Hydrobiologia (2009) 624:81–90
DOI 10.1007/s10750-008-9668-6

PRIMARY RESEARCH PAPER

Distribution of epipelic diatoms in artificial fishponds along environmental and spatial gradients

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Received: 17 September 2008 / Revised: 2 December 2008 / Accepted: 4 December 2008 / Published online: 17 December 2008

Abstract Although epipelic diatoms play a key role in primary production of many ecosystems, many aspects of their biodiversity, ecology and geographical distribution are poorly understood. The present study is based on sampling of 45 man-made fishponds in the Czech Republic covering an environmental gradient from oligo/dystrophic highland ponds within protected areas to the eutrophic/hypertrophic lowland ponds used for intensive fish production. Diatom distribution patterns assessed using biomass and species composition variables were assessed along environmental and geographical gradients. In total, 185 epipelic diatom taxa were found in the investigated samples. The differences in species composition between sites were correlated with environmental parameters, but not with the geographic distance of the localities. This pattern might suggest that niche-based control, rather than the effect of dispersal limitation, is the main driving force in the species composition of epipelic diatoms in fishponds. The alpha-diversity of sites correlated with altitude, nitrogen and chlorophyll *a* concentrations but did not correlate with the area of the ponds. The significant relationships between local abundance of species and their regional occupancy were very similar to previous studies of diatoms in boreal streams. In addition, these data concur with patterns known for multicellular organisms suggesting that in this respect diatoms may not differ from groups of organisms with larger body sizes.

Keywords Epipelon · Diatoms · Geographic distribution

Introduction

Fishponds are man-made shallow water bodies in which water level, fish stock and, to some extent, nutrient and fish-food input are under human control (Fott et al., 1980). Moreover, fishpond ecosystems exhibit fast changes and are susceptible to unpredictable random external disturbances (Weimann, 1942). The Central European fishponds have been constructed since the Middle Age, and since then they have often lost any artificial appearance, looking nowadays like small lakes within the landscape (Kořínek et al., 1987). However, with their ca. 250–750 years, they are still much younger than most comparable natural stagnant freshwaters (lakes, wetland pools). This freshwater habitat type can be

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Handling editor: J. Padisak

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found in several European countries (e.g. Austria, Poland, Germany, Hungary, France, Croatia and Russia) and are typically more abundant than larger lakes by about 100:1 (Oertli et al., 2005). In the Czech Republic, they represent the single most common type of stagnant water habitat (total area 510 km^2; Pokorný et al., 2006) replacing a large proportion of former wetland ecosystems (Fig. 1). The most recent articles, particularly focused on invertebrates or macrophytes, highlighting the importance of ponds for the provision of habitat to support freshwater biodiversity (Céréghino et al., 2008a, b; Davies et al., 2008; De Bie et al., 2008). The phytobenthos of fishponds is structurally dominated by epipelic microalgal assemblages. Epipelic algae represent a specific functional group adapted to living on and between fine-grained substrata. The study of epipelon was pioneered within freshwater habitats by Round (1953), but epipelic algae in general have received relatively little attention in comparison to studies of phytoplankton (Poulíčková et al., 2008a). Thus, the distribution patterns of benthic algae in fishponds remain largely unexplored (Lysáková et al., 2007; Hašler et al., 2008; Poulíčková et al., 2008a, b).

On the other hand, the distribution patterns of freshwater microalgae have recently been the subject of several studies, specifically investigating the local abundance versus regional occupancy patterns of species assemblages and the relation of species composition similarities between individual localities to their spatial structure and environmental characteristics (e.g. Soininen, 2007; Soinien et al., 2007). The relation of local abundance versus regional occupancy of species and the frequency distribution of species occupancy across the investigated region are useful characteristics of distribution patterns in microalgal species (Heino & Soininen, 2006). In diatoms, Soininen & Heino (2005) illustrated a similar positive relationship between species local abundance and regional occupancy. However, comparative data from other habitat types than boreal streams are lacking.

It has recently been demonstrated that dispersal limitations do affect the global distribution of freshwater diatoms (Telford et al., 2006; Vyverman et al., 2007). Moreover, traditional "cosmopolitan" and "euryvalent" species (species complexes) consist of pseudo-cryptic diatom species with restricted distribution (Evans et al., 2008; Poulíčková et al., 2008c). Thus, diatoms now may appear as the group with possibly much less cosmopolitanism than hypothesized by Finlay et al. (2002). Generally, groups largely with cosmopolitan distribution of species should have flat species–area curves with little increase of the species richness at the level of regions, continents or at the global level. On the other hand, species–area curves of groups with strong geographic limits of distribution increase strongly from the regional to global levels (Finlay et al., 2002). Thus, strong spatial

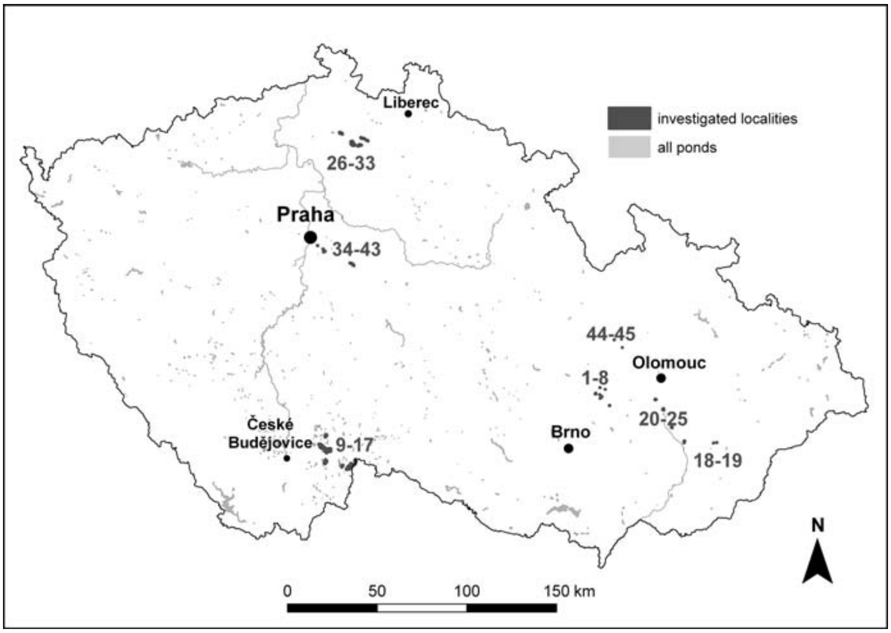

Fig. 1 Map showing total area and distribution of all fishponds in the Czech Republic (*grey areas*) and investigated localities (*black areas*). For locality numbers see Table 1

control of diatom distribution at the regional level should indicate their pronounced geographically restricted species distribution pattern.

The present study uses an epipelic diatom dataset from 45 Czech fishponds and aims to address the following questions:

(a) Do the epipelic diatom communities in man-made fishponds exhibit strong spatial structuring at the regional level (suggesting neutrality) or are they structured by environmental features (suggesting the niche-based control)?
(b) Which environmental factors correlate with the alpha-diversity of fishpond epipelic diatoms and is there any effect of pond size on the single site alpha-diversity of epipelic diatoms?
(c) Is the relationship between the local abundance and the regional frequency, and the species–occupancy frequency distribution of fishpond epipelic diatoms similar to those observed in boreal streams (Soininen & Heino, 2005)?

Material and methods

In May 2007, we sampled 45 fishponds in the Czech Republic (Fig. 1) covering a gradient from oligo/dystrophic highland ponds within protected areas (localities Pavlov, U 3 krátkých) to hypertrophic lowland ponds used for intensive fish production (Naděje, Starý Kanclíř). The geographic positions, area and selected environmental data of the ponds are summarized in the Table 1. Other measured environmental variables and species composition of other algal groups (Cyanobacteria, desmids, euglenophytes) were published elsewhere (Hašler et al., 2008). Selected environmental variables (pH, conductivity) were measured in situ using field instruments (WTW, Germany). Samples for chemical analyses were stored in sterile plastic bottles. Total phosphorus and nitrogen were analysed with a DR 2000 spectrophotometer by HACH (Hach, 1993; Hašler et al., 2008).

Sediment samples were collected using a glass tube, as described by Round (1953), and transported to the laboratory in polyethylene bottles. The mud–water mixtures were then poured into plastic boxes and allowed to stand in the dark for at least 5 h. The supernatant was then removed by suction and the mud covered with lens tissue. Under continuous low-level illumination (ca. 5 μmol photons m^{-2} s^{-1}), epipelic algae moved up through the first layer of lens tissue (separating detritus and inorganic particles) and became attached to the second layer of lens tissue placed on top. Captured diatoms were cleaned with a mixture of concentrated sulphuric and nitric acids and mounted in Naphrax as described previously by Poulíčková & Mann (2006). Diatom species were identified according to Krammer & Lange-Bertalot (1986, 1988, 1991a, b). Relative abundances of individual diatom species were estimated by counting 400 valves from each sample.

The Mantel tests of matrix correlations were used for testing the relationships between matrices of distance in species composition (evaluated using Bray–Curtis quantitative distance measure), environmental distance (matrix of Euclidean distances of ranked values of individual parameters) and the geographic distance of the localities (in kilometres). We used both the full (two matrices) Mantel tests and the partial (three matrices) Mantel tests with either the effect of environmental similarity or the geographic distance taken as the co-variate in testing the relation of the above-mentioned matrices in *zt* ver. 1.0 (Bonnet and Van de Peer, 2002). Altogether 10,000 permutations were used to assess the permutation *P*-value of significance in matrix correlations. The correlations of species composition distance, environmental and geographic distances were illustrated using linear regression models. Linear correlations of alpha-diversity indices and the environmental factors were evaluated in PAST, ver. 1.80. (Hammer et al., 2001). Alpha-diversity was evaluated using Shannon and Menhinick indices after Magurran (2004). The evenness of the diatom community was assessed using the Simpson index and species dominance using the 1-Simpson index (Hammer, 2002; Magurran, 2004).

Results

In total, 185 diatom taxa were recorded across the study sites. The most common epipelic diatoms were "cosmopolitan" species (sensu Krammer & Lange-Bertalot, 1986, 1988, 1991a, b) or species complexes (see Poulíčková & Mann, 2006; Potapova & Hamilton, 2007; Mann et al., 2008): *Navicula capitata* Ehrenb., *N. gregaria* Donkin, *Amphora copulata* (Kütz.) Schoem. et Archibald, *Achnanthidium minutissimum*

Table 1 Basic characteristics of investigated localities

No.	Locality	GPS	Altitude (m a.s.l.)	Area (m^2)	Cond (µS cm^{-1})	pH	TN (mg l^{-1})	Chl-*a* (µg l^{-1})
1	Drahany	N 49;25;54;8 E 16;52;34;9	380	35,200	195	7.38	6.5	16.12
2	Protivanov	N 49;28;12;2 E 16;48;41;7	615	24,222	201	9.93	6.5	6.38
3	Obora	N 49;27;44;3 E 16;47;54;9	610	12,300	175	7.50	0.8	3.78
4	U 3 krátkých	N 49;28;47;5 E 16;47;35;0	610	6,700	112	6.76	0.3	5.53
5	Suchý 1 náves	N 49;28;52;5 E 16;45;49;5	673	680	290	10.90	5.9	265.47
6	Suchý 2 tobogán	N 49;28;54;5 E 16;45;40;2	674	55,200	125	7.82	0.9	6.17
7	Pavlov	N 49;30;57;7 E 16;47;23;6	680	9,400	200	7.28	1.9	9.40
8	Buková	N 49;30;39;4 E 16;49;51;4	630	2,000	181	9.41	5.1	32.84
9	Naděje	N 49;07;07;7 E 14;44;31;3	430	656,548	220	8.89	0.7	10.68
10	Velký Tisý	N 49;04;04;2 E 14;42;25;6	429	2,247,877	245	8.33	0.5	45.01
11	Malý Tisý	N 49;03;13;8 E 14;44;57;0	435	213,225	245	8.18	3.0	70.40
12	Rožmberk	N 49;02;53;3 E 14;45;43;6	441	4,270,631	205	8.59	1.9	29.95
13	Opatovický	N 48;59;13;9 E 14;46;43;4	445	1,323,151	215	7.60	1.1	34.06
14	Starý kanclíř	N 48;58;05;6 E 14;53;43;6	455	339,028	165	10.38	1.8	140.49
15	Hejtman	N 48;57;32;4 E 14;56;20;8	469	800,000	132	7.65	0.4	19.26
16	Staňkov	N 48;58;31;9 E 14;57;26;7	483	1,969,555	133	9.16	1.0	25.79
17	Špačkov	N 48;58;31;9 E 14;57;26;7	483	412,628	188	7.76	2.4	66.19
18	Bezedník	N 49;17;58;2 E 17;43;35;1	323	4,153	461	9.10	0.1	4.05
19	Horní Ves	N 49;17;45;0 E 17;42;03;7	316	10,779	429	8.10	0.9	9.34
20	Záhlinice 1	N 49;17;14;6 E 17;28;41;1	198	120,525	670	7.93	3.3	69.00
21	Záhlinice 2	N 49;17;14;6 E 17;28;41;1	198	127,905	770	7.78	1.7	88.13
22	Chropyně	N 49;21;25;4 E 17;22;14;1	207	189,476	422	7.68	1.5	28.02

Table 1 continued

No.	Locality	GPS	Altitude (m a.s.l.)	Area (m^2)	Cond (μS cm^{-1})	pH	TN (mg l^{-1})	Chl-*a* (μg l^{-1})
23	Tovačov	N 49;26;06;8 E 17;17;35;6	206	359,850	267	7.38	2.3	97.52
24	Hrdibořice 1	N 49;28;56;1 E 17;13;31;2	213	30,362	726	7.94	1.9	64.38
25	Hrdibořice 2	N 49;28;56;1 E 17;13;31;2	213	49,824	729	8.00	1.5	37.48
26	Máchovo jezero	N 50;34;34;4 E 14;39;00;0	266	2,631,963	303	8.70	1.3	11.20
27	Břehyňský hráz	N 50;34;32;9 E 14;41;35;7	266	807,966	203	7.09	0.4	10.60
28	Černý	N 50;36;30;6 E 14;45;46;1	279	10,507	306	7.69	0.9	2.30
29	Vavrouškův	N 50;36;35;4 E 14;45;01;9	287	30,482	293	8.05	0.3	8.76
30	Strážovský	N 50;36;38;3 E 14;44;29;8	279	40,000	299	7.77	0.1	6.31
31	Tůň u letiště	N 50;36;51;0 E 14;43;48;1	289	9,246	221	7.50	0.1	6.73
32	Hradčanský	N 50;37;05;6 E 14;42;26;5	287	79,690	245	7.57	0.1	13.46
33	Novozámecký	N 50;37;44;7 E 14;32;12;1	261	541,141	332	8.90	0.8	7.68
34	Hostivař-vedl.	N 50;02;23;3 E 14;31;53;6	262	9,396	437	8.46	1.8	26.08
35	Hamerský	N 50;03;08;3 E 14;29;16;7	220	36,565	748	7.47	2.6	48.32
36	před Vrahem	N 50;01;50;9 E 14;32;53;4	263	27,036	722	7.17	2.5	42.57
37	Vrah	N 50;01;44;1 E 14;32;50;9	274	24,503	543	7.32	2.2	33.25
38	Homolka	N 50;01;38;4 E 14;32;42;1	212	12,364	660	9.82	3.4	6.73
39	Milíčov	N 50;01;34;0 E 14;32;27;0	302	23,955	778	7.65	2.0	19.13
40	Požár	N 49;59;15;5 E 14;45;24;2	419	37,656	556	7.59	2.9	5.06
41	Louňovický	N 49;59;07;0 E 14;45;59;7	412	64,661	511	8.17	2.0	45.59
42	Jevanský	N 49;58;43;7 E 14;47;13;8	395	176,150	431	8.50	2.2	59.79
43	Pařez	N 49;59;05;5 E 14;46;33;5	418	38,482	534	7.39	2.5	19.30
44	Líšnice	N 49;45;42;0 E 16;51;39;0	320	15,000	457	7.56	1.7	45.82

Table 1 continued

No.	Locality	GPS	Altitude (m a.s.l.)	Area (m^2)	Cond ($\mu S\ cm^{-1}$)	pH	TN ($mg\ l^{-1}$)	Chl-*a* ($\mu g\ l^{-1}$)
45	Obectov	N 49;43;39;0 E 16;55;43;0	329	500	296	7.26	3.7	185.06

Cond conductivity, *TN* total nitrogen, *Chl*-a chlorophyll *a* concentration

(Kütz.) Czarn. agg., *Navicula cryptocephala* Kütz. agg. and *Sellaphora pupula* (Kütz.) Mereschk. agg. The samples from oligotrophic/dystrophic protected ponds (often with low pH and conductivity; e.g. Břehyňský, Pavlov) were characterized by the occurrence of *Brachysira vitrea* (Grunow) Ross, *Pinnularia viridis* (Nitzsch) Ehrenb., *P. microstauron* (Ehrenb.) Cleve and *Tabellaria flocculosa* (Roth) Kützing. Assemblages from eutrophic ponds (Naděje, Rožmberk, Malý Tisý) were characterized by a dominance of *N. cryptocephala*, *N. capitata*, *N. gregaria*, *Nitzschia palea* (Kütz.) W. Smith. The representation of *S. pupula* agg. was very low (usually <1%) with the single exception of the Obectov locality that had 74% of *S. pupula* agg. cells in the epipelic community. Rare taxa included *Entomoneis ornata* (J.W.Bailey) Reimer (localities Obora, Suchý 2, Břehyňský) and *Amphipleura pelucida* (Kütz.) Kütz. (Hradčanský, Tůň u letiště).

Table 2 Results of Mantel tests of matrix correlations

	r	*P-value*
Species composition versus geographic distance	−0.009	0.41
Species composition versus environmental distance	**0.233**	**0.0002**
Geographic distance versus environmental distance	**0.138**	**0.0017**
Species composition versus geographic distance with environmental distance effect controlled	−0.028	0.25
Species composition versus environmental distance with geographic distance effect controlled	**0.235**	**0.0002**

Significant correlations are indicated in bold

The results of Mantel tests of matrix correlation (Table 2) illustrated strong relations between the species composition and environmental factors. The relation of environmental distance and species composition was highly significant both in two-matrices Mantel test (Fig. 2a) and in the partial Mantel test with the geographic distance taken as the co-variate. However, the species compositions of the samples were not correlated with their spatial position (Fig. 2b). In other words, the closer localities did not have more similar diatom species composition when

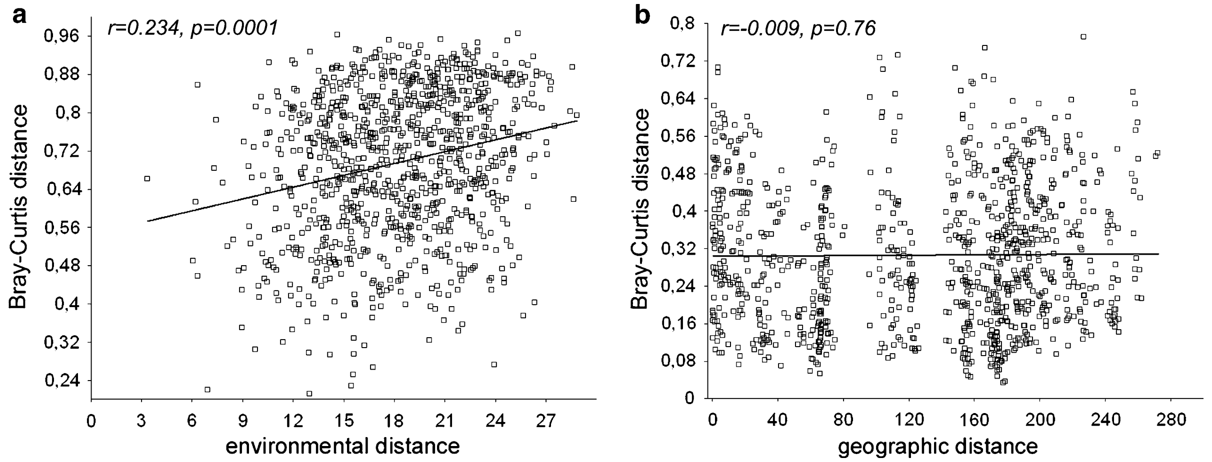

Fig. 2 Relation of species composition distances of fishpond epipelic diatoms from the Czech Republic between individual sites and their environmental (**a**) and geographic distances (**b**) in kilometre. The linear correlation *r* and the respective *P*-values are indicated in *upper left* of the graphs

Table 3 Linear correlations of diversity measures and environmental variables

	Shannon index	Menhinick index	Evenness	Dominance	Altitude	Pond area	Conductivity	pH	Total P	Total N	Chlorophyll *a*	Transparency
Shannon index	–	**0.60*****	**0.95*****	**−0.95*****	**−0.34***	−0.01†	0.14†	−0.01†	−0.21†	−0.28†	−0.26†	−0.11†
Menhinick index		–	**0.46****	**−0.46****	**−0.50*****	−0.12†	0.18†	−0.22	−0.27†	**−0.40****	**−0.34***	−0.09†
Evenness			–	**−1.00*****	−0.20†	0.04†	0.07†	0.04†	−0.19†	−0.28†	−0.26†	−0.08†
Dominance				–	0.20†	−0.04†	−0.07†	−0.04†	0.19†	0.28†	0.26†	0.08†
Altitude					–	0.06†	**−0.63*****	0.26†	−0.01†	0.25†	0.09†	0.26†
Pond area						–	**−0.30***	0.16†	−0.11†	−0.19†	−0.08†	−0.06†
Conductivity							–	−0.13†	**0.38***	0.10†	0.05†	**−0.44****
pH								–	0.24†	**0.35***	**0.34***	−0.09†
Total P									–	**0.45****	**0.62*****	**−0.55*****
Total N										–	**0.43*****	−0.21†
Chlorophyll *a*											–	−0.23†

Individual values indicate correlation coefficients between evaluated variables

* P-value = 0.01–0.05, ** P-value = 0.001–0.01, *** P-value < 0.001, † P-value > 0.05

Significant values are indicated in bold

compared to the more distant ones (Table 2). At the same time, geographic distances of ponds were positively correlated with their environmental distance. Species diversity indices did not correlate with pond area (Table 3). The alpha-diversity indices (evaluated by Shannon and Menhinick indices) were negatively correlated with site altitude, and there was a significant negative correlation between Menhinick diversity index and the total nitrogen and chlorophyll *a* concentrations (the *P*-values of the correlation of Shannon index with these measures were slightly above the 0.05 level). Altitude was negatively correlated with site conductivity. The total nitrogen, total phosphorus and chlorophyll *a* concentrations were strongly positively correlated with each other. In addition, total phosphorus and conductivity were strongly negatively correlated with water transparency, and conductivity was positively correlated with the total phosphorus concentrations (Table 3).

The local maximum species abundance and the local mean species abundance were positively correlated with regional frequency (i.e. % of the localities with the presence of the particular species). This positive correlation was slightly stronger for the local maximum abundance, but it was highly significant for both the local abundance measures (Fig. 3). The species–occupancy frequency distribution (Fig. 4) was in agreement with the "satellite-mode", distribution model, i.e. a high proportion of species occurred at a small number of sites.

Discussion

In their study of meta-community structure in boreal wetland ponds, Soinien et al. (2007) recently suggested two distinct models for distribution patterns of freshwater microalgae in natural ponds:

(a) The neutrality model concurring with Hubbell's (2001) theory. This model is typical of strongly spatially structured meta-communities with pronounced regional distance decay (negative correlation of similarity in species composition with geographic distance of localities). This pattern suggests that species are spatially limited in their dispersal, but it assumes that there are no differences in fitness of individuals within the assemblages (Hubbell, 2001).

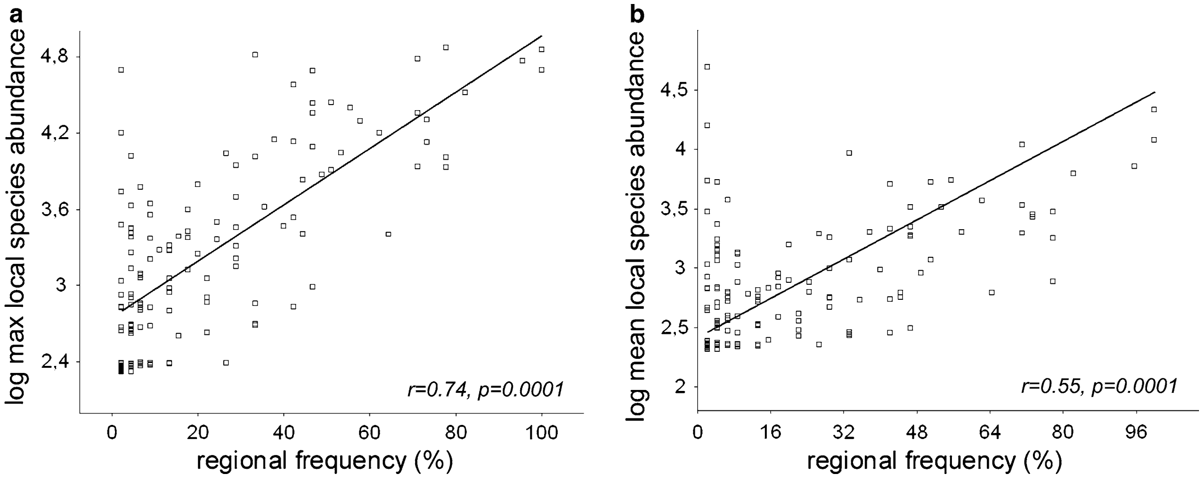

Fig. 3 The relationship between maximum (**a**) and mean (**b**) local abundance and regional occupancy (frequency) of epipelic fishpond diatom species of the Czech Republic. The linear correlation *r* and the respective *P*-values are indicated in *lower right*

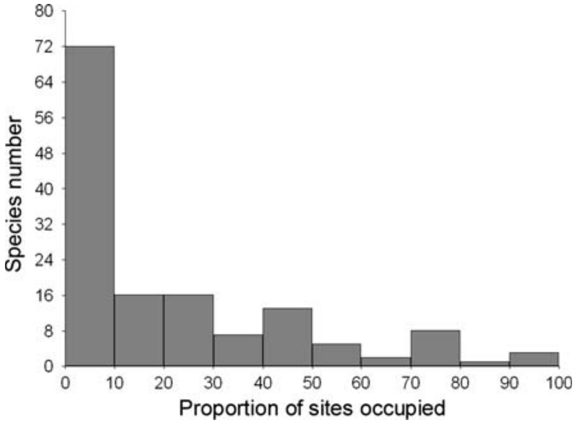

Fig. 4 The species–occupancy frequency distribution of fishpond epipelic diatoms in the Czech Republic

(b) The niche-based model assuming that individuals have different fitness in different environmental conditions. In this model, species composition similarities between pairs of localities correlate primarily with similarities in their local environmental characteristics rather than with the geographic distances. This model assumes that dispersal limitations does not matter (at least within an investigated region), and so, the species pools of individual localities are more or less identical to the overall regional species pool. Finlay (2002) and Finlay et al. (2002) extended this model to the global scale assuming cosmopolitan distribution in most protist species with dimensions of less than 1 mm.

In our study, the differences in species composition between sites (evaluated by the Bray–Curtis distance measure) were correlated with environmental distance, but they were not related to the geographic distance of the localities. This pattern might suggest, at least at the regional level of the Czech Republic, that niche-based control rather than the effect of dispersal limitations on the species composition of epipelic diatoms in fishponds is important. Within the Czech Republic (ca. hundreds of kilometres without obvious dispersal barriers as, for example mountain ridges), the effects of dispersal limits on epipelic diatom metapopulations can be ignored. However, we should still bear in mind the relatively young age of individual fishpond habitats (ca. 250–750 years). In this relatively very short evolutionary time, local speciation events, detectable via morphology-based diatom taxonomy, may not have taken place (see, e.g. Soininen, 2007 for diatoms speciation estimates of about 10^3–10^4 years). In addition, most of the fishponds in the Czech Republic have experienced drastic ecological changes in the past decades as a result of large-scale eutrophication and intensive fish-production management (Pechar, 1995), having strong influence on biota (Allan, 2004; Declerck et al., 2006). This could further support the "young age-effect" which may be superseded by spatially controlled variation in diatom species composition. The published datasets detailing the diatoms of natural lakes generally illustrate obvious spatial effects (Fallu et al., 2002; Bouchard et al., 2005) indicating dispersal limitations between localities. Thus, the "young age-effect" of man-made fishponds that highlights the environmental control over the spatial control of the diatoms species composition could, for the present, be the most plausible explanation of this pattern.

In organisms with ubiquitous dispersal and distribution, the pattern of species frequency distribution across localities should be characterized by a high proportion of "core species", i.e. species present at most of the localities. However, Soininen & Heino (2005) illustrated that the "satellite mode" (sensu Hanski, 1982) of diatom species frequency distribution held with most species occurring in a low proportion of sites in boreal streams. Thus, they concluded that regional distribution patterns of stream diatoms "may not be fundamentally different from those described previously for multicellular organisms" and suggested that this may even be a more general pattern for other habitat types and species groups. Given the difference in morphological and ecological structure of the diatom community coupled with the obvious differences between man-made fishponds and boreal streams, the pattern of diatom species regional frequency distribution in artificial fishponds may provide a test system from which a more general distribution model for freshwater diatoms may be constructed.

The significant correlations between local abundance of species and their regional occupancy in this study were similar to those illustrated by Soininen & Heino (2005) in their boreal streams study. In addition, these findings are in agreement with patterns observed in multicellular organisms, suggesting that diatoms may not differ from other groups of biota with larger body sizes. The overwhelming number of satellite species (present in just a few sites across the region) in a situation where there is no spatial effect on species composition similarity implies rather narrow ecological tolerances (niche breadths) of epipelic diatom species, similarly to conclusions based on the investigation of the boreal streams data of Soininen & Heino (2005). This observed distribution pattern clearly indicated the importance of habitat variety among Central European fishponds for the sustainability of epipelic diatom biodiversity. Whether the environmentally driven species composition control of fishpond epipelic diatoms reflects the absence of dispersal limitations at the regional level or it may really be a result of their relatively young age in comparison with most natural stagnant freshwater habitats, remains to be confirmed or rejected in future studies.

Acknowledgements This study was supported by grant nos. 206/07/0115 and 206/08/0389 of Czech Science Foundation, partly by the research project of the Czech Ministry of Education no. 0021620828. We would like to thank Dr. J. Burian (Department of Geoinformatics, Olomouc) for preparing a map of all fishpond distribution and Dr. Bryan Spears (Centre for Ecology & Hydrology, Edinburgh) for helping to improve the clarity of the manuscript.

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