

Sustaining abundance and distributional patterns of benthic diatoms from streams in Kentucky, USA

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Abstract

A sustainable approach to the preservation of natural aquatic communities requires detailed understanding of primary producers in those communities. Diatom species abundance depends on the ecological conditions and species' ability to distribute and grow at conditions close to its optima. The abundance-distribution relationship of diatom species was studied along an anthropogenic gradient in Kentucky streams. Mean relative abundance of diatoms found in reference streams decreased with an increase of nutrients and chloride, while distribution remained wide. Diatoms from the non-reference streams had higher diversity, but even with wide distribution, they had low abundance. Species that were most common and most abundant were species that occurred in streams in low human impact watersheds. Relative abundance of these species decreased with the increasing of nutrients and chloride concentrations; however, they persisted in habitats with high human disturbance. Non-reference sites had higher diversity, higher richness and lower evenness than reference sites. These results do warrant concern in regards to conservation, where the native low nutrient, low diversity sites in the State of Kentucky are the desired attribute.

Keywords: periphyton, diatoms, community structure, reference and non-reference streams, low nutrient streams.



1 Introduction

The relationship between species abundance (relative, absolute or percent cover) and distribution has been studied for many years [1–3] on the premise that dynamics of resource exploitation by species in local communities are connected with their regional distribution. Almost without exception [4], species with wide distribution, i.e. present at a large proportion of sites in a defined region, tend to be more abundant than species with restricted distribution [5, 6]. In this context, abundance is the average abundance at sites, where the species population is observed. For scenarios where all species can exist in all sites, either positive [5] or no [7] correlation between abundance and distribution of species has been observed in many groups of organisms [7]. A positive correlation between species abundance and distribution contradicts the presumed relationship if ecological specialization was important. Specialization is the ability of a species to exploit and maintain populations in unique environmental conditions [6]. Specialists have higher mean abundances at unique sites, which would result in no or negative correlations between species abundance and distribution in a region.

Microbial bioassessment and algal conservation are valued tools in current applied ecology [8]. Study of the abundance-distribution relationship in periphyton is needed because species abundance changes greatly along environmental gradients and relative abundance is often reported in large-scale surveys [9]. Survey studies report algal species distribution patterns, but distribution refers to the correspondence between abundance and environmental characteristics. In those studies usually dominant species are weighted more than species with lower abundance in an ecoregion [10]. Periphyton abundance and distribution are a result of complex interactions [11], physical disturbance [12], substrate conditions [13], grazing [14], and nutrient concentrations and ratios [15]. Addressing relationships between species abundance and distribution (as frequency of occurrence) could be valuable for the understanding of changes in ecosystems.

Diatoms are an excellent group for testing the abundance-distribution relationships, because they are mostly microscopic, widely distributed and every species has the potential of establishing populations under a given set of environmental conditions, while presenting species specific traits along environmental gradient n [16]. Diatom species composition is sensitive to environmental changes [17]. Consideration of both ecological preferences and historical occurrences could provide the accurate understanding of diatom abundance and distribution [18]. The abundance and distribution relationship of periphytic diatoms within an ecoregion have not been addressed.

Species in streams with minimal human impact can be defined as reference species [16]. Diatoms from those streams are likely to be reference diatoms of the area or region. Those diatoms presumably existed in streams prior anthropogenic alterations. Reference species are expected to have a broad niche under reference conditions, while specialists (potentially introduced to a region) will have narrow distribution, according to the fundamental niche



differentiation [19]. Diatoms are a very diverse group of algae with an estimated hundreds of thousands number of species [9]. It is unrealistic to expect few diatom species to be declared 'most valuable' for protection, rather in current bioassessment, the desire to protect and restore reference communities and conditions, regardless of their diversity, is considered an important ecological goal [20].

The goal of this study was to describe the relationship between relative abundance and distribution of diatom species in streams along a human disturbance gradient. Diatoms with high mean relative abundance were expected to have a narrow distribution at a small number of sites due to specialization (species specific autecology). Diatom community organization in reference streams was predicted to be similar, while diatom communities between reference and non-reference streams were expected to differ.

2 Material and methods

Samples from 44 streams from the Knobs ecoregion (northwestern Kentucky and southeastern Indiana) were collected during the April–June periods in 1996 and 1997 (Table 1 and Fig. 1). A total of 69 statistically independent samples were analyzed for the abundance – distribution pattern. Four streams were designated as reference sites and were sampled during both years (Table 1). Those sites were completely enclosed in nature preserves or human disturbance in the watersheds was low.

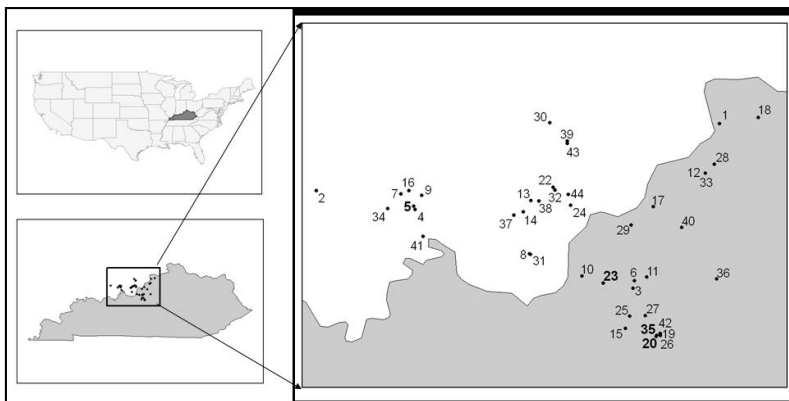


Figure 1: Map USA, the State of Kentucky and of Knobs ecoregion (northwestern Kentucky and southeastern Indiana) with sampling sites given as numbers, reference sites in bold, sites correspond with numbers in Table 1.

Each stream was visited weekly for 8 weeks. At each visit, pH and conductivity (CON) were measured with a YSI meter (YSI Incorporated, Yellow Springs, Ohio, USA); water temperature was determined with a thermometer;

and canopy cover (CAN) was assessed with a spherical canopy densiometer. Samples for chloride and nutrients were collected in 2 125-mL acid-rinsed polyethylene bottles. Water in one sample was filtered in the field through 0.45 µm pore-size filters to measure dissolved nutrients. Nutrient samples were stored on ice until returning to the lab where they were frozen until analysis.

Table 1: Site locality and identification for sites samples each year in Knobs ecoregion US, sites in bold are considered reference.

ID	SITE NAME	site	WATERSHED	STREAM	COUNTY	LAT	LONG	1996	1997
1	Barebone Creek	BBCR	Ohio River	Barebone	Trimble	38.59	85.4		•
2	Bird Hollow	BIHO	Little Blue River	Bird Hollow	Crawford	38.36	86.77	•	•
3	Bluelick Creek	BLCR	Ohio River	Bluelick Creek	Bullitt	38.03	85.69	•	
4	Bogard Creek	BOCR	Little Blue River	Bogard Creek	Crawford	38.29	86.43	•	•
5	Brushy Creek	BRC	Little Blue	Brushy	Crawford	38.31	86.44	•	•
6	Brooks Run	BRRU	Ohio River	Brooks Run	Bullitt	38.05	85.69	•	
7	Brownstown	BTCR	Little Blue River	Brownstown	Crawford	38.35	86.48	•	•
8	Buck Creek	BUCR	Buck Creek	Buck Creek	Harrison	38.14	86.04	•	•
9	Camp Fork Creek	CAFO	Little Blue River	Camp Fork	Crawford	38.34	86.41	•	•
10	Cain Run	CARU	Ohio River	Cain Run	Jefferson	38.07	85.87	•	
11	Cedar Creek #1	CEC1	Salt River	Cedar Creek	Bullitt	38.06	85.65	•	
12	Cedar Creek #2	CEC2	Salt River	Cedar Creek	Bullitt	38.42	85.45	•	•
13	Corn Creek	COCR	Indian River	Corn Creek	Harrison	38.33	86.04		•
14	Crandall Branch	CRBR	Indian River	Crandall	Harrison	38.29	86.07	•	•
15	Crooked Creek	CRCR	Salt River	Crooked	Bullitt	37.89	85.72	•	•
16	Dog Creek	DOCR	Little Blue River	Dog Creek	Crawford	38.36	86.45	•	•
17	Goose Creek	GOCR	Ohio River	Goose Creek	Jefferson	38.3	85.62	•	•
18	Hardy Creek	HRCR	Ohio River	Hardy Creek	Trimble	38.61	85.27		•
19	Harrison Fork	HAFO	Ohio River	Harrison Fork	Nelson	37.87	85.6		•
20	Harts Run	HAR	Salt River	Harts Run	Bullitt	37.86	85.61	•	•
21	Hite Creek	HTCR	Ohio River	Hite Creek					•
22	Jersey Park Creek	JPCR	Indian River	Jersey Park	Floyd	38.37	85.96	•	•
23	Knob Creek	KNC	Ohio River	Knob Creek	Bullitt	38.04	85.79	•	•
24	Little Indian Creek	LIIN	Indian River	Little Indian	Floyd	38.31	85.91	•	
25	Long Lick Creek	LLCR	Salt River	Long Lick	Bullitt	37.93	85.71	•	•
26	Lower Wilson	WICR	Salt River	Lower Wilson	Nelson	37.87	85.61	•	•
27	Lickskilllet Creek	LSCR	Salt River	Lickskilllet	Bullitt	37.93	85.65	•	•
28	MB Harrods	HACR	Ohio River	MB Harrods	Oldham	38.45	85.42		•
29	MF Beargrass	MFBG	Ohio River	MF Beargrass	Jefferson	38.24	85.7	•	•
30	MF Blue River	MFBL	Blue River	MF Blue River	Washington	38.59	85.98		•
31	MF Buck Creek	MFBU	Buck Creek	MF Buck	Harrison	38.14	86.04	•	•
32	MF Indian Creek	MFIN	Indian River	MF Indian	Floyd	38.36	85.96		•
33	NF Harrods Creek	NFHA	Ohio River	NF Harrods	Oldham	38.42	85.45		•
34	Otter Creek	OTCR	Little Blue River	Otter Creek	Crawford	38.3	86.53	•	•
35	Overalls Creek	OVC	Salt River	Overalls	Bullitt	37.87	85.6	•	•
36	Pryors Fork	PRFO	Ohio River	Pryors Fork	Trimble	38.06	85.41		•
37	Racoon Branch	RABR	Indian River	Racoon	Harrison	38.28	86.1	•	•
38	Richland Creek	RICR	Indian River	Richland	Floyd	38.32	86.01	•	•
39	SF Blue River	SFBR	Blue River	SF Blue River	Washington	38.53	85.92		•
40	Stinking Fork	STFO	Little Blue River	Stinking Fork	Crawford	38.23	85.53	•	•
41	Turkey Fork	TUFO	Little Blue River	Turkey Fork	Crawford	38.2	86.4	•	•
42	Upper Wilson	UWIL	Salt River	Upper Wilson	Nelson	37.87	85.6		•
43	Whiskey Run	WHR	Ohio River	Whiskey Run	Washington	38.52	85.92		•
44	Yellow Fork	YEF	Indian River	Yellow Fork	Floyd	38.35	85.91		•

Benthic algae were sampled during 1 of the 8 weeks of sampling, which was timed so that algae had greater than 7 days to recover after the last storm event.



Benthic algae were removed from five 3-rock clusters in riffles with a spoon and toothbrush placed into a container and split for chlorophyll *a* and enumeration. Subsamples for chlorophyll *a* were stored on ice until returning to the lab, where they were frozen until processing. Algal samples (n=69) for enumeration were preserved with M3 in the field [21]. Rock surfaces from which benthic algae were scraped were measured in the field.

2.1 Laboratory assays

Water samples were analyzed for chloride, nitrate (NO_3), and ammonium (NH_4) using a Skalar[®] auto-analyzer. Soluble reactive phosphorus (SRP) was measured using a Hitachi[®] U-2001 spectrophotometer. Alkalinity (ALK) was assessed according to standard methods APHA [21]. Silica was determined with ascorbic acid method on a Skalar[®] auto-analyzer [21]. To determine total phosphorus (TP) and total nitrogen (TN) concentrations, particulate matter in water samples was oxidized with persulfate and analyzed for SRP and NO_3 . Chlorophyll *a* was measured as measured spectrophotometrically after extraction from the periphyton samples with 90% buffered acetone [21].

Algal subsamples were analyzed for diatom species composition. Permanent diatom slides were prepared by acid-cleaning to increase the clarity of observing diatoms and mounting in Naphrax resin (RI 1.74, Northern Biological Supplies L., Ipswich, UK). A minimum of 600 diatom valves were identified and counted in each slide. Correct taxonomic identification in the dataset was ensured following a QAQC protocol. A second analyst independently counted samples from the reference streams and four random streams in each year. Proportional relative abundances of diatom taxa in each sample were determined.

Diatoms from reference streams are species that occurred naturally in Kentucky (or not introduced). In the reference sites, human disturbance is considered negligible [20], so diatoms from those sites were defined as reference taxa. Those species are the species that occur in many water bodies, fossil records and habitats. Extensive counts were performed to account for as many rare taxa as possible in the four reference streams. After the original 600 count and the QAQC count, a third count continued until at least five taxa were enumerated with 100 valves (which in diverse sites reached a count of >2500 valves). This protocol ensured accounting for all dominant taxa (more than 5% relative abundance in each count), allowed observation of more taxa in the count and was independent of a predetermined number count.

2.2 Data analyses

The relationship between species abundance and distribution was tested with regression analysis. Following the terminology of the core-satellite hypothesis [5], a core species was a common diatom that appeared in more than 90% of the sites, while a satellite species appeared in less than 10% of the sites. Species in the middle (found in more than 10 % and less than 90% of the sites) were called intermediate, but those intermediate taxa had the potential to become part of the later categories. We varied those categories increasing the sites for



core species up 4 folds (more than 80%, 70% core and 60% core) and followed characteristics of the newly classified number of species in each category. Based on the number of species in each category, different distribution patterns are discriminated (skewed to the left or right, unimodal, or bimodal). All categories can vary in abundance.

The physico-chemical differences between reference and non-reference sites were tested with a Mann-Whitney nonparametric test. Average species similarity (aveS) within reference and non-reference sites or dissimilarity (ave δ) between the two groups of sites was evaluated with SIMPER procedure (Primer-E Ltd. [22]). This allowed examining the contribution of each diatom species to either similarity within or dissimilarity between reference and non-reference sites. Standard deviation of the means were estimated for S and δ , respectively SD(S) and SD(δ). For both measures, how consistently a diatom species contributes to either aveS or ave δ was measured with the ratios aveS/SD(S) and ave δ /SD(δ) respectively. When SD(S) and SD(δ) were small the ratios were large and the respective diatom species not only contributed much for the similarity or dissimilarity, but was also consistent in doing so. Diatom species with high discriminating ratios (either aveS /SD(S) or ave δ /SD(δ)) were called discriminating species [23] and are reported. Statistical analyses were performed with SYSTAT[®] version 10 [24] unless stated otherwise.

3 Results

3.1 Species abundance-distribution relationship

A positive relationship was observed between diatom species abundance and distribution in the survey, more abundant species occupied a larger percent of the sites than less abundant species (regression analysis: $R^2 = 0.68$, $p < 0.01$; Fig. 2a). A total of 189 diatom species were recorded. Three taxa were observed in more than 90 % of the sites sampled. *Achnantheidium minutissimum* was observed at all sites and had the highest mean relative abundance in the survey (20.8%). The other two core species in this study, *Nitzschia dissipata* and *Gomphonema angustatum*, had 6.5 and 15.5% mean relative abundances, respectively. Sixty-nine percent of the observed taxa were defined as rare because they appeared in less than one percent of sites. All rare taxa had mean relative abundances less than 4.2% (Fig. 2b).

The observed positive relationship between abundance and distribution was not due to sampling error or aggregation. The coefficient of variation was negatively related to species distributions (Table 2). Regression analysis: Model: $R^2 = 0.98$, $F_{2, 188} = 5095.22$, $p < 0.0001$. Diatoms with high abundance were found in more sites and had smaller coefficient of variation. The analysis showed that the parameters differed from zero.



Table 2: Test of the influence of sampling on the abundance-distribution relationship for Kentucky stream diatoms. Species-specific coefficient of variation (CV) and average abundance (\bar{x}_{all}) were calculated across all sites. SE- standard error, p – significance level.

Variable	Estimate	SE	p
Intercept	0.04	0.09	0.66
$\ln(\ln(\bar{x}_{all}))$	0.99	0.03	<0.0001
$-2*\ln(CV)$	1.99	0.03	<0.0001

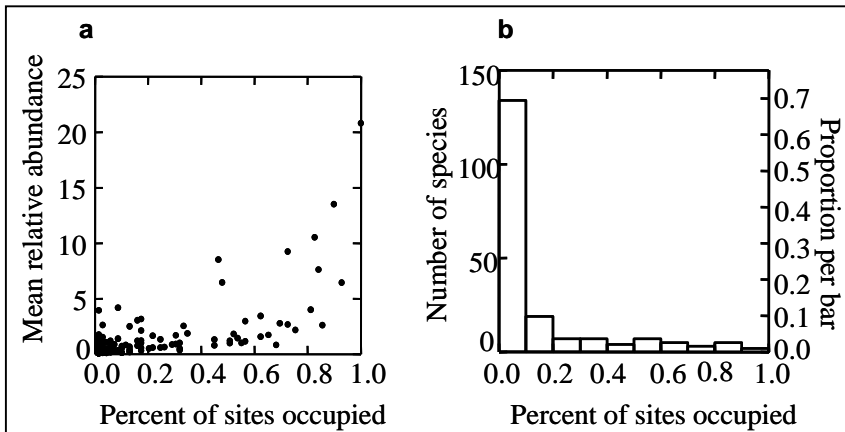


Figure 2: Relationship between diatom species abundance and distribution (as percent of sites occupied) in the survey for all samples ($n=69$); a. A scatter plot of mean relative abundance for the sites occupied; b. A histogram number of species and percent sites occupied (second y axes represents the proportion of taxa in the bars) against their distribution.

3.2 Relation of core-satellite species to ecological conditions

Temperature, canopy cover (measure of light) and pH were not different between the reference and non-reference streams. Silica was higher in the reference streams. All other physico-chemical variables in the reference sites were significantly lower compared to sites with human influence (Table 3). Multiple regression analysis: Model $R^2=0.43$, $F_{2, 188}=71.93$, $p<0.0001$. Conductivity and chloride were 1.5 times higher in the non-reference sites compared to the reference sites. Nutrients were several orders of magnitude higher also.

In reference streams taxa observed (richness) in counts varied from 15 to 26 taxa (mean evenness 0.55 ± 0.03 SE, range 0.41 to 0.66), while in sites with human influence there were 14 to 45 diatom taxa were observed (mean evenness 0.67 ± 0.01 SE range 0.36 to 0.82). Diatom species membership at reference sites was less diverse than at all sites.

Table 3: Physicochemical measurements in reference and non-reference sites. Mann-Whitney test, p = significance level.

Variables	Reference sites				Non-reference sites				p
	mean	±SE	min	max	mean	±SE	min	max	
air temperature °C	15.9	2.1	6	32	15.8	0.7	3	36	n.s
water temperature °C	13.6	1	6.8	19.7	14.3	0.5	5	25.9	n.s
canopy cover (%)	24.36	3.69	0	87	29.02	1.3	0	88	n.s.
conductivity (µS cm ⁻¹)	220	17.9	107	322	345	16	105.2	804	<0.001
alkalinity (mg L ⁻¹)	75.3	7.6	51	120	113.5	6.3	12	208	0.02
pH	8	0	8	8	8.1	0	7	9	n.s
Chloride (meq L ⁻¹)	2.5	1	0.8	7.1	7.3	0.7	1.6	21.3	0.01
NO ₃ (µg L ⁻¹)	204.7	67.9	27.8	789.6	957.0	123.9	19.2	6645.2	0.01
NH ₄ (µg L ⁻¹)	12.7	2.4	2.1	32.6	23.9	3.5	3.8	263.0	<0.001
TN (µg L ⁻¹)	308.1	75.5	2.6	876.0	1131.8	131.0	38.0	7358.0	0.04
SRP µg L ⁻¹	6.6	1.4	1.0	20.6	31.6	11.7	0.0	940.9	<0.001
TP (µg L ⁻¹)	9.3	1.9	2.6	27.1	51.1	16.7	2.3	1379.9	0.01
SI (mg L ⁻¹)	8.9	0.8	5.0	12.0	6.5	0.3	1.0	17.0	0.01
NP (molar ratio)	86.3	24.5	0.5	298.0	107.0	18.2	4.6	688.0	n.s

In reference and non-reference sites, *Cymbella affinis* occurred in 80% of the samples, but had mean relative abundance of 14.9% and 8.8% respectively (Tables 4 and 5). *Achnanthyidium deflexum* appeared in 82% of non-reference and 88% of reference sites. *Achnanthyidium deflexum* and *Achnanthyidium minutissimum* were the most abundant taxa in reference streams. Only *A. minutissimum* and *Cymbella* sp. *K* appeared in all reference samples, but differed in mean relative abundance 38% to 2.8% respectively.

The observed differences in species richness between reference and non-reference sites contributed to 68% dissimilarity between the two groups. Twenty-seven taxa (15% of all identified) contributed for 90% of the dissimilarity, with 50% of it contributed by four taxa (Table 4). The highest discriminating species in the between sites dissimilarity was *Cymbella affinis* (ratio 8.67). Additional dissimilarity was contributed by *Gomphonema angustatum*, *Achnanthyidium minutissimum* and *A. deflexum*. All four discriminating taxa appeared in both reference and non-reference taxa.

Within non-reference streams, average similarity among sites was lower, 31% (Table 5a). Thirteen taxa accounted for 90% of the accounted similarity. *Achnanthyidium minutissimum* accounted only 30.6% of similarity among the non-reference sites. Three discriminating species in non-reference sites had high similarities and low standard deviations: *A. minutissimum*, *G. angustatum* and *Cymbella affinis* (discriminating ratios 9.15, 6.75 and 5.60 respectively, Table 5a). Average similarity among reference streams was 48%. Four taxa contributed to 90% of the similarity, with over 60% contributed by *A. minutissimum* alone (Table 5b). *Achnanthyidium minutissimum* and *Gomphonema angustatum* were the two discriminating species in reference sites, because of their high similarity and low standard deviation measures (discriminating ratios 16.44 and 8.38 respectively, Table 5b). Low nutrient taxa decreased only 13 % with 4 fold increase of the core sites, while the satellite species were predominantly high nutrient taxa (Figure 3).



Table 4: Diatom species average dissimilarity (ave δ) between non-reference and reference sites, contribution from each species; species are ordered in decreasing contribution with 90% cumulative contribution (Cum%) as a cut-off percentage; meanRAnr- mean relative abundance in non-reference sites, compare with mean RA in reference sites Appendix B; (SD) δ – standard deviation of the δ (*ith* species) values; ave δ /SD(δ) - discriminating ratio, highest in bold; $\sum(\text{ave}\delta)\%$ - average percent contribution to similarity by the (*ith* species).

Taxon	meanRAnr	ave δ	ave δ (SD)	δ /SDSD	$\sum \text{ave } \delta\%$	Cum%
<i>Achnantheidium minutissimum</i>	18.6	12.67	1.79	7.08	18.7	18.7
<i>Gomphonema angustatum</i>	11.6	8.42	1.08	7.80	12.5	31.2
<i>Cymbella affinis</i>	8.8	6.85	0.79	8.67	10.1	41.3
<i>Achnantheidium deflexum</i>	5.9	5.97	1.36	4.39	8.8	50.1
<i>Gomphonema olivaceum</i>	7	3.27	0.75	4.36	4.8	54.9
<i>Nitzschia dissipata</i>	6.6	3.04	0.93	3.27	4.5	59.5
<i>Nitzschia inconspicua</i>	4.5	2.25	0.41	5.49	3.3	62.8
<i>Rhoicosphenia abbreviata</i>	6.5	1.75	0.47	3.72	2.6	65.4
<i>Navicula veneta</i>	3.5	1.75	0.67	2.61	2.6	68
<i>Cymbella</i> sp. K	1.8	1.57	1	1.57	2.3	70.3
<i>Synedra rumpens</i>	0.1	1.41	0.59	2.39	2.1	72.4
<i>Navicula cryptotenella</i>	3.5	1.22	0.6	2.03	1.8	74.2
<i>Navicula minima</i>	2.5	1.17	0.52	2.25	1.7	75.9
<i>Amphora pediculus</i>	2.8	1.13	0.53	2.13	1.7	77.6
<i>Navicula gregaria</i>	1.9	0.95	0.25	3.80	1.4	79
<i>Encyonema silesiacum</i>	0.6	0.94	1	0.94	1.4	80.4
<i>Surirella minuta</i>	1.8	0.92	0.66	1.39	1.4	81.8
<i>Achnanthes ventralis</i>	0.2	0.86	0.56	1.54	1.3	83
<i>Cymbella delicatula</i>	0.2	0.77	0.92	0.84	1.1	84.2
<i>Gomphonema minutum</i>	1	0.69	0.48	1.44	1	85.2
<i>Meridion circulare</i>	0.4	0.68	0.84	0.81	1	86.2
<i>Diatoma vulgare</i>	1.8	0.64	0.45	1.42	1	87.1
<i>Reimeria sinuata</i>	1	0.52	0.73	0.71	0.8	87.9
<i>Nitzschia frustulum</i>	1	0.49	0.31	1.58	0.7	88.6
<i>Fragilaria vaucheriae</i>	0.3	0.48	0.47	1.02	0.7	89.3
<i>Synedra ulna</i>	0.7	0.45	0.51	0.88	0.7	89.9
<i>Nitzschia sociabilis</i>	1.2	0.37	0.64	0.58	0.6	90.6

4 Discussion

In this study a positive abundance-distribution relationship was observed for benthic diatoms. The observed patterns were due to the species-specific abundance and distribution relationship of relatively small number of diatom species. *Achnantheidium minutissimum* had highest mean relative abundance in



Table 5: Diatom species average similarity (aveS) contributed from each species for: a. non-reference sites, and b. reference sites; species are ordered in decreasing contribution with 90% cumulative contribution (Cum%) as a cut-off percentage; (SD)S – standard deviation of the S (ith species) values; aveS/SD(S) – discriminating ratio, highest in bold; $\sum(\text{aveS})\%$ – average percent contribution to similarity by the (ith species).

Taxon	aveS	SD(S)	aveS/SD(S)	$\sum \text{aveS}\%$	Cum%
a.					
Achnantheidium minutissimum	10.43	1.14	9.15	30.62	30.6
Gomphonema angustatum	4.86	0.72	6.75	14.28	44.9
Nitzschia dissipata	3.21	0.93	3.45	9.44	54.3
Cymbella affinis	2.91	0.52	5.60	8.55	62.9
Gomphonema olivaceum	2.57	0.68	3.78	7.53	70.4
Achnantheidium deflexum	1.79	0.49	3.65	5.26	75.7
Navicula veneta	1.14	0.6	1.90	3.36	79.1
Navicula cryptotenella	0.71	0.52	1.37	2.09	81.1
Navicula minima	0.66	0.49	1.35	1.92	83.1
Cymbella sp. K	0.62	0.54	1.15	1.81	84.9
Surirella minuta	0.59	0.62	0.95	1.74	86.6
Nitzschia inconspicua	0.59	0.22	2.68	1.73	88.3
Amphora pediculus	0.59	0.46	1.28	1.73	90.1
b.					
Achnantheidium minutissimum	29.26	1.78	16.44	61.5	61.5
Achnantheidium deflexum	6.86	0.9	7.62	14.4	75.9
Gomphonema angustatum	6.03	0.72	8.38	12.7	88.6
Cymbella sp. K	0.82	0.48	1.71	1.7	90.3

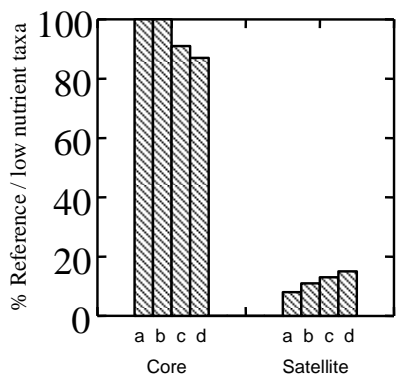


Figure 3: Distribution of species membership low nutrient (reference) requirements in different site number designations of core (C) and satellite species (S): a. C>90%, S<10%; b. C>80%, S<20%; c. C>70%, S<30%; and d. C>60%, S<40%.



the survey and was found at all sites. Core species comprised only 2% of the diatom community, while the majority of diatoms were satellite species. The large number of rare taxa observed did not change the positive correlation between abundance and distribution.

Diatom communities from reference streams had low diversity and high similarity. Reference and non-reference diatom communities were highly dissimilar. A relatively small number of diatom taxa contributed to the observed dissimilarity. Diatoms observed in the reference sites were observed in many non-reference sites, but in significantly lower abundance. All non-reference diatoms were in lower abundance regardless of the number of sites they appeared.

With an increase in nutrients, eutrophic species grow faster when compared with diatom species from the reference community. The robustness of the pattern was confirmed with the experimental results. In the abundant literature addressing the abundance-distribution relationships, only one relates to algae. Lewis [25] found an asymmetric relationship for phytoplankton, which was skewed to the right with most taxa in a few sites. That distribution was independent of mean abundance and resource supply. The relationship was specific for green algae, bluegreen algae, and diatoms and varied with grazer conditions. In the present study we found a strong positive relationship between abundance and distribution, common taxa were most abundant and had wider distribution.

Biologically the appearance of *Achnanthes minutissimum* at all sites and with high mean relative abundance can be explained with the relatively fast growth of this diatom and high tolerance for low nutrient concentrations. Tradeoff theory suggests that there should be optimal conditions, so if *A. minutissimum* was at optimal growth in the reference sites, different taxa should have high abundance at the non-reference sites. The mean abundance of *A. minutissimum* in the reference sites was significantly higher compared to all sites.

The observed pattern did not follow the core-satellite hypothesis [5], which predicts a bimodal abundance-distribution pattern. This pattern has been observed in different organisms and along multiple gradients [26, 27], but it was not evident for benthic diatoms. Diatoms with high abundance were found in more sites and had a smaller coefficient of variation. Thus, the predictions of ecological specialization were not supported [28]. Sample collection, sampling area, and the number of samples were appropriate to study the abundance-distribution relationship [27]. However, the degree of environmental heterogeneity was minimized by sampling only riffles, rocks, and streams within an ecoregion.

Diatom species with high mean relative abundance had the widest distribution. Species were expected to be most abundant in relatively few habitats in a region if species specialized with optimal performance in specific environmental conditions. Contrary to this prediction, a positive correlation was observed between diatom abundance and breadth of their distribution in the Knobs ecoregion of Kentucky and southern Indiana. A positive relationship



between relative abundance and distribution was observed. Few taxa were abundant and they had broad distributions, the majority (79%) of the observed diatom species had low abundance and appeared in few sites (less than 10% of sites).

Acknowledgements

We would like to thank Drs S. T. Rier (Bloomsburg University) and C. M. Riseng (University of Michigan) for collecting the samples as part of the STAR-EPA grant to RJS and Carrie DeJaco (Queens University of Charlotte) for initial sample identification. The manuscript benefited from the critical reviews of Drs D. Hall, G. Mittelbach and T. Burton (Michigan State University). This research was done and presented as partial fulfillment of the dissertation research of KMM at Michigan State University.

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