Spatial and temporal variation in the ecological stoichiometry of aquatic organisms in an urban catchment

Author

Tsoi, Wing Y, Hadwen, Wade L, Fellows, Christine S

Published

2011

Journal Title

Journal of the North American Benthological Society

DOI

10.1899/10-085.1

J. N. Am. Benthol. Soc., 2011, 30(2):533–545

DOI: 10.1899/10-085.1
Published online: 29 March 2011

Spatial and temporal variation in the ecological stoichiometry of aquatic organisms in an urban catchment

Wing Y. Tsoi[1], Wade L. Hadwen[2], AND Christine S. Fellows[3]
Australian Rivers Institute, Griffith School of Environment, Griffith University, Nathan Campus, Queensland 4111, Australia

Abstract. Urban land use has increased dramatically over the past few decades. Urban streams are distinguished from forested or agricultural streams, in particular, by their more variable and unpredictable hydrologic pattern. The resulting high variability in nutrient loading is likely to alter the elemental composition of primary producers and, ultimately, to change the elemental composition of other foodweb components. Ecological stoichiometry is a useful framework for improving our understanding of the mass balance of multiple key elements in ecosystems. To this end, the C:N:P of key foodweb components were measured in Oxley Creek, an urban catchment in southeastern Queensland, Australia. Ten stream reaches were sampled to explore the spatial variation of C:N:P of abundant taxonomic groups across the catchment. Four of these sites were sampled weekly (for 8 wk) to examine temporal variation in elemental composition. Our results suggested that spatial and temporal variation in elemental composition of primary producers and some animal taxa were highly dependent on local (i.e., site) conditions. This local dependence makes determination of catchment-wide drivers of stoichiometric variability difficult, but our results do suggest that site-based influences in urban streams can generate substantial variability in the C:N:P content of in-stream biota. In the context of other studies that have been undertaken principally in forested streams, this application of ecological stoichiometry promises to further our understanding of the effects of urbanization on stream food webs and the stability of elemental flow.

Key words: elemental ratios, C:N:P, urban stream, homeostasis, food webs, primary producers, macroinvertebrates, fish.

Urbanization has long been recognized as a degrading influence on stream ecosystems (Heaney and Huber 1984). Urban streams are at risk from urban landuse practices that result in changes to a range of physical and chemical characteristics (Paul and Meyer 2001, Peterson et al. 2001, Feminella and Walsh 2005). Urbanization generally changes stream hydrographs by increasing the frequency of short-duration, high-flow events (Walsh et al. 2005, Brown et al. 2009). Moreover, high concentrations of nutrients can be delivered to urban streams during these intense flow events (Grimm et al. 2005, Kaye et al. 2006). These changes alter the spatial and temporal availability of nutrients to aquatic biota (Sterner and Elser 2002), effects that are likely to alter the elemental composition of autotrophic producers (Turner and Rabalais 1991, Vitousek and Farrington 1997) and, ultimately, to change the stoichiometry of other foodweb components (Singer and Battin 2007).

Knowledge of how elemental composition of in-stream biota responds to nutrient loading is growing rapidly (Ramírez and Pringle 2006, Singer and Battin 2007, Ventura et al. 2008). The elemental composition of primary producers tracks changes in concentrations of dissolved nutrients in a variety of aquatic ecosystems (Healey and Hendzel 1980, Stelzer and Lamberti 2001, Fink and Von Elert 2006). Stoichiometric theory is based on the assumption that animals maintain their elemental composition within a relatively small range (strict homeostasis), regardless of the elemental composition of their food (Urabe and Watanabe 1992, Sterner and Hessen 1994 , Elser et al. 1996). However, several recent studies have provided evidence to suggest that homeostasis is less strict than previously thought in primary consumers (Cross et al. 2003, Liess and Hillebrand 2005) and across multiple trophic levels (Small and Pringle 2010). Deviations of animals from strict homeostasis in response to nutrient enrichment suggests that changes in nutrient

[1] E-mail addresses: i.tsoi@griffith.edu.au
[2] w.hadwen@griffith.edu.au
[3] Deceased

loading may lead to substantial spatial and temporal variation in the elemental composition of stream foodweb components across trophic levels (Small and Pringle 2010).

Stoichiometry has received less attention in streams in urban than in forested or agricultural catchments, and no foodweb studies of ecological stoichiometry have been done in urban streams to date. We examined the elemental composition (C:N:P) of key foodweb components in urban streams of the Oxley Creek catchment, in southeastern Queensland, Australia. We sought to investigate the degree to which elemental composition varied spatially and temporally across trophic levels. We assumed that the variation in elemental composition of consumers would be smaller than that of their food sources (i.e., a higher degree of homeostasis in consumers than in primary producers). Based on recent studies of freshwater organisms (Bowman et al. 2005, Liess and Hillebrand 2005, Small and Pringle 2010), we expected that increases in anthropogenic nutrient inputs caused by landuse change would decrease C:N and C:P of primary producers. We also expected that differences in C:N:P of primary producers would generate concomitant variability in C:N:P of their consumers.

Methods

Study sites

Our study was conducted in the highly urbanized Oxley Creek catchment in southeastern Queensland, Australia (Fig. 1). Oxley Creek has a catchment area of 260 km^2 and is one of the major lowland tributaries of the Brisbane River (OCCA 1999). The region has a subtropical climate, and mean annual temperature ranges from 15.5 to 25.4°C. Average annual precipitation is 947.3 mm. About 70% of the annual precipitation occurs in summer (October to March), often during high-intensity, short-duration rainfall events. The upper catchment includes areas of undisturbed forest but is dominated by agricultural land use. Land use is rural–residential in the middle catchment and residential, industrial, and commercial in the lower catchment (OCCA 1999). Extensive urbanization of the Oxley Creek catchment has increased impervious areas within the catchment, thereby increasing runoff volume, frequency, and peak discharges, especially in the lower catchment (OCCA 1999).

All of the study sites were small streams (<3rd-order) in the lower catchment with channel beds composed of silt, sand, and scattered cobble. Landuse categories were quantified in ArcView (version 9.3; Environmental Systems Research Institute, Redlands, California) from analysis of Statewide Landcover and Trees Study (SLATS) data from 1999 (Department of Environment and Resource Management, Queensland Government, Brisbane, Australia) coupled with subcatchment boundaries delineated for the Oxley Creek catchment (T. J. Pietsch, Australian Rivers Institute, unpublished data). Landuse statistics for each site were determined by quantifying the percentage of upstream subcatchment occupied by each landuse type. Based on these percentages, 3 major landuse types were identified: residential, industrial, and natural vegetation. Because of the mixed land use in the lower Oxley Creek catchment, study sites were classified into 4 landuse categories: residential dominant (R), mixed industrial and residential (I), natural vegetation dominant (V), and mixed residential, industrial, and natural vegetation (M) (Table 1).

Collection of biota and elemental analysis

Sampling was done in 2 stages (Table 1). In the 1st stage, ten 50-m-long stream reaches (riffle or run) were sampled between 10 December and 19 December 2007 to investigate the spatial variation in elemental composition of abundant taxa across sites. At each site, representatives of the most abundant taxa were sampled in pool and run habitats from a representative 50-m-long reach. These taxa included in-stream primary producers (filamentous algae and submerged macrophytes), aquatic macroinvertebrates, and fish. In the 2nd stage, 4 of the original sites were sampled weekly for 8 wk (17 January–7 March 2008) to assess temporal variation in stoichiometry of primary producers (filamentous algae, rock biofilm) and primary consumers (atyid shrimps, planorbid and physid snails).

Replicate samples ($n = 3$ wherever possible) of all biota were sampled at each site on each sampling occasion. Filamentous algae and submerged macrophytes were collected by hand. Rock biofilm was sampled by scrubbing algae from a single rock with a brush and rinsing with distilled water until no obvious biomass remained. Macroinvertebrates were sampled by dip net (250-μm mesh size) in riffles, around snags, and in edge habitats. Snails and some mayfly and caddisfly taxa were picked by hand from substrates. Fish were collected with a small seine net (2 m long, 1-mm mesh size) in shallow open water and baited fish traps near snags. All samples were placed in labelled Ziploc® bags and immediately stored on ice in a cooler. Upon return to the laboratory, all samples were stored frozen at −20°C until preparation. Algae were identified to broad morphological categories (filamentous algae and

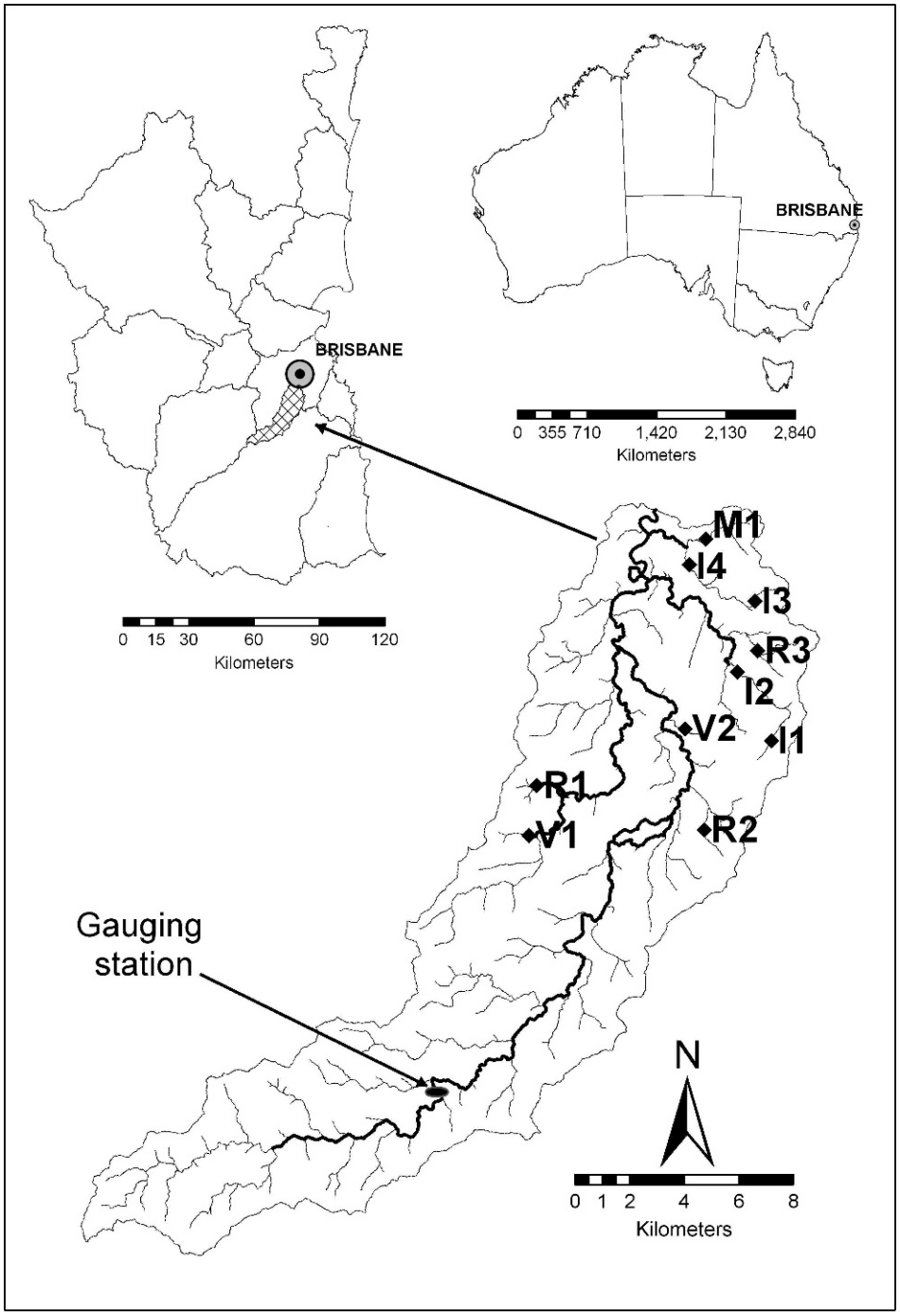

FIG. 1. Sites in the Oxley Creek Catchment, southeastern Queensland, Australia, where key foodweb components were collected during 2007 to 2008.

biofilm), macroinvertebrates were identified to family, and fish were identified to species.

In the laboratory, all samples of biota were rinsed with distilled water to remove foreign materials. Shells or exoskeletons were removed from mollusks and crustaceans to obtain the entire soft-body tissue for analysis. Fish were scaled and filleted, and a portion of the dorsal muscle tissue was used for analysis to exclude nondietary sources of C (Hadwen and Bunn 2005). All samples were dried in a 60°C oven to constant mass before being ground to a homogenous powder. Individual large animals (>4 mg) were treated as 1 sample, whereas smaller animals (<4 mg) were pooled to obtain enough

Table 1. Site codes used in the spatial and temporal stages of the study, and landuse categories and water-column nutrient concentrations ($n = 1$) for the spatial study. Site codes are named by dominant landuse categories, where V = natural vegetation dominant, R = residential dominant, I = mixed industrial and residential, M = mixed residential, industrial, and natural vegetation. Sites are ordered from upstream to downstream.

Site code		Landuse categories (%)			Nutrient concentration		
Spatial	Temporal	Residential	Industrial	Natural vegetation	NH_4-N	NO_3-N	PO_4^{3-}
V1	V1	28%	1%	70%	0.057	0.133	0.005
V2	–	30%	6%	54%	0.038	0.083	0.012
R1	–	78%	0%	14%	0.050	0.029	0.007
R2	R2	98%	0%	1%	0.024	0.018	0.005
R3	–	99%	0%	0%	0.040	0.031	0.009
M1	M1	70%	8%	9%	0.119	0.258	0.011
I1	I1	65%	33%	0%	0.043	2.626	0.004
I2	–	65%	33%	0%	0.027	0.037	0.053
I3	–	65%	28%	6%	0.083	0.249	0.004
I4	–	62%	28%	6%	0.041	0.030	0.009

material for analysis. Larger samples were ground with a ring grinder and smaller samples were ground by hand with a mortar and pestle.

For analysis of C and N content, all dried and ground samples were weighed into tin capsules and combusted in a EuroEA 3000 (EuroVector, Milan, Italy) elemental analyser. The resulting CO_2 and N_2 gases were separated chromatographically and fed into an IsoPrime (Micromass, Cheadle, UK) isotope ratio mass spectrometer. The results obtained for C and N were then expressed as % by mass for each sample. For analysis of P content, the method of Stelzer and Lamberti (2001) was used. All dried and ground samples were combusted in a muffle furnace (Lenton Thermal Designs, Hope Valley, UK) at 500°C for 1 h. The samples were then digested in 2 mL of 1N HCl at 80°C for 30 min. Thirty mL of deionized water were added, and the resulting solution was analysed in a SmartChem200 discrete chemical analyser (Westco Scientific Instruments, Brookfield, Connecticut). The results, expressed as mg/L of orthophosphate (PO_4^{3-}), were converted to total P content of the sample based on the mass of the ground sample and the solution volume and were then expressed as % by mass. All C, N, and P contents (represented as % by mass) were finally converted to molar values to express C:N, C:P, and N:P.

Water-quality and environmental variables

At each site and sampling occasion, temperature and conductivity were measured with a portable conductivity meter (TPS, Brisbane, Australia). Water samples were collected for turbidity analysis in the laboratory with a Hach 2100AN turbidimeter (Hach, Inc., Loveland, Colorado). Water samples for analysis of dissolved nutrients (NH_4-N, NO_3-N + NO_2-N [NO_3-N], and soluble reactive P [SRP]) were collected and filtered through 0.45-μm cellulose-acetate membranes at each site. All samples were stored on ice until returned to the laboratory where they were stored at −20°C until analyzed. All dissolved nutrient samples were analyzed on a SmartChem200 (Westco Scientific Instruments) discrete chemical analyser. The results were expressed as mg N/L (NO_3-N and NH_4-N) and mg PO_4^{3-}/L (SRP).

Gauge height data from the only gauged site within the Oxley Creek catchment (New Beith site on the main stem of Oxley Creek) were used to characterize catchment-wide stream-flow conditions during the study period. Daily gauge heights for the study period were obtained from the Department of Environment and Resource Management (DERM 2008).

Statistical analysis

Our analyses focused on examining the variability in elemental composition of the biota and its relationships with water-quality and environmental variables. All elemental ratios were $\log(x + 1)$-transformed to satisfy the normality and homoscedasticity assumptions of parametric tests. One-way analysis of variance (ANOVA) was done in SAS (version 9.1; SAS Institute, Cary, North Carolina) to test for differences among spatial sites and landuse categories and within temporal sites in ambient nutrient concentrations and C:N, C:P, and N:P of foodweb components. The significance level was set at 0.05 in all ANOVAs (Zar 1999). Where statistically significant differences were detected, post hoc Tukey's Honestly Significant Difference (Tukey's HSD) comparisons were used to determine the source of the

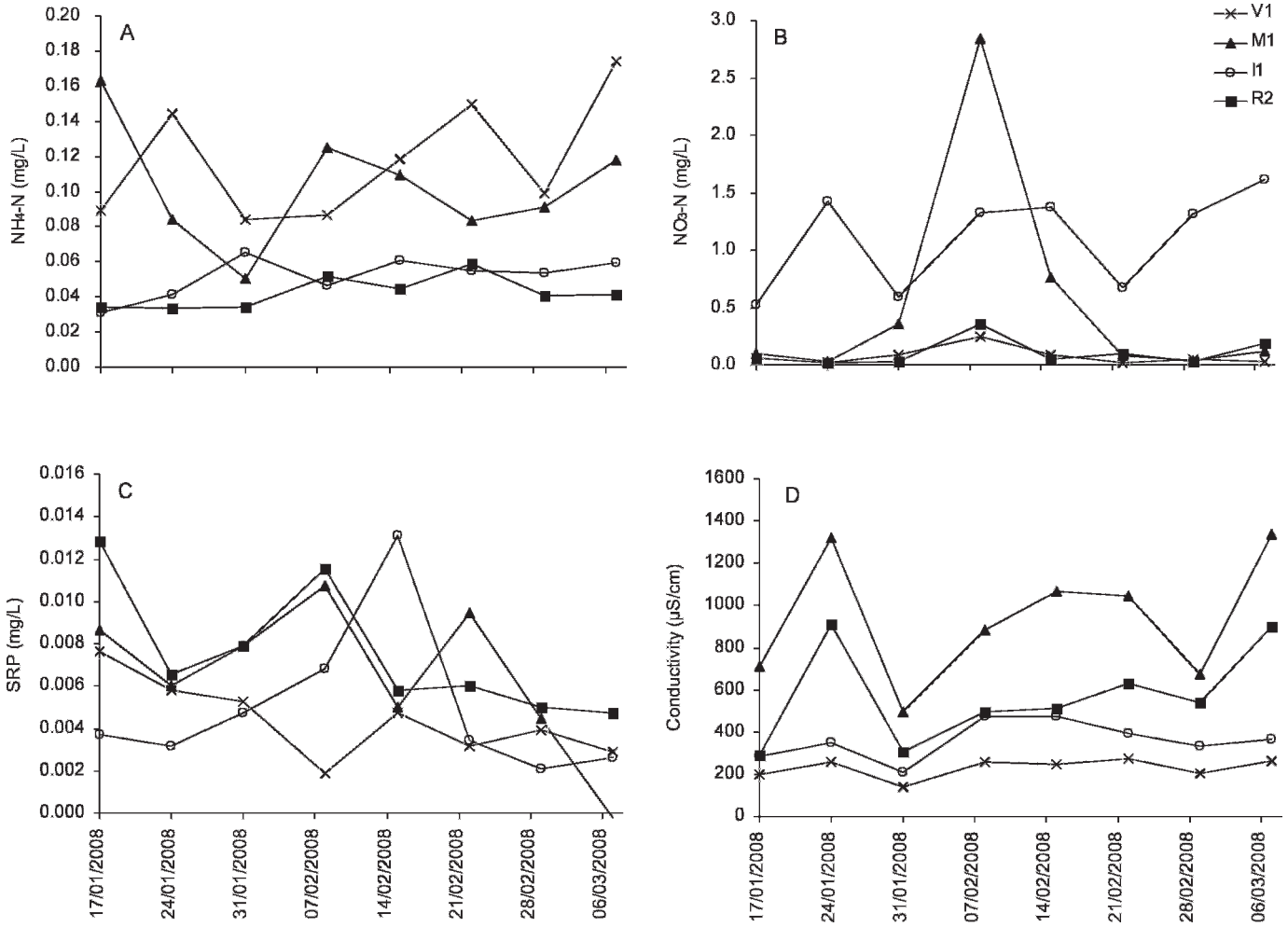

FIG. 2. Temporal fluctuations in NH_4-N (A), NO_3-N (B), soluble reactive P (SRP) (C), and conductivity (D) from 4 sites sampled between 17 January and 7 March 2008 in the Oxley Creek catchment. $n = 1$ for all variables.

significant differences. Coefficients of variation (CVs) of C:N, C:P, and N:P were calculated to compare variability among taxonomic groups. Simple linear regression analysis was used to examine relationships between the elemental composition of biota and the percentages of landuse categories, and the environmental factors of nutrient concentrations, stage level, conductivity, and turbidity.

Results

Environmental variables and stoichiometric variability

In the spatial study, the broad landuse categories identified around each sampling site did not explain the observed differences in NH_4-N, NO_3-N and SRP concentrations throughout the catchment (Table 1). In the temporal study, NH_4-N, NO_3-N, and SRP concentrations and conductivity varied over the 8-wk sampling period (Fig. 2A–D). Similar trends in the rise and fall of conductivity were observed across all sites, but values at sites V1 and I1 were generally less variable than those at sites M1 and R2 (Fig. 2D).

The C:N:P of filamentous algae and biofilm were not correlated with landuse category, stage level, ambient dissolved nutrient concentrations, conductivity, or turbidity when all sites were analyzed as 1 data set (e.g., Fig. 3A). When tests were done separately for each site over the temporal study period, some significant relationships were found between conductivity and C:N and C:P at some of the sites. The temporal variation in C:N of filamentous algae from site R2 ($R^2 = 0.7226$, $p < 0.05$) was strongly correlated with conductivity (Fig. 3B). However, the observed relationships between filamentous algae and conductivity were not consistent across all sites.

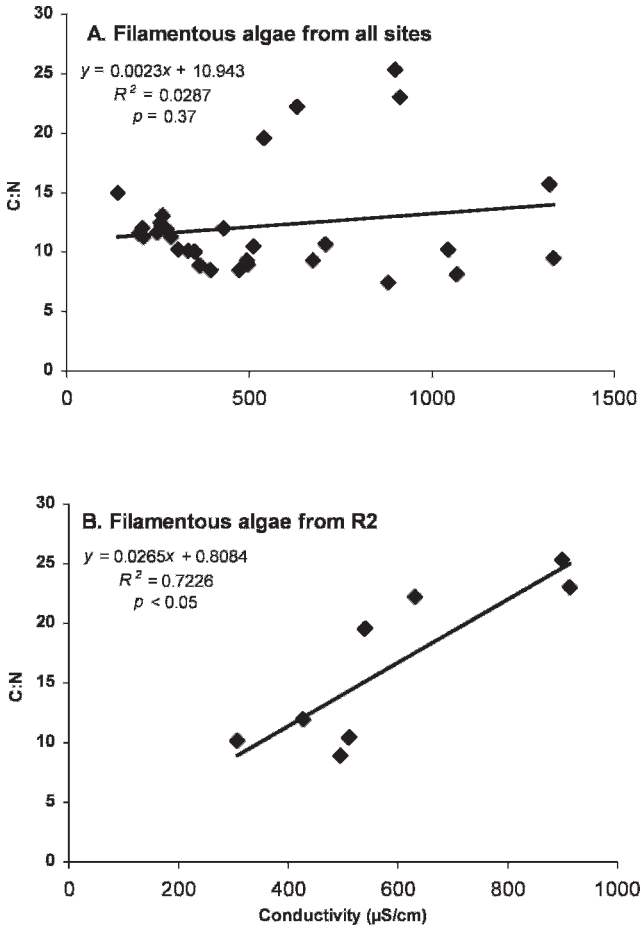

FIG. 3. Relationships between conductivity and C:N of filamentous algae sampled from all temporal sites (A) and temporal site R2 (B) in the Oxley Creek catchment between 17 January and 7 March 2008.

Stoichiometric variation among sites

C:N, C:P, and N:P of the 12 most commonly encountered taxa were assessed to examine spatial variation among the 10 sites sampled in stage 1 of the study (Appendix). The CVs for C:N, C:P, and N:P of primary producers were higher than those for consumers. Among sampled primary producers, C:N of the filamentous algae, *Nitella* sp., and the aquatic macrophyte, *Egeria densa*, differed significantly among sites (ANOVA, $p \leq 0.01$). Among primary consumers, C:P and N:P of atyid shrimp differed significantly among sites (ANOVA, $p \leq 0.01$). Among predators, C:N of coenagrionids (ANOVA, $p < 0.05$) and notonectids (ANOVA, $p < 0.01$) differed significantly among sites. Among the commonly encountered fish taxa (the top consumers sampled), no ratio differed among sites. Across all taxonomic groups, C:N was more stable than C:P or N:P, as shown by the greater CVs for C:P or N:P than C:N.

Stoichiometric variation through time

Elemental composition of both primary producers and animals fluctuated considerably through time. C:N and C:P of filamentous algae and C:N of biofilm were highly variable at all 4 sites over the 8-wk period (ANOVA, $p < 0.001$; Fig. 4A–D). The extent of this temporal variation differed among sites, and, as a result, no consistent trends were found in the rise and fall of C:N:P through time.

We observed some significant variations in the elemental composition of invertebrates in the temporal study. The extent of temporal variability of stoichiometric ratios of physid snails was higher than that of atyid shrimp, but only C:P of physid snails varied significantly over time, and only at site R2 (ANOVA, $p < 0.001$; Fig. 5A, B). C:N and C:P of atyid shrimp at site V1 and site R2 varied significantly over the 8-wk period (ANOVA, $p < 0.001$; Fig. 5C, D). Stoichiometric ratios of planorbid snails did not vary significantly among sites or over time.

Discussion

Overview

The variation in elemental composition of food sources was higher than that of consumers, a result supporting our expectation that consumers would exhibit a higher degree of homeostasis than their food sources. C:P and N:P of primary producers showed a wider range of physiological plasticity in our study than has been reported elsewhere (e.g., C:P range: 99–603, N:P range: 10–49; Kahlert 1998, Kahlert et al. 2002). One explanation for the greater variability in P than N in the Oxley Creek catchment, at least at the time of our study, is that P was less available than N in this system. Elser et al. (2000a) suggested that stream biota may be relatively plastic in their capacity to store P in their tissues when it is abundant to compensate for future periods when it is scarce.

Invertebrates from different trophic levels showed variable degrees of homeostasis in our study. In the temporal study, C:P and N:P of mollusk grazers (Physidae) was variable. In the spatial study, C:P and N:P of decapod collectors (Atyidae) and C:N of predatory damselflies (Coenagrionidae) and backswimmers (Notonectidae) was variable. These results suggest that, within the invertebrate taxa, deviation from strict homeostasis occurs not only among herbivorous primary consumers (Cross et al. 2003, Liess and Hillebrand 2005) but also among different trophic levels (Small and Pringle 2010). On the other hand, the low elemental plasticity observed in fish-muscle samples supports the idea that strict homeo-

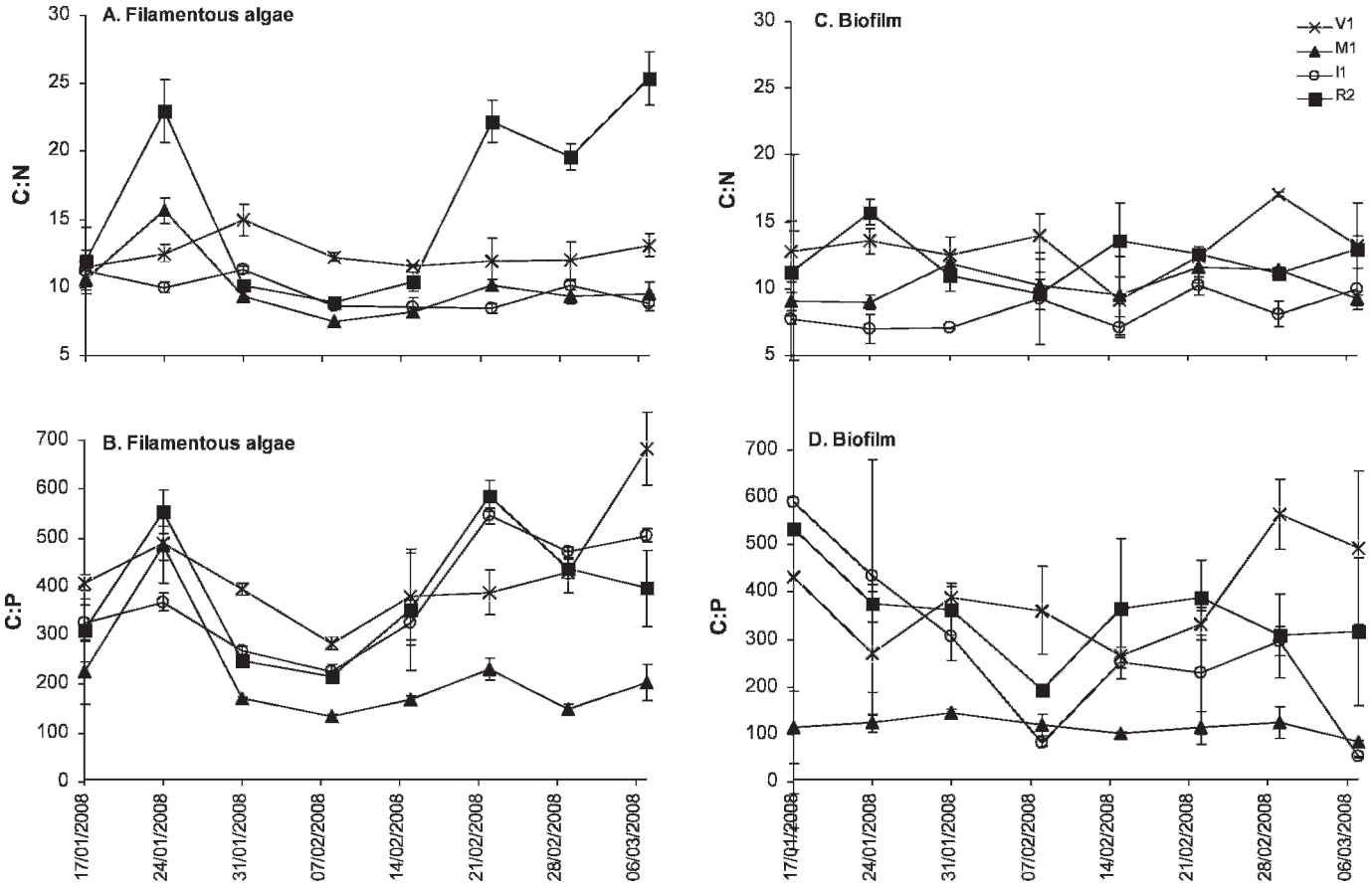

FIG. 4. Temporal variation in mean (±1 SE) C:N (A, C) and C:P (B, D) for filamentous algae (A, B) and biofilm (C, D) samples collected from 4 sites in the Oxley Creek catchment between 17 January and 7 March 2008.

stasis of top consumers might be linked to their relatively complex physiologies. However, for predatory species (like many fish), low variability also might be a consequence of the reduced stoichiometric variability of prey items (primary consumers) when compared to the variability observed in primary producers (Elser et al. 2000b, Frost et al. 2003).

Environmental variables and primary producer stoichiometry

We expected that ambient nutrient concentrations would vary throughout the Oxley Creek catchment because of differences in upstream land uses among sampled sites. The ranges of NH_4-N and NO_3-N concentrations in our study were similar to the ranges reported in studies of other urban streams in Australia, whereas the range of SRP concentrations was smaller in our study than in others (e.g., NH_4-N: range = 0.009–0.245, NO_3-N: range = 0.167–2.898, SRP: range = 0.002–0.329; Walsh et al. 2001). However, landuse categories and percentages of different land uses did not explain the variability in measured nutrient concentrations at sites sampled in our study. This lack of observable relationships could be related to the variable and unpredictable hydrologic patterns in urban systems. The Oxley Creek catchment is likely to experience localized hydrologic change more quickly and frequently than natural streams because of more efficient transport of runoff from impervious surfaces (OCCA 1999). Highly variable flows can lead to high variability in ambient nutrient concentrations. As a result, the likelihood of detecting and understanding flow-mediated changes in nutrient loads and concentrations is lower than it might be in forested streams. Another possible reason for the apparent lack of relationships among percentages of land uses and nutrient concentrations is that the approach used to assess upstream land uses (percentage of upstream land use, i.e., lumped method) could mask the disproportionate influence of land near the stream or connected by overland flow (Peterson et al. 2010). The Oxley Creek catchment is a relatively small urban catchment with multiple land uses in the lower

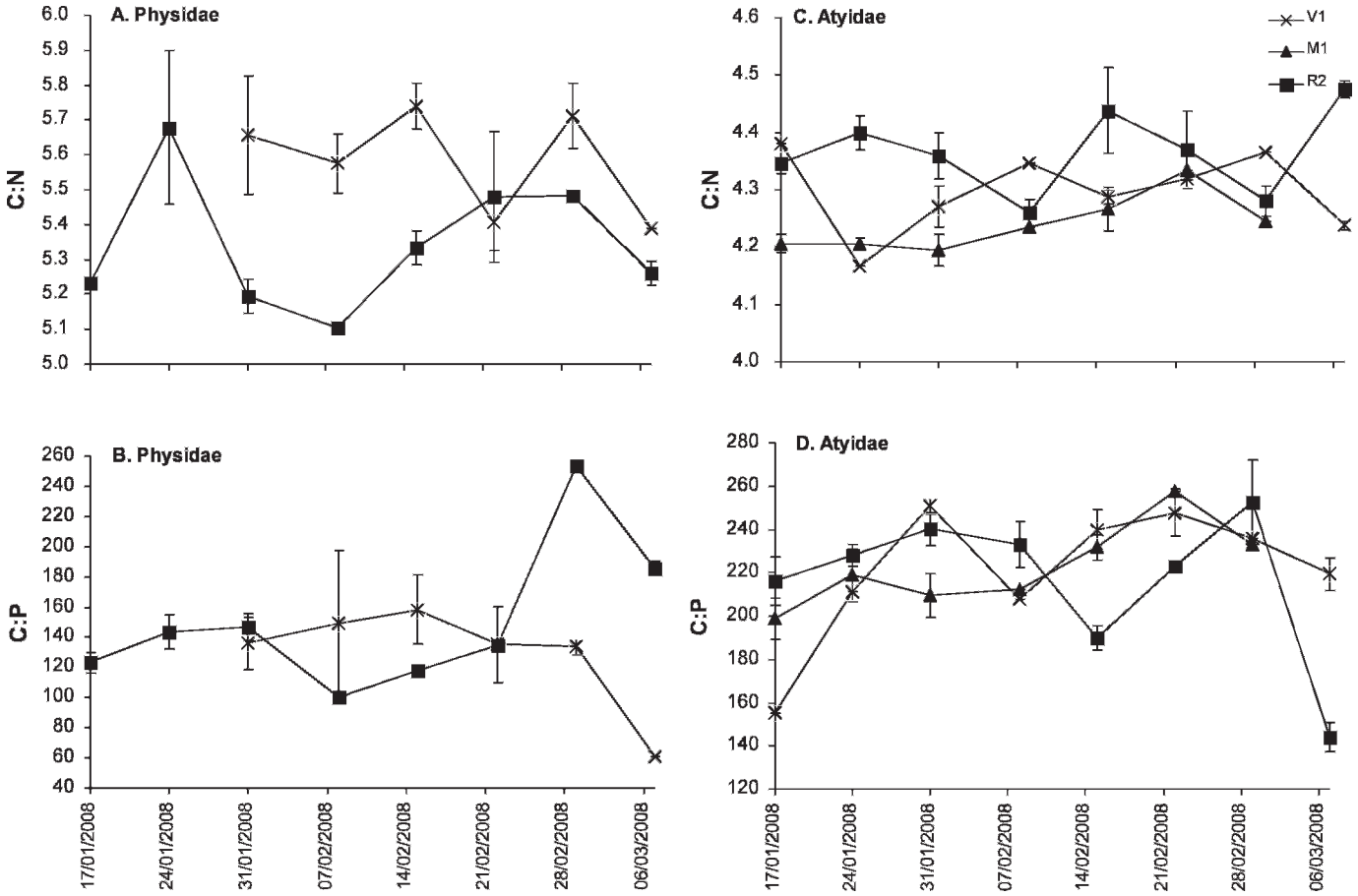

FIG. 5. Temporal variation in mean (±1 SE) C:N (A, C) and C:P (B, D) of snail (Physidae) (A, B) and shrimp (Atyidae) (C, D) samples collected from 4 sites in the Oxley Creek catchment between 17 January and 7 March 2008.

catchment, and the catchments of most of our study sites were not dominated exclusively by one landuse type. Therefore, the lumped method, which allocates equal weight to land uses regardless of where they occur in the catchment could misrepresent the probable linkages between the stream and land uses in the catchment (Peterson et al. 2010). Peterson et al. (2010) suggested that landscape metrics weighted by distance to the stream may provide a better description of the linkages between land use and in-stream ecological conditions, especially in urbanized catchments with multiple land uses, but these approaches are still in their infancy and have yet to be tested in a complex urban stream setting.

We hypothesized that increases in anthropogenic nutrient inputs might decrease C:N and C:P of primary producers. Some support for this hypothesis was observed in the spatial component of our study. C:N of filamentous algae was lower at site I1 than at any other site, a result that corresponds well with the fact that the NO_3-N concentration at site I1 was among the highest measured across all 10 sites. Therefore, filamentous algae could have assimilated more N in the high-nutrient environment at site I1 than at other sites. Similarly, C:P of filamentous algae was lower at site I2 than at any other site, and water-column SRP was higher at site I2 than at any other site. Nevertheless, no statistical relationships were found between nutrient concentrations and C:N:P of filamentous algae or other primary producers in our study.

Despite the absence of clear relationships between nutrient concentrations and stoichiometric ratios, some relationships were found between conductivity and C:N and C:P of filamentous algae when tests were done separately for each site. At site R2, peaks and troughs of conductivity and C:N and C:P of filamentous algae were similar over the 8-wk period. Conductivity is directly proportional to the concentrations and types of ions present in water. It represents ionic forms of nutrients in water that are not readily altered by biological processes. Biggs and Price (1987) observed a close positive relationship between filamentous algal biomass and conductivity

in New Zealand rivers. Moreover, conductivity was elevated and correlated with increasing urban intensity (Wang and Yin 1997, Herlihy et al. 1998, Brown et al. 2009, O'Brien and Wehr 2009). The similar trends in filamentous algal C:N and C:P and conductivity captured in the temporal phase of our study suggest that conductivity may be an important environmental indicator in urban streams. However, little information appears to be available in the literature on the relationship between conductivity and elemental ratios. Further research is needed to investigate if the relationship between conductivity and stoichiometry differs between urban and nonurban streams.

The differences in fluctuations in conductivity and stoichiometric ratios of filamentous algae among the 4 temporal sites explain the absence of significant explanatory relationships across the entire data set and suggest that site-level variability may be more easily explained than catchment-wide patterns of stoichiometric change. The probable importance of site-specific variability is reinforced by the fact that temporal changes in gauge-height data in our study (from a single site) were not mirrored by fluctuations in conductivity or stoichiometric ratios of filamentous algae. Furthermore, no single mechanism or process appears to have affected the C:N:P of filamentous algae predictably over time. Instead, our findings suggest that the site-specific complexity and interactivity of factors that influence algal C:N:P need to be better understood and should be taken into account when assessing food webs using a stoichiometric perspective in an urban catchment.

Primary producers and consumers stoichiometry

We hypothesized that variation in consumer elemental ratios could be a response to varying elemental ratios of their potential food sources caused by the substantial temporal variety in nutrient loading in urban catchments. C:N of snails (Physidae) and shrimp (Atyidae) appeared to follow roughly the observed patterns in biofilm C:N at R2. However, no statistical relationships were found between C:N:P of biofilm and consumers in our study.

One possible reason for the absence of primary producer–consumer stoichiometric relationships is differences in the tissue turnover rates of elements in different taxa (Pinnegar and Polunin 1999). A lag period between uptake of nutrients and change in consumer tissue nutrient concentrations has been demonstrated, but the implications of such a lag period remain unresolved for many taxa (Jardine et al. 2005, Matthews and Mazumder 2005). Furthermore, little information on the ontogenetic variation in elemental composition in these taxa is available in the literature. Such information could provide insights into the observed patterns (Sterner and Elser 2002). Further study is needed to evaluate the nature and consistency of lag periods and ontogenetic variation in consumer stoichiometric response to changes in the elemental composition of food sources under laboratory and field conditions.

A lag effect coupled with the site-specific variability and unpredictable hydrologic pattern of urban streams make the likelihood of detecting and understanding flow-mediated changes in nutrient loads and concentrations and subsequent stoichiometric changes in organisms lower than in less-modified forested systems (e.g., Small and Pringle 2010). Therefore, the spatial and temporal variation of animal C:N:P throughout the Oxley Creek catchment (and the drivers of this variation) requires further investigation.

Conclusions

Our study provides one of the first assessments of the elemental composition of biota in urban streams. On the basis of our findings, we suggest that elemental stoichiometry could be a useful framework for understanding the high variability in urban stream ecosystems. No significant relationships were found among landuse categories, nutrient concentrations, and C:N:P of biota, but the spatial and temporal variability in C:N:P of primary producers and some invertebrate taxa in our study suggest that changes in elemental stoichiometry could be a useful indicator of the highly variable physiochemical conditions that characterize urban streams. Moreover, the absence of catchment-wide patterns of elemental stoichiometry in this urban study highlights the individuality of urban streams and the multitude of land uses in urban catchments, relative to those of forested streams. Thus, coarse measures of upstream land use are less likely to be predictive of site-specific conditions in urban streams.

Future research should focus on examining how and why the observed spatial and temporal variation of C:N:P occurs. Particular emphasis should be placed on the roles of flow, nutrient concentrations, and conductivity in influencing organismal elemental ratios. In addition, our limited knowledge of tissue turnover rates and the lag time between consumption of particular sources and the appearance of those elemental components in the C:N:P of consumer tissues significantly reduces our capacity to make strong predictions of elemental flows in ecosystems. Whether our findings are unique to Australian stream

environments or taxa or to urban streams more broadly is yet to be determined. Future studies in forested and urban streams and a wider range of aquatic habitats are required to gain a better understanding of both the general principles of ecological stoichiometry and how it can be applied to improve our understanding of ecological processes in natural and urbanized environments.

Acknowledgements

This paper is dedicated to the memory of Christine Fellows, whose contributions to the project were invaluable. Special thanks to 2 anonymous referees, Robert Hall, and Pamela Silver for their constructive comments on the manuscript. We thank Cliff Dahm and Fran Sheldon for their valuable input at the beginning of the project. We also thank Mark Kennard, Tim Pietsch, Rene Diocares, Noreen Dejoras, Scott Byrnes, Yi Ru Chen, Michael Newham, Joe McMahon, and numerous volunteers for help in the field, laboratory, and data analyses. The project was funded in part by the Griffith School of Environment and the eWater Cooperative Research Centre. This project was conducted under ethics permit (ENV-08-07) in accordance with Griffith University animal ethics standards.

The State of Queensland (Department of Natural Resources and Mines) 2005. The Department of Natural Resources and Mines gives no warranty in relation to the data (including accuracy, reliability, completeness or suitability) and accepts no liability (including without limitation, liability in negligence) for any loss, damage or costs (including consequential damage) relating to any use of the data.

Literature Cited

Biggs, B. J. F., and G. M. Price. 1987. A survey of filamentous algal proliferations in New Zealand rivers. New Zealand Journal of Marine and Freshwater Research 21:175–191.

Bowman, M. F., P. A. Chambers, and D. W. Schindler. 2005. Changes in stoichiometric constraints on epilithon and benthic macroinvertebrates in response to slight nutrient enrichment of mountain rivers. Freshwater Biology 50:1836–1852.

Brown, L. R., T. F. Cuffney, J. F. Coles, F. Fitzpatrick, G. McMahon, J. Steuer, A. H. Bell, and J. T. May. 2009. Urban streams across the USA: lessons learned from studies in 9 metropolitan areas. Journal of the North American Benthological Society 28:1051–1069.

Cross, W. F., J. P. Benstead, A. D. Rosemond, and J. B. Wallace. 2003. Consumer-resource stoichiometry in detritus-based streams. Ecology Letters 6:721–732.

DERM (Department of Environment and Resource Management). 2008. Gauge height data for Oxley Creek. State of Queensland, Department of Natural Resources and Management, Brisbane, Australia. (Available from: http://www.derm.qld.gov.au/water/monitoring/current_data/)

Elser, J. J., D. Dobberfuhl, N. A. MacKay, and J. H. Schampel. 1996. Organism size, life history, and N:P stoichiometry: towards a unified view of cellular and ecosystem processes. BioScience 46:674–684.

Elser, J. J., W. F. Fagan, R. F. Denno, D. R. Dobberfuhl, A. Folarin, A. Huberty, S. Interlandi, S. S. Kilham, E. McCauley, K. L. Schulz, E. H. Siemann, and R. W. Sterner. 2000a. Nutritional constraints in terrestrial and freshwater food webs. Nature 408:578–580.

Elser, J. J., W. J. O'Brien, D. R. Dobberfuhl, and T. E. Dowling. 2000b. The evolution of ecosystem processes: growth rate and elemental stoichiometry of a key herbivore in temperate and arctic habitats. Journal of Evolutionary Biology 13:845–853.

Feminella, J. W., and C. J. Walsh. 2005. Urbanization and stream ecology: an introduction to the series. Journal of the North American Benthological Society 24:585–587.

Fink, P., and E. Von Elert. 2006. Physiological responses to stoichiometric constraints: nutrient limitation and compensatory feeding in a freshwater snail. Oikos 115: 484–494.

Frost, P. C., S. E. Tank, M. A. Turner, and J. J. Elser. 2003. Elemental composition of littoral invertebrates from oligotrophic and eutrophic Canadian Lakes. Journal of the North American Benthological Society 22:51–62.

Grimm, N. B., R. W. Sheibley, C. L. Crenshaw, C. N. Dahm, W. J. Roach, and L. H. Zeglin. 2005. N retention and transformation in urban streams. Journal of the North American Benthological Society 24:626–642.

Hadwen, W. L., and S. E. Bunn. 2005. Food web responses to low-level nutrient and 15N-tracer additions in the littoral zone of an oligotrophic dune lake. Limnology and Oceanography 50:1096–1105.

Healey, F. P., and L. L. Hendzel. 1980. Physiological indicators of nutrient deficiency in lake phytoplankton. Canadian Journal of Fisheries and Aquatic Sciences 37: 442–453.

Heaney, J. P., and W. C. Huber. 1984. Nationwide assessment of urban runoff impact on receiving water quality. Water Resources Bulletin 20:35–42.

Herlihy, A. T., J. L. Stoddard, and C. B. Johnson. 1998. The relationship between stream chemistry and watershed land cover data in the Mid-Atlantic region, US. Water, Air, and Soil Pollution 105:377–386.

Jardine, T. D., R. A. Curry, K. S. Heard, and R. A. Cunjak. 2005. High fidelity: isotopic relationship between stream invertebrates and their gut contents. Journal of the North American Benthological Society 24:290–299.

Kahlert, M. 1998. C:N:P ratios of freshwater benthic algae. Archiv für Hydrobiologie Supplementband 51:105–114.

Kahlert, M., A. T. Hasselrot, H. Hillebrand, and K. Pettersson. 2002. Spatial and temporal variation in the biomass and nutrient status of epilithic algae in Lake Erken, Sweden. Freshwater Biology 47:1191–1215.

KAYE, J. P., P. M. GROFFMAN, N. B. GRIMM, L. A. BAKER, AND R. V. POUYAT. 2006. A distinct urban biogeochemistry? Trends in Ecology and Evolution 21:192–199.

LIESS, A., AND H. HILLEBRAND. 2005. Stoichiometric variation in C:N, C:P, and N:P ratios of littoral benthic invertebrates. Journal of the North American Benthological Society 24:256–269.

MATTHEWS, B., AND A. MAZUMDER. 2005. Temporal variation in body composition (C:N) helps explain seasonal patterns of zooplankton $\delta^{13}C$. Freshwater Biology 50: 502–515.

O'BRIEN, P. J., AND J. D. WEHR. 2009. Periphyton biomass and ecological stoichiometry in streams within an urban to rural land-use gradient. Hydrobiologia 657:89–105.

OCCA (OXLEY CREEK CATCHMENT ASSOCIATION). 1999. Oxley Creek Catchment Management Plan. Oxley Creek Catchment Association Inc, Brisbane, Australia. (Available from: http://www.oxleycreekcatchment.org.au/)

PAUL, M. J., AND J. L. MEYER. 2001. Streams in the urban landscape. Annual Review of Ecology and Systematics 32:333–365.

PETERSON, B. J., W. M. WOLLHEIM, P. J. MULHOLLAND, J. R. WEBSTER, J. L. MEYER, J. L. TANK, E. MARTÍ, W. B. BOWDEN, H. M. VALETT, A. E. HERSHEY, W. H. MCDOWELL, W. K. DODDS, S. K. HAMILTON, S. GREGORY, AND D. D. MORRALL. 2001. Control of nitrogen export from water sheds by headwater streams. Science 292:86–90.

PETERSON, E. E., F. SHELDON, R. DARNELL, S. E. BUNN, AND B. D. HARCH. 2010. A comparison of spatially explicit landscape representation methods and their relationship to stream condition. Freshwater Biology. doi:10.1111/j.1365-2427.2010.02507.x

PINNEGAR, J. K., AND N. V. C. POLUNIN. 1999. Differential fractionation of $\delta^{13}C$ and $\delta^{15}N$ among fish tissues: implications for the study of trophic interactions. Functional Ecology 13:225–231.

RAMÍREZ, A., AND C. M. PRINGLE. 2006. Fast growth and turnover of chironomid assemblages in response to stream phosphorus levels in a tropical lowland landscape. Limnology and Oceanography 51:189–196.

SINGER, G. A., AND T. J. BATTIN. 2007. Anthropogenic subsidies alter stream consumer-resource stoichiometry, biodiversity, and food chains. Ecological Applications 17:376–389.

SMALL, G. E., AND C. M. PRINGLE. 2010. Deviation from strict homeostasis across multiple trophic levels in an invertebrate consumer assemblage exposed to high chronic phosphorus enrichment in a Neotropical stream. Oecologia (Berlin) 162:581–590.

STELZER, R. S., AND G. A. LAMBERTI. 2001. Effects of N:P ratio and total nutrient concentration on stream biofilm community structure, biomass, and elemental composition. Limnology and Oceanography 46:356–367.

STERNER, R. W., AND J. J. ELSER. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, New Jersey.

STERNER, R. W., AND D. O. HESSEN. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. Annual Review of Ecology and Systematics 25:1–29.

TURNER, R. E., AND N. N. RABALAIS. 1991. Changes in Mississippi River water quality this century: implications for coastal food webs. BioScience 41:140–147.

URABE, J., AND Y. WATANABE. 1992. Possibility of N or P limitation for planktonic cladocerans: an experimental test. Limnology and Oceanography 37:244–251.

VENTURA, M., L. LIBORIUSSEN, T. LAURIDSEN, M. SØNDERGAARD, M. SØNDERGAARD, AND E. JEPPESEN. 2008. Effects of increased temperature and nutrient enrichment on the stoichiometry of primary producers and consumers in temperate shallow lakes. Freshwater Biology 53:1434–1352.

VITOUSEK, P. M., AND H. FARRINGTON. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. Biogeochemistry 37:63–75.

WALSH, C. J., A. H. ROY, J. W. FEMINELLA, P. D. COTTINGHAM, P. M. GROFFMAN, AND R. P. MORGAN. 2005. The urban stream syndrome: current knowledge and the search for a cure. Journal of the North American Benthological Society 24:706–723.

WALSH, C. J., A. K. SHARPE, P. F. BREEN, AND J. A. SONNEMAN. 2001. Effects of urbanization on streams of the Melbourne region, Victoria, Australia. I. Benthic macroinvertebrate communities. Freshwater Biology 46: 535–551.

WANG, X., AND Z. YIN. 1997. Using GIS to assess the relationship between land use and water quality at a watershed level. Environment International 23:103–114.

ZAR, J. H. 1999. Biostatistical analysis. 4th edition. Prentice–Hall, Upper Saddle River, New Jersey.

Received: 22 June 2010
Accepted: 18 January 2011

APPENDIX. Mean (±1 SD) elemental ratios for the 12 most commonly encountered taxa from 10 sites. CV = coefficient of variation. Bold indicates statistically significant differences among sites. Values with the same superscript are not significantly different.

		Overall				Spatial sites	
Taxon	Ratio	Grand mean	Range	CV(%)	*p*-value	V1	V2
Filamentous algae	C:N	13.0 ± 3.1	8.0–19.9	23.5	**<0.01**	11.5 ± 0.2[c,d]	17.3 ± 0.8[a]
	C:P	455.7 ± 284.0	74.4–1158.3	62.3	0.17	638.6 ± 333.0	609.2 ± 226.1
	N:P	35.6 ± 21.5	5.7–88.4	60.4	0.23	55.9 ± 30.0	35.6 ± 14.0
Nitella sp.	C:N	11.8 ± 1.2	10.4–14.7	10.1	**<0.01**	11.0 ± 0.9[b]	12.4 ± 0.3[a,b]
	C:P	521.3 ± 260.2	195.2–1075.5	49.9	0.07	642.2 ± 337.6	443.7 ± 169.1
	N:P	45.4 ± 24.2	13.3–92.9	53.3	0.08	59.9 ± 33.7	36.0 ± 14.5
Egeria densa	C:N	14.2 ± 4.5	9.7–23.6	31.9	**0.01**	–	–
	C:P	363.4 ± 177.6	170.2–619.4	48.9	**<0.01**	–	–
	N:P	24.9 ± 7.6	15.2–37.2	30.5	0.08	–	–
Physidae	C:N	5.6 ± 0.1	5.5–5.8	2.1	0.07	–	–
	C:P	134.1 ± 22.7	102.3–167.1	16.9	0.26	–	–
	N:P	24.0 ± 4.3	17.8–30.0	17.9	0.27	–	–
Planorbidae	C:N	5.6 ± 0.5	5.3–7.4	9.0	0.61	5.4 ± 0.1	–
	C:P	150.0 ± 35.5	97.9–234.7	23.7	0.46	122.6 ± 10.5	–
	N:P	26.7 ± 5.8	18.3–41.3	21.8	0.22	22.8 ± 1.9	–
Atyidae	C:N	4.5 ± 0.1	4.4–4.7	2.4	0.07	4.4	4.4 ± 0.1
	C:P	199.7 ± 53.0	111.8–285.7	26.5	**0.01**	111.8[b]	200.6 ± 35.3[a,b]
	N:P	44.7 ± 12.5	25.2–65.1	27.9	**0.01**	25.2[b]	45.3 ± 9.0[a,b]
Notonectidae	C:N	5.6 ± 0.3	5.2–6.1	5.1	**<0.01**	–	–
	C:P	202.0 ± 32.0	159.2–278.2	15.8	0.62	–	–
	N:P	36.2 ± 5.8	26.5–46.6	16.1	0.32	–	–
Coenagrionidae	C:N	5.1 ± 0.1	4.9–5.3	2.6	**0.03**	–	–
	C:P	188.7 ± 2.6	124.5–299.5	27.9	0.09	–	–
	N:P	36.8 ± 9.8	25.2–56.9	26.6	0.12	–	–
Cordulliidae	C:N	5.3 ± 0.3	4.8–5.9	5.8	0.44	5.4 ± 0.3	5.4
	C:P	182.3 ± 42.6	134.6–282.7	23.4	0.60	186.5 ± 52.4	179.9
	N:P	34.5 ± 8.3	25.5–54.1	24.2	0.63	34.5 ± 10.6	33.2
Gambusia holbrooki	C:N	4.3 ± 0.1	4.0–4.4	2.1	0.28	4.3 ± 0.0	–
	C:P	458.4 ± 216.1	186.2–962.6	47.1	0.49	400.7 ± 130.6	–
	N:P	107.6 ± 51.5	46.5–234.6	47.8	0.96	93.1 ± 30.5	–
Xiphophorus maculates	C:N	4.3 ± 0.1	4.0–4.5	2.8	0.06	4.3 ± 0.1	–
	C:P	218.2 ± 103.5	95.2–366.4	47.4	0.33	148.5 ± 90.4	–
	N:P	51.1 ± 24.7	22.3–84.4	48.4	0.33	34.9 ± 21.7	–
Xiphophorus helleri	C:N	4.3 ± 0.1	4.1–4.5	1.9	0.78	4.3 ± 0.0	–
	C:P	317.8 ± 107.4	129.8–600.6	33.8	0.60	319.5 ± 82.4	–
	N:P	74.1 ± 24.5	30.6–138.3	33.0	0.59	74.9 ± 19.1	–

APPENDIX. Extended.

Spatial sites			Spatial sites				
R1	R2	R3	M1	I1	I2	I3	I4
10.9 ± 0.8[d]	–	18.1 ± 1.8[a]	11.7 ± 1.0[c,d]	8.7 ± 0.6[e]	11.0 ± 0.4[d]	14.2 ± 0.6[b]	13.6 ± 0.6[b,c]
411.7 ± 82.7	–	481.1 ± 125.1	229.8 ± 99.4	777.5 ± 609.6	179.9 ± 61.3	383.7 ± 117.7	389.9 ± 122.5
38.1 ± 9.7	–	26.3 ± 4.3	20.3 ± 9.9	56.0 ± 43.5	16.4 ± 6.0	27.2 ± 9.3	44.8 ± 13.5
10.9 ± 0.6[b]	11.4 ± 0.1[b]	–	–	11.2 ± 0.7[b]	13.7 ± 1.3[a]	–	–
345.7 ± 88.4	914.2 ± 155.6	–	–	442.8 ± 126.5	339.1 ± 129.6	–	–
32.1 ± 9.4	80.0 ± 12.7	–	–	39.1 ± 8.7	25.1 ± 10.2	–	–
11.5 ± 1.2[b]	19.7 ± 3.3[a]	–	–	–	–	11.4 ± 0.3[b]	–
317.4 ± 106.7[b]	575.4 ± 38.9[a]	–	–	–	–	197.4 ± 36.8[b]	–
27.8 ± 9.1	29.5 ± 2.8	–	–	–	–	17.3 ± 2.7	–
5.6	5.7	–	–	–	–	5.8	5.5 ± 0.0
167.1	135.6	–	–	–	–	102.3	133.3 ± 15.3
30.0	23.7	–	–	–	–	17.8	24.2 ± 2.9
–	6.1 ± 1.1	5.5 ± 0.0	–	5.6 ± 0.1	–	–	5.5 ± 0.2
–	139.2 ± 40.2	148.1 ± 15.2	–	190.7 ± 52.7	–	–	149.2 ± 17.6
–	22.7 ± 3.9	27.0 ± 2.7	–	34.1 ± 8.7	–	–	27.1 ± 2.3
–	4.6 ± 0.0	–	4.4 ± 0.0	–	–	4.5 ± 0.1	–
–	152.4 ± 23.3[b]	–	264.2 ± 30.5[a]	–	–	232.4 ± 14.1[a]	–
–	33.0 ± 5.1[b]	–	60.4 ± 6.8[a]	–	–	51.9 ± 2.7[a]	–
–	–	5.4 ± 0.2[b]	5.4 ± 0.2[b]	–	5.9 ± 0.2[a]	–	5.9 ± 0.2 [a]
–	–	211.1 ± 21.2	203.7 ± 10.6	–	222.2 ± 53.5	–	177.6 ± 18.8
–	–	39.0 ± 3.3	37.9 ± 2.6	–	37.7 ± 8.3	–	30.3 ± 4.1
–	–	–	5.0 ± 0.1[a]	5.2 ± 0.1[a,b]	5.0 ± 0.1[a,b]	5.2 ± 0.1[b]	–
–	–	–	134.2 ± 13.1	213.3 ± 13.0	176.6 ± 30.5	230.7 ± 75.5	–
–	–	–	26.8 ± 2.1	41.4 ± 3.1	35.1 ± 5.9	44.1 ± 14.7	–
5.4 ± 0.3	–	5.4 ± 0.2	5.0 ± 0.1	5.3 ± 0.5	5.3 ± 0.3	5.0	5.3 ± 0.4
144.5 ± 6.8	–	236.7 ± 40.9	176.2 ± 11.6	184.9 ± 43.1	165.4 ± 28.9	271.6	152.6 ± 16.0
26.9 ± 1.2	–	43.8 ± 8.6	35.6 ± 3.1	34.8 ± 6.9	31.3 ± 6.2	54.1	28.6 ± 1.6
4.3 ± 0.1	4.3 ± 0.0	–	4.3 ± 0.1	–	–	4.1 ± 0.1	4.3
544.2 ± 223.6	436.0 ± 288.7	–	431.5 ± 102.0	–	–	512.9 ± 402.6	358.2
126.3 ± 50.3	102.3 ± 67.9	–	99.8 ± 22.6	–	–	124.6 ± 98.0	83.8
–	–	–	4.4 ± 0.1	–	–	4.2 ± 0.1	4.3 ± 0.1
–	–	–	227.9 ± 121.4	–	–	196.8 ± 125.6	299.8 ± 46.2
–	–	–	51.9 ± 28.4	–	–	47.8 ± 31.8	69.8 ± 11.7
4.3 ± 0.0	4.2 ± 0.0	4.3 ± 0.1	–	4.3 ± 0.2	4.3 ± 0.1	–	4.3 ± 0.0
412.9 ± 191.7	314.0 ± 35.4	375.6 ± 50.6	–	253.3 ± 42.1	283.1 ± 94.2	–	265.9 ± 144.3
95.6 ± 43.7	74.6 ± 8.4	87.0 ± 10.9	–	58.9 ± 7.7	65.7 ± 21.2	–	62.2 ± 33.2