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Patterns of abundance and co-occurrence in aquatic plant communities

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Abstract Aquatic plants are well suited as subjects for studies on the distribution and abundance of co-occurring species, especially due to the simple structure of their communities, well defined toposequences and relatively easily measurable environmental factors. Here we show that underwater plants occurring in semi-natural lakes form stable communities, where species interactions dominate over dispersal dynamics to form a modular community structure with a high degree of zonation (turnover) and low within-module species richness. In turn, human-induced disturbance largely destroyed the modular structure. Our results indicate that (1) species abundance distributions (SADs) of underwater plant communities are well described by the lognormal model; (2) environmental characters did not significantly influence the SADs of underwater plant communities; (3) log-series SADs do not indicate specific types of community organization; (4) in our lake communities only few satellites (tourists) occur; (5) the co-occurrence of species is highly dependent on the turnover across lakes and water depth zones; and (6) species zonation is a function of lake properties.

Keywords Aquatic plants · Modular community structure · Satellite species · Species abundance distributions · Species co-occurrence · Species dispersal dynamics · Zonation

Introduction

An ecological community contains the individuals of species that potentially interact within a single patch or local area of habitat (Leibold et al. 2004), while a meta community is a set of local communities that are linked by dispersal of multiple interacting species (Wilson 1992). One of the tasks of community ecology is to disentangle the local and regional factors that influence the patterns of distribution and abundance of these species (Weiher and Keddy 1999; Chase 2003; Boschilia et al. 2008). Patterns of abundance are usually described by means of relative species abundance distributions (SADs), which are often visualized by rank order–abundance plots (RADs) (McGill et al. 2007; Ulrich et al. 2010). RADs were found to follow two major types of distribution (Ulrich et al. 2010; Silva et al. 2010) that have been linked to specific patterns of resource use (Tokeshi 1999), habitat characteristics (Magurran 2004; McGill et al. 2007), and dispersal regimes (Zillio and Condit 2007). Lognormal type abundance distribution seems to occur in rather stable and closed communities (Tokeshi 1999; Hubbell 2001; Ulrich et al. 2010), while log-series distributions describe dispersal-driven open assemblages (Fisher et al. 1943; Zillio and Condit 2007; Ulrich et al. 2010). So far, SADs have not been studied for underwater plant communities occurring in lakes.

Several authors observed relative higher numbers of rare and abundant species with respect to those with intermediate abundance in communities structured by the trade-off between species interactions and dispersal (Hanski 1982; Magurran and Henderson 2003; Ulrich and Ollik 2004). Such a core and satellite pattern (Hanski 1982) is expected in heterogeneous communities (Magurran and Henderson 2003) where some of the species are linked by strong interactions (core species), while other species attend the community infrequently and at low abundances (satellite or tourist species). Communities lacking satellite species should be rather closed and exhibit lognormal species abundance distri-

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butions (Magurran and Henderson 2003; Ulrich and Ollik 2004), while communities without a clear group of core species are often artificial assemblages of species with high degrees of spatial or temporal turnover. Due to the limited dispersal abilities of most underwater plant species, we hypothesize that our lake communities lack the satellite group (Barrett et al. 1993; Santamaria 2002; Szymeja and Bazydło 2005; Szymeja and Gałka 2008).

In animal and terrestrial plant communities, patterns of species co-occurrence are linked to environmental gradients (Ulrich 2009) and mutual interactions (Bascompte and Jordano 2007; Presley et al. 2010). The still ongoing discussion about ecological assembly rules (Diamond 1975) focused on the question to what degree interspecific competition shapes patterns of species turnover (beta-diversity) and segregation. Recent meta-analytical studies (Gotelli and McCabe 2002; Ulrich and Gotelli 2007, 2010) found the majority of meta communities to be shaped by either random or negative species associations but not by joint occurrences in response to a particular environmental factor. Thus, at least in closed communities, competitive forces (past and present) seem to dominate over aggregative forces. Therefore we use species co-occurrence analysis (Gotelli and Graves 1996) to infer how strong segregative and aggregative forces shape underwater communities and whether differences in community structure can be linked to environmental factors.

Here we focus on underwater plant communities—a neglected guild in community ecology (Simberloff and Dayan 1991) although the constituting species are potentially well suited to infer the interplay between biotic and environmental factors. These communities have a simple few-species composition and a clear to-posesquence. Their environmental features are relatively easily to measure. We assume that underwater plants live in sufficiently stable habitats (Szymeja 1994a; Murphy 2002) where species interactions dominate over dispersal dynamics to form a community structure with groups of co-occurring species (a modular structure) with a high degree of zonation (species turnover) and low within-module species richness. This leads to four basic hypotheses about the community structure of underwater plant communities:

1. We predict a prevalence of lognormal SADs as an indication of closed and stable communities structured by species interactions. We ask whether and

how environmental characters affect these distributions.

2. Lognormal SADs are associated with a prevalence of species with intermediate abundances (McGill et al. 2007; Henderson and Magurran 2010). Thus we do not expect bimodal richness—abundance distributions typical of a core-satellite pattern.
3. Under the assumption of strong species interactions and competitive forces we expect a prevalence of negative species associations.
4. Habitat gradients within lakes and habitat gradients among lakes influence the structure of macrophyte communities. If species occurrences follow these gradients we expect a modular community organization and thus clearly defined patterns of species turnover among lakes and along with water depth.

Materials and methods

Study area and sampling

In July and August 2010, submerged aquatic plants from five lakes in north-western Poland, located in the Pomeranian Lakeland along the southern shores of the Baltic Sea, were sampled by scuba diving. The lakes are post-glacial, oligo- and mesotrophic, predominantly located in forests, well-preserved, without significant human pressure, and vary in terms of surface area (30.0–79.0 ha), maximum depth (5.0–19.0 m), water pH (5.50–8.86), conductivity (27.2–249.0 $\mu\text{S cm}^{-1}$), sediment pH (5.22–8.02), sediment conductivity (16.8–459.0 $\mu\text{S cm}^{-1}$), organic matter content (0.25–90.67 %) and sediment hydration (12.94–95.96 %). The selected lakes exhibit gradients from acid to alkaline and from shallow to fairly deep (cf. Table 1). Lakes Dymno and Krasne are semi-natural while Lakes Dobrogoszcz, Strupino, and Trzebielsk show visible symptoms of anthropopressure. Such a choice of lakes enabled us to obtain samples from a broad spectrum of aquatic plant communities.

In each of the lakes, a single strip (transect), 250 m wide and with a depth depending on the maximum depth of occurrence of macrophytes, was marked out on the bottom. Each transect was divided into depth zones of 1.0 m, where five sediment samples and five 0.5 l

Table 1 Features of lakes

Lake	Area (ha)	Maximum depth (m)	Geographic coordinates		Number of depth zones	Sediment properties (min–max)			
						pH	Conductivity ($\mu\text{S cm}^{-1}$)	Organic matter (%)	Hydration (%)
Trzebielsk	72.0	19.0	53°59'N	17°22'E	5	7.34–7.68	297.0–459.0	2.62–42.30	66.62–89.02
Dymno	79.0	18.0	53°55'N	17°30'E	9	7.43–8.02	40.0–351.0	0.45–90.67	12.84–87.77
Strupino	42.6	9.1	54°20'N	17°59'E	5	6.89–7.71	84.6–370.0	0.51–39.87	22.54–93.27
Dobrogoszcz	53.3	6.6	54°08'N	18°20'E	5	5.37–6.66	25.5–158.3	0.25–22.37	19.40–86.63
Krasne	30.0	5.0	53°52'N	17°17'E	5	5.22–6.85	16.8–60.6	0.61–74.93	25.42–95.96

sediment water samples were taken. In the sediment, pH, conductivity, organic matter (OM, %) and hydration (%) were measured according to methods proposed by Wetzel (2001). The evaluation of the environmental conditions in the lakes under study was performed on the basis of 145 water and 145 sediment samples from 29 depth zones.

In each of the lakes, we placed a total of 100 times a quadratic diver (0.1 m^2) every 1.0 m in order to record all plant species present (cf. Madsen and Adams 1988; Madsen 1993; Szmaja 1994a, b). In total, we took 2,900 plant samples from 290 m^2 of lake bottom. For the following analyses we used pooled samples for each of the 29 studied depth zones in the five lakes.

Data analysis

For each lake and for the total community we constructed ordinary presence–absence and abundance matrices (Gotelli and Graves 1996) with species in rows and water depth in columns. To analyze the core-satellite patterns, we plotted species number to occurrence and abundance using \log_2 occurrence and abundance classes. To infer the influence of environmental variables on the distribution of species abundances we fitted for each lake lognormal and log-series distributions to the observed species rank order–abundance (Whittaker) distributions (Ulrich et al. 2010). Goodness-of-fit was quantified from sums of ordinary least squares (SS) and we used the quotient of $\text{rfit} = \text{SS}_{\log\text{normal}}/\text{SS}_{\log\text{-series}}$ to assess whether a given distribution was better fitted by a lognormal or by a log-series. Values of rfit less than one indicate a better fit of the lognormal distribution.

Patterns of species co-occurrence were quantified by the C-score (Stone and Roberts 1990), that is an averaged count of all checkerboard $\{\{1,0\},\{0,1\}\}$ submatrices. The larger the C-score, the more, on average, species pairs are segregated in their occurrences (Ulrich and Gotelli 2007). We assessed the coherence of occurrence patterns across lake depth classes with the embedded absences metric proposed by Presley et al. (2010), which is a count of the number of species absences embedded by species occurrences after ordering the matrix according to the first axis of correspondence analysis. The smaller the number of embedded absences is, the more coherent the ranges of species occurrences are. To infer the degree of spatial species turnover (beta-diversity) we used the coefficient of correlation r of the row and column numbers of non-empty cells in the ordinated matrix and quantified the degree of turnover by the associated coefficient of determination r^2 as proposed by Ulrich and Gotelli (2013). Statistical significances were in all cases obtained from a null model approach using the conservative fixed–fixed (FF) null model that retains observed row and column totals during randomization. Randomization was done with the independent swap algorithm (Gotelli 2000) that sequentially swaps $\{\{1,0\},\{0,1\}\}$ submatrices to their $\{\{0,1\},\{1,0\}\}$ coun-

terparts. We used 10mn swaps (m number of species, n number of depth classes) for each random matrix (Ulrich and Gotelli 2010). For each lake we generated 1,000 randomized matrices and compared the observed metric scores with the respective upper and lower tail distributions of the randomized matrices. We also calculated standardized effect sizes (SES) $Z = (x - \mu)/\sigma$. SES scores that are approximately normally distributed indicate statistical significance at the 5 % error level below -2.0 or above 2.0 (two-tailed test). The calculations were made in the *Turnover* software applications (Ulrich 2011).

We used canonical correspondence analysis based on species abundances (Legendre and Legendre 1998) to assess the spatial species turnover across lakes and across depth zones within each lake. We considered sediment pH, conductivity, organic matter content and hydration as environmental variables.

Table 2 Species and abundances in all 2,900 lake samples

Species	Abbreviation	Abundance
<i>Ceratophyllum demersum</i> L.	Cd	26
<i>Chara aspera</i> (Dech.) Willd.	Cha	101
<i>Chara contraria</i> A. Braun ex Kützing.	Chc	369
<i>Chara fragilis</i> Desvaux (= <i>Ch. globularis</i> Thuillier)	Chf	792
<i>Chara rudis</i> A. Braun.	Chr	325
<i>Chara tomentosa</i> L.	Cht	516
<i>Drepanocladus aduncus</i> (Hedw.) Warnst.	Da	112
<i>Eleocharis palustris</i> (L.) Roem. &Schult.	Ep	11
<i>Elodea canadensis</i> L.	Ec	585
<i>Fontinalis antipyretica</i> Hedw.	Fa	109
<i>Isoetes lacustris</i> L.	Il	377
<i>Juncus bulbosus</i> L.	Jb	49
<i>Littorella uniflora</i> (L.) Asch.	Lu	163
<i>Lobelia dortmanna</i> L.	Ld	129
<i>Luronium natans</i> (L.) Raf.	Ln	117
<i>Myriophyllum alterniflorum</i> DC	Ma	238
<i>Myriophyllum spicatum</i> L.	Ms	18
<i>Myriophyllum verticillatum</i> L.	Mv	292
<i>Najas marina</i> L.	Nm	144
<i>Nitella flexilis</i> (L.) Agardh.	Nf	369
<i>Nitellopsis obtusa</i> (Desvaux) J. Groves.	No	188
<i>Nuphar lutea</i> (L.) Sibth. & Sm.	Nl	1
<i>Nymphaea alba</i> L.	Na	1
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	Pha	18
<i>Polygonum amphibium</i> L.	Pa	4
<i>Potamogeton compressus</i> L.	Pco	63
<i>Potamogeton crispus</i> L.	Pc	56
<i>Potamogeton friesii</i> Rupr.	Pf	25
<i>Potamogeton lucens</i> L.	Pl	43
<i>Potamogeton obtusifolius</i> Mert. et Koch	Po	101
<i>Potamogeton pectinatus</i> L.	Pp	297
<i>Potamogeton x zizi</i> Koch ex Roth	Pz	70
<i>Sphagnum denticulatum</i> Bridel.	Sd	323
<i>Stratiotes aloides</i> L.	Sa	267
<i>Warrnstorfia exannulata</i> (Schimp.) Loeske	We	224
Filamentous algae	A	13

Table 3 The species × depth class matrix (entries are abundances) for all lakes combined ordinated by reciprocal averaging

S	K4	K5	K3	K2	K1	Do1	Do2	Do4	Do3	Do5	S1	S2	D7	D8	S3	S5	D9	D6	S4	S4	D5	D4	D3	T2	T1	T3	D2	T4	D1	T5	Occurrences
We	75	67	51	31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Nl	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Sd	87	83	85	54	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Jb	0	0	0	48	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Ep	0	0	0	6	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Ln	0	0	41	20	43	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Pha	0	0	0	2	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Na	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Il	59	62	84	34	46	60	32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
Ld	0	0	0	44	16	69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Lu	0	0	0	46	13	86	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Pa	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
A	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Ma	0	0	0	0	0	70	78	39	35	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Pz	0	0	0	0	0	1	12	26	25	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5
Ec	0	0	0	0	0	65	95	85	86	87	75	52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	9
Chf	0	0	0	0	0	16	93	0	85	93	0	14	88	70	43	75	0	91	50	40	0	21	13	0	0	0	0	0	0	0	14
Pco	0	0	0	0	0	0	4	0	0	0	34	9	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Po	0	0	0	0	0	0	5	0	0	10	28	15	0	0	31	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	6
Pl	0	0	0	0	0	0	0	0	0	0	25	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Nf	0	0	0	0	0	0	0	0	0	0	0	0	94	81	0	81	56	57	0	0	0	0	0	0	0	0	0	0	0	0	5
Da	0	0	0	0	0	0	0	0	0	0	0	0	16	79	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Fa	0	0	0	0	0	0	0	0	0	0	0	0	0	35	0	0	74	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Mv	0	0	0	0	0	0	0	0	0	0	53	54	0	0	63	53	0	0	69	0	0	0	0	0	0	0	0	0	0	0	5
Sa	0	0	0	0	0	0	0	0	0	0	41	59	0	0	47	11	0	0	17	12	3	9	1	0	0	0	0	0	0	0	12
Cht	0	0	0	0	0	0	0	0	0	0	67	56	0	0	48	32	0	0	39	0	1	9	0	54	86	52	21	23	28	0	13
No	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41	0	4	14	0	6	36	11	24	52	13	38	0	10
Pp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28	0	0	0	51	0	6	38	0	36	36	0	0	0	0	0	6
Chc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	98	100	82	0	0	0	0	0	59	2	28	0	6
Chr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	40	6	41	34	34	53	10	76	17	41	4	11
Pf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	10	0	0	0	3
Nm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	9	13	43	0	75	0	3	6
Ms	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0	5	3	4	1	0	6
Pc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	21	0	27	0	2	4
Cha	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	0	0	0	0	0	0	2
Cd	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	61	0	2
Species	3	3	5	9	10	9	8	3	4	5	7	8	3	4	8	5	4	5	6	6	5	7	7	9	5	9	7	10	7	5	2

Numbers in column names refer to depth in meters
K Krasne, *Do* dobrogoszcz, *D* dymno, *S* strupino, *T* trzebielsk
 Species abbreviations refer to Table 2

Results

Abundance distributions

In the five lakes we found 35 species of aquatic plants belonging to 18 families (Table 2), of which Potamogetonaceae (7 species) and Characeae (7) were most species rich. Additionally, we considered filamentous algae. Most abundant were *Chara fragilis* (792 occurrences), *Elodea canadensis* (585) and *Chara tomentosa* (516) (Table 2). None of the species colonized four or all five lakes, 5 species occurred in three, 15 in two lakes, and 16 species were lake specific (Table 3).

Numbers in column names refer to depth in meters: *K* Krasne, *Do* Dobrogoszcz, *D* Dymno, *S* Strupino, *T* Trzebielsk. Species abbreviations as in Table 2

Species abundance distributions of the whole meta-community followed the log-normal type (Ulrich et al. 2010) with a small number of species with very low or high abundances and a large number of moderately

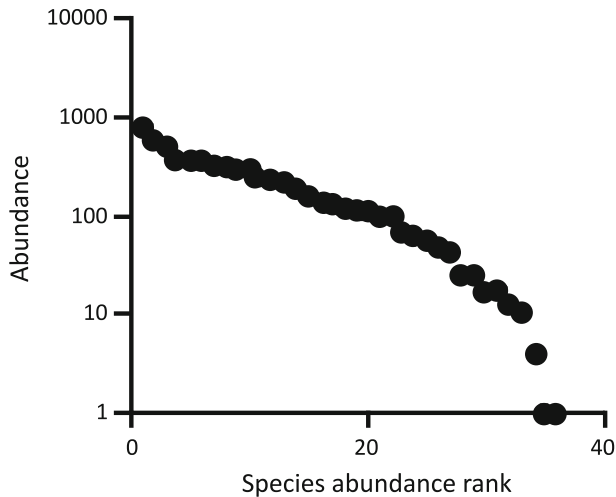


Fig. 1 Species abundance—rank order (Whittaker) plot of 35 plant species across all lakes and samples

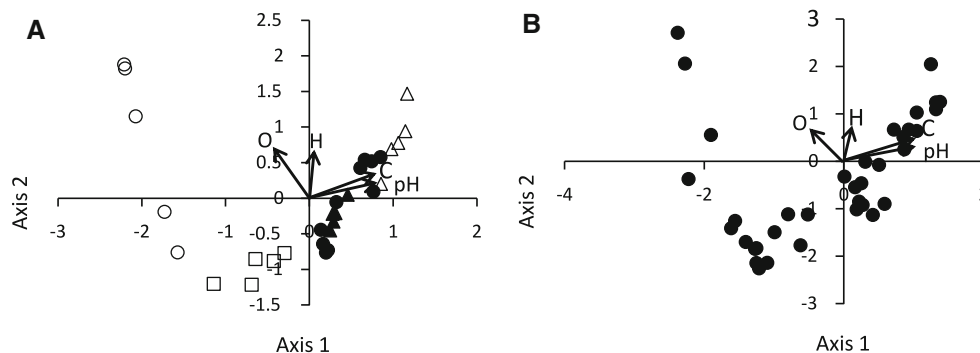


Fig. 2 Correspondence analysis based on all depth classes separates lakes (a) filled dots Dymno, open dots Krasne, filled triangles Strupino, open triangles Trzebielsk, open squares Dobrogoszcz) according to the first two axes that are defined mainly by the

abundant species (Fig. 1). Correspondence analysis based on Table 3 separated our lakes mainly according to pH and sediment conductivity (Fig. 2a). Community composition followed this major environmental gradient (Fig. 2b).

In turn, patterns of species abundances within single lakes were not significantly modified by environmental gradients. SADs of 21 of the 29 depth classes with at least five species had rfit scores of less than 1 and were therefore better fitted by a lognormal than a log-series distribution (Fig. 3). The relative fit of both models did not significantly depend on either sediment pH (Fig. 3a), sediment conductivity (Fig. 3b), sediment organic matter content (Fig. 3c), or water depth (Fig. 3d) (all $P > 0.1$, $r^2 < 0.05$). Species richness was also not correlated with these four environmental variables (all $P > 0.1$, data not shown).

Neither with respect to species occurrences (Fig. 4a) nor when using abundances (Fig. 4b) did a typical core-satellite pattern emerge. Species with intermediate numbers of occurrences or abundances were most numerous (Fig. 4). Most frequent were *Chara fragilis* and *Chara tomentosa*, which occurred in 14 and 13 depth zones, respectively. Only three species (*Nuphar lutea*, *Nymphaea alba* and *Polygonum amphibium*) occurred in one depth zone only.

Co-occurrence of species along environmental gradients

Our analyses revealed a distinct zonation of species occurrences (Table 3), especially in the lakes with strong environmental gradients (Dymno and Krasne). These lakes were characterized by high species turnover (quantified by the r^2 metric; Table 4) across depth classes (1–9 m for Dymno; 1–5 m for Krasne) and a comparatively strong degree of negative species associations (C-score). The low numbers of embedded absences (EmbAbs) indicates that species occurrences were depth specific and not scattered across depth zones. *Chara aspera*, *Myriophyllum spicatum*, and *Potamogeton friesii*

gradients of sediment pH and conductivity *C* (axis 1) and sediment hydration *H* and sediment organic matter content *O* (axis 2). Species abundances follow this trend (b) to form lake specific plant communities as defined in Table 3

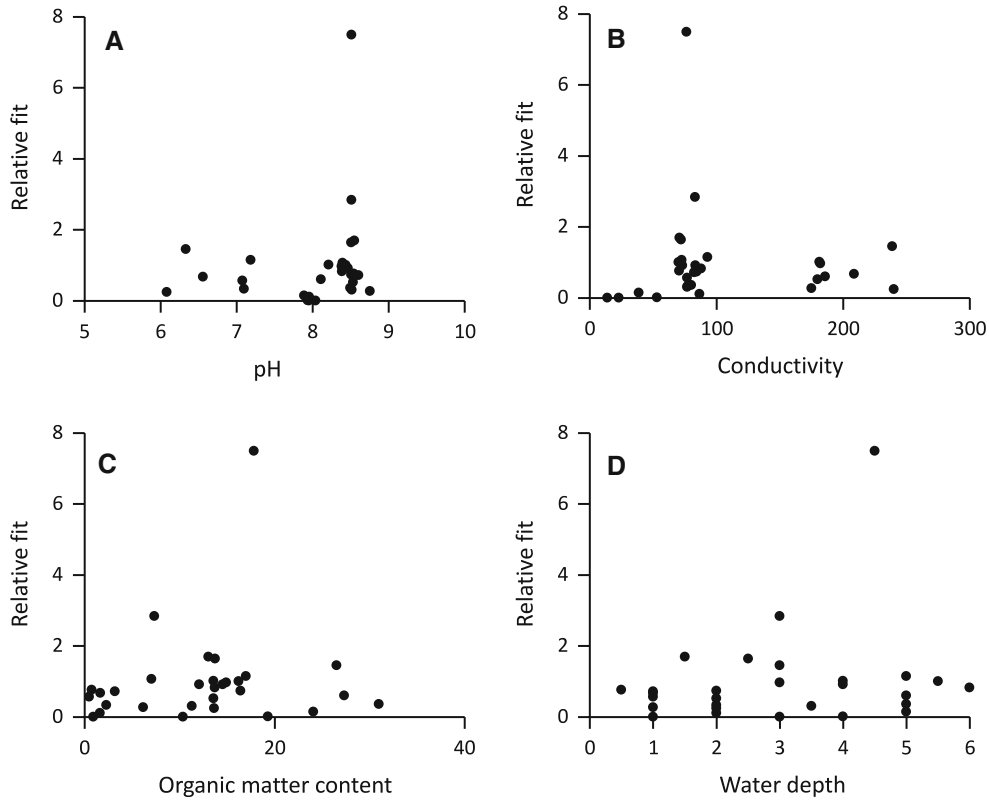


Fig. 3 Relative fits (rfit) of lognormal (fitn) and log-series abundance distributions (fitl) ($rfit = fitn/fitl$) of 29 within depth class communities with at least five species in dependence of four

important sediment variables. Values of rfit < 1 indicate a better fit of the lognormal distribution

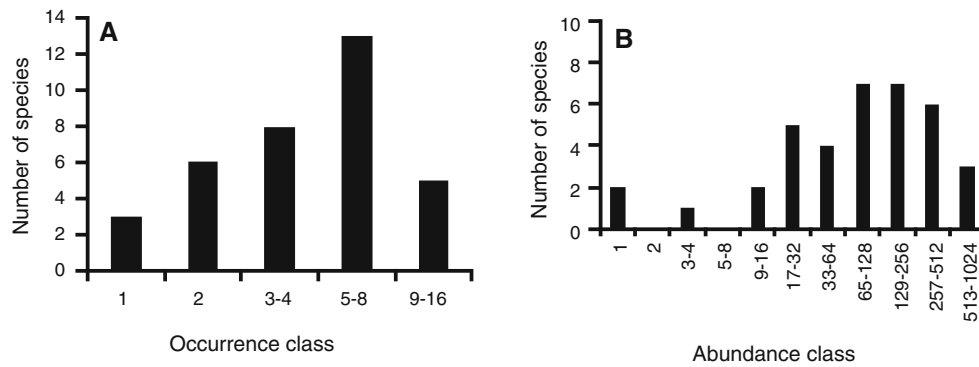


Fig. 4 Numbers of plant species in binary occurrence (a) and abundance (b) across depth zones of lakes (a) and samples (b). Occurrences are based on the total number of depth classes among the five lakes (maximally 29)

occurred only in shallow waters below 3 m, while *Nitella flexilis*, *Drepanocladus aduncus*, and *Fontinalis antipyretica* colonized the water depth below 6 m. *Stratiotes aloides*, *Chara rudis* and *Chara contraria* preferred shallow and intermediate waters. *Nitellopsis obtusa*, *Najas marina*, and *Chara fragilis* were found at intermediate water depths only.

A different pattern emerged in Lakes Trzebielsk, Dobrogoszcz, and Strupino. The tendency towards negative co-occurrence vanished and we did not find a clear zonation and depth specific clustering (Table 4).

Instead, patterns of species co-occurrences across depth classes appeared to be random with respect to the FF null model.

Discussion

The plant communities of our study lakes were best described by a lognormal type SAD (Fig. 1). Lognormal SADs are common in closed competition structured animal (Magurran and Henderson 2003) and terrestrial

Table 4 Score and SES values (Z) of three metrics of species co-occurrence in species—depth class matrices for five lakes and for all lakes combined

Metric	Lake											
	Dymno		Trzebielsk		Krasne		Dobrogoszcz		Strupino		All	
	Score	SES	Score	SES	Score	SES	Score	SES	Score	SES	Score	SES
C-score	0.020*	10.260*	0.007	1.530	0.006*	5.170*	0.002	0.960	0.005	0.850	0.040*	13.274*
EmbAbs	0.015*	-5.887*	0.000	-1.440	0.000	-1.540	0.100	0.120	0.000	-2.200	0.451*	-10.843*
R ²	0.528*	7.136*	0.110	0.320	0.400*	3.170*	0.130	0.250	0.150	1.670	0.756*	12.071*

C-score species segregation metric, EmbAbs Embedded absences metric, R² metric of species turnover
Significant scores ($P < 0.01$)

plant (Silva et al. 2010) communities. Our results from submerged plant communities add to the impression that lognormal distributions form by universal processes acting on animal and plant communities that are independent of habitat and taxon peculiarities. About two-thirds of the single lake communities were best described by the lognormal model (Fig. 3). We hypothesize this prevalence of lognormal SADs to be caused by the specificities of the lake environment characterized particularly by strong light gradients that favor a marked zonation in plant occurrences and community structure (Banaś et al. 2012). Accordingly, Ulrich et al. (2010) reported a tendency towards lognormal SADs particularly at local scales and stable species occurrences. The fact that we did not find any significant correlations of rfit on important environmental variables that might indicate gradients towards less suited or disturbed habitat conditions is an indication that these lakes are sufficiently in equilibrium to support stable community structures. However, it should be mentioned that the detection probability of a certain type of abundance distribution depends heavily on the total number of species (Wilson et al. 1998). Our local communities contained between 3 and 11 species and thus, communities with at least 5 species were used for comparison. Previous work (Ulrich et al. 2010) showed that this is the minimum number of species that allows at least for comparison of model fit.

From a theoretical perspective, log-series distributions should prevail in disturbed and input driven environments (Hill and Hammer (1998), e.g., in the shallow littoral zones of lakes, where strong and frequent wave activity causes a significant transformation of population and community structure (Szmeja 1994b; Szmeja and Gałka 2008). We think that this type of species abundance distribution in aquatic plant communities might also be formed as a result of human pressure on lakes, e.g., in the early stages of eutrophication, acidification or toxication, especially during the elimination or exchange of species and the formation of short-lived substitute communities.

According to Hanski (1982), two groups of species play an important role in the formation of communities: the so-called satellite species and those participating in the construction of the community core. None of these

groups dominated in our study and thus the distribution of species abundance in our aquatic plant communities was close to the unimodal (Fig. 4b). A similar distribution was obtained by Heino and Virtanen (2006) in bryophyte communities occurring in streams. Bimodal distributions emerge in heterogeneous communities under the influence of two contrasting processes: immigration and local reproduction that favors local persistence (Magurran and Henderson 2003). The high number of species with intermediate occurrence (Fig. 4a) in our lake communities thus does not point to a strong influence of dispersion as a major driver of community structure.

We found the highest number of species in the intermediate abundance classes (Fig. 4b). This is a typical situation in terrestrial plant (Cadotte and Lovett-Doust 2007) and animal (Simberloff and Martin 1991) communities, but also in aquatic animals (Harvey 1981; Tokeshi 1992). In turn, in terrestrial arthropod communities the lowest abundance class is frequently most species rich (Ollik 2008; Ulrich et al. 2010). In our research submerged macrophyte plants live in sufficiently stable habitats where species interactions dominate over dispersal dynamics. This fact is linked to limited dispersion within the lake (Szmeja 1994c, 2010; Santamaria 2002; Szmeja et al. 2010) and relatively high numbers of species that are depth zone specific (Schwarz et al. 2000).

The pattern of species co-occurrence within and across lakes was segregated with a high degree of turnover across lakes. The latter tendency is apparently related to the gradients in water and sediment conditions (Table 1). Our analysis partly recovered the well-known zonation of aquatic plants (Banaś et al. 2012) (Table 4). However, within lakes a clear zonation occurred only in Lakes Dymno and Krasne, which are least influenced by human activities. In these lakes we found a modular community organization with clearly defined subcommunities along the depth gradient (Table 3). The lack of modularity in the other three lakes, however, demonstrates that species zonation is lake specific and possibly dependent on human-induced disturbance regimes.

In conclusion, our study shows that underwater plants occurring in lakes form stable communities, where species interactions dominate over dispersal dynamics to form a modular community structure with a

high degree of zonation (turnover) and a low within module species richness. In lakes subject to long-term human pressure the plant communities did not have an obvious modular structure. Probably, environmental stress factors dominate over species interactions.

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