontinuous variables such as disturbance events including unusual weather conditions (Wiegleb et al., 2014b; Demars et al., 2014). At the level of the catchment, frequency of species (Wiegleb, 1981, 1983b; Kohler et al. 2003), frequency and distribution of communities (Holmes, 1983; Paal et al., 2007) as well as spatial variables (connectivity, isolation) can be studied (Demars and Harper, 2005).

However, the reach level is also embedded into a second nested hierarchy leading via the riverine landscape (Van de Weyer, 2001) to the physiographic unit. For characterizing and comparing spatial units of the size of physiographic units (5000–6000 km²), the most appropriate metrics is relative frequency. Measures of abundance and cover are strongly dependent of the applied sampling method and short-term change in the vegetation (Staniszewski et al., 2006; Pentecost et al., 2009). Still, the spatio-temporal variation of reach-based data was broadly underestimated (Wiegleb et al., 2014a; Demars et al., 2014). Recognizing in addition the natural variability of macrophyte vegetation at the regional level requires that species frequencies of the wider geographical area in which a physiographic unit is embedded must be known. This can only be reached by using a standardized sampling method, high taxonomic precision and inclusion of all species actually found in the aquatic habitat.

We assumed that within our study area physiographic units are different enough to show different stream vegetation. We used the accumulated data to test a set of plausible hypotheses, which can be interpreted as assembly and response rules in the sense of Keddy (1992). The hypotheses (H) relate to properties of the macrophyte vegetation of the whole study area (H1–H3), variation of species and growth form frequencies in space at the scale of the physiographic unit (H4 and H5), and mechanistic factors explaining the maintenance and change in the observed patterns (H6–H8):

H1. The vegetation of the study area will consist of a set of core species of high (>50%) and satellite species of medium frequency (>15%). This pattern will be stable over time (10 years).

H2. Variation in species frequencies over time (10 years) will be low. Rank-order of species and the proportions among growth forms will be stable.

H3. Core and satellite species will comprise both hydrophytes and helophytes. Helophytes are expected to form an integral component of stream vegetation.

H4. Variation of species frequencies among physiographic units will peak at intermediate species frequencies.

H5. Variation of frequencies of functional groups will show a lower variation among physiographic units than species.

H6. Major geographical gradients such as topography and climate will strongly influence species composition and floristic similarity. The basic patterns of similarity between physiographic units will be stable over 10 years.

H7. Alkalinity will have a strong influence on the differentiation of vegetation among physiographic units.

H8. The basic patterns of richness and diversity of the physiographic units will not follow simple gradients. It will remain stable over time (10 years).

Materials and methods

Study area and study sites

The study was carried out in the northwest German lowlands and adjacent higher grounds (Fig. 1). The study area had an east–west extension of ca. 360 km and a north–south extension of ca. 410 km. The longest distance between two points (southwest–northeast) was 480 km. Three main types of physiographic units were distinguished: alluvial plains, ranging from 0 to 15 m above sea level; sandy glacial lowlands, ranging from 10 to 170 m; and higher grounds of mostly Mesozoic origin, locally ranging up to 500 m. All sample sites were located below 200 m, still reflecting true lowland conditions (Holmes, 1983). Annual averages for temperature between 1971 and 2000 were (DWD, 2014): Düsseldorf 10.3 °C, Hannover 9.2 °C, Bremen, 9.2 °C, Hamburg 9.0 °C, and Kiel 8.5 °C. Annual precipitation was for Düsseldorf 759 mm, Hannover 642 mm, Bremen 672 mm, Hamburg 773 mm, and Kiel 750 mm. While there is a pronounced temperature gradient in south–north direction, the pattern of precipitation is more complex.

For the delimitation of the physiographic units we used the updated classification kindly provided by Bundesamt für Naturschutz (BfN). For the present purpose, we enumerated the units from 1 to 25. In the 1980s, we distinguished 12 units (14–25), while in the 1990s we distinguished 13 units (1–13). A full list of all physiographic units, their numbers and main characteristics is given in the Supplementary material Table S2. Classifications slightly differed among periods. In the 1980s both units D30 and D36 were split into two separate units. The northern boundary of the study area was the German–Danish border. The eastern boundary mostly followed the border between the former West and East Germany. The western boundary was the German–Dutch border. While these borders were dictated by political factors the southern boundary follows the border between the north German higher grounds and the true south German uplands. It runs almost exactly in west–east direction along the 51.5° northern latitude, comprising the northern part of unit D35, which we regarded as a separate unit in the 1990s.



Fig. 1. Overview of the study area, showing the current delimitation of German physiographic units (by courtesy of Bundesamt für Naturschutz, 2011) and the boundary of the study area. Numbers D21–D36 denote the physiographic units studied.

Field surveys

The field surveys were carried out between 1978 and 1990. We analyzed two data sets from different periods (A: 1978–1983; B: 1988–1990). Data set A consists of a total of 2018 samples, 1143 samples from Lower Saxony and adjacent North-Rhine-Westphalia (Herr et al., 1989), and 875 samples from Schleswig-Holstein (Herr, 1981; Herr and Wiegleb, 1984). Because of financial restrictions it took six years to complete the survey. Data set B consists of 988 samples from the whole study area mostly taken in 1990 with the exception of two units, which were sampled in 1988 (Zander et al., 1992). In that study we were not allowed to carry out an exhaustive mapping of all rivers because of legal restrictions. Instead, 16 river catchments were selected in a way covering all physiographic units with at least 30 reaches. In data set A, on average one site per 5–10 stream km was sampled, while in data set B on average one site per 20 km was sampled. Zonation analysis had shown (Wiegleb, 1984) that river zones usually extended 10–15 km and sample sites 20 km

apart were mostly spatially independent. For both data sets A and B we collected information on geographical coordinates, morphology, shading, water chemistry and hydrology. Of these data only alkalinity and altitude above sea level were used for statistical analyses. Altitude above sea level, width and depths were used for the exclusion of aberrant sample sites (see below).

In both studies reaches were preselected on topographical maps 1:50,000 in order to avoid observer bias in the data set. Both data sets can be regarded as random samples from the same population. Both covered the main catchments of northwest Germany, small catchments leading to the North Sea or Baltic Sea, respectively, as well tributaries of the large rivers Elbe, Weser, Ems and Rhine. Both data sets comprise upper and lower courses, main rivers and tributaries as well as narrow streams and wider rivers. Full identity of sites was not intended as the study focused on similarities between units, neither between catchments nor river types. Both sampling campaigns had an overlap of ca. 35% of the sampling sites due to the lack of bridges in rural areas. In data set A the southwestern part

is underrepresented, while in data set B gaps are scattered more regularly over the study area. The average time of remapping the same physiographic unit was 9.2 years.

The following types of waters were excluded from both surveys ('macrophyte free waters', Van de Weyer, 2001): the large rivers Rhine, Weser and Elbe; tidal reaches along the North Sea coast, e.g. the lower reaches of the rivers Ems, Hunte, Oste and Stör; and completely shaded upper courses of streams below 5 m width. In addition, intensively managed artificial water courses such as irrigation and drainage ditches as well as navigable canals were excluded. Sampled reaches had a width from 5–25, rarely 50 m, belonging to the types of 'small and medium sized lowland streams' (Baattrup-Pedersen et al., 2006), also called 'sandy lowland brooks' and 'medium-sized lowland streams', respectively (Birk and Willby, 2011).

All macrophytes growing in the water or rooting below the water surface were sampled. We included all hydrophytes in the sense of Willby et al. (2000), helophytes which behave like hydrophytes ('amphiphytes' in the sense of Kohler et al., 1996) in the study area and hydrophytic 'cryptogams'. Accidental helophytes and land plants growing on eroded banks were excluded. Cover was estimated in the field using the decimal Londo scale (Londo, 1976). Reaches of 50–70 m length were sampled bank-to-bank either by hand or with a telescopic rake, while walking along the reach on both sides and wading in the stream. Most reaches were located upstream of bridges or other well accessible points (Wiegleb, 1983a; Wiegleb et al., 2014a).

Nomenclature of taxa follows Jäger (2011) for Tracheophyta-Euphylllopytina (vascular plants in part), Koperski et al. (2000) for Bryophyta, and Blümel and Raabe (2004) for Charophyta. *Potamogeton berchtoldii* and *P. pusillus* were treated as one taxon, *P. pusillus*. *P. berchtoldii* was by far the more frequent species in water courses. In a few cases, the taxon comprises *P. pusillus* or supposed *P. berchtoldii* hybrids (Herr and Wiegleb, 1985). The taxon *Ranunculus peltatus* comprises several hybrids with other *Ranunculus* species (*R. aquatilis*, *R. penicillatus*, *R. fluitans*; G. Wiegleb, J. Zalewska-Gaïocz, unpublished results, 2013). Specimens of *Potamogeton*, *Ranunculus*, *Callitriche* and other critical groups were deposited in Herbarium LMO (Landesmuseum Natur und Mensch, Oldenburg).

Data preparation and analysis

For the purpose of characterizing the vegetation of the study area we converted all cover data to presence/absence data. We calculated the frequency percentages of all species for the total data set as well as for data sets A and B separately. Species frequencies could mostly be extracted from available sources (Herr et al., 1989; Zander et al., 1992). Additional unpublished material was provided by W. Herr. We counted absolute frequencies of species per unit, which were transferred to percentages for the statistical analyses. Species which did not reach a frequency of at least 10% in at least one physiographic unit were no longer considered. We did not expect any discriminating function among units from uniformly distributed rare species. For all units species richness and Shannon diversity were calculated based on the 59 species \times 25 units' matrix. From pooling of species for physiographic units we expected a considerable noise reduction.

All variables were tested for normal distribution. Species frequencies were not normally distributed according to both Kolmogorov–Smirnov- and Shapiro–Wilk-test. Data were $\log(x+1)$ -transformed for further analyses. For testing whether data sets A and B were similar enough to allow for combined analysis we applied three statistical methods. We used Wilcoxon's *U* test for testing whether the median values of species frequencies significantly differ between the observation periods. We used Spearman' rank correlation coefficient for testing whether significant

differences in the rank order of species existed between observation periods. And we looked at the shape of the rank–frequency curves drawn separately for both data sets. In addition, we compared the total number of species as well as the rank order of the most frequent species and functional groups.

We drew the rank–frequency curve for the whole data set for the identification of core and satellite species and their affiliation to functional groups. The shape of the rank–frequency curve was compared to existing models such as the broken stick distribution (Wiegleb et al., 2014a). In combination with the preceding analysis this allowed conclusions on hypotheses H1–H3.

For the analysis of variation of species frequencies among units we drew a scatter gram displaying frequency vs. variance of frequencies for all species. We calculated standard deviation, variance and variance/mean ratio for all species. Frequencies were aggregated for three functional groups: nine morphological growth forms (Wiegleb, 1991; Wiegleb et al., 2014a), three types of space occupancy (emergent, floating, submerged; Mesters, 1995) and two life forms (hydrophytes and helophytes; Wiegleb, 1991). Standard deviation, variance and variance/mean ratio were calculated as well. Order of magnitude of variance/mean ratios of species, growth forms, spatial occupancy types and life forms were directly compared. In addition, we applied non-parametric one-way ANOVA (Kruskal–Wallis test) to examine whether the patterns of variation among species were significantly different from the pattern observed among functional groups. This allowed us to make a judgment on H4–H5.

For the classification and ordination of physiographic units, all 59 species were equally considered regardless of their status as hydrophyte or helophyte. We did not apply the option 'down-weighting of rare species', as rare species were already eliminated. Detrended Correspondence Analysis (DCA) and Cluster Analysis (linkage within clusters, squared Euclidian distances, standardization by z-scores; not shown) were used for separate ordination and classification of units from both sampling periods in order to detect common gradients or clusters. It was shown again that the data sets A and B were similar enough to allow combined analyses. DCA and CA were also applied to the total data set to survey the stability of gradients and clusters. As this did not yield any additional information, the results are not shown. Conclusion on H6 was now possible.

Canonical Correspondence Analysis (CCA) was used for constrained ordination of all units in relation to selected environmental variables. CCA ordination allows analyzing and displaying the effect of selected independent variables on units, species and additional variables such as diversity. The following geographical variables were used: Average altitude above sea level (m, Zander et al., 1992), average alkalinity (meq L^{-1} ; Herr, 1981; Wiegleb, 1984; Zander et al., 1992), the west–east gradient (1 – coastal areas and Rhine valley: D21, D24, D25, D26, northern part of D35; 2 – central areas: D22, D27, D30, D34, western part of D36; 3 – eastern areas: D23, D28, D31, D32, D33; eastern part of D36), and the south–north gradient (1 – south of northern edge of the higher grounds: D33, D34, D35, D36; 2 – directly north of the higher grounds to a line River Weser–River Aller: D30, D31, D32; 3 – mostly between River Weser and River Elbe: D25, D26, D27, D28; 4 – north of River Elbe: D21, D22, D23, D24). Time was introduced into the analysis as consecutive year (1–13) in order to supervise the time effect on the data set. Environmental data were also $\log(x+1)$ -transformed. Variance explanation of all variables including their marginal and conditional effects was carefully observed. Interpretation of CCA diagrams allowed conclusions on hypotheses H7 and H8.

Statistical tests, correlation and regression analyses as well as cluster analysis were carried out using IBM SPSS Statistics 21 (IBM Germany, Ehningen). For DCA and CCA ordinations, CANOCO 4.51 was used (ter Braak and Šmilauer, 2002).

Table 1

Frequency of the 21 most frequent species in the 1980s, 1990s and the total data set (classification of functional groups follows Wiegleb, 1991; Kohler et al., 1996; Mesters, 1995).

Species	% 1980s	% 1990s	% total	Growth form	Life form	Spatial occupancy
<i>Phalaris arundinacea</i>	70.3	88.2	79.6	Graminid	Helophyte	Emergent, submerged
<i>Callitriche platycarpa</i>	55.8	60.8	58.4	Peplid	Hydrophyte	Submerged, floating
<i>Sparganium emersum</i>	56.3	55.8	56.0	Vallisnerid	Hydrophyte	Floating, submerged
<i>Lemna minor</i>	48.0	58.9	53.7	Pleustophyte	Hydrophyte	Floating
<i>Myosotis scorpioides</i>	40.1	64.7	52.9	Herbid	Helophyte	Emergent, submerged
<i>Agrostis stolonifera</i>	22.6	70.1	47.3	Graminid	Helophyte	Emergent, submerged
<i>Glyceria fluitans</i>	38.4	41.1	39.8	Graminid	Helophyte	Floating, emergent
<i>Elodea canadensis</i>	36.7	42.7	39.8	Potamid	Hydrophyte	Submerged
<i>Glyceria maxima</i>	31.5	33.3	32.5	Graminid	Helophyte	Emergent, floating
<i>Sparganium erectum</i>	25.8	37.0	31.6	Graminid	Helophyte	Emergent
<i>Berula erecta</i>	19.8	34.7	27.5	Herbid	Helophyte	Emergent, submerged
<i>Potamogeton natans</i>	27.6	18.3	22.7	Nymphaeid	Hydrophyte	Floating, submerged
<i>Sagittaria sagittifolia</i>	18.9	25.9	22.6	Vallisnerid	Hydrophyte	Submerged, floating
<i>Nuphar lutea</i>	23.6	20.3	21.9	Nymphaeid	Hydrophyte	Floating, submerged
<i>Rorippa amphibia</i>	13.3	25.5	19.6	Herbid	Helophyte	Emergent, submerged
<i>Potamogeton pectinatus</i>	16.8	20.7	18.9	Potamid	Hydrophyte	Submerged
<i>Potamogeton crispus</i>	13.5	21.5	17.7	Potamid	Hydrophyte	Submerged
<i>Nasturtium officinale</i>	9.9	23.5	17.0	Herbid	Helophyte	Emergent, submerged
<i>Persicaria hydropiper</i>	19.3	13.5	16.3	Herbid	Helophyte	Emergent, submerged
<i>Rumex hydrolapathum</i>	10.6	19.3	15.1	Herbid	Helophyte	Emergent
<i>Alopecurus geniculatus</i>	14.7	14.4	14.5	Graminid	Helophyte	Floating, emergent

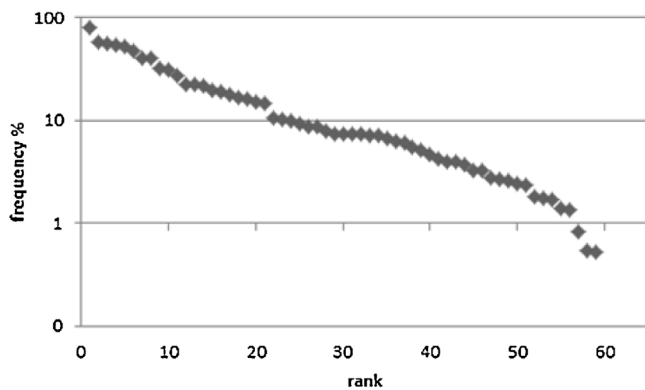


Fig. 2. Rank–frequency curve of the 59 selected species based on their frequencies (in %) in the total data set.

Results

Frequency and frequency variation of species

Fifty-nine species matching the predefined criterion were found in the study area. Fig. 2 shows the rank–frequency curve for the whole data set. The curves for the 1980s and 1990s, respectively, looked similar (see Supplementary material, Fig. S1). In the logarithmic scaling there was an almost linear decrease in frequency with light steps after the 6th and 21st species. After the 51st species we observed a sharp decline. The long tail of less frequent species (around 200), whose distribution was not analyzed in this study, is not shown.

Table 1 shows the frequencies of the 21 most frequent species including their affiliation to functional groups (growth form, life form, spatial occupancy). *Phalaris arundinacea* was the most frequent species (79.6%), followed by *Callitriche platycarpa*, *Sparganium emersum*, *Lemna minor* and *Myosotis scorpioides*. All other species occurred in less than 50% but more than ca. 15% of the sites. 12 of 21 species were helophytes, which were more frequently found in an emergent growth form than under submerged conditions. Nine of 21 species were true hydrophytes, which were only exceptionally found as terrestrial forms in the study area. Both graminids and herbids were represented with six species. Potamids (3), vallisnerids (2) and nymphaeids (2) followed. As to spatial

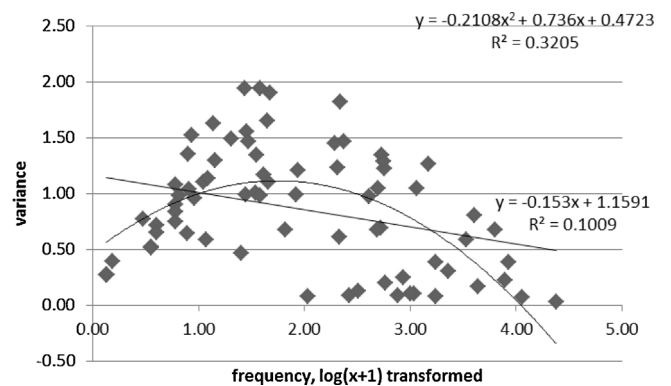


Fig. 3. Relation between total frequency and variance of species among all regions, $\log(x+1)$ transformed frequency data. The linear and polynomial trend lines serve for orientation.

occupancy, nine species were predominantly found in emergent, seven in floating and only five in submerged state. Almost all species occurred in at least two of these states.

Of the frequent species, *Sagittaria sagittifolia*, *Potamogeton crispus* and *Potamogeton pectinatus* showed a decadal increase of more than 20%. *Elodea canadensis*, *C. platycarpa* and *S. emersum* were found with similar frequencies in both observation periods. Only *Potamogeton natans* decreased in frequency by more than 20%. Of the less frequent species (Table S1) *Myriophyllum spicatum*, *Callitriche hamulata*, *Callitriche obtusangula* and *Elodea nuttallii* increased, while *Potamogeton alpinus*, *P. lucens*, *P. perfoliatus*, *R. fluitans* and *R. penicillatus* decreased. *Utricularia australis* was not found in the 1990s, being the only species not occurring in both data sets. Mean frequency percentages in the 1980s were significantly lower than in the 1990s ($p < 0.005$). Rank correlation showed that rank order of species frequencies did not differ between both sample periods ($\rho = 0.838$; $p < 0.001$).

Fig. 3 shows the relation between total frequency of each species and the variation of frequencies among all units. The coefficient of determination (R^2) of the polynomial trend line exceeds the one for the linear trend line. The most even distribution (variance/mean ratio < 0.06) was found for frequent species such as *P. arundinacea*, *M. scorpioides* and *C. platycarpa*. Highly uneven distributions (variance/mean ratio > 1.2) were found for some rare species of different growth form, such as *Callitriche cophocarpa*, *Nitella mucronata*, *U.*

Table 2

Significance of differences between species variance and variance of three functional groups (growth forms, spatial occupancy type, life form) among physiographic unit. p -Values are derived from Kruskal–Wallis test (Kruskal–Wallis non-parametric one way ANOVA).

	Growth form	Spatial occupancy type	Life form
Species	<0.001	0.005	0.025
Growth form	–	0.564	0.658
Spatial occupancy type	–	–	0.996

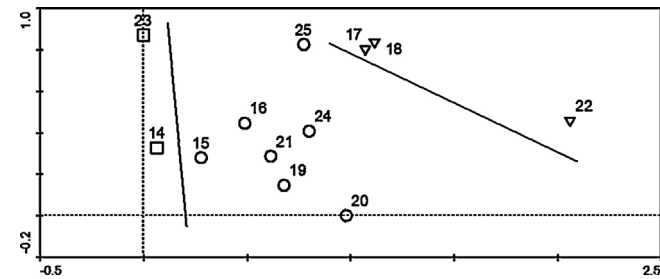


Fig. 4. DCA ordination of physiographic units 14–25 (1980s). Solid lines indicate the distinction between alluvial plains (left, open quadrats), glacial lowland (center, open circles) and higher grounds (right, open triangles). 1st axis explains 33.3%, 2nd axis explains 9.2% of species frequency variance. Units in the 1980s were: 14 – Southern part of D24, D25; 23 – D21 (alluvial plains); 15 – D26; 16 – D30; 21 – D31; 19 – D27; 24 – D22; 20 – D28; 25 – D23 (glacial lowlands); 17 – Western part of D36; 18 – D32, D33; 22 – Eastern part of D36 (higher grounds).

australis and *Zannichellia palustris*, but mostly among hydrophytic species of medium frequency such as *Fontinalis antipyretica*, *R. penicillatus*, *R. fluitans*, *R. peltatus*, *Spirodela polyrhiza*, *P. lucens* and *Hydrocharis morsus-ranae*.

Variance of species was on average higher than of growth forms ($p < 0.001$), space occupancy types ($p = 0.005$) and life forms ($p = 0.025$; Table 2). Variances of growth forms, space occupancy types and life forms did not differ significantly ($p > 0.05$ for all pairs compared). Within growth forms, herbids, graminids, peplids and potamidids showed the lowest variance/mean ratio among physiographic units (< 0.072). Variance/mean ratio was intermediate in myriophyllids, nymphaeids, vallisnerids and pleustophytes (0.11–0.33), while it was high in cryptogams (0.55). Among space occupancy types floating leaved species had the highest variance/mean ratio (0.085). Variance/mean ratio of helophytes and hydrophytes was low as well (0.035 and 0.050, respectively). Variance/mean ratios of all function groups were much lower than for species.

Ordination of units

Fig. 4 shows the DCA ordination of the units in data set A (1980s). Higher grounds units 17, 18 and 22 are found at the right side of the diagram, alluvial plain units 14 and 23 on the left side. Glacial lowland units are located in between. Only one gradient is visible, as most of the variance explanation (33.3%) is accounted for the first axis, only 9.2% for the second axis. Fig. 5 shows the DCA ordination of the units in data set B (1990s). Higher grounds units 1–3 are located on the right side of the diagram as well, being closely associated with units 4, 5 and 13. The alluvial plain unit 8 is found on the left side of the diagram. Glacial lowlands are situated in the center of the ordination diagram. Here, the first axis accounted for 24.6% of the variance, while the second axis explained 18.8%. Total variance explanation of the first two axes was similar for both ordinations (42.5 vs. 43.5%).

Fig. 6 shows a CCA biplot of all units showing both the main geographical and temporal gradients as well as isolines of the Shannon diversity. The first axis, explaining 25.4% of the variance, was highly

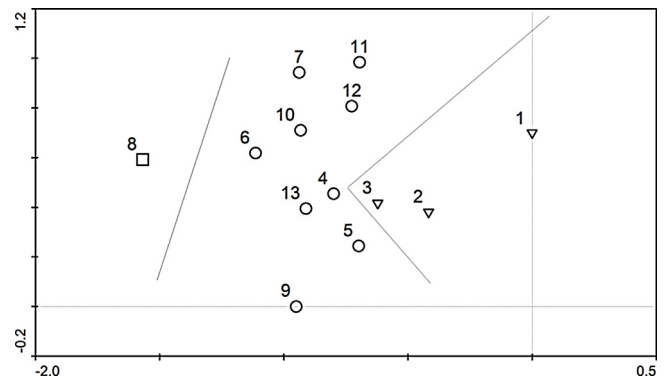


Fig. 5. DCA of physiographic units 1–13 (1990s). Solid lines indicate the distinction between alluvial plains (left, open quadrat), glacial lowland (center, open circles) and higher grounds (right, open triangles). 1st axis explains 24.6%, 2nd axis explains 18.8% of species frequency variance. Units in the 1990s were: 8 – D21, D24, D25 (alluvial plain); 6 – Southern part of D30; 7 – Northern part of D30, D26; 9 – D31; 10 – D27; 11 – D28; 13 – D23; 12 – D22; 4 – D34; 5 – Northern part of D35 (all glacial lowlands); 1 – Eastern part of D36; 2 – D32, D33; 3 – Western part of D36 (higher grounds).

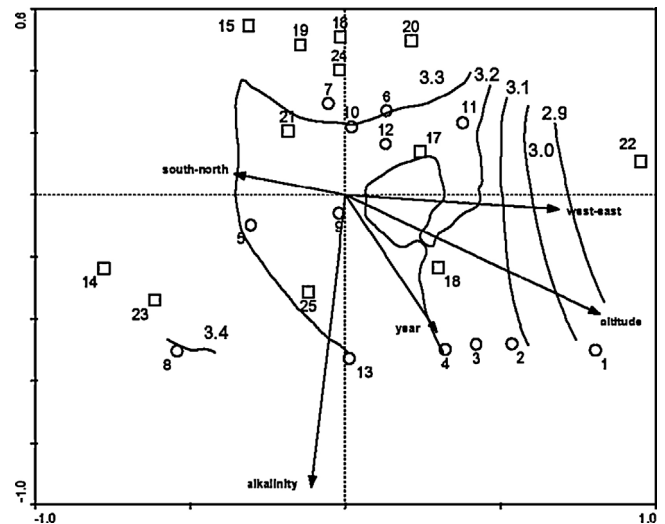


Fig. 6. CCA biplot of all regions in both sampling periods. Open triangles denote units of the 1980s, open circles of the 1990s. 1st axis explains 25.4%, 2nd axis explains 10.4%. Contours show lines of equal Shannon diversity. Conditional effects of all independent variables were significant.

correlated to the altitudinal gradient, while the second axis (10.4%) was related to alkalinity. The north–south gradient points into the opposite direction as the altitudinal gradient. Higher grounds units of both sample periods (1, 2, 3, 18, and 22) including one unit close to the higher grounds (4) are concentrated at the right side of the diagram. Typical alluvial plain units of both sample periods (8, 14, and 23) are shown on the left side. Both alluvial plain units formed by young nutrient rich sediments and higher grounds units within the reach of Mesozoic limestone are found at the lower side of the diagram, while the units made up by sandy glacial deposits are clumped in the center of the upper part. They were characterized by a similar stock of species for both sample periods. Altitude and alkalinity contributed best to the distinction of units, however conditional effects of all independent variables were significant ($p < 0.002$ to $p = 0.03$). Diversity is generally lower in higher grounds units. High values of $H' > 3.3$ can be reached both in alkaline alluvial streams and acidic streams running through units formed by glacial deposits.

Fig. 7 shows the position of species in the CCA ordination diagram. Three different vegetation groups are distinguishable. On the

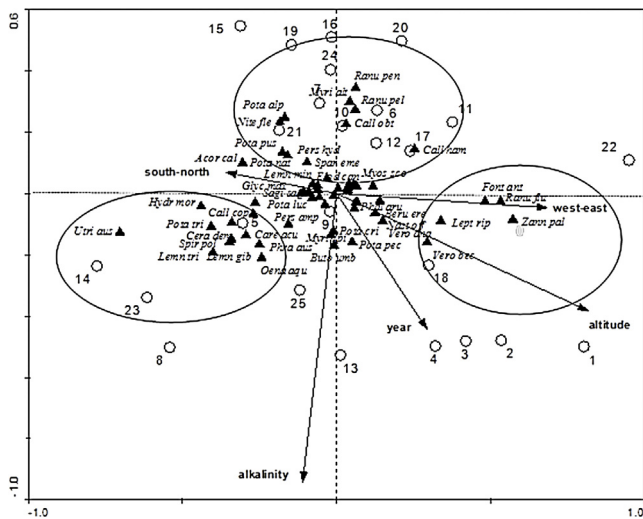


Fig. 7. CCA triplot showing the physiographic units (open circles), environmental variables (arrows) and species positions (closed triangles). Ellipses indicate the most characteristic species for each flora: left (alluvial plains), right (higher grounds), center (glacial lowlands). 1st axis explains 25.4%, 2nd axis explains 10.4% of total variance.

lower left side, pleustophytes such as *U. australis*, *Lemna gibba* and *H. morsus-ranae* were associated with helophytes such as *Phragmites australis* and *Carex acuta* as well as parvipotamids such as *Potamogeton trichoides*. All these species occurred in relative slow flowing streams in alluvial and glacial plains. On the lower right side, *Z. palustris* and *R. fluitans*, mosses such as *F. antipretica* and *Leptodictyum riparium* and small helophytes such as *Veronica beccabunga* were found, characterizing fast flowing reaches in the higher grounds. In the upper central part of the diagram *Nitella flexilis*, *P. alpinus*, *Myriophyllum alterniflorum*, *R. peltatus*, *R. penicillatus* and *C. obtusangula* were associated. This species group was typical for glacial lowland areas, where the streams are still influenced by ground water inflow (Wiegleb, 1983b; Brux et al., 1988). *C. hamulata* took an intermediate position between the second and third group, while *Butomus umbellatus* and *P. pectinatus* were intermediate between the first and second group.

Discussion

Frequency and frequency variation of species

With our method we were able to sample the species pool of small to medium-sized water courses in northwest Germany. Vegetation in the 1980s and 1990s did not differ among observations periods with respect to important properties such as the number of frequent species, the rank–frequency relations and main geographical gradients. This enabled us to compare the vegetation of physiographic units in space and time. The only considerable difference between the two data sets was the higher average frequency of the 59 most frequent species, especially of helophytes. This can be interpreted as a sampling artifact. Even within a group of well-trained researchers, differences in the notion of the ‘current water level’ may occur.

The rank–frequency curve of the total data set resembled a broken-stick distribution (Wilson, 1991), also known for rank–abundance curves (Wiegleb et al., 2014a; Baatrup-Pedersen et al., 2006). As species frequency and average abundance are positively correlated, in particular for hydrophytes (Riis and Sand-Jensen, 2002; Demars et al., 2014), we can assume that frequent species contribute more to the standing biomass. The presence of six core species and 15 satellite species (H1) indicates that

colonization is somehow limited but frequent species do not exclude each other, they only use the resources or space differently. There are not many more species available in the species pool. For additional species, mostly laterally invading helophytes, habitats become available only accidentally. This causes the long tail of very rare species.

The core species *P. arundinacea*, *C. platycarpa*, *S. emersum*, *L. minor*, *M. scorpioides* and *Agrostis stolonifera* appear in many published species lists from lowland areas all over north central Europe (Great Britain: Haslam, 1978; Holmes, 1983; Denmark: Riis et al., 2000; Baatrup-Pedersen et al., 2003, 2008; Southern Sweden: Kohler et al., 1996; Poland: Szoszkiewicz et al., 2002, 2010; Slovakia: Hrivnák et al., 2010; Latvia: Grinberga, 2011; Estonia: Kõrs et al., 2012; Paal and Trei, 2004; Paal et al., 2007). Despite floristic changes along the west–east gradient the basic composition of river vegetation remains similar within the temperate region of northern Europe. The inventory of species was particularly similar to the vegetation type RBSQ A, as defined by Holmes (1983) for southern British lowlands (RBSQ stands for River/Bank/Selected Species/Quantitative). Differences are only found with respect to the recognition of frequent helophytes, which may have methodological reasons.

The marginal delimitation of the sample site has a strong influence on the sampling result (see Staniszwski et al., 2006; Breugnot et al., 2008; Kõrs et al., 2012). Sampling all species below the current water level leads to the inclusion of a larger proportion of helophytes. Helophytes make up a high percentage (12 of 21) of most frequent species. Helophytes form an integral part of the aquatic stream community (H3). Under largely undisturbed conditions, helophytes would form large stands in and alongside the margins of the stream (see Herr et al., 1989; Paal et al., 2007). The helophyte free river is regarded as an artifact of an intensively managed landscape, were weed cutting, bank construction or grazing by domestic animals destroyed the natural vegetation structure. Helophyte rich stands are often particularly species rich (Wiegleb et al., 1989; Paal and Trei, 2004). Helophytes may facilitate the survival of small submerged species, such as narrow leaved *Potamogeton* or *Lemna trisulca*, and are thus crucial to the maintenance of biodiversity in streams. Many helophytes are forming submerged morphotypes in the main water course (see Table 1), such as *P. arundinacea*, *M. scorpioides*, *A. stolonifera*, *Glyceria fluitans*, *Berula erecta*, *Nasturtium officinale*, *Persicaria hydropiper* and *Glyceria maxima*. This indicates a sufficient supply with CO₂ (Sand-Jensen and Frost-Christensen, 1998; Demars and Trémolières, 2009). Regional variation in adaptation to the aquatic life was observed for *Sparganium erectum*, which is less hydrophytic in our area than in southern Germany, while *B. umbellatus*, *G. maxima* and *P. arundinacea* were more often found as fully submerged forms than elsewhere (G. Wiegleb, K. van de Weyer; own observations).

Even though changes in species frequency occurred within a decade, most frequent species kept their position in the rank order. The high degree of floristic stability was also indicated by the similarity between rank–frequency curves of both periods. During the observation period no major vegetation breakdown was observed. In contrast to southern Germany (Van de Weyer and Hussner, 2008) the northwest German lowlands were also relatively immune against invasion. Since then only the neophyte *E. nuttallii* has increased in frequency (Steffen et al., 2013). On the other hand, *R. penicillatus* has become rare in glacial plains (H. Brux, W. Herr, G. Wiegleb, unpublished data, 2012, 2013), where it grew abundantly in the 1980s. Both findings confirmed trends already visible in the 1990s.

The relation between frequency of species and variation among units (H4) had never been studied before, as straight-forward measures of analyzing variation in frequency of areas of unequal size and irregular shape are not available (Gotelli and Graves, 1996;

Legendre, 2008). We expected to find a hump-back curve. At low frequencies the variation cannot be high, while in a ubiquitous species occurring almost everywhere at high frequencies variation must be low as well. Our finding confirmed these assumptions. Some outliers were associated with rare species of restricted geographical distribution or pleustophytes. Uneven distribution of medium-frequent species among units may be related to either insufficient dispersal abilities (lacking recolonization after disturbance) or general unsuitability of some units for some species.

Shifting from a taxonomic to functional view (H5), physiographic units shared only four growth forms over the whole observation period, i.e. graminids, herbids (both helophytes), peplids and potamids (both hydrophytes). The respective niches were present everywhere. Despite the lower variance in all functional groups as compared to species no full niche equivalence among units was found. Niches for myriophyllids, nymphaeids and vallisnerids may be partially lacking in some units, while pleustophytes and cryptogams may be completely absent from units, where their niches are nowhere realized.

Ordination of units

In accord with the stability of the total flora of the study area the units showed similar similarity patterns during both observation periods (H6). This is particularly expressed by the altitudinal gradient from the alluvial plains to the higher grounds, being more or less congruent with the north–south gradient. Higher grounds units and alluvial plains were more robust against change than glacial plains. Still, the degree of change at the scale of the region is low, compared to the drastic changes which occurred locally during the observation period (Wiegleb et al., 2014a). At the reach level, temporal autocorrelation for most properties of the vegetation (species composition, dominance, growth form spectrum) is lost after 3–5 years (Wiegleb et al., 2014a; Demars et al., 2014). After 7–10 years autocorrelation may even be negative indicating a different system state. If we assume that reaches within a physiographic unit are showing unsynchronized stochastic vegetation fluctuations caused by local management interventions and discharge events we may conclude that the net effect of local fluctuations lead to a high degree of resistance and resilience at the regional level as predicted by McCluney et al. (2014). This indicated that the colonization extinction-dynamics of the three components of the species pool (regional, longitudinal, and lateral) was still intact.

In the CCA ordination a second axis was identified, namely the alkalinity axis (H7). Temporal changes were more pronounced at higher altitudes and higher alkalinities. In our analysis, 'alkalinity' stands for a whole array of chemical parameters which are usually closely intercorrelated such as alkalinity, pH, nitrate and phosphate (see Wiegleb, 1984; Demars and Harper, 1998, 2005; Demars and Edwards, 2009; Wiegleb et al., 2014b). We assume that among the chemical variables inorganic carbon availability has a higher importance than nitrogen or phosphorus limitation (see Demars and Thiébaud, 2007; Demars and Trémolières, 2009; Demars et al., 2012). The importance of alkalinity for large-scale discrimination among units and river systems had already been reported by Wiegleb (1984) and was later confirmed by Riis et al. (2000), Baattrup-Pedersen et al. (2008) and Lewin and Szoszkiewicz (2012). The fact that the basic structure of ordination diagrams (with the main axes 'current velocity' and 'alkalinity') is preserved over various spatial scales indicates a form of self-similarity. An analysis of more than 300 sites in our study area showed that none of the species found in northwest Germany has any significant relation to phosphorus concentrations of the water (Steffen et al., 2014). Nor did changes in nutrient concentrations have any influence on the stochastic changes in cover, richness, species

composition, dominance and growth form over 21 years (Wiegleb et al., 2014a; Demars et al., 2014).

Diversity was best maintained in the 'true lowlands' (alluvial plains and sandy glacial lowlands), regardless of species composition (H6). The glacial lowland units 11/20, 12/24 and 6/7/16 all comprised more than 90% of the 59 most frequent species and were the hotspots of macrophyte diversity in northwest Germany. Reaches where more than 20 species were found are located along the edges of these three units, bordering alluvial plains (Herr et al., 1989). Local species richness was strongly related to occurrence of frequent species. That is why we did not explore the effect of rare species on the discrimination among units.

Species frequency at the scale of the unit is dependent of the species pool and of both spatial dependence and autocorrelation (Wilson and Anderson, 2001; Legendre et al., 2002; Demars and Thiébaud, 2007). Spatial dependence refers to explanatory variables such as alkalinity and altitude, for which the unit is regarded as homogeneous. Spatial autocorrelation would reflect the influence of neighboring units. In addition, temporal autocorrelation describes the fact that established species will prevail, at least within the limit of their physiological tolerance, which is usually not exceeded. To all terms several error terms must be added, e.g. unknown effective habitat parameters (e.g. grazing), unknown range of dispersal abilities of species, or insufficient knowledge about the species pool prior to the start of the study.

Under the assumption of homogeneity as to important geofactors neither size of the unit nor sampling intensity should influence species percentages, at least not of the frequent species. The units used here are homogeneous by definition for parameters such as geology, geomorphology, hydrology and geochemistry. In addition we assumed that they are homogeneous with respect to anthropogenic influence, as all sampled reaches are characterized by altered habitat conditions in the sense of O'Hare et al. (2006). Still they may violate the *ceteris paribus* clause as defined by Gotelli and Graves (1996). They may not be homogeneous for other parameters which influence macrophyte frequency and abundance. Such parameters are groundwater inflow or crossing of large rivers. These 'non-regional' effects may decrease the expected individuality of a unit (Borcard et al., 2004). Connection of river systems by canals beyond the limits of single units may also blur the picture (Herr et al., 1989).

Conclusions

In accord with our expectation, vegetation of adjacent physiographic units was sufficiently different to identify characteristic species compositions. Thus the physiographic unit meets the requirements of an 'appropriate macrosystem' in the sense of Thorp (2013) and McCluney et al. (2014). In surface water management and protection under the WFD statistical information of this kind will be helpful for the definition of regionally differentiated reference states (see Baattrup-Pedersen et al., 2008). So far, published surveys did not allow any judgment about which species are frequent, rare, or typical, nor which sites are representative for which river system or physiographic unit in northern Germany (e.g. Schaumburg et al., 2004; Baattrup-Pedersen et al., 2008; Birk and Willby, 2010). Our data suggest that context independent river typologies may lead to inadequate judgment on reference states and indicator values. A sandy lowland brook in one unit will have a different vegetation from a sandy lowland brook in another unit, indicating a non-stationary spatial process in the sense of Fielding and Bell (1997). This may be caused by functionally similar species occupying the same niches. Similar sites are often colonized by one species of the following three growth forms, peplids (all *Callitriche* species), myriophyllids (small *Ranunculus* species or

M. alterniflorum) and parvopotamids (*P. pectinatus*, *P. trichoides* or *P. berchtoldii*). They may simultaneously show maximum floristic dissimilarity and maximum functional similarity. Many species show characteristic distributional gaps because of lacking niches in certain physiographic units. They are not bound to river types but to a combination of hydrological factors, which may appear independently in a variety of types.

The occurrence of frequent species such as *S. emersum* and *E. canadensis* does not indicate disturbed conditions. If their frequency in a physiographic unit is around 90% they will inevitably occur both in disturbed and undisturbed as well in potamal and rhithral reaches because of the mass effect or longitudinal autocorrelation (see O'Hare et al., 2006; Birk and Willby, 2010). Only frequent occurrence as monodominant stands may raise some concern. Taxa which are rare or do not occur in a unit cannot be used for classification and assessment. This holds for aquatic mosses which showed low frequencies in our study area, similar as in Poland (Szoszkiewicz et al., 2010). Still they play an important role in the system of quality assessment proposed for Germany by Schaumburg et al. (2004).

On the other hand, more information about helophyte distribution and abundance must be gathered in order to include them into assessment schemes of lowland rivers. More attention should be paid to the factor of carbon availability. In the 1990s pH values rarely exceeded 8.2 in the study area, while recently pH values of 9.1 were frequently found in four of our physiographic units (Steffen et al., 2014). This must have a negative influence on the growth potential of submerged helophytes as well as of hydrophytes without floating leaves or the ability to assimilate hydrogen carbonate. Even a dominant climax species such as *S. emersum* may decline under such circumstances.

Acknowledgments

Sampling of data set A was funded by Niedersächsischer Landesbetrieb für Wasserwirtschaft, Küsten- und Naturschutz (Fachbehörde für Naturschutz, Hannover) from 1978 to 1982 and by Schleswig-Holsteinisches Landesamt für Naturschutz und Landschaftspflege (Kiel) from 1983 to 1984. Sampling data set B was funded by Bundesministerium für Umwelt, Naturschutz und Reaktorsicherheit (BMU, Bonn) from 1988 to 1991. We thank H.J. Dahl and A. Krause for the great support during that time. U. Euler, P. Finck and A. Ssymank (BfN, Bonn) provided the updated map of physiographic units. We thank B.O.L. Demars and S. Birk for many valuable comments on macrophyte ecology, statistical analyses and indicator value of aquatic plants. A. Baatrup-Pedersen, K. Szoszkiewicz, A. Kohler and H.-U. Dahms commented on previous versions of the paper. R. Becker, K. Kanongdate, A. Lehmann, P. Moog, D. Todeskino, H.-G. Wagner, and U. Wohlfahrt assisted with the field work. M. Filetti helped with the design of the figures. Sampling of *R. penicillatus* from 2012 to 2014 was initiated and supported by J. Zalewska-Gaioć.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.limno.2014.12.005>.

References

- Baatrup-Pedersen, A., Larsen, S.E., Riis, T., 2003. Composition and richness of macrophytic communities in small Danish streams – influence of environmental factors and weed cutting. *Hydrobiologia* 495, 171–179.
- Baatrup-Pedersen, A., Szoszkiewicz, K., Nijboer, R., O'Hare, M., Ferreira, T., 2006. Macrophyte communities in unimpacted European streams: variability in assemblage patterns, abundance and diversity. *Hydrobiologia* 566, 179–196.
- Baatrup-Pedersen, A., Springe, G., Riis, T., Larsen, S.E., Sand-Jensen, K., Larsen, L.M.K., 2008. The search for reference conditions for stream vegetation in northern Europe. *Freshwater Biol.* 53, 1890–1901.
- Barendregt, A., Bio, A.M.F., 2003. Relevant variables to predict macrophyte communities in running waters. *Ecol. Model.* 160, 205–217.
- Beck, M.W., Vondracek, B., Hatch, L.K., 2013. Environmental clustering of lakes evaluate performance of macrophyte index of biotic integrity. *Aquat. Bot.* 108, 16–25.
- Birk, S., Willby, N., 2010. Towards harmonization of ecological quality classification: establishing common grounds in European macrophyte assessment for rivers. *Hydrobiologia* 652, 149–163.
- Birk, S., Willby, N., 2011. WFD intercalibration phase 2: milestone 6 report. <https://www.uni-due.de/imperia/md/content/aquatische.oekologie/cbrivigig-macrophytes-milestone6-dec2011-final.pdf> (accessed 05.03.14).
- Birk, S., Bonne, W., Borja, A., Bruce, S., Courrat, A., Poikane, S., Solimini, A., van den Bund, W., Zampoukas, N., Hering, D., 2012. Three hundred ways to assess Europe's surface waters: an almost complete overview of biological methods to implement the Water Framework Directive. *Ecol. Indic.* 18, 31–41.
- Blümel, C., Raabe, U., 2004. Vorläufige Checkliste der Characeen Deutschlands. *Ros-tocker Meeresbiol. Beiträge* 13, 9–26.
- Borcard, D., Legendre, P., Avois-Jacquet, C., Tuomisto, H., 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85, 1826–1832.
- Breugnot, E., Dutartre, A., Laplace-Treytore, C., Hauri, J., 2008. Local distribution of macrophytes and consequences for sampling methods in large rivers. *Hydrobiologia* 610, 13–23.
- Bruh, H., Herr, W., Todeskino, D., Wiegleb, G., 1988. A study on structure and dynamics of communities with *Potamogeton alpinus* Balbis in water bodies of the northern part of the Federal Republic of Germany. *Aquat. Bot.* 32, 23–44.
- Decornet, J.M., (Thèse docteur Etat Sciences) 1979. Contribution à l'étude hydrobiologique de deux rivières de Lorraine: l'Orne et le Rupt de Mad. (Aperçu phytosociologique. La flore macrophytologique. Relations avec la qualité des eaux), 5 vol. Université de Metz, Metz, 724 pp.
- Demars, B.O.L., Harper, D.M., 1998. The aquatic macrophytes of an English lowland river system: assessing response to nutrient enrichment. *Hydrobiologia* 384, 75–88.
- Demars, B.O.L., Harper, D.M., 2005. Distribution of aquatic vascular plants in lowland rivers: separating the effects of local environmental conditions, longitudinal connectivity and river basin isolation. *Freshwater Biol.* 50, 418–437.
- Demars, B.O.L., Edwards, A.C., 2009. Distribution of aquatic macrophytes in contrasting river systems: a critique of compositional-based assessment of water quality. *Sci. Tot. Environ.* 307, 975–990.
- Demars, B.O.L., Potts, J.M., Tremolières, M., Thiébaud, G., Gougelin, N., Nordmann, V., 2012. River macrophyte indices: not the Holy Grail. *Freshwater Biol.* 57, 1745–1759.
- Demars, B.O.L., Thiébaud, G., 2007. Distribution of aquatic plants in the Northern Vosges rivers: implications for biomonitoring and conservation. *Aquat. Conserv. Mar. Freshwater Ecosyst.*, <http://dx.doi.org/10.1002/acq.844>, 14 pp.
- Demars, B.O.L., Trémolières, M., 2009. Aquatic macrophytes as bioindicators of carbon dioxide in groundwater fed rivers. *Sci. Tot. Environ.* 407, 4752–4763.
- Demars, B.O.L., Wiegleb, G., Harper, D.M., Bröring, U., Bruh, H., Herr, W., 2014. Aquatic plant dynamics in lowland river networks: climate change, management and connectivity. *Water* 2014 (6), 1–41.
- DWD (Deutscher Wetterdienst), 2014. Klimadiagramme. <http://www.klimadiagramme.de/Deutschland.html>
- European Environment Agency, 2014. Ecoregions for rivers and lakes. <http://www.eea.europa.eu/data-and-maps/figures/ecoregions-for-rivers-and-lakes>
- Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ. Conserv.* 24, 38–49.
- Gotelli, N.J., Graves, G.R., 1996. Null Models in Ecology. Smithsonian Inst. Press, Washington, 368 pp.
- Granke, O., Schmiedinger, W., Walentowski, H., 2004. Konzept und Schlüsselkriterien für die Bewertung der Biodiversität von Wald-Lebensräumen in Deutschland. *Waldökologie Online* 1, 25–28.
- Grinberga, L., 2011. Macrophyte species composition in streams of Latvia under different flow and substrate conditions. *Estonian J. Ecol.* 60, 194–208.
- Haslam, S.M., 1978. *River Plants*. Cambridge University Press, Cambridge.
- Herr, W., (diploma thesis) 1981. Die Fließgewässervegetation im Einzugsgebiet der Treene. Carl-von-Ossietzky Universität Oldenburg.
- Herr, W., Todeskino, D., Wiegleb, G., 1989. Übersicht über Flora und Vegetation der nie-dersächsischen Fließgewässer unter besonderer Berücksichtigung von Naturschutz und Landschaftspflege. *Naturschutz und Landschaftspflege in Niedersachsen* 18, 145–283.
- Herr, W., Wiegleb, G., 1984. Vegetationskundliche Untersuchungen zur biologisch-ökologischen Situation Schleswig-Holsteinischer Fließgewässer. Band 2: Tabellenband. In: Report on Behalf of the Landesamt für Naturschutz und Landschaftspflege-Schleswig-Holstein, Oldenburg.
- Herr, W., Wiegleb, G., 1985. Die Potamogetonaceae niedersächsischer Fließgewässer, Teil 2. *Göttinger Floristische Rundbriefe* 19, 2–16.
- Holmes, N., 1983. Typing British Rivers According to Their Flora. Nature Conservancy Council, Huntingdon, UK.
- Hrivnák, R., Otahelova, H., Valachovič, M., Palove-Balang, P., Kubinska, A., 2010. Effect of environmental variables on the aquatic macrophyte composition pattern in streams: a case study from Slovakia. *Fundam. Appl. Limnol.* 177 (2), 115–124.
- Jäger, E., 2011. *Rothmaler. Exkursionsflora von Deutschland. Gefäßpflanzen Grundband*. Spektrum, Heidelberg.

- Keddy, P.A., 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veget. Sci.* 3, 157–164.
- Kohler, A., Sipos, V., Björk, S., 1996. Makrophyten-Vegetation und Standorte im humosen Bräkné-Fluss (Südschweden). *Bot. Jahrb. Syst.* 118, 451–503.
- Kohler, A., Sonntag, E., Köder, M., Pall, K., Veit, U., Zeltner, G.H., Janauer, G., 2003. Macrophyte distribution in the River Vils (Oberpfalz, Bavaria). *Large Rivers* 14, 33–53.
- Koperski, M., Sauer, M., Braun, W., Gradstein, S.R., 2000. Referenzliste der Moose Deutschlands. *Schriftenreihe für Vegetationskunde* 34, 519.
- Körs, A., Vilbaste, S., Käiro, K., Pall, P., Piirso, K., Truu, J., Viik, M., 2012. Temporal changes in the composition of macrophyte communities and environmental factors governing the distribution of aquatic plants in an unregulated lowland river (Emajõgi, Estonia). *Boreal Environ. Res.* 17, 1–13 (online).
- Legendre, P., 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *J. Plant Ecol.* 1, 3–8.
- Legendre, P., Dale, M.R.T., Fortin, M.J., Gurevitch, J., Hohn, M., Myers, D., 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* 25, 601–615.
- Lewin, I., Szoszkiewicz, K., 2012. Drivers of macrophyte development in rivers in an agricultural area: indicative species reactions. *Cent. Eur. J. Bot.* 7, 731–740.
- Londo, G., 1976. The decimal scale for relevés of permanent quadrats. *Vegetatio* 33, 61–64.
- McCluney, K.E., Pof, N.L., Palmer, M.A., Thorp, J.H., Poole, G.C., Williams, B.S., Williams, M.R., Baron, J.S., 2014. Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. *Front. Ecol. Environ.* 12 (1), 48–58.
- Mesters, C.L.M., 1995. Shifts in macrophyte species composition as a result of eutrophication and pollution in Dutch transboundary streams over the past decades. *J. Aquat. Ecosyst. Health* 4, 295–305.
- O'Hare, M.T., Baatrup-Pedersen, A., Nijboer, R., Szoszkiewicz, K., Ferreira, T., 2006. Macrophyte communities of European streams with altered physical habitat. *Hydrobiologia* 566, 197–210.
- Paal, J., Trei, T., 2004. Vegetation of Estonian water courses; the drainage basin of the southern coast of the Gulf of Finland. *Ann. Bot. Fennici* 41, 157–177.
- Paal, J., Trei, T., Viik, M., 2007. Vegetation of Estonian watercourses, III. Drainage basins of the Moonsund Sea, the Gulf of Riga and Saaremaa Island. *Ann. Bot. Fennici* 44, 321–344.
- Pentecost, A., Willby, N., Pitt, J.A., 2009. River macrophyte sampling: methodologies and variability. Report SC070051/R1. Environment Agency, Bristol.
- Riis, T., Sand-Jensen, K., 2002. Abundance-range size relationship in stream vegetation in Denmark. *Plant Ecol.* 161, 175–183.
- Riis, T., Sand-Jensen, K., Vestergaard, O., 2000. Plant communities in lowland Danish streams: species composition and environmental factors. *Aquat. Bot.* 66, 255–272.
- Sand-Jensen, K., Frost-Christensen, H., 1998. Photosynthesis of amphibious and obligately submerged plants in CO₂-rich lowland streams. *Oecologia* 117, 31–39.
- Schaumburg, J., Schranz, C., Foerster, J., Gutowski, A., Hofmann, G., Meilinger, P., Schneider, S., Schmedtje, U., 2004. Ecological classification of macrophytes and phytobenthos for rivers in Germany according to the Water Framework Directive. *Limnologica* 34, 283–301.
- Staniszewski, R., Szoszkiewicz, K., Zbierka, J., Lesny, J., Jusik, S., Clarke, R.T., 2006. Assessment of sources of uncertainty in macrophyte surveys and the consequence for river classification. *Hydrobiologia* 566, 235–246.
- Steffen, K., Becker, T., Herr, W., Leuschner, C., 2013. Diversity loss in the macrophyte vegetation of northwest German stream and rivers between the 1950 and 2010. *Hydrobiologia* 713, 1–17.
- Steffen, K., Leuschner, C., Müller, U., Wiegleb, G., Becker, T., 2014. Relationships between macrophyte vegetation and physical and chemical conditions in northwest German running waters. *Aquat. Bot.* 113, 46–55.
- Steusloff, U., 1939. Zusammenhänge zwischen Boden, Chemismus des Wassers und Phanerogamenflora in fließenden Gewässern der Lüneburger Heide um Celle und Uelzen. *Arch. Hydrobiol.* 35, 70–106.
- Szoszkiewicz, K., Karolewicz, K., Lawniczak, A., Dawson, F.H., 2002. An assessment of the MTR aquatic plant bioindication system for determining the trophic status of Polish rivers. *Polish J. Environ. Stud.* 11, 421–427.
- Szoszkiewicz, K., Jusik, S., Lawniczak, A.E., Zgola, T., 2010. Macrophyte development in unimpacted lowland rivers in Poland. *Hydrobiologia* 656, 117–131.
- ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination. Microcomputer Power, New York.
- Thorp, J.H., 2013. Metamorphosis in river ecology: from reaches to macrosystems. *Freshwater Biol.* 59, 200–210.
- Tremp, H., 2009. Geostatistische Analyse der Strahlwirkung in Fließgewässern am Beispiel der Wasserpflanzen. In: Deutsche Gesellschaft für Limnologie (DGL). *Erweiterte Zusammenfassungen der Jahrestagung 2008 (Konstanz)*, pp. 518–523.
- Weber-Oldecop, D.W., (diss. TU Hannover) 1969. *Wasserpflanzengesellschaften im östlichen Niedersachsen*.
- Van de Weyer, K., 2001. Klassifikation der aquatischen Makrophyten der Fließgewässer von Nordrhein-Westfalen gemäß den Vorgaben der EU-Wasser-Rahmen-Richtlinie, vol. 30. Landesumweltamt NRW, Merkblätter, 108 pp.
- Van de Weyer, K., 2008a. Aquatische Makrophyten in Fließgewässern des Tieflandes-Mögliche Maßnahmen zur Initiierung der Strahlwirkung. *Schriftenreihe des Deutschen Rates für Landschaftspflege (2007)* 81, 67–70.
- Van de Weyer, K., 2008b. Fortschreibung des Bewertungsverfahrens für Makrophyten in Fließgewässern in Nordrhein-Westfalen gemäß den Vorgaben der EG-Wasser-Rahmen-Richtlinie. LANUV-Arbeitsblatt 3. Landesamt für Natur, Umwelt und Verbraucherschutz. Nordrhein-Westfalen, Düsseldorf.
- Van de Weyer, K., Hussner, A., 2008. Die aquatischen Neophyten (Gefäßpflanzen, Armeuchteralge und Moose) Deutschlands – eine Übersicht. In: Deutsche Gesellschaft für Limnologie (DGL). *Erweiterte Zusammenfassungen der Jahrestagung 2007 (Münster)*, Werder 2008, pp. 225–228.
- WFD, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy, Brussels.
- Wiegleb, G., 1981. Struktur, Verbreitung und Bewertung von Makrophytengesellschaften niedersächsischer Fließgewässer. *Limnologica (Berlin)* 13, 427–448.
- Wiegleb, G., 1983a. Recherches méthodologiques sur les groupements végétaux des eaux courantes. *Colloques Phytosociologiques* 10 (Végétations Aquatiques, Lille 1981), 69–83.
- Wiegleb, G., 1983b. A phytosociological study of the macrophytic vegetation of running waters in Western Lower Saxony (FRG). *Aquat. Bot.* 17, 251–274.
- Wiegleb, G., 1984. A study of the habitat conditions of the macrophytic vegetation in selected river systems in Western Lower Saxony (FRG). *Aquat. Bot.* 18, 313–352.
- Wiegleb, G., 1988. Analysis of flora and vegetation in rivers – concepts and applications. In: Symoens, J.J. (Ed.), *Handbook of Vegetation Science Application to Aquatic Vegetation and Water Management*, 15/1. Nijhoff, Dordrecht, pp. 311–330.
- Wiegleb, G., 1991. Die Lebens- und Wuchsformen der makrophytischen Wasserpflanzen und deren Beziehungen zu Ökologie, Verbreitung und Vergesellschaftung der Arten. *Tuexenia* 11, 135–148.
- Wiegleb, G., Herr, W., Todeskino, D., 1989. Ten years of vegetation dynamics in two rivulets in Lower Saxony. *Vegetatio* 82, 163–178.
- Wiegleb, G., Bröring, U., Filetti, M., Brux, H., Herr, W., 2014a. Long-term dynamics of macrophyte dominance and growth form types in two northwest German lowland streams. *Freshwater Biol.* 59, 1012–1025.
- Wiegleb, G., Bröring, U., Filetti, M., Gnauck, A., Brux, H., Luther, B., 2014b. Long-term prediction of macrophyte community development in lowland streams using artificial neural networks. In: Thinh, N.X. (Ed.), *Modellierung und Simulation von Ökosystemen, Workshop Kölpinsee 2013*. Rhombos Verlag, Berlin, pp. 217–238.
- Willby, N.J., Abernethy, V.J., Demars, B.O.L., 2000. An attribute-based classification of European hydrophytes and its relationship to habitat utilisation. *Freshwater Biol.* 43, 43–74.
- Wilson, J.B., 1991. Methods for fitting dominance/diversity curves. *J. Veg. Sci.* 2, 35–46.
- Wilson, J.B., Anderson, B.J., 2001. Species-pool relations: like a wooden light bulb. *Folia Geobot.* 36, 35–44.
- Zander, B., Wohlfahrt, U., Wiegleb, G., 1992. *Typisierung und Bewertung von Fließgewässervegetation der Bundesrepublik Deutschland*. Band I: Text. Carl-von-Ossietzky Universität, Oldenburg.