Thresholds in macroinvertebrate biodiversity and stoichiometry across water-quality gradients in Central Plains (USA) streams

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Abstract. N and P often limit primary and secondary production in ecosystems, but they also can cause eutrophication and negatively influence sensitive species above a certain level or threshold point. Aquatic biodiversity can have negative threshold relationships with water-quality variables at large scales, but the specific mechanism(s) driving these threshold relationships are not well established. We hypothesized that resource quality (i.e., C:P) might partly drive primary consumer (grazer and detritivore) richness thresholds by altering competitive interactions among species with differing resource demands, but might have less influence on predator richness. We estimated total N (TN), total P (TP), and turbidity thresholds for macroinvertebrate richness across trophic levels and feeding groups in Central Plains (USA) streams. We also determined if mean taxon body C:P of groups with diversity losses were negatively related to TP, a pattern that would suggest that eutrophic communities were dominated by a few species with high dietary P demands. Primary consumers were more sensitive to TN and TP (threshold mean = 1.0 mg N/L and 0.06 mg P/L) than secondary consumers (threshold mean = 0.09 mg P/L), a result supporting the resource quality hypothesis. Turbidity reduced richness regardless of feeding mode (threshold mean = 4.7 NTU), a result suggesting that turbidity and nutrient thresholds were driven by different factors. The TP-richness threshold could be driven partially by changes in food quality because the mean body C:P of shredding and collector-gathering taxa declined as TP increased (threshold mean = 0.07 and 0.75 mg P/L, respectively). Mean scraper C:P was not related to TP, a result indicating other factors might be responsible for the scraper richness threshold. Our results suggest that changes in resource quality could contribute to large-scale losses in biodiversity in nutrient-enriched lotic ecosystems. Within shredder and collector-gatherer macroinvertebrate feeding groups, P-rich food might allow faster growing taxa with high body P demands to out-compete slower growing taxa adapted to lower quality food resources. This pattern suggests that biotic integrity is directly linked to nutrients in streams and that toxicity, low dissolved O_2, and increased turbidity might not be the only mechanisms leading to reductions in diversity as nutrient concentrations increase.

Key words: breakpoints, nutrient criteria, species richness, bioassessment, eutrophication, water quality.

Increased nutrients are the leading cause of impairment in many freshwater aquatic ecosystems (USEPA 1998, Dodds and Welch 2000), and effects of nutrient enrichment on aquatic species composition are of particular interest to environmental managers and ecologists concerned with maintaining biotic integrity and diversity. Recent regional-scale studies examining freshwater biotic community structure across nutrient gradients have reported threshold or wedge-shaped patterns in biotic diversity and index metrics (King and Richardson 2003, Wang et al. 2007, Weigel and Robertson 2007). Specifically, the total number of species and the proportion of sensitive species can decrease rapidly above a certain threshold nutrient concentration.

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Reduced biodiversity in streams with high nutrient levels is commonly thought to be caused by direct nutrient toxicity (i.e., primarily NO_3^- or NH_3 toxicity; Camargo and Alonso 2006) or indirect nutrient toxicity via increases in primary production and reduced dissolved O_2 (Dodds and Welch 2000). In addition, suspended sediments, which can be positively associated with nutrients, can settle on the stream bottom and coat the respiratory organs or gills of sensitive biota (Lemly 1982). Increases in stream temperature associated with removal of riparian trees in impacted systems also can cause respiratory stress (Sweeney 1978) and alter growth and development (Hogg and Williams 1996). All of these mechanisms can play a role in reducing macroinvertebrate diversity in nutrient-enriched streams. However, recent experimental evidence suggests that changes in food quality associated with stream nutrient enrichment also might cause shifts in community structure and decrease diversity (Gafner and Robinson 2007, Singer and Battin 2007). We propose that this resource quality mechanism might play a part in observed regional nutrient-threshold patterns, particularly at lower levels of nutrient enrichment.

Significant nutrient imbalances occur between stream primary consumers and their algal and detrital food resources (Cross et al. 2003, Evans-White et al. 2005) and can cause nutrient limitation of growth and production (Stelzer and Lamberti 2002, Cross et al. 2006). Primary consumers with a high nutrient demand (low body C:N or C:P) are more likely to be limited by low-quality food than primary consumers with a lower nutrient demand (Sterner and Elser 2002). Nutrient enrichment of stream autotrophic (Kahlert 1998, Stelzer and Lamberti 2001) and detrital (Meyer and Johnson 1983, Suberkropp and Arsuffi 1984, Stelzer et al. 2003) food resources occur as dissolved nutrient concentrations increase. Food resource enrichment might release species with high nutrient demands from growth constraints and give them a competitive advantage over species with lower nutrient demands. Recent experimental whole-stream dissolved nutrient and food resource (e.g., seston, algae, or detritus) enrichment studies have demonstrated shifts in benthic macroinvertebrate communities toward lower diversity (Gafner and Robinson 2007, Singer and Battin 2007) and toward primary consumer species with higher growth rates and P demands (Cross et al. 2006, Singer and Battin 2007). However, to our knowledge, no studies have examined whether nutrient enrichment of food resources might partly drive patterns of macroinvertebrate community structure on a regional scale across a eutrophication gradient.

Aquatic shredding detritivores might be more sensitive than other feeding groups to the resource quality mechanism because nutrient imbalances between detritivores and detritus are larger than those between other consumers and food resources (Cross et al. 2003, Evans-White et al. 2005). Shredders can have a higher body C:P and a lower P demand than collector and predator feeding groups (Cross et al. 2003, Frost et al. 2006). Body P content is positively linked to organismal growth rates (Elser et al. 2000, 2003), and the trade-off for exploiting these low-quality food resources efficiently might be slower growth (Cross et al. 2003, Frost et al. 2006). Experimental evidence has indicated that growth of low C:P shredding taxa is more likely than growth of high C:P taxa to respond positively to nutrient enrichment (Cross et al. 2006). Therefore, faster-growing species with low body C:P might out-compete slower-growing species with high body C:P across a eutrophication gradient.

Our objective was to determine if benthic macroinvertebrate richness declined in a threshold manner with increasing nutrient and turbidity concentrations in Central Plains streams. In addition, we examined whether evidence for the food resource quality mechanism existed at regional scales. Nutrient imbalances are greater between primary consumers and their food resources than between predators and primary consumers (Sterner and Elser 2002). Therefore, we expected that nutrient thresholds would be confined to primary consumers if the resource mechanism was important. In addition, we expected that primary consumer species with low body C:P would become dominant as P concentrations in streams increased. We also expected that this relationship would be particularly strong for feeding groups depending upon detritus. Last, we expected that turbidity, a surrogate measure of suspended sediments, should negatively affect macroinvertebrate species across all feeding modes and trophic levels.

Methods

Our Central Plains study region included streams in 13 level III ecoregions (Omernik 1995) in Kansas, Nebraska, and Missouri (i.e., Environmental Protection Agency [EPA] Region VII; Fig. 1A, B). Stream watershed size varied from 136 to 8.16×10^6 ha. Benthic macroinvertebrates were collected from March to November by several agencies over many years (Table 1). Median values of water-chemistry data (total N [TN], total P [TP], and turbidity) collected within 30 d and 2 km of a benthic macroinvertebrate sample were linked to that individual macroinvertebrate sample unless a point

A

ECO_NAME

☐	Central Great Plains
▨	Central Irregular Plains
▨	Central Oklahoma/Texas Plains
▨	Driftless Area
▨	Flint Hills
▨	Interior River Valleys and Hills
▨	Mississippi Alluvial Plain
▨	Nebraska Sand Hills
▨	Northwestern Glaciated Plains
■	Northwestern Great Plains
▨	Ozark Highlands
▨	Southwestern Tablelands
▨	Western Corn Belt Plains
▨	Western High Plains

B
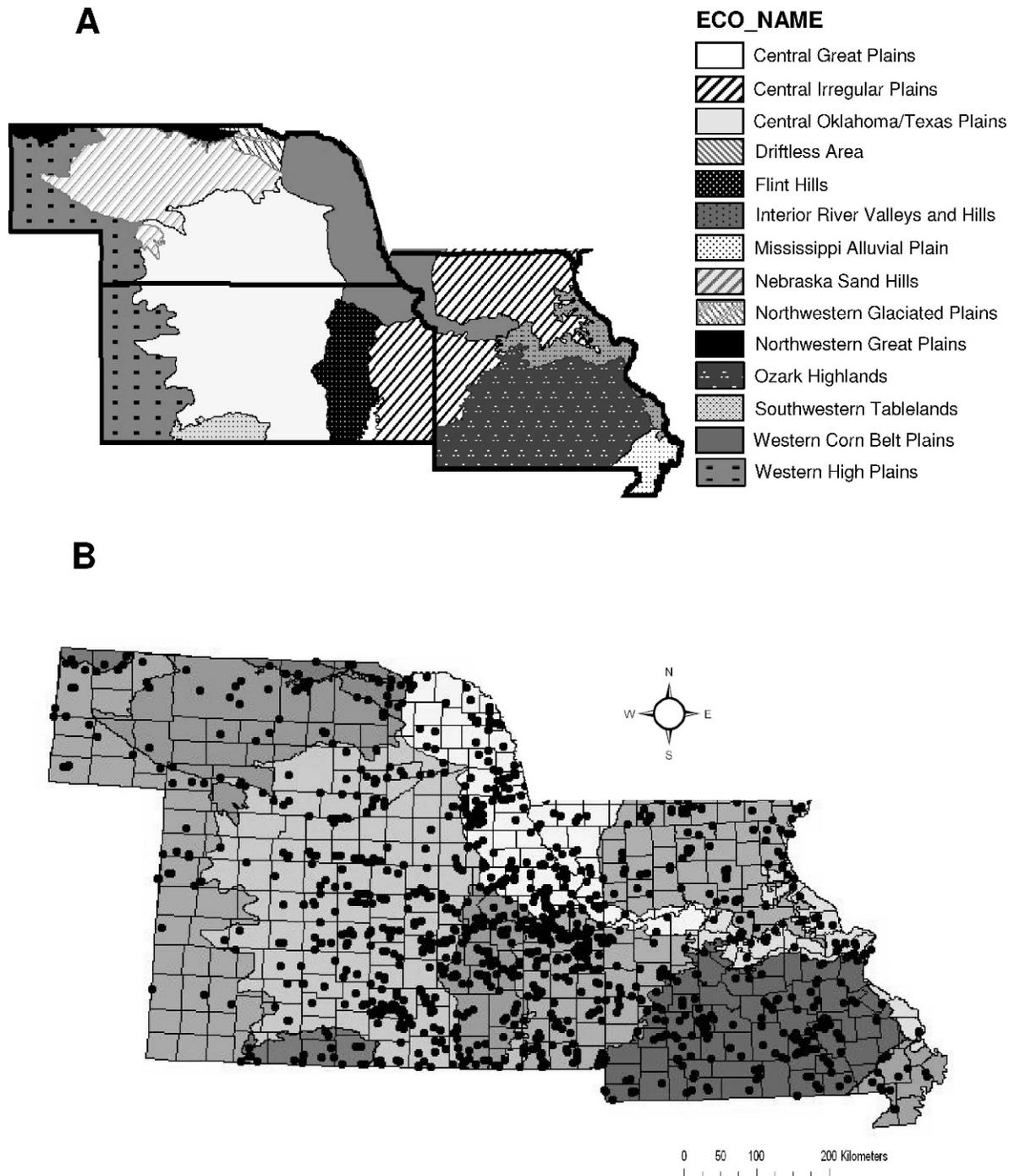
FIG. 1. A.—Level III ecoregions (ECO_NAME) in the Central Plains (USA) study region. The ECO_NAME legend fills are for panel A only. B.—Stream water-chemistry and biota sampling locations included in our study.

source (power plant, etc.) bisected the reach between the water and the macroinvertebrate sampling sites. Coupling 1 macroinvertebrate sample with aggregated, instead of synoptic, water-chemistry data enabled us to at least double the sample size of the database.

Water-chemistry data were obtained from various state agencies that had US EPA certified laboratories with established internal quality-assurance procedures. Water-column TN was measured with a persulfate or a Kjeldahl digest. TP was measured primarily with a persulfate digest. Medians of TN, TP,

TABLE 1. Number of sites, number of sampling events, years, and months each agency sampled.

Agency	No. sites	No. sampling events	Years	Months
Central Plains Center for BioAssessment	87	87	2001	July
Kansas Wildlife and Parks	76	95	1994–2002	June–September
Kansas Department of Health and Environment	54	198	1990–2003	April–November
Missouri Department of Environmental Quality	43	77	1997–2001	March, September, October
Nebraska Department of Environmental Quality	23	26	1993–2001	August–October
Total	283	483		

and turbidity were calculated from the total population of all samples, pooled across all years of record, and all replicates taken for each site in the database (1 median data point/stream site) were used to examine patterns across sites. This method reduced the chance that data from sites that had been resampled often might skew the results. Median TN:TP (by mass) was calculated as the median value of all calculated TN:TP values for a particular stream site. Turbidity is highly correlated with total suspended solids, which are composed primarily of inorganic particles in this region (Dodds and Whiles 2004). Therefore, turbidity was used as a proxy for suspended sediments in our analysis. Across the Central Plains stream sites, TN ranged from 0.04 to 32.80 mg/L, TP ranged from 0.005 to 8.7 mg/L, TN:TP (by mass) ranged from <1 to 6021, and turbidity ranged from 0.3 to 718 nephelometric turbidity units (NTU) (Fig. 2A–D).

More than 75% of benthic macroinvertebrates were sampled from 4 level III ecoregions: Central Great Plains (CGP), Central Irregular Plains (CIP), Flint Hills (FH), and Ozark Highlands (OH). Most agencies collected timed samples with a 500-μm D-net in dominant habitat types. Nebraska Department of Environmental Quality (NDEQ) also used Hess, Hester–Dendy, and Surber samplers to sample macroinvertebrates in several habitat types (i.e., multiple habitat, pool, riffle, glide/pool, riffle/pool, and overhanging vegetation). NDEQ sample richness estimates were comparable to those estimated by other agencies in the same ecoregions (i.e., Kansas Department of Health and Environment and Kansas Department of Wildlife and Parks) even though they used different sampling methods. Most macroinvertebrate taxa were identified to genus and species, excluding those in the families Tubificidae, Turbellaria, Naididae, and Enchytraeidae.

A variety of richness metrics were reported (Table 2). Total macroinvertebrate richness (MTAXA), which represents a count of all taxa found at a site on a date, was calculated for our study. Each macroin-

vertebrate taxon was assigned 1 of the following functional feeding traits: collector-gatherer, collector-filterer, scraper, shredder, predator, parasite, or piercer (Barbour et al. 1999). Primary consumers included individuals with a collector-gatherer, collector-filterer, scraper, or shredder functional feeding designation. Secondary consumers included individuals with a predator, parasite, or piercer feeding designation. All taxa within the secondary consumer group feed primarily on food resources with a high nutrient content (other animals).

Macroinvertebrate molar body C:P data were compiled from other published studies (Frost et al. 2003, Cross et al. 2003, Evans-White et al. 2005, Singer and Battin 2007; Appendix; available online from: http://dx.doi.org/10.1899/08-113.1.s1). Macroinvertebrate body C:P can vary within species and can be sensitive to food resource content for some taxa, but distinct differences among taxa remain (Cross et al. 2003). Literature values have been used previously to examine taxonomic variation in C:P and to calculate threshold elemental ratios (Frost et al. 2006). Each species from the literature was sorted based on family and functional feeding group. Mean body C:P was calculated for each unique family and functional feeding group across studies, and the same literature-based mean value was assigned to all macroinvertebrate taxa within a unique family and functional feeding group. One mean C:P value was used for all taxa within a family that had a scraper, collector-filterer, and collector-gatherer classification because no data have been reported to indicate that macroinvertebrate body C:P differs among these functional feeding groups (Cross et al. 2003, Frost et al. 2006). For chironomids, primary consumer taxa were assigned a nontanypodinae C:P value and predators were assigned a tanypodinae C:P value. Authors of 2 studies reporting macroinvertebrate C:P (Cross et al. 2003, Singer and Battin 2007) had experimentally elevated the nutrient content of food resources. Therefore, macroinvertebrate C:P in the elevated and the
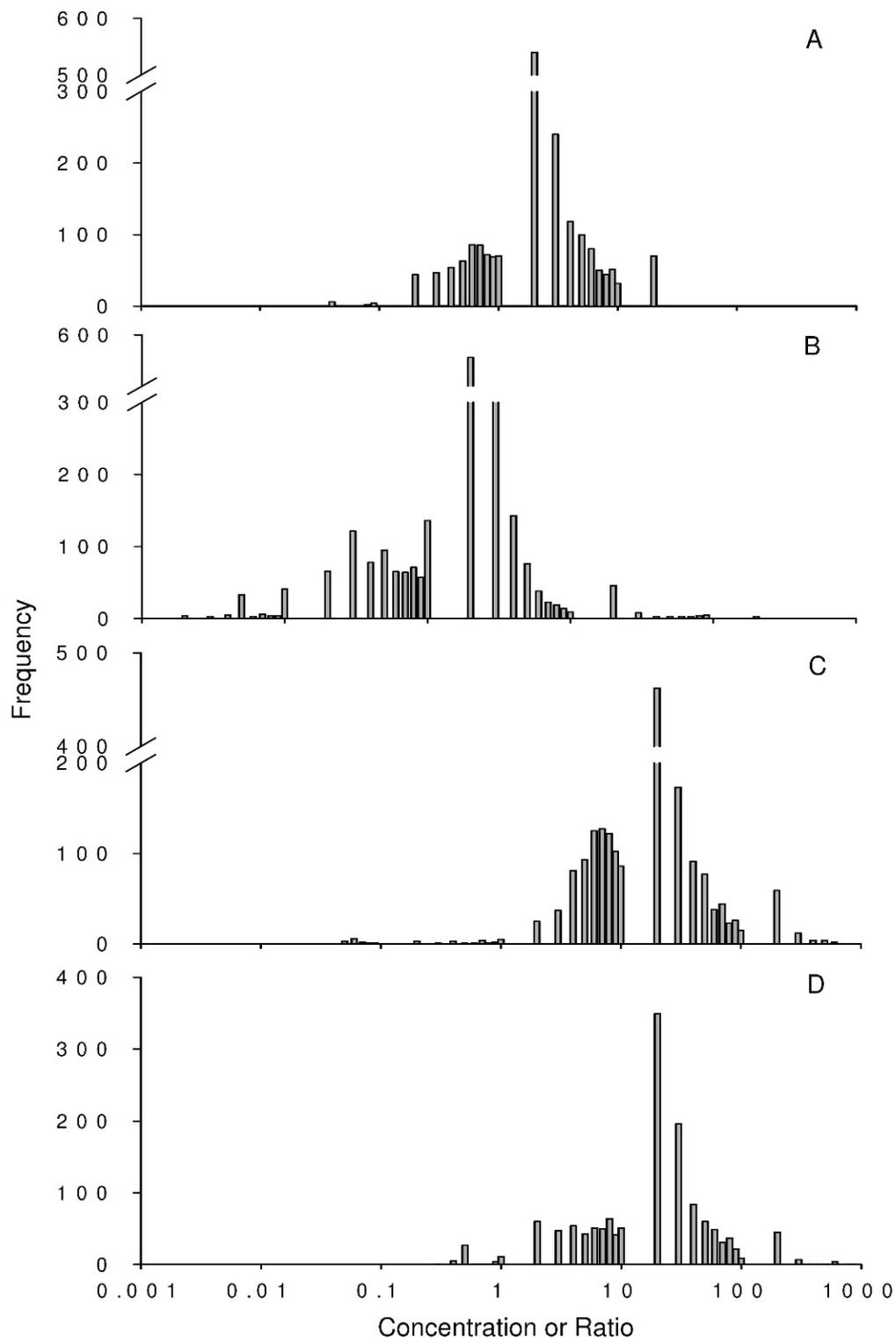
FIG. 2. Frequency histograms for median total N (TN; mg/L) (A), total P (TP; mg/L) (B), TN:TP (C; by mass), and turbidity (D; NTU) in Central Plains streams.

Table 2. Metric abbreviations, means, ranges, and standard deviations (STD) for benthic macroinvertebrate richness metrics paired with total N (TN), total P (TP), and turbidity measurements. n = sample size.

Variable	Abbreviation	TN			TP			Turbidity		
		Mean	Range ($n = 274$)	STD	Mean	Range ($n = 468$)	STD	Mean	Range ($n = 287$)	STD
Number of taxa	MTAXA	45	5–132	29	39	4–128	24	46	5–132	28
Number of primary consumer taxa	CTPRIM	25	1–80	17	21	0–72	14	24	0–80	16
Number of predator taxa	CTPRED	10	0–30	6	10	0–30	6	10	0–30	7
Number of scraper taxa	CTSCR	13	0–46	9	5	0–22	4	5	0–22	4
Number of filter taxa	CTFIL	5	0–12	3	5	0–12	3	5	0–12	3
Number of shredder taxa	CTSHR	4	0–15	3	3	0–15	3	4	0–15	3
Number of gatherer taxa	CTGATH	11	0–35	8	8	0–34	7	10	0–35	8

ambient food resource treatments were averaged and that average was treated as a replicate in the overall community mean calculated for each sampling event. If no literature value was available for a taxon with a unique functional feeding group, that taxon was not included in the C:P analysis. Mean body C:P of all species present at each site were computed and examined across TP concentrations.

Statistical analyses

Biological threshold estimation across water-quality gradients was a multistep process. First, we examined Spearman rank and Pearson correlations with a Bonferroni-corrected α (i.e., α divided by the number of dependent variables) to determine if richness metrics and mean taxa C:P were significantly correlated with water-quality measures (Wang et al. 2007). Spearman rank correlations were always higher than Pearson correlations indicating nonlinear relationships among macroinvertebrate and water-quality data. Inspection of scatter plots confirmed the presence of nonlinear relationships. A nonparametric changepoint analysis (nCPA; Qian et al. 2003, King and Richardson 2003) was used to estimate threshold water-quality levels for dependent variables with significant correlations to water-quality variables. Nonparametric tests are usually more robust for analyzing nonlinear and heteroscedastic data similar to our data set. nCPA was chosen over another common nonparametric threshold technique (Garvey et al. 1998) because it allowed calculation of an uncertainty estimate around the threshold value. nCPA uses a bootstrap simulation that resamples with replacement the original data set and recalculates the changepoint or threshold 1000 times (treefit and nboot commands; MATLAB R2007b/2007; The MathWorks Inc., Natick, Massachusetts). The resulting data set can be used to estimate uncertainty in the

threshold value reported as a cumulative probability of <5%, 50%, or 95% of a community shift occurring below a certain value (King and Richardson 2003). The reported cumulative probabilities were chosen to allow comparisons to previous threshold studies (Wang et al. 2007, Weigel and Robertson 2007). However, the level of risk that ecologists, managers, and policy-makers are willing to accept will vary depending on a variety of scientific and societal conditions and might be more or less stringent (King and Richardson 2003).

Macroinvertebrate data included in the Central Plains database were collected across many seasons, but macroinvertebrate communities can be seasonally variable (Linke et al. 1999, Ŝporka et al. 2006). Therefore, the possibility that seasonal patterns in richness and water quality might contribute to macroinvertebrate threshold patterns was assessed by examining patterns in richness and water quality across seasons (spring = March–May, summer = June–August, autumn = September–November) with a 1-way analysis of variance (ANOVA) with a Tukey-adjusted multiple comparison test. Seasons with similar richness and water-quality patterns were grouped according to the ANOVA results, and the threshold analysis described above was repeated.

Benthic macroinvertebrate samples were collected from streams with highly variable watershed size. Linear regression between watershed area and total macroinvertebrate richness was used to determine whether watershed size was a significant factor driving diversity. Correlations among TN, TP, and turbidity might also lead to spurious correlations between biotic variables and TN, TP, or turbidity. Spearman rank correlations with the medians database were used to assess interdependencies among these water-quality variables. Threshold analyses also were done between biotic diversity and TP at a subset
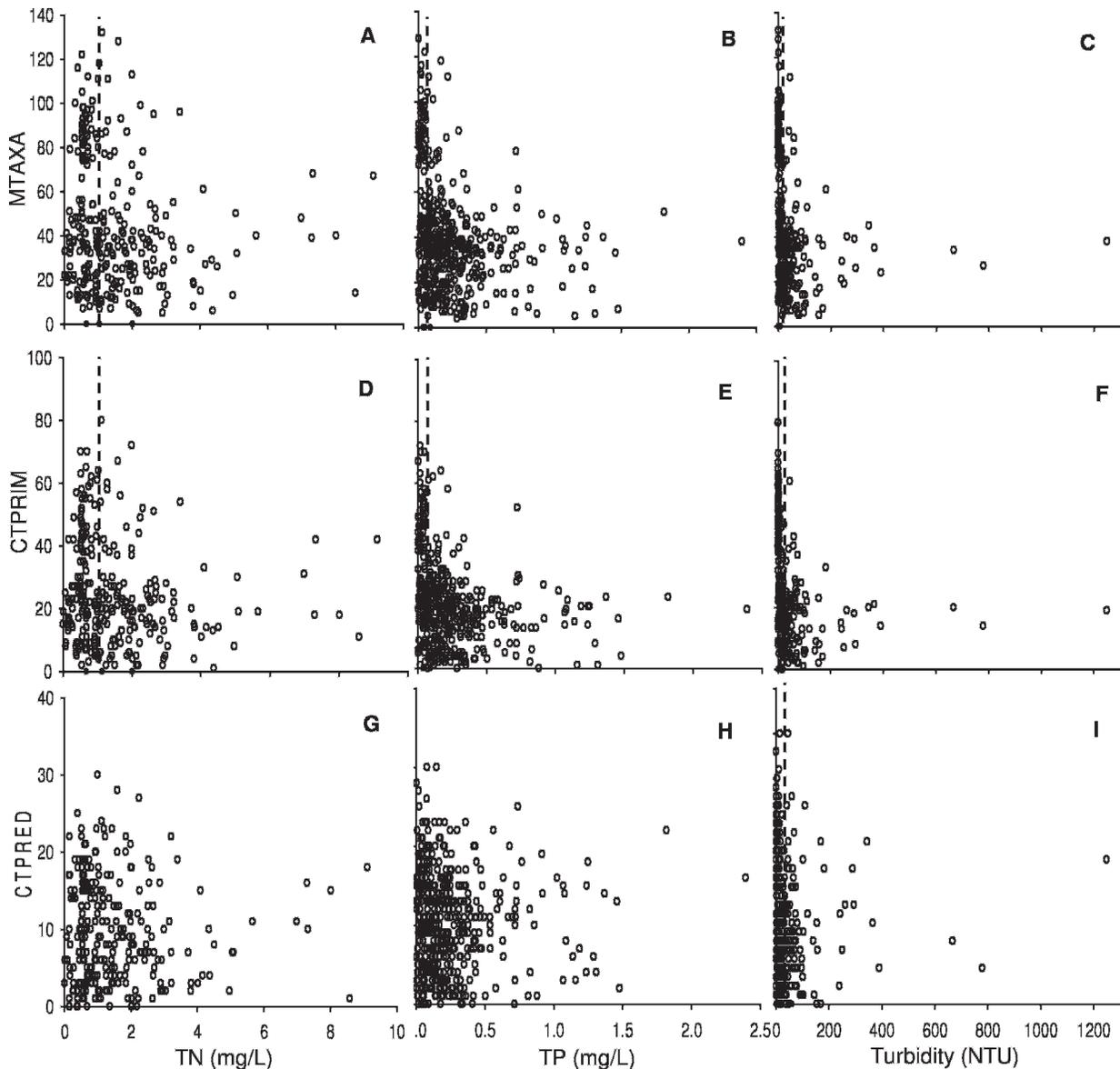
FIG. 3. The total number of benthic macroinvertebrate taxa (MTAXA) (A, B, C), primary consumer taxa (CTPRIM) (D, E, F), and predator taxa (CTPRED) (G, H, I) vs total N (TN) (A, D, G), total P (TP) (B, E, H), TN:TP (C), and turbidity (C, F, I) for the Central Plains database. Dotted vertical lines represent the nonparametric changepoint analysis (nCPA) 50% threshold estimates.

of sites with low turbidity (<10 NTU) to determine whether the TP threshold remained.

Results

The mean and variability in macroinvertebrate richness (MTAXA) in Central Plains streams often dropped abruptly across the gradient of water-quality variables (Fig. 3A–I, Table 3). The correlation between primary consumer richness (CTPRIM) and nutrients was higher than the correlation between predator richness (CTPRED) and nutrients. Correlations be-

tween richness and nutrient concentrations varied among functional feeding groups of primary consumers (Table 3). Collector-gatherers were the main feeding group negatively affected by TN. Collector-gatherer (CTGATH), scraper (CTSCR), and shredder (CTSHR) richness were negatively correlated with TP. Collector-filterer richness (CTFIL) was not significantly related to TP. Turbidity reduced richness of all macroinvertebrate taxa (MTAXA) and all feeding groups.

We expected that macroinvertebrate communities would be dominated by primary consumers with low body C:P as TP increased. Counter to our hypothesis,

Table 3. Spearman rank correlation coefficients (r) and p-values and nonparametric changepoint analysis threshold estimates (5% = threshold ≤ value 5% of the time, 50% = threshold ≤ value 50% of the time, 95% = threshold ≤ value 95% of the time) for Central Plains benthic macroinvertebrate richness metrics (see Table 2 for definitions of abbreviations). Boldface indicates statistically significant ($p < 0.05$) correlation. – indicates no threshold detected.

Independent variable	Dependent variable	Spearman rank		Threshold		
		r	p	5%	50%	95%
Total N (mg/L)	MTAXA	**−0.17**	**0.004**	0.65	**1.04**	2.01
	CTPRIM	**−0.17**	**0.005**	0.68	**1.14**	2.01
	CTGATH	**−0.23**	**<0.001**	0.68	**0.93**	1.67
	CTSCR	−0.14	0.020	–	–	–
	CTSHR	−0.09	0.120	–	–	–
	CTFIL	−0.04	0.508	–	–	–
	CTPRED	−0.09	0.124	–	–	–
	Average				**1.04**	
Total P (mg/L)	MTAXA	**−0.31**	**<0.001**	0.04	**0.05**	0.09
	CTPRIM	**−0.36**	**<0.001**	0.04	**0.05**	0.09
	CTGATH	**−0.43**	**<0.001**	0.04	**0.06**	0.08
	CTSCR	**−0.31**	**<0.001**	0.03	**0.05**	0.10
	CTSHR	**−0.19**	**<0.001**	0.04	**0.05**	0.06
	CTFIL	−0.11	0.020	–	–	–
	CTPRED	−0.12	0.011	–	–	–
	Average				**0.05**	
Turbidity (NTU)	MTAXA	**−0.51**	**<0.001**	1.69	**2.85**	7.93
	CTPRIM	**−0.53**	**<0.001**	1.69	**4.42**	8.40
	CTGATH	**−0.56**	**<0.001**	1.81	**4.93**	7.96
	CTSCR	**−0.47**	**<0.001**	0.60	**1.79**	4.38
	CTSHR	**−0.41**	**<0.001**	0.85	**4.55**	10.25
	CTFIL	**−0.30**	**<0.001**	1.57	**10.75**	19.50
	CTPRED	**−0.37**	**<0.001**	1.60	**4.55**	15.50
	Average				**4.83**	

mean total primary consumer body C:P in the Central Plains database was not correlated with TP ($r = -0.05$, $p = 0.24$). However, negative relationships were found between mean macroinvertebrate C:P and TP within individual functional feeding groups (Fig. 4A–D). Collector-gatherer and shredder communities, whose diversity had a negative threshold relationship with TP, tended to have lower mean body C:P as TP increased. The threshold shift in mean shredder taxa body C:P was similar to the threshold calculated for richness (Fig. 4A, B, Table 3). The shift in mean body C:P for collector-gatherers occurred at a higher concentration than the threshold estimated for diversity (Fig. 4C, D). TP had no significant effect on mean scraper taxa body C:P ($r = 0.02$, $p = 0.72$).

Seasonal trends in the macroinvertebrate database might partly drive threshold patterns. Spring and autumn samples had higher richness than summer samples (Fig. 5A). Spring and autumn seasons were associated with lower TP (Fig. 5C) and turbidity (Fig. 5D) than the summer season, but TN did not differ significantly among seasons (Fig. 5B). When summer data were analyzed separately from spring and autumn data, patterns were similar between the spring and autumn samples and the whole Central Plains database (Tables 3, 4). However, CTSCR and CTSHR were negatively affected by TN, and CTPRED was negatively affected by TP when only spring and autumn data were considered. Analysis of summer data alone found few significant negative correlations (Table 4).

Spring and autumn patterns in functional feeding group mean C:P across TP gradients were similar to those calculated with data combined from all seasons (Fig. 4). The negative relationship between CTGATH and TP in the summer (Table 4) did not coincide with a shift in mean collector-gatherer body C:P ($r = 0.02$, $p = 0.77$). In addition, no significant relationship existed between mean predator body C:P and TP ($r = -0.06$, $p = 0.35$) even though predator richness was reduced across the same gradient (Table 4).

Benthic macroinvertebrate richness was not related to watershed area ($R^2 = 0$, $p = 0.55$, $n = 471$). Turbidity was positively correlated with TP ($r = 0.46$, $p < 0.001$, $n = 1379$) and TN ($r = 0.24$, $p < 0.001$, $n = 1337$), and TN and TP were positively correlated ($r = 0.49$, $p < 0.001$, n
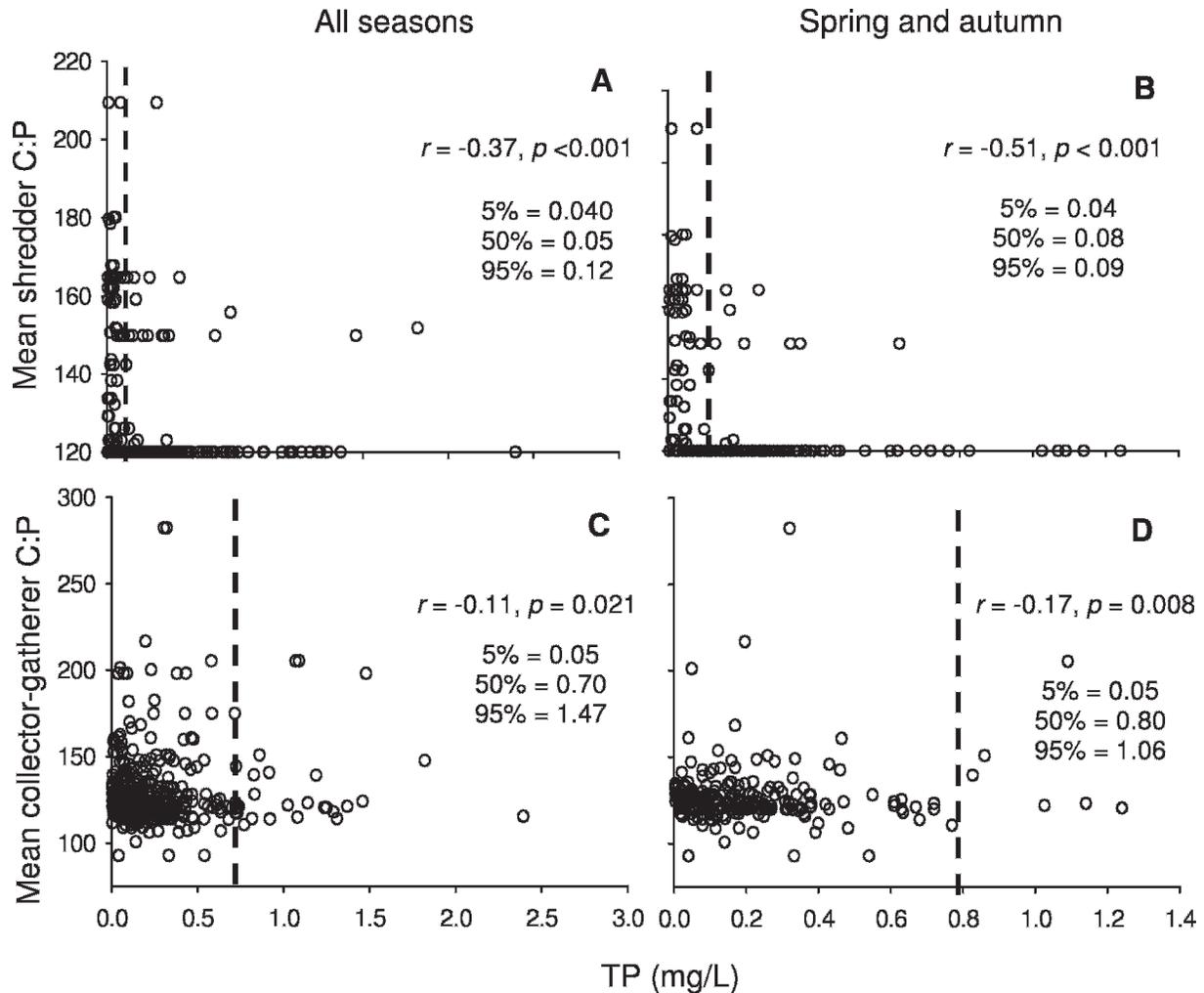
FIG. 4. Mean shredder (A, B) and collector-gatherer (C, D) body C:P (molar) across total P (TP) concentrations for samples collected from all seasons (A, C) and from spring and autumn seasons only (B, D). Dotted vertical lines represent the nonparametric changepoint analysis (nCPA) 50% threshold estimates. Spearman rank correlation coefficients (r) and p-values (p) and nCPA 5% (threshold $\leq$ value 5% of the time), 50% (threshold $\leq$ value 50% of the time), and 95% (threshold $\leq$ value 95% of the time) values are also included.

= 1869). Therefore, threshold relationships between biological variables and a particular water-quality variable (i.e., TN, TP, or turbidity) could have been confounded by correlations of that variable with another water-quality variable (i.e., TN, TP, or turbidity). Macroinvertebrate richness and C:P were negatively correlated with TP at sites that had low turbidity (<10 NTU; Table 5). Thresholds were similar or lower than those calculated across the full range of turbidity in the Central Plains database (Table 3). In addition, similar patterns were observed for macroinvertebrate C:P across primary consumer functional feeding groups (Fig. 4, Table 5).

Discussion

We found a negative threshold relationship between macroinvertebrate diversity and stream nutrient concentrations. Authors of previous studies have reported similar threshold declines in macroinvertebrate richness as N and P concentrations increased (Wang et al. 2007, Weigel and Robertson 2007). Wang et al. (2007) reported macroinvertebrate richness threshold values of 0.86 mg TN/L and 0.04 mg TP/L (Spearman rank correlations = -0.35 and -0.21, respectively) from wadeable streams in Wisconsin. Weigel and Robertson (2007) reported macroinverte-
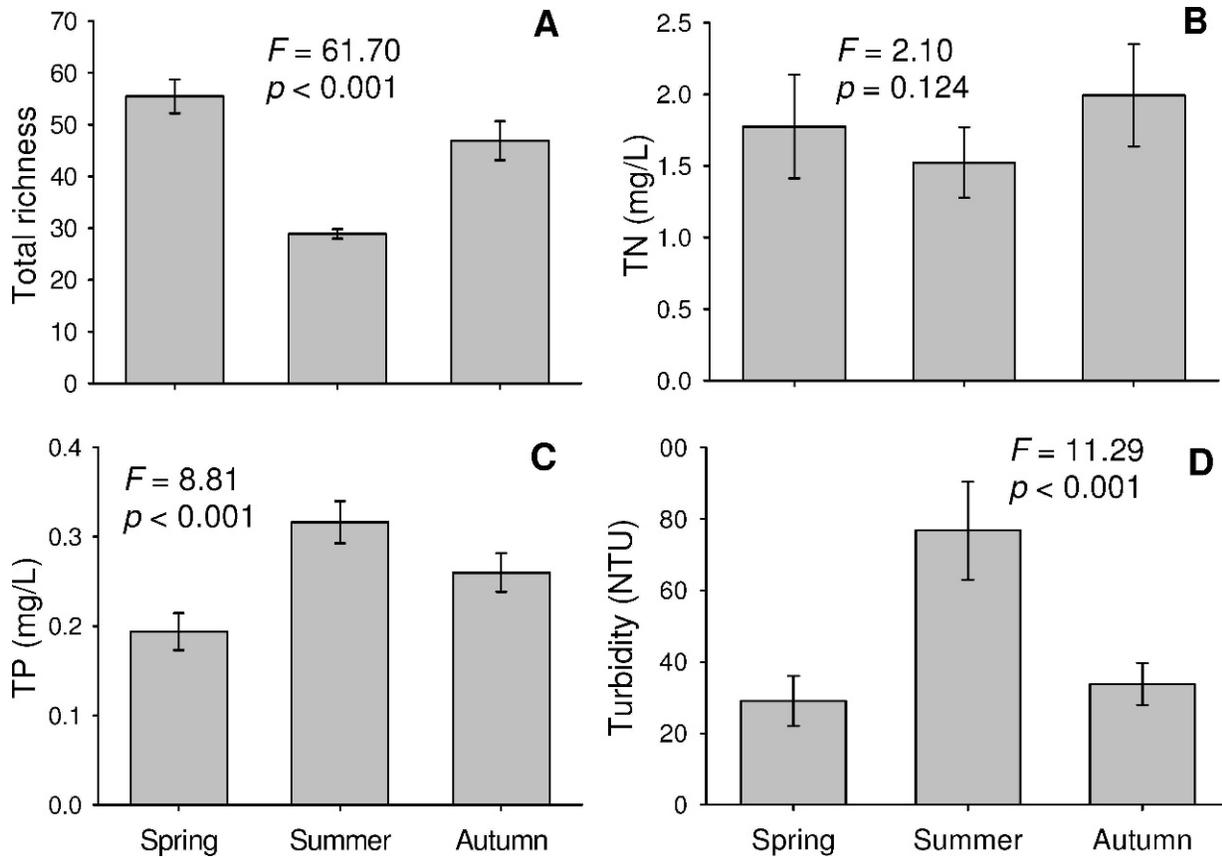
FIG. 5. Mean (±1 SE) richness (A), total N (TN) (B), total P (TP) (C), and turbidity (D) and associated analysis of variance results across seasons in the Central Plains database.

brate richness threshold values of 1.92 mg TN/L and 0.15 mg TP/L (Spearman rank correlations = −0.44 and −0.55, respectively) for nonwadeable Wisconsin streams. The similarity between the Central Plains and Wisconsin stream TN and TP threshold concentrations and correlation coefficients suggest a broad agreement in threshold values for the mid-continental US. These threshold nutrient concentrations could be used to develop nutrient criteria for this region, and might be combined with experimental data to gain a better understanding about the main factors driving the threshold relationships (King and Richardson 2003).

Patterns in macroinvertebrate diversity were probably not driven by watershed area because the 2 variables were not significantly related. However, all water-quality variables were positively correlated, so nutrient effects were difficult to separate from turbidity or sedimentation effects. Wang et al. (2007) determined that nutrients accounted for only 22% of the variation explained by environmental factors in their study of benthic macroinvertebrate patterns across water-quality gradients. Catchment features,

such as watershed area, and instream habitat features, such as silt substrate or embeddedness, explained ~42% of the variation. Results of a previous study in Ozark streams indicated that sedimentation was an important factor driving reductions in macroinvertebrate richness (Rabeni et al. 2005). Specifically, the richness of all feeding groups excluding shredders was negatively affected by sedimentation. In our study, the richness of all functional feeding groups was negatively affected by turbidity. However, nutrients affected feeding group richness differently; primary consumer richness was more often negatively affected by nutrients than was predator richness. In addition, significant TP threshold patterns remained when sites with low turbidity concentrations were analyzed. Both lines of evidence suggest that nutrient thresholds in our study could have been caused directly by nutrients and not by turbidity.

Several patterns in our study support the hypothesis that changes in resource quality could influence macroinvertebrate diversity threshold patterns. First, we found that diversity thresholds across gradients of TN and TP were dependent upon feeding group, a

TABLE 4. Spearman rank correlation coefficients (r) and p-values and nonparametric changepoint analysis threshold estimates (5% = threshold $\leq$ value 5% of the time, 50% = threshold $\leq$ value 50% of the time, 95% = threshold $\leq$ value 95% of the time) for richness metrics (see Table 2 for definitions of abbreviations) in the spring and autumn and the summer in the Central Plains. Boldface indicates statistically significant ($p < 0.05$) correlation. – indicates no threshold detected.

Independent variable	Dependent variable	Spring and autumn data					Summer data				
		Spearman rank		Threshold			Spearman rank		Threshold		
		r	p	5%	50%	95%	r	p	5%	50%	95%
Total N (mg/L)	MTAXA	**−0.38**	**<0.001**	0.60	**0.93**	2.33	−0.04	0.636	–	–	–
	CTPRIM	**−0.32**	**<0.001**	0.13	**1.90**	3.22	0.07	0.489	–	–	–
	CTGATH	**−0.36**	**<0.001**	0.63	**0.93**	2.05	−0.05	0.644	–	–	–
	CTSCR	**−0.23**	**0.006**	0.13	**2.00**	2.67	−0.11	0.203	–	–	–
	CTSHR	**−0.25**	**0.002**	0.41	**0.93**	1.72	0.00	0.985	–	–	–
	CTFIL	−0.09	0.296	–	–	–	0.00	0.947	–	–	–
	CTPRED	**−0.21**	**0.010**	–	–	–	−0.03	0.705	–	–	–
	Average				**1.34**						
Total P (mg/L)	MTAXA	**−0.56**	**<0.001**	0.05	**0.08**	0.09	0.00	0.962	–	–	–
	CTPRIM	**−0.54**	**<0.001**	0.04	**0.05**	0.08	−0.13	0.046	–	–	–
	CTGATH	**−0.59**	**<0.001**	0.04	**0.06**	0.08	**−0.20**	**0.002**	0.00	**0.06**	0.09
	CTSCR	**−0.45**	**<0.001**	0.03	**0.05**	0.09	−0.12	0.063	–	–	–
	CTSHR	**−0.34**	**<0.001**	0.03	**0.05**	0.08	0.03	0.696	–	–	–
	CTFIL	−0.10	0.112	–	–	–	−0.03	0.598	–	–	–
	CTPRED	**−0.28**	**<0.001**	0.03	**0.09**	0.10	0.13	0.047	–	–	–
	Average				**0.06**					**0.060**	
Turbidity (NTU)	MTAXA	**−0.61**	**<0.001**	0.60	**4.55**	7.81	−0.16	0.070	–	–	–
	CTPRIM	**−0.62**	**<0.001**	0.85	**4.55**	7.96	**−0.30**	**<0.001**	1.20	**11.50**	15.00
	CTGATH	**−0.63**	**<0.001**	1.65	**4.55**	7.96	**−0.27**	**<0.001**	1.75	**9.50**	10.75
	CTSCR	**−0.57**	**<0.001**	0.50	**1.71**	3.00	**−0.23**	**0.006**	1.20	**11.50**	89.85
	CTSHR	**−0.47**	**<0.001**	0.40	**4.55**	7.96	−0.17	0.048	–	–	–
	CTFIL	**−0.36**	**<0.001**	0.45	**8.15**	9.95	−0.15	0.080	–	–	–
	CTPRED	**−0.39**	**<0.001**	0.60	**4.55**	9.00	−0.19	0.027	–	–	–
	Average				**4.02**					**10.83**	

result indicating that feeding mode might play a mechanistic role. Second, primary consumers were negatively affected by increasing nutrient concentrations and predators generally were not. This pattern supports our hypothesis that predators would be less sensitive to TN and TP than primary consumers because they have a smaller nutrient imbalance between their body tissue and their food resource

TABLE 5. Sample size, Spearman rank coefficients (r), p-values, and nonparametric changepoint analysis results (nCPA; 5% = threshold $\leq$ value 5% of the time, 50% = threshold $\leq$ value 50% of the time, 95% = threshold $\leq$ value 95% of the time) for benthic macroinvertebrate richness and C:P across a total P gradient in the Central Plains. All sample events included in the analysis had a turbidity <10 NTU. See Table 2 for definitions of abbreviations. – indicates no threshold detected.

Variable	n	Spearman rank		nCPA		
		r	p	5%	50%	95%
MTAXA	87	−0.29	0.007	0.03	0.06	0.14
CTPRIM	87	−0.27	0.013	0.01	0.04	0.14
CTGATH	87	−0.26	0.017	0.01	0.01	0.45
CTSCR	87	−0.38	<0.001	0.01	0.01	0.06
CTSHR	87	−0.23	0.032	0.01	0.11	0.60
Primary consumer C:P	87	−0.20	0.067	0.01	0.1	0.58
Scraper C:P	81	−0.08	0.485	–	–	–
Shredder C:P	77	−0.34	0.002	0.01	0.06	0.08
Gatherer C:P	86	−0.18	0.099	0.01	0.26	1.15

(Sterner and Elser 2002, Frost et al. 2006). When predators did have a significant negative threshold relationship with TP (spring and autumn samples only; Table 4), mean predator C:P was not related to TP, a result suggesting that the resource quality mechanism was not driving the pattern. Third, mean shredder and collector-gatherer taxa C:P had negative threshold relationships with TP, and these shifts in stoichiometry coincided with shifts toward lower richness. Specifically, shredder communities shifted from communities with diverse assemblages of trichopteran, plecopteran, and dipteran species to communities with primarily chironomids (e.g., *Brillia*, *Cricotopus*). This pattern is consistent with previous experimental results in which shredder and collector-gatherer taxa with faster growth rates and lower body C:P responded more positively to nutrient elevations than taxa with slower growth rates and higher body C:P (Cross et al. 2006, 2007, Singer and Battin 2007). Therefore, our study provides evidence that patterns from these smaller-scale experiments might apply at the regional scale.

Food resource quality was not measured directly in our study, but higher quality at higher nutrient levels was assumed. This assumption is supported by the literature (Suberkropp and Arsuffi 1984, Kahlert 1998, Stelzer and Lamberti 2001, Cross et al. 2003) and probably also is valid in Central Plains streams. Algal biomass in temperate streams increased across a gradient of nutrient concentrations up to a point (0.48 mg N/L and 0.04 mg P/L; Dodds et al. 2002, 2006). Above that point, algal biomass did not increase (Dodds et al. 2002, 2006). Only ~11% of TN and ~21% of TP concentrations measured in Central Plains streams fell below these maximum algal biomass thresholds (Fig. 2A, B), a result indicating that nutrients might be saturating algal growth and primarily altering algal nutrient concentrations.

Nutrient gradients also might alter detrital quality. Nutrients can stimulate bacterial and fungal growth, which can increase detrital food quality (Meyer and Johnson 1983, Arsuffi and Suberkropp 1989, Stelzer et al. 2003). Baldy et al. (2007) found that microbial biomass and CO_2 production on leaf litter increased along a dissolved P gradient and then reached a plateau between 0.02 and 0.04 mg/L soluble reactive P (SRP). Rosemond et al. (2002) also found that the half-saturation constant for litter decay across 16 tropical stream sites with differing SRP concentrations was between 0.007 and 0.013 mg/L SRP. The plateau concentration might differ among stream systems, but many of the Central Plains streams had concentrations above the highest threshold level found in the literature (0.040 mg SRP/L). Thus, many of the

macroinvertebrate richness nutrient thresholds in our study occurred at concentrations above those needed to increase the nutrient content of their algal and detrital food resources.

Thresholds between richness or stoichiometry and water quality occurred more often in spring and autumn than in summer samples. In the summer, only 13% and 6% of the sites had median TP and turbidity concentrations below estimated threshold concentrations. The percentage of sites with concentrations below the estimated threshold concentrations was higher in the spring (TP: 41, turbidity: 16%) and autumn (TP: 24, turbidity: 21%). Therefore, fewer thresholds in the summer compared to spring and autumn might reflect a lack of sites sampled in the summer season with water-quality concentrations below biotic thresholds. Thresholds for animals, such as shredders and collector-gatherers, that include detritus in their diets might be seasonally dependent because detrital inputs are seasonal, and the life histories of many taxa are timed with resource availability in the stream. Some agencies in the Central Plains did focus on summer sampling, and this sampling protocol could erroneously indicate that taxon richness is not sensitive to stream water quality. Our data suggest that autumn and spring samples are more indicative of stream biotic integrity.

Conclusions

Thresholds have been found at multiple scales in biology and ecology, and environmental managers are increasingly using them in ecosystem management (Groffman et al. 2006) in terrestrial (e.g., With and King 1999, Hobbs and Harris 2001, Briske et al. 2006) and in aquatic ecosystems (e.g., Dodds 2006, King and Richardson 2003). In aquatic ecosystem management, thresholds are being considered for use primarily in establishing nutrient criteria. However, the coupling of large-scale threshold patterns and experimental data might elucidate cause–effect linkages between biological patterns and specific stressors (King and Richardson 2003). Our study allowed us to scale-up from previous experimental research (Cross et al. 2006, 2007, Singer and Battin 2007) and our results suggest that alteration of food resource quality could be partially driving patterns in aquatic communities across nutrient gradients, particularly for detritivore taxa. Our results also provide evidence supporting the hypothesis that physiological nutrient threshold patterns across taxa and feeding groups (Frost et al. 2006) might drive nutrient threshold patterns at larger scales. Elevated nutrient concentrations in streams could be increasing food resource

quality above the level at which many stream taxa evolved and could be contributing to losses of biodiversity. A stoichiometric view of stream trophic state will be essential to managing eutrophication (Dodds 2007), and our results further support this argument. Future research should further examine the stoichiometry of competitive interactions across nutrient gradients in a more controlled setting to further address this hypothesis.

Acknowledgements

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