

# Linking nutrient enrichment and streamflow to macrophytes in agricultural streams

Christopher A. Mebane · Nancy S. Simon ·  
Terry R. Maret

Received: 18 March 2013 / Revised: 4 September 2013 / Accepted: 14 September 2013  
© Springer Science+Business Media Dordrecht (outside the USA) 2013

**Abstract** Efforts to limit plant growth in streams by reducing nutrients would benefit from an understanding of the relative influences of nutrients, streamflow, light, and other potentially important factors. We measured macrophytes, benthic algae, nutrients in water and sediment, discharge, and shading from 30 spring-fed or runoff-influenced streams in the upper Snake River basin, ID, USA. We hypothesized that in hydrologically stable, spring-fed streams with clear water, macrophyte and benthic algae biomass would be a function of bioavailable nutrients in water or sediments, whereas in hydrologically dynamic, runoff-influenced streams, macrophyte and benthic algae biomass would further be constrained by flow disturbance and light. These hypotheses were only partly supported. Nitrogen, both in sediment and water, was positively correlated with macrophyte biomass, as was loosely sorbed phosphorus (P) in sediment. However,

P in water was not. Factors other than nutrient enrichment had the strongest influences on macrophyte species composition. Benthic algal biomass was positively correlated with loosely sorbed sediment P, lack of shade, antecedent water temperatures, and bicarbonate. These findings support the measurement of bioavailable P fractions in sediment and flow histories in streams, but caution against relying on macrophyte species composition or P in water in nutrient management strategies for macrophytes in streams.

**Keywords** Aquatic macrophytes · Benthic algae · Eutrophication · Phosphorus fractionation · Nitrogen · Flow regime · Streams

**Electronic supplementary material** The online version of this article (doi:10.1007/s10750-013-1693-4) contains supplementary material, which is available to authorized users.

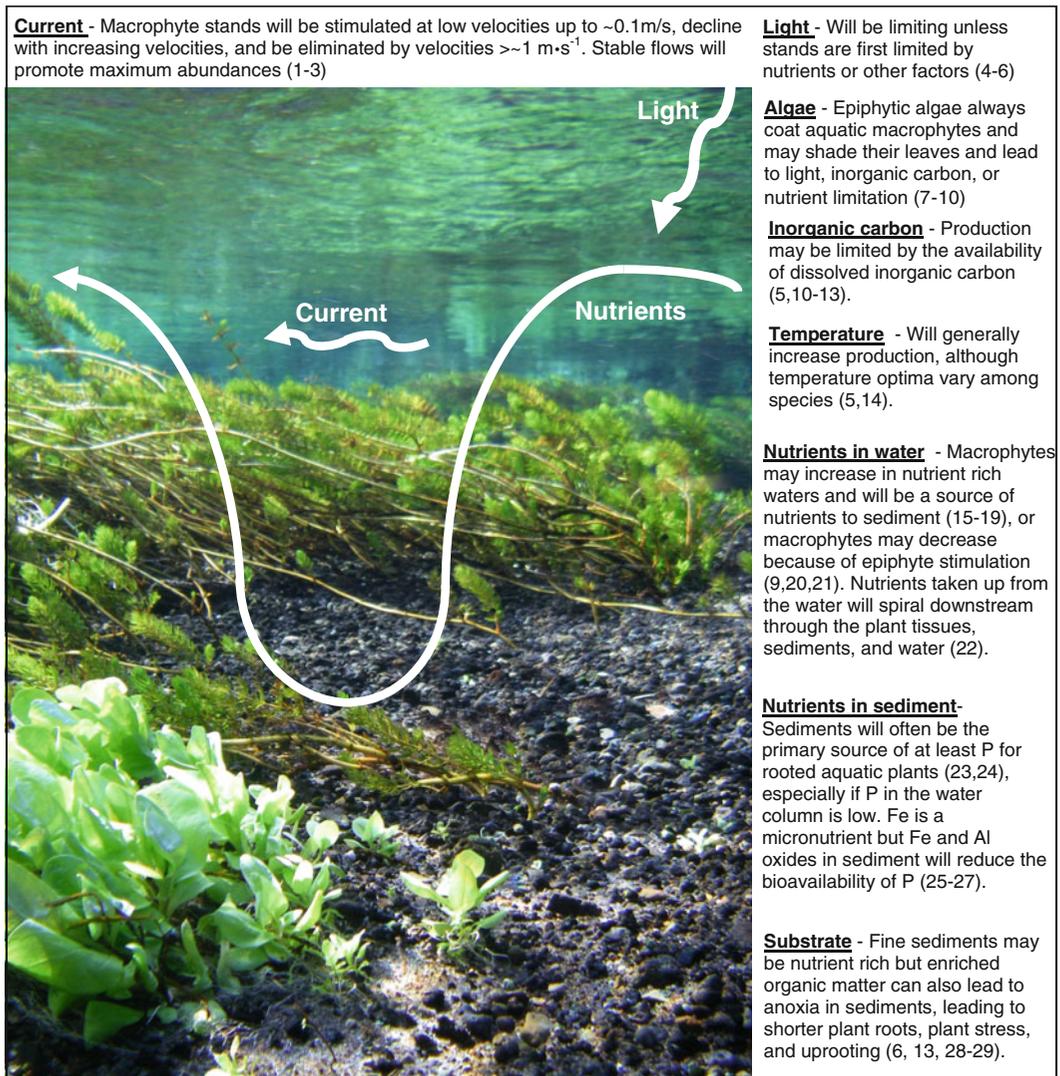
Handling editor: Sidinei Magela Thomaz

C. A. Mebane (✉) · T. R. Maret  
U.S. Geological Survey, 230 Collins Road, Boise,  
ID 83702, USA  
e-mail: cmebane@usgs.gov

N. S. Simon  
National Research Program, U.S. Geological Survey,  
Reston, VA, USA

## Introduction

Nutrient enrichment of streams and rivers is a widespread concern in agricultural and urban settings. In North America, much recent research has attempted to relate nutrient enrichment in the water columns of streams to benthic algae and other biologic variables (USEPA, 2000; Dodds, 2007; Maret et al., 2010; Munn et al., 2010; Chambers et al., 2012). However, nutrient enrichment in streams likely involves complex interactions between water column-nutrients, sediment-nutrients, attached algae and aquatic macrophytes (Hilton et al., 2006), and nutrient assessment



**Fig. 1** Conceptual model of the primary factors expected to influence macrophyte biomass in flowing waters. Numbers in parentheses refer to 1 Chambers et al. (1991), 2 Biggs (1996), 3 Madsen et al. (2001), 4 Canfield & Hoyer (1988), 5 Carr et al. (1997), 6 Squires & Lesack (2003), 7 Fitzgerald (1969), 8 Cattaneo & Kalff (1980), 9 Hilton et al. (2006), 10 Madsen & Sand-Jensen (1991), 11 Jones et al. (2002), 12 Wright & Mills

(1967), 13 Raun et al. (2010), 14 Rasmussen et al. (2011), 15 O'Hare et al. (2010), 16 Sosiak (2002), 17 Carr et al. (2003), 18 Thiébaud & Muller (2003), 19 Pelton et al. (1998), 20 Sand-Jensen & Borum (1991), 21 Wersal & Madsen (2011), 22 Clarke (2002), 23 Carignan & Kalff (1980), 24 Chambers et al. (1989), 25 Geurts et al. (2008), 26 Gensemer & Playle (1999), 27 Barko & Smart (1986), 28 Jones et al. (2012), photo from site 18

approaches that ignore sediments and macrophytes may be incomplete.

Aquatic macrophyte beds have long been recognized as fundamental parts of stream ecosystems by providing substrate for periphyton and associated secondary production by macroinvertebrate grazers, which in turn support fish and other predators (Butcher, 1933; Carpenter & Lodge, 1986). The

distribution and abundance of macrophyte beds in streams are a function of the stream environment, yet the beds may act as biological engineers and in turn structure physical, chemical, and biological aspects of streams (Gurnell, 2013). Macrophyte beds tend to retain sediments and the high productivity of macrophyte beds in turn may increase nutrient processing, increase the residence time of phosphorus (P) within a

given stream reach, and increase denitrification capacity and ultimate nitrogen removal (N) from streams (Clarke, 2002; Birgand et al., 2007; Feijoó et al., 2011). These features contribute to efforts to restore and protect macrophyte beds in rivers (Hilton et al., 2006; Franklin et al., 2008). However, macrophytes can also flourish in streams to the point that they become a major nuisance. Dense macrophyte stands can block water intakes, interfere with irrigation water delivery in canals, raise water levels in stream channels, and cause flooding (Chambers et al., 1999).

Many previous studies have investigated macrophyte abundance in streams and have reported current, nutrients, light, and substrate to be important factors influencing macrophyte abundance (Fig. 1). However, reports have been contradictory on the relative importance of these factors, or even whether a factor had a positive or negative influence on macrophyte abundances.

The objectives of our study were to determine whether nutrients, streamflow, or other environmental variables best explained macrophyte abundance in streams in an agriculturally dominated landscape. More specifically, we hypothesized that (1) in hydrologically stable, spring-fed streams with clear water, macrophyte and benthic algae biomass would be a function of bioavailable nutrients in water or sediments; and (2) in hydrologically dynamic, runoff-influenced streams, macrophyte and benthic algae biomass would further (also) be constrained by flow disturbance, light, and substrate. We selected a suite of field and laboratory measurements that we expected would capture the expected interplay of current, light, nutrients, and substrate, and we selected study sites that we anticipated would encompass a broad range of conditions. We present our results here from a broad perspective aimed at describing apparently important relations between environmental variables and macrophyte abundance. More detailed results and study area particulars that might be of only regional interest are presented in the Electronic Supplemental Materials.

## Methods

Our study streams are located in an agriculturally dominated river basin in the arid western United States, the upper Snake River basin in Idaho and Nevada (Online Resources 1 and 2). Thirty sites were

selected with the goal of obtaining a range of nutrient conditions from streams with different types and intensities of agricultural land uses. We selected sites from among the two prevalent stream types occurring in the study area, streams that are influenced by annual spring snowmelt runoff and spring-fed streams. The spring-fed streams had long-term base flow index (BFI) values ranging from 0.94 to 1.00. The BFI is the ratio of base flow to total flow volume for a given time period, where an ephemeral stream would have a BFI value of 0 and a stream with constant flows would have a BFI of 1 (e.g., Riis et al., 2008; Tesoriero et al., 2013). The runoff-influenced sites had BFI values ranging from 0.50 to 0.91 over the entire period of records for each site, which ranged from 4 to 96 years. The spring-fed streams have relatively stable flows and temperatures year around, clear waters, and also have a strong gradient of N concentrations depending on how much irrigation recharge water they receive (Clark & Ott, 1996). Here we considered streams to be “spring-fed” if (1) their peak flows were less than twice their late summer flows, (2) if the streams arose from either distinct vents, or (3) alluvial spring-fed streams that arose from diffuse seeps and springs without tributary contributions from higher elevation terrain. At sites with distinct vents, our sample reaches were at least 100 m downstream of the vents, which is beyond the ecological transition of springs to spring-fed streams (von Fumetti et al., 2007).

The runoff-receiving stream sites represent a gradient of agricultural influences ranging from streams serving as conveyances of irrigation wastewater to streams in natural conditions that are managed as wildlife and watershed reserves. The percentages of watershed areas upstream of each of the 30 sample locations allocated to agricultural land use, defined as cultivated crops or confined pasture, ranged from 0 to 92%. However, “percent agricultural land use” at a 1:100,000 scale from a remote sensing-based national land cover database ([www.mlr.gov](http://www.mlr.gov)), is a crude measure of agricultural disturbance to streams because the type and intensity of agricultural practices that directly or indirectly affect the water quality and physical habitat can vary widely. Thus, we also used a more focused agricultural intensity index which combined four variables: percent agricultural land use, percent riparian agricultural land use within 100 m of the channel based on interpretation of aerial orthophotos, and estimates of TN and TP inputs to the

watershed. The four variables were combined into an index on a 0–100 point scale, where 0 represents no agricultural influences and 100 represents maximum agricultural intensity (Waite, 2013). Index scores for our study sites ranged from 0 to 95.

### Physical, chemical, and biological measurements

Our methods are detailed in Online Resource 1, but briefly, each site consisted of a stream reach  $\geq 150$  m in length. Physical and chemical measurements included nutrients in water and sediment, channel characteristics including substrate sizes and light availability, and discharge. Phosphorus in sediment was analyzed by sequential extractions in order to identify the fraction most bioavailable to plants following the approach of Ruttenberg (1992), as modified for freshwater (Simon et al., 2009). Stream-flow history at sites was obtained by locating sampling sites near long-term stream gages where available (16 of 30 sites). For the remaining sites, we installed temporary stream gages in late winter prior to the snowmelt runoff, which provided a short-term ( $\sim 120$  days) seasonal flow history prior to our biological sampling in late summer. Biological measurements included benthic algae collected from 25 rock scrapes per site. Macrophyte channel cover was visually estimated at 55 points per reach (11 transects with five samples points each), and macrophytes were collected for species counts and biomass measurements by clipping all plant material above the substrate from five quadrats along each of three transects within the reach (Online Resource 1). For simplicity, we refer to sites only by a number and whether the stream was spring-fed or runoff-influenced. More site information is given in Online Resources 2 and 3.

### Data analysis

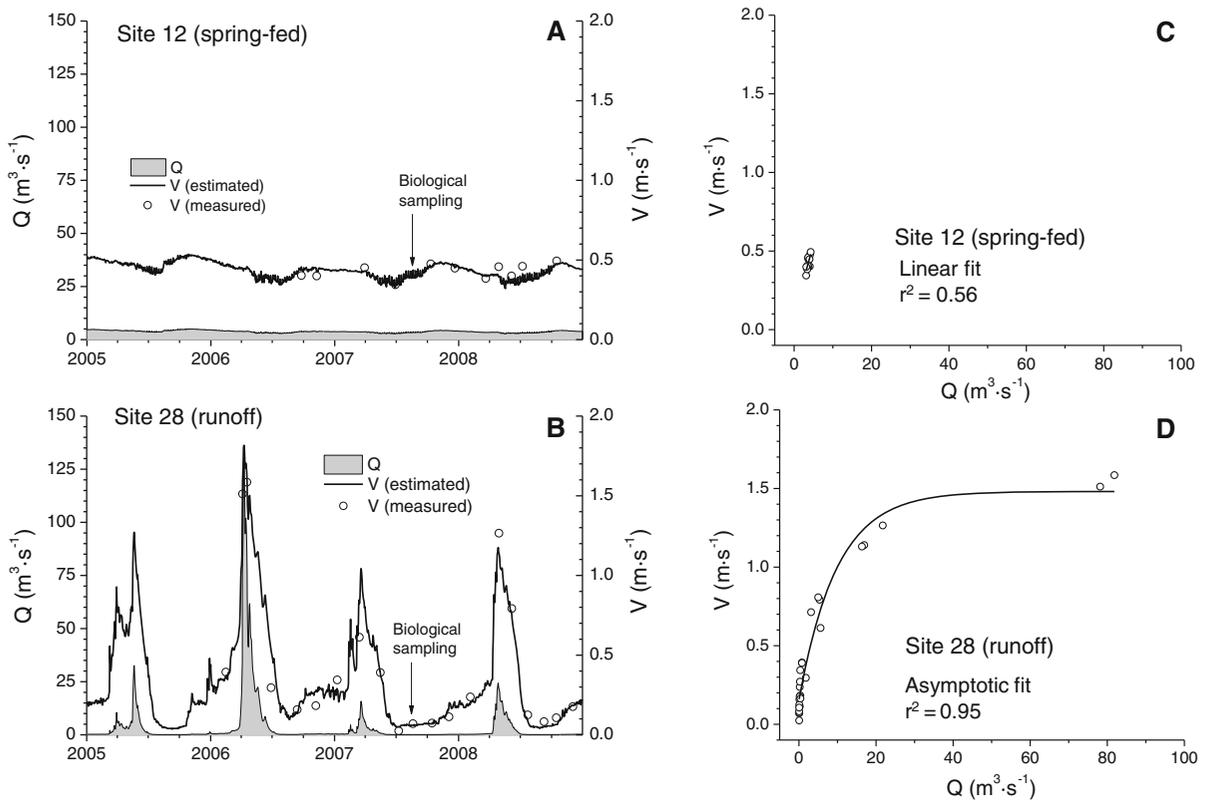
We focused our interpretations on those variables that are conceptually important to plant growth in streams (Fig. 1). These included measures of light, current, substrate type, nutrients in sediment and water as well as inorganic carbon availability, and algal density. To determine if extreme velocities occurring prior to our summer 2007 macrophyte sampling may have been more influential than the average velocities at the time of sampling (e.g., Gaines & Denny, 1993), we

constructed estimates of the maximum average cross-channel velocities occurring at our sites during the snowmelt runoff prior to sampling. This was done by developing a regression equation between the average cross-channel velocities measured as part of our discharge measurements and stage or discharge at each of the sites and applying the regressions to the continuous records of discharge or stage for each site.

We analyzed data through raw data graphing, multivariate ordinations of species composition, and multiple regression models (Clarke, 1993; Warton, 2008; O'Hare et al., 2010). The ordinations were constructed to explore associations between environmental variables and species occurrence. These include the Biota-Environmental (Bio-Env) optimization procedure which identifies the best subset of environmental variables that explain the biotic pattern. The procedure provides the highest rank correlation obtainable between the Bray–Curtis similarity matrix of the macrophyte taxa and the matrix of environmental data (Clarke et al., 2008). Multiple regression models were constructed to relate the abundances of macrophytes to potentially predictive variables. Model variables were selected among (1) the four major categories of variables that our conceptual model and bivariate correlations indicated should be important, i.e., those relating to light, current, sediment-nutrients, and water-nutrients (Fig. 1); and (2) within each of those categories, the single variable that had the strongest correlation with macrophyte biomass; and (3) was not strongly correlated ( $r < 0.5$ ) with another variable. We similarly examined benthic algae biomass.

### Results

Maximum velocity estimates at stream transects were acceptable at 22 of 30 sites with  $r^2$  coefficients of determination ranged from 0.56 to 0.97. At the remaining eight sites, the maximum measured average cross-channel velocities were used to estimate maximum velocities. Spring-fed sites had poor relations between discharge and velocity because they tended to have little change in either flow or velocity, and at two sites, the continuous velocity estimates were confounded by beaver damming. Estimated velocity histories are compared to discrete velocity measurements in Fig. 2 for two contrasting sites, one with nearly uniform velocities (0.4–0.5 m s<sup>-1</sup>), a relatively



**Fig. 2** Contrasting discharge and velocity histories at a spring site with stable flows and velocities and abundant macrophyte growth (site 12) and a site with annual velocity peaks, extreme differences in discharge, and sparse macrophytes (site 28)

weak discharge-velocity regression and abundant macrophytes, and the second, a runoff site with highly variable velocities ( $0.04\text{--}1.8\text{ m s}^{-1}$ ), had a very strong discharge-velocity regression, and sparse macrophytes. At low flows, velocities in the runoff site increased sharply with increasing discharge, but at very high flows velocities reached a maximum asymptote (Fig. 2). Similar nearly asymptotic discharge-velocity patterns were found at all the runoff sites.

#### Macrophyte species composition and environmental correlates

We identified 13 macrophyte taxa in the 30 synoptic study sites with seven common taxa encountered in sufficient abundances to estimate biomass. The most common taxon was the Sago pondweed, *Stuckenia pectinata* (L.) Börner, also known as *Potamogeton pectinatus* (Table 1).

In the principal components analysis (PCA), there was a rough delineation between spring-fed and runoff-

influenced sites, with the first two principal components explaining 51% of the total variation in the ordination (Fig. 3A). Spring-fed sites tended to be associated with higher concentrations of loosely sorbed P in sediments, and higher total nitrogen (TN) in both sediment and water. Runoff-influenced sites tended to have higher aluminum (Al) in sediment, maximum velocities ( $V_m$ ), and higher ratios of maximum flows to late summer baseflows ( $Q_m:Q$ ). *Mimulus*, *Veronica*, *Nasturtium*, and *Stuckenia* were associated with spring-fed sites (positive loading on the 1st principal component) and *Ranunculus* was only found at runoff sites. Sites associated with negative loading on the 2nd principal component included those with higher agricultural intensity (Ag), higher bicarbonate ( $\text{HCO}_3^-$ ), higher benthic algae biomass (Chla), higher proportions of fine-grained sediments (Fines), less riparian shading (Open), and higher *Stuckenia* biomass. *Veronica* and *Mimulus* were distinguished by positive loading on the 2nd principal component, in opposition to the negative loadings for *Stuckenia* and benthic algae (Fig. 3A).

**Table 1** Submerged aquatic plant collections for biovolume to biomass conversions

Species	Common name	Percentage of stream sites where species collected	Proportion moisture, average $\pm$ SD	Number of dry weight samples
<i>Stuckenia pectinata</i> <sup>a</sup>	Sago pondweed	53.3	0.91 $\pm$ 0.04	16
<i>Ranunculus aquatilis</i>	White water-buttercup	13.3	0.91 $\pm$ 0.01	3
<i>Nasturtium officinale</i>	Watercress	13.3	0.90 $\pm$ 0.07	3
<i>Veronica anagallis-aquatica</i>	Water speedwell	10.0	0.89	1
<i>Cladophora</i> sp.	Cladophora	6.7	0.91 $\pm$ 0.07	2
<i>Elodea canadensis</i>	Common waterweed	6.7	0.89	1
<i>Mimulus</i> sp.	Monkey-flower	3.3	0.91 $\pm$ 0.04	3

<sup>a</sup> Synonymous with *Potamogeton pectinatus*. We follow Kaplan's (2008) revision to "*Stuckenia pectinata* (L.) Börner" although we recognize that some authorities continue to consider this taxon properly in the genus "*Potamogeton*" (e.g., Raun et al., 2010; Jones et al., 2012). Other taxa that were noted at sites but were not collected in sample quadrats included *Potamogeton richardsonii* (Richardson's pondweed), *Chara vulgaris* (stonewort), *Myriophyllum sibiricum* (northern milfoil), *Ceratophyllum* sp. (coontail), *Lemna minor* (duckweed), and aquatic mosses

Ordinations based on Bray–Curtis similarities of macrophyte taxa biomass showed distinctive groupings among some sites (Fig. 3B). The large spring-fed sites 12, 18, and 20 grouped together, as did two small clusters of runoff-influenced sites. A large cluster of *Stuckenia* dominated streams consisted of both spring-fed and runoff sites, and included several sites with high agricultural intensity rankings (Fig. 3B). The ordination of the environmental data in Fig. 3C showed some similar clusters.

A subset of five environmental variables identified through the Biota–Environmental matching procedure provided the highest rank correlation ( $\rho$ ) obtainable between the macrophyte taxa similarity matrix and the matrix of environmental data. The best five explanatory variables which yielded a  $\rho$  value of 0.48,  $P = 0.01$ , were elevation (Elev), the agricultural intensity index (Ag), maximum velocity in the year prior to sampling (Vm), aluminum in sediment (Al), and % fine-grained sediments (Fines).

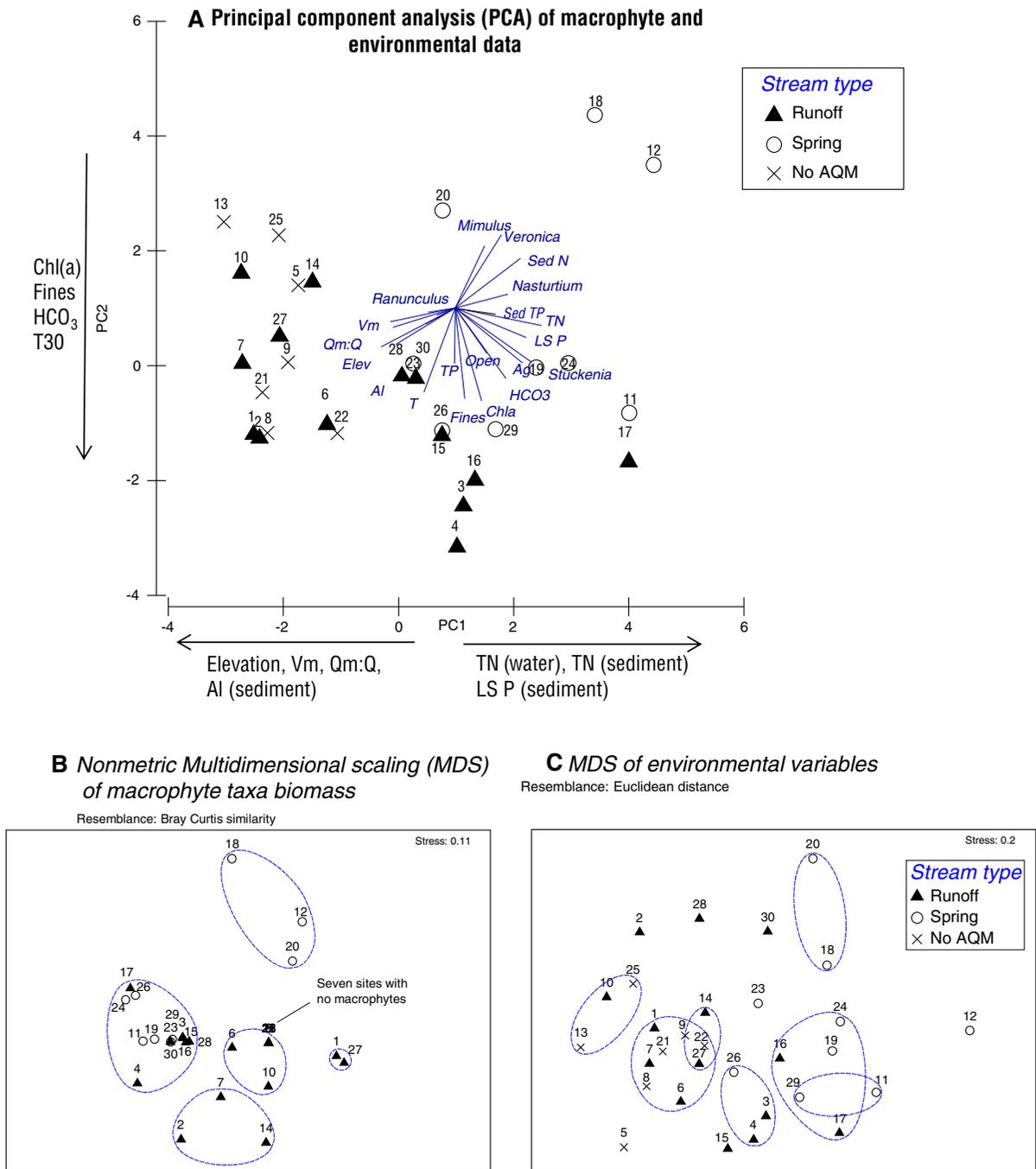
#### Macrophyte biomass and environmental co-variates

Overall macrophyte abundances, pooled for all species, varied widely in our study streams during the late summer sampling. The reach-wide mean percentage of stream channel surface areas covered by macrophyte beds ranged from 0 to 89% and mean biomass in

sample reaches ranged from 0 to over 1,800 g m<sup>-2</sup> (dry weight).

Wide ranges of abiotic variables were also measured. Total P concentrations in water ranged from 10 to 159  $\mu\text{g l}^{-1}$  and TN ranged from 110 to 3,908  $\mu\text{g l}^{-1}$ . Total N tended to be dominated by dissolved forms in spring-fed sites or sites receiving substantial agricultural runoff, with more variability in runoff-influenced sites. In the spring-fed sites, the median dissolved inorganic nitrogen (DIN), as a percentage of TN, was 87% versus a median of 23% for the runoff sites. The median dissolved OP was 77 versus 63% of TP in spring-fed and runoff sites, respectively. Nutrients in sediment varied by about a factor of 10 both for loosely sorbed P and total sediment nitrogen (Online Resource 3). Selected co-variates are plotted against macrophyte biomass in Fig. 4. Spring-fed sites are distinguished because these sites are little affected by runoff and associated high velocities, and were expected to be more responsive to nutrient enrichment.

Shading limited macrophyte abundance at some sites. Sites with less than about 70% unshaded channels consistently had low or no macrophytes present, and all sites that had abundant macrophytes had open channels (>80% unshaded, Fig. 4a). Turbidity was low at most of our sites (median 2.5, range 0.07–31 nephelometric turbidity units (NTUs)). Macrophyte abundance was low in turbid sites with >~10 NTUs, and the spring-fed sites which had the



**Fig. 3** Multivariate ordinations of macrophyte species composition and environmental variables. **A** Principal component analysis (PCA); the vector direction and length reflect the relative importance of that variable on either of the first two principal components. **B** Nonmetric multidimensional scaling (MDS) ordination of macrophyte species composition

superimposed with hierarchical clusters for 50% Bray–Curtis similarity. **C** MDS plot of environmental variables. The best environmental variables for explaining the macrophyte species composition were elevation (Elev), agricultural intensity index (Ag), maximum velocity (Vm), aluminum (Al), and % fine-grained sediments (Fines)

**Table 2** Multiple regression models for macrophyte and periphyton biomass

Model 1. Predicted variable: log (macrophyte biomass  $\text{g m}^{-2}$ ):  $r^2$  0.75, adjusted  $r^2$  0.71, SE ( $\epsilon$ ) 0.57, IRP 2.6 groups

Explanatory variables ( $x_k$ )	Coefficient ( $\beta_k$ )	Std. coefficient	<i>P</i>
Intercept ( $\beta_0$ )	2.38		
Log (TN)	0.923	0.37	0.004
Sqrt (Sed Al/P ratio)	-0.181	-0.34	0.007
Log ( $Q_{\max}/Q$ )	-0.530	-0.31	0.009
Asin (open)	0.987	0.24	0.038

Model 2. Predicted variable: Sqrt (periphyton chlorophyll *a* biomass  $\text{mg m}^{-2}$ ):  $r^2$  0.58, adjusted  $r^2$  0.52, SE ( $\epsilon$ ) 2.15, IRP 2.0 groups

Variable	Coefficient	Std. coefficient	<i>P</i>
Intercept	-0.23		
Log (LS <i>P</i> )	4.06	0.36	0.02
T30	0.397	0.34	0.03
Asin (open)	3.26	0.28	0.07
HCO <sub>3</sub>	0.0085	0.24	0.10

The adjusted  $r^2$  is an  $r^2$  that penalizes models for including more explanatory variables (Helsel & Hirsch, 2002). IRP index of resolution power; the number of different groups of the whole range of dependent values can be predicted with 95% confidence (Prairie, 1996)

highest abundances tended to have very clear water (Fig. 4b).

The highest macrophyte biomasses occurred at sites with nearly stable flows, and macrophyte biomasses declined at sites with increasing flow disturbance, as defined by the ratio of flows at the spring runoff maxima to flows at the time of sampling. Sites which experienced peak flows of at least a factor of 10 higher than late summer base flows usually had sparse or no macrophyte beds (Fig. 4c). Maximum velocities occurring in the year prior to the macrophyte sampling were negatively correlated with macrophyte biomass (Fig. 4d), and macrophytes were sparse at sites where velocities  $>1 \text{ m s}^{-1}$  had occurred.

Total N in water was strongly correlated with macrophyte biomass, as was N in sediment (Fig. 4e, g). Total N and DIN were highly correlated with each other ( $r = 0.93$ ) even though DIN as a percent of TN was extremely variable, ranging between 3 and 97%. Similarly, TP and OP were highly correlated ( $r = 0.93$ ), but in contrast to TN and DIN, TP in

**Fig. 4** Macrophyte biomass in relation to selected measures of light, current, sediment-nutrients, and water-nutrients: **a** percent of channel that is unshaded, **b** turbidity, **c** ratio of peak flows in the year prior to sampling to flows at the time of sampling ( $Q_{\max}/Q_{\text{sample}}$ ), **d** maximum water velocity in the year prior to sampling, **e** total N in water, **f** loosely sorbed P in sediment, **g** total N in sediment, and **h** ratio of Al to total P in sediments. *Circled numbers* are springbrooks, *other numbers* are runoff streams. Pearson's *r* correlation coefficients are with transformed data, with the data transformations, in X-Y order, in parentheses

water was not correlated with macrophyte biomass (Online Resource 1).

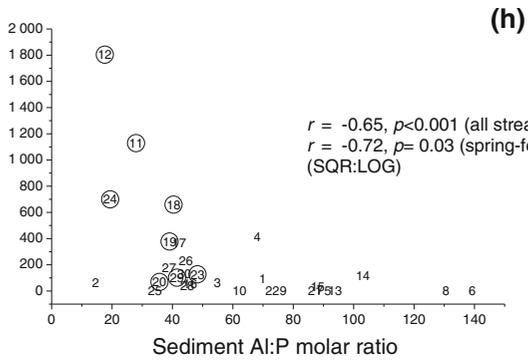
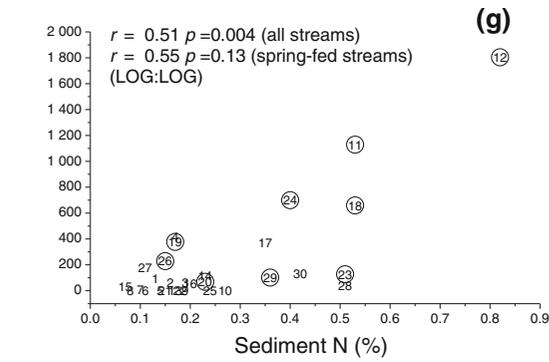
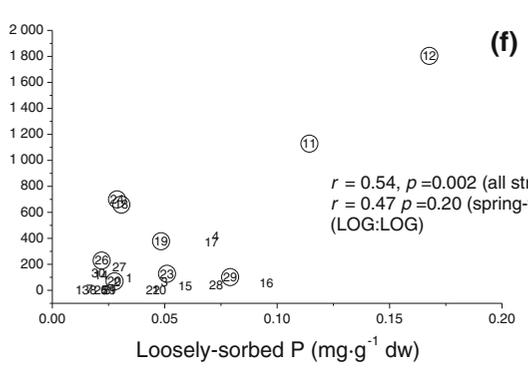
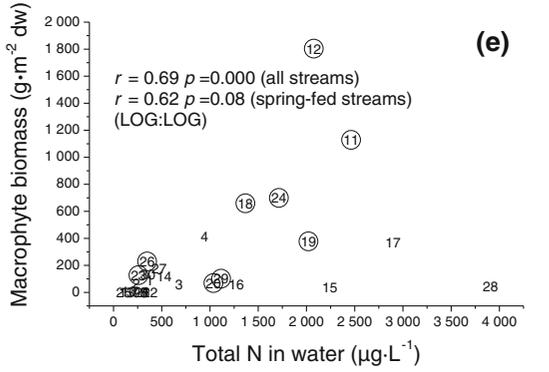
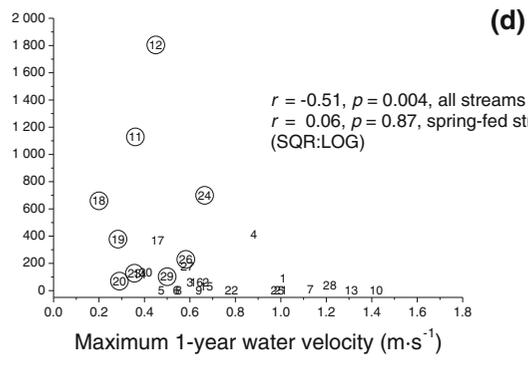
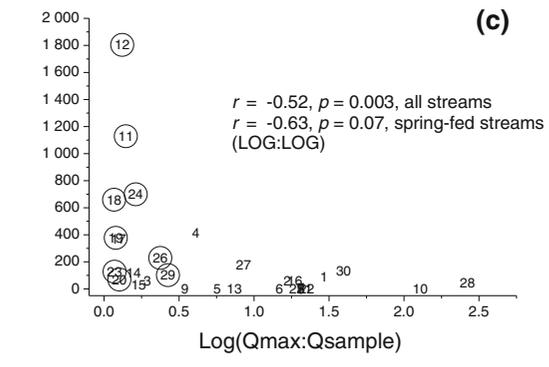
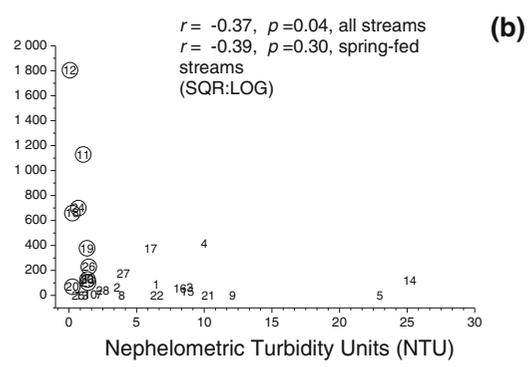
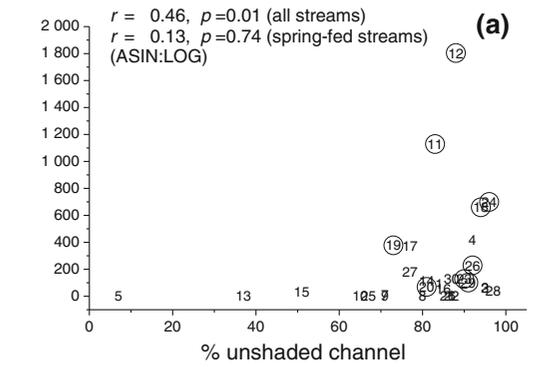
Loosely sorbed P in sediment was correlated with macrophyte biomass (Fig. 4f). Similarly, when total P in sediment was normalized to either Al or Fe concentrations to estimate bioavailable P, correlations with macrophyte biomass were stronger than was the correlation with total sediment P ( $r = 0.65$  for Al:P ratios, 0.60 for Fe:P ratios, versus 0.45 for total sediment P and macrophyte biomass, respectively (Fig. 4h; Online Resource 1).

Periphyton biomass was not strongly correlated with macrophyte biomass. Periphyton biomass in turn was positively correlated with loosely sorbed P in sediment, antecedent stream temperature, bicarbonate, and percent of the channel without shade. Other variables that we had anticipated might be strongly correlated with macrophyte abundance but were not included antecedent temperature, inorganic carbon, and fine sediment (Fig. 1; Online Resource 1).

#### Multiple regression models

We expected overall abundance of all macrophyte taxa in streams to be a function of at least four factors: light availability, current, nutrients in sediment, and nutrients in water (Fig. 1). We constructed a multiple linear regression model that reflected each of these factors, using the variables among each of these factors that had the strongest correlation with macrophyte biomass. The variables used were: % unshaded channel; current as  $Q_{\max}/Q$ ; sediment Al:P ratio, and TN in water.

A multiple linear regression model using these four independent variables to predict macrophyte biomass was able to account for 75% of the observed macrophyte biomass values (Table 2, model 1). The relative importance of the variables to the multiple regression ranged from 0.37 to 0.24 on a scale of 0–1 for the standardized coefficients. With benthic algae, loosely sorbed P in



sediments, stream temperature for the 30 days preceding sampling, % unshaded channel, and dissolved inorganic carbon as bicarbonate were the most important variables, respectively (Table 2, model 2).

## Discussion

Comparisons of our measurements of macrophyte abundance as percent areal cover on transect points or biomass showed that for most sites, the two measures were highly correlated (Online Resource 1). These results suggest that if a relative indication of macrophyte standing crop or productivity is sufficient for the purposes of a survey, the less-laborious percent areal cover is a reasonable measure even though it does not directly reflect the height of plants in the macrophyte beds.

### Macrophyte taxa composition and environmental co-variates

Much of the use of aquatic plants in biological assessment of water quality has been as an indicator of trophic status based upon species composition and diversity. Eutrophication has been implicated in declines in macrophyte diversity in streams and rivers (Steffen et al., 2013), and various nutrient classification-based trophic indices and species classifications have been developed (Thiébaud, 2008; Demars & Edwards, 2009). The support for this approach from our study area was equivocal. In the PCA of our data, *Stuckenia* biomass, TN in water, and loosely sorbed P in sediment did all contribute positively to the first principal component. However, the subset of environmental variables which provided the best biota-environmental match with the macrophyte species composition (agricultural intensity, maximum velocity, sediment aluminum, and % fine-grained sediments) did not include any direct measures of nutrients in water or sediment. Generally, both the PCA and MDS biota-environmental matching indicated that factors other than nutrient enrichment were the strongest influences on macrophyte species occurrence.

This conclusion is congruent with reports of ambiguous relationships in streams between macrophyte species composition-based indices and nutrient status or other water quality conditions (Demars et al., 2012). For example, in the low gradient, nutrient-rich

streams of Argentina's pampas region, nutrients (nitrate) and ionic strength were indeed the most important factors linked to macrophyte species composition (Feijóo & Lombardo, 2007). In contrast, in French and Danish streams, respectively, Demars & Thiébaud (2008) and (Riis et al., 2000) found that alkalinity exerted stronger influences on plant distribution than did nutrients in water. Also in French streams, Grasmück et al. (1995) found that geochemical parameters such as watershed geology, channel slope, and water clarity had stronger influence on macrophyte species composition than did parameters associated with nutrients. In more hydrologically dynamic New Zealand streams, the hydrologic regime (flood frequency) controlled the species composition and abundance of macrophytes, with no significant correlations between nutrients or alkalinity, and vegetation variables (Riis & Biggs, 2003). Although we found no other studies that were directly comparable to ours, i.e., that included flow history and nutrients in sediment and water, these findings from other areas are generally congruent with our findings that macrophyte species composition was less responsive to nutrient conditions than was total macrophyte biomass.

### Macrophyte biomass and environmental co-variates

#### *Flow and velocity*

Macrophytes were sparse or absent from streams which had springtime peak flows that exceeded late summer base flows by a factor of 10 or more. This is consistent with other observations of increased macrophyte abundance in streams with low and stable flows and long periods between disturbances, such as streams with reduced peak spring flows in regulated rivers or spring-fed streams (Biggs, 1996; French & Chambers, 1997; Biggs et al., 2005; Riis et al., 2008). The timing of high flow events is an important constraint on extensive macrophyte development (Biggs, 1996; Riis & Biggs, 2003; Robinson et al., 2009). Because high flows in our streams were from spring snowmelt rather than storms, the annual timing of high flows was similar for all sites. However, across our study area, peak flows in 2007 were lower than average, and peak flows in 2006 were higher than average, based on the previous 30 years of record. The

interannual differences in peak flows between 2006 and 2007 were large at some sites. For instance at runoff site 28, a peak flow of  $15.8 \text{ m}^3 \text{ s}^{-1}$  was recorded in 2007 but the peak flow in 2006 was almost an order of magnitude greater at  $132 \text{ m}^3 \text{ s}^{-1}$  (Fig. 3). This gives a 1-year  $Q_{\text{max}}/Q_{\text{sample}}$  ratio of 266 compared to a 2-year  $Q_{\text{max}}/Q_{\text{sample}}$  ratio of 2,210. Thus, while about a factor of 10 difference in annual flow magnitudes appeared to constrain development of extensive macrophyte beds, it could be that the less frequent, higher magnitude flow differences were what actually constrained macrophyte development.

Peak velocities occurring in the spring prior to the late summer sampling had a generally negative correlation with macrophyte biomass. Macrophytes were sparse or absent at sites where the peak velocities in the spring prior to sampling exceeded about  $1 \text{ m s}^{-1}$ . The apparent limiting threshold of about  $1 \text{ m s}^{-1}$  for macrophyte beds to develop corresponds with results from transplant experiments in the unregulated Pembina River, Alberta, Canada. There, macrophyte biomass decreased linearly with increasing current velocity up to  $1 \text{ m s}^{-1}$ , after which macrophytes were no longer present (Chambers et al., 1991). Average velocity measurements at the time of our summertime macrophyte collections tended to be very low and had no interpretive value in runoff streams. If only the stable velocity, spring-fed streams were considered, macrophyte biomass and average velocities were positively correlated (Fig. 4h), which is consistent with the idea that, if not extreme, current improves nutrient access in macrophyte beds.

### Light

Light availability, as measured by turbidity or as openness, i.e., percent of the stream channel that was unshaded by riparian vegetation or terrain, was clearly related to macrophyte biomass (Fig. 4a, b). However, our shallow streams had mostly open canopies and at least moderately clear water, and light was not as strong of a variable as in other areas where depth, shade, or turbidity appear to have been more defining. For instance, in low gradient, mostly forested streams with a wide gradient of TP and TN concentrations, percent riparian canopy cover accounted for over 90% of the variability in macrophyte standing crop (Canfield & Hoyer, 1988). In that study, macrophytes were

sparse when less than 50% of the stream surface was open to the sky, which was similar to our results.

Macrophyte biomass was expected to be low where benthic algal biomass was high, based on expected competition for light, inorganic carbon, and nutrients (Fig. 1). This expectation assumed that benthic periphyton is proportional to epiphytic periphyton because macrophytes simply provide a neutral substrate for periphyton to attach (Cattaneo & Kalff, 1979; Winter & Duthie, 2000; Hilton et al., 2006). This expectation seemed to hold for specific taxa, *Veronica* and *Mimulus*, which were separated from benthic algae biomass in the PCA ordination (Fig. 3a). However, this was not the case for benthic algae and *Stuckenia*, which were similarly oriented in the PCA. *Stuckenia* was the most commonly collected taxa, and when considering overall macrophyte biomass, the expectation of a negative correlation between macrophyte and benthic algae biomass was not borne out in our data.

### Nutrients in water

Phosphorus and nitrogen are most bioavailable in their dissolved inorganic forms, such as phosphate, nitrate, and ammonium (Biggs, 2000). Ammonium, the form of N in water most bioavailable to plants and thus most readily removed from the water column by uptake, was  $<10 \mu\text{g l}^{-1}$  in most samples and had no obvious relation to macrophyte biomass. Orthophosphate or DIN could potentially be related to macrophyte productivity because macrophyte stems and leaves have a thin cuticle through which nutrients can diffuse (Pelton et al., 1998). However, because OP and DIN concentrations measured late in the growing season may simply reflect the leftover nutrients that are surplus to macrophytes and algae, OP and DIN concentrations could have no correlation with or be negatively correlated with macrophytes and periphyton abundances. In our data, OP and TP in water were highly correlated ( $r = 0.93$ ).

Uptake of DIN in streams is rapid and dissolved organic nitrogen (DON) probably occurs in streams both as a refractory pool derived primarily from soils and a labile internally recycled pool which is readily bioavailable (Brookshire et al., 2005). Despite the large differences in DIN and TN concentrations in our samples, correlations between DIN and TN with macrophyte biomass were similar, supporting the idea that DIN does not solely reflect bioavailable N. There

was a consistent concentration dependence to the DIN:TN ratios. Below about  $700 \mu\text{g l}^{-1}$  TN, DIN made up less than half of the TN, and above about  $1,000 \mu\text{g l}^{-1}$  TN, almost all the TN was DIN. In N-saturated streams more DIN would be transported downstream without being transformed to organic forms (Brookshire et al., 2005). This suggests that our study streams were N saturated by about  $1,000 \mu\text{g l}^{-1}$  TN.

Total N in water had the strongest correlation with macrophyte biomass of any variables we examined, and TP was not correlated at all with macrophyte biomass. This could be related to macrophytes obtaining P through sediments rather than water. Alternatively it could reflect N limitation, which at least for benthic algae is common in our study area (Marcarelli et al., 2009). The prevalence of volcanic rock in our study area likely contributes to elevated P in water relative to natural conditions in non-volcanic areas (Wright & Mills, 1967; Dillon & Kirchner, 1975). The reasonably strong correlations between TN in water with macrophyte biomass or TN in sediment with macrophyte biomass (Fig. 4) is consistent with ideas that some macrophytes can alternatively obtain N from both water and sediment (Carr & Chambers, 1998).

#### *Nutrients in sediment*

Nitrogen in sediment showed a wedge-like pattern with macrophyte biomass, similar to a factor-ceiling distribution. Phosphorus in sediment, as total P, was also correlated to macrophyte biomass. However, deviations from this general pattern were common, which was similar to Carr & Chambers (1998) observation that macrophyte biomass in the South Saskatchewan River, Canada, was only weakly related to total sediment P. Our attempts to interpret the bioavailable fraction of sediment P as loosely sorbed P from the sequential extractions improved the correlation strength with both macrophyte and periphyton biomass. Similarly, normalizing total sediment P to Al or Fe also improved the strength of correlations with macrophyte biomass.

Iron and Al in riparian soils often control the release of P to shallow groundwater, which in turn is often the major source of dissolved P in stream water (Lyons et al., 1998). The use of Fe:P ratios has been used as an approach for estimating the mobility of P in sediments

to overlying water and the bioavailability of P in sediments for aquatic macrophytes (Jensen et al., 1992; Geurts et al., 2008). The streams with the highest macrophyte biomass correspond with low Fe:P ratios, and sites with Fe:P molar ratios greater than about 6 all had very low macrophyte biomass. This is similar to Jensen et al.'s (1992) observation that surface sediments with Fe:P molar ratios below about 5.5 seemed unable to retain P from release to the overlying water, and sediments with Fe:P molar ratios above 8 released very little P to the overlying water. Aluminum in sediment showed a generally negative pattern with macrophyte biomass, as did Al:P molar ratios. Macrophytes were sparse at sites with Al:P molar ratios  $>70$  (Fig. 4h, Online Resource 1).

Loosely sorbed P in sediment from sequential extractions is intended to measure the bioavailable fraction of P in sediment. Macrophyte biomass mostly increased linearly with increasing concentrations of loosely sorbed P. The loosely sorbed P obtained from the  $\text{MgCl}_2$  extraction seemed to be a good operational approach to measuring bioavailable P in sediments. Because the  $\text{MgCl}_2$  extraction was the first of the sequential extractions of P from sediments, the data for loosely sorbed P concentrations are obtained easily and the full extraction sequence provided little more useful information. We think this is a better measure of bioavailable P than stronger digestions such as NaOH extractions for “exchangeable P” that may include Al and Fe bound P fractions that are probably less bioavailable (Boström et al., 1988).

#### *Other factors*

Substrate particle size is closely related to sediment nutrient content and also is related to bed stability and the anchoring attachment of plants in streams (Riis & Biggs, 2003; Jones et al., 2012). In our data, the percentage of the channel substrate composed of fine-grained sediments was indeed associated with higher *Stuckenia* biomass (Fig. 3a). Reciprocal relations were expected between the establishment of macrophyte beds and fine sediment (Fig. 1). So long as light is not obstructed, increased fine sediments will tend to benefit the plants through increased nutrient concentrations in sediment, and macrophyte beds in turn will tend to cause increased fine sediments by reducing the velocity of stream water and trapping fine particles (Gregg & Rose, 1982; Jones et al., 2012). Organic

carbon (OC) in sediments was positively correlated with macrophyte biomass in our data, but this may simply reflect the tight correlation between OC and N in sediment (Online Resource 1). Plant detritus is the source of both organic C and N, and therefore we expect the concentrations of these elements in sediment to be correlated. Despite abundant nutrients, highly organic sediments can impede macrophyte abundance because consumption of oxygen during bacterial degradation of organic matter results in low concentrations of oxygen in the sediment leading to poor solute transport and shorter roots that uproot easily (Raun et al., 2010).

Dissolved inorganic carbon can promote macrophyte populations, and macrophytes are often abundant in streams with abundant carbonates, independent of anthropogenic nutrient sources (Fig. 1). Overall macrophyte biomass was not significantly correlated with bicarbonate (Online Resource 1). Macrophytes might be expected to grow better at warmer temperatures (Fig. 1). However, average temperatures for the 30-day period prior to macrophyte and periphyton collections were positively correlated with periphyton biomass but not with macrophyte biomass (Online Resource 1).

#### Multiple regression models of macrophyte and algae biomass

Multiple regression models were able to account for about 75 and 54% of the observed variability in macrophyte biomass and benthic algae chlorophyll *a* biomass, respectively (Table 2). Statistical macrophyte biomass models from field studies are sometimes weak (e.g., Carr & Chambers, 1998; Sosiak, 2002; Carr et al., 2003). In field studies such as these and our study, it may be possible that important relations are present but are not obvious from the data because of multiple factors or measurement errors. For example, macrophyte biomass in the Bow River (Alberta, Canada) greatly declined over 14 years following the installation of enhanced wastewater nutrient removal. Despite the large decline, correlations between nutrient concentrations in water and macrophyte biomass were weak, explaining only up to about 15% of the variability in macrophyte biomass (Sosiak, 2002). Similarly with a process-based model, calibrations of predicted macrophyte or benthic algae biomass were not very close to observations (Robinson et al., 2009).

Benthic algal biomass was positively correlated with channel openness, loosely sorbed P in sediments, antecedent temperature, and bicarbonate (Table 2; Online Resource 4). Unlike the macrophyte biomass model, flow variability and nutrients in water were not important factors in the algae model. The stronger correlation between algal biomass and loosely sorbed P in sediment than TP in water suggests that loosely sorbed P may be a more meaningful measure of the P available to benthic algae than was P in water during the growing season. Two reasons occur to us why this might be so. First, the sediments probably act as nutrient diffusing substrates, and the loosely sorbed P in sediment reflects the ongoing availability of P to the stream. Second, phosphorus in water during the growing season would only reflect the P that was surplus to algal uptake, and thus we would not expect this leftover P in water to be strongly correlated with benthic algae.

#### Conclusions

We had hypothesized that in hydrologically stable, spring-fed streams with clear water, macrophyte and benthic algae biomass would be a function of bioavailable nutrients in water or sediments. This was only supported in part. Nitrogen, both in sediment and water, was positively correlated with macrophyte biomass. While TP in water was not correlated with macrophyte biomass, loosely sorbed P in sediment was. Similarly sediment TP, expressed as either Fe:P ratios or Al:P ratios, was correlated with macrophyte biomass across both spring-fed and runoff streams. We further had hypothesized that in hydrologically dynamic, runoff-influenced streams, macrophyte and benthic algae biomass would also be constrained by flow disturbance, light, and substrate. Flow disturbance history and channel shading were strong constraints on macrophyte but substrate size was not a strong influence on total biomass in the streams studied. Factors other than nutrient enrichment had the strongest influences on macrophyte species composition.

Two lessons learned could be useful elsewhere. First, macrophyte biomass measurements were highly correlated with visual estimates of macrophyte cover, which were much less laborious. This suggests that if a relative indication of macrophyte standing crop or productivity is sufficient for the purposes of a survey,

the percent areal cover is a reasonable measure. Second, the loosely sorbed P obtained from the  $MgCl_2$  extraction seemed to be a good operational approach to measuring bioavailable P in sediments, and was much easier than the sequential extractions of P from sediments.

**Acknowledgments** Financial support for the study was from the U.S. Geological Survey's National Water Quality Assessment (NAWQA) Program.

## References

- Barko, J. W. & R. M. Smart, 1986. Sediment-related mechanisms of growth limitation in submersed macrophytes. *Ecology* 67: 1328–1340.
- Biggs, B. J. F., 1996. Hydraulic habitat of plants in streams. *Regulated Rivers: Research & Management* 12: 131–144.
- Biggs, B. J. F., 2000. Eutrophication of streams and rivers: dissolved nutrient-chlorophyll relationships for benthic algae. *Journal of the North American Benthological Society* 19: 17–31.
- Biggs, B. J. F., V. I. Nikora & T. H. Snelder, 2005. Linking scales of flow variability to lotic ecosystem structure and function. *River Research and Applications* 21: 283–298.
- Birgand, F., R. W. Skaggs, G. M. Chescheir & J. W. Gilliam, 2007. Nitrogen removal in streams of agricultural catchments – a literature review. *Critical Reviews in Environmental Science and Technology* 37: 381–487.
- Boström, B., J. M. Andersen, S. Fleischer & M. Jansson, 1988. Exchange of phosphorus across the sediment–water interface. *Hydrobiologia* 170: 229–244.
- Brookshire, E. N. J., H. M. Valett, S. A. Thomas & J. R. Webster, 2005. Coupled cycling of dissolved organic nitrogen and carbon in a forest stream. *Ecology* 86: 2487–2496.
- Butcher, R. W., 1933. Studies on the ecology of rivers. I. On the distribution of macrophytic vegetation in the rivers of Britain. *Journal of Ecology* 21: 58–91.
- Canfield, D. E. Jr & M. V. Hoyer, 1988. Influence of nutrient enrichment and light availability on the abundance of aquatic macrophytes in Florida streams. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1467–1472.
- Carignan, R. & J. Kalff, 1980. Phosphorus sources for aquatic weeds: water or sediments? *Science* 207: 987–989.
- Carpenter, S. R. & D. M. Lodge, 1986. Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany* 26: 341–370.
- Carr, G. M. & P. A. Chambers, 1998. Macrophyte growth and sediment phosphorus and nitrogen in a Canadian prairie river. *Freshwater Biology* 39: 525–536.
- Carr, G. M., H. C. Duthie & W. D. Taylor, 1997. Models of aquatic plant productivity: a review of the factors that influence growth. *Aquatic Botany* 59: 195–215.
- Carr, G. M., S. A. E. Bod, H. C. Duthie & W. D. Taylor, 2003. Macrophyte biomass and water quality in Ontario rivers. *Journal of the North American Benthological Society* 22: 182–193.
- Cattaneo, A. & J. Kalff, 1979. Primary production of algae growing on natural and artificial aquatic plants: a study of interactions between epiphytes and their substrate. *Limnology and Oceanography* 24: 1031–1037.
- Cattaneo, A. & J. Kalff, 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnology and Oceanography* 25: 280–289.
- Chambers, P. A., E. E. Prepas, M. L. Bothwell & H. R. Hamilton, 1989. Roots versus shoots in nutrient uptake by aquatic macrophytes in flowing waters. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 435–439.
- Chambers, P. A., E. E. Prepas, H. R. Hamilton & M. L. Bothwell, 1991. Current velocity and its effect on aquatic macrophytes in flowing waters. *Ecological Applications* 1: 249–257.
- Chambers, P. A., R. E. DeWreede, E. A. Irlandi & H. Vandermeulen, 1999. Management issues in aquatic macrophyte ecology: a Canadian perspective. *Botany* 77: 471–487.
- Chambers, P. A., D. J. McGoldrick, R. B. Brua, C. Vis, J. M. Culp & G. A. Benoy, 2012. Development of environmental thresholds for nitrogen and phosphorus in streams. *Journal of Environmental Quality* 41: 7–20.
- Clark, G. M. & D. S. Ott, 1996. Springflow effects on chemical loads in the Snake River, south-central Idaho. *Water Resources Bulletin* 32: 553–563.
- Clarke, K. R., 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18: 117–143.
- Clarke, S. J., 2002. Vegetation growth in rivers: influences upon sediment and nutrient dynamics. *Progress in Physical Geography* 26: 159–172.
- Clarke, K. R., P. J. Somerfield & R. N. Gorley, 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota–environment linkage. *Journal of Experimental Marine Biology and Ecology* 366: 56–69.
- Demars, B. O. L. & A. C. Edwards, 2009. Distribution of aquatic macrophytes in contrasting river systems: a critique of compositional-based assessment of water quality. *Science of the Total Environment* 407: 975–990.
- Demars, B. O. L. & G. Thiébaud, 2008. Distribution of aquatic plants in the Northern Vosges rivers: implications for biomonitoring and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18: 619–632.
- Demars, B. O. L., J. M. Potts, M. Trémolières, G. Thiébaud, N. Gougelin & V. Nordmann, 2012. River macrophyte indices: not the Holy Grail! *Freshwater Biology* 57: 1745–1759.
- Dillon, P. J. & W. B. Kirchner, 1975. The effects of geology and land use on the export of phosphorus from watersheds. *Water Research* 9: 135–148.
- Dodds, W. K., 2007. Trophic state, eutrophication and nutrient criteria in streams. *Trends in Ecology and Evolution* 22: 669–676.
- Feijóo, C. S. & R. J. Lombardo, 2007. Baseline water quality and macrophyte assemblages in Pampean streams: a regional approach. *Water Research* 41: 1399–1410.
- Feijóo, C., A. Giorgi & N. Ferreiro, 2011. Phosphate uptake in a macrophyte-rich Pampean stream. *Limnologia* 41: 285–289.

- Fitzgerald, G. P., 1969. Some factors in the competition or antagonism among bacteria, algae, and aquatic weeds. *Journal of Phycology* 5: 351–359.
- Franklin, P., M. Dunbar & P. Whitehead, 2008. Flow controls on lowland river macrophytes: a review. *Science of the Total Environment* 400: 369–378.
- French, T. D. & P. A. Chambers, 1997. Reducing flows in the Nechako River (British Columbia, Canada): potential response of the macrophyte community. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2247–2254.
- Gaines, S. D. & M. W. Denny, 1993. The largest, smallest, highest, lowest, longest and shortest: extremes in ecology. *Ecology* 74: 1677–1692.
- Gensemer, R. W. & R. C. Playle, 1999. The bioavailability and toxicity of aluminum in aquatic environments. *Critical Reviews in Environmental Science and Technology* 29: 315–450.
- Geurts, J. J. M., A. J. P. Smolders, J. T. A. Verhoeven, J. G. M. Roelofs & L. P. M. Lamers, 2008. Sediment Fe:PO<sub>4</sub> ratio as a diagnostic and prognostic tool for the restoration of macrophyte biodiversity in fen waters. *Freshwater Biology* 43: 2101–2116.
- Grasmück, N., J. Haury, L. Léglize & S. Muller, 1995. Assessment of the bio-indicator capacity of aquatic macrophytes using multivariate analysis. *Hydrobiologia* 300–301: 115–122.
- Gregg, W. W. & F. L. Rose, 1982. The effects of aquatic macrophytes on the stream microenvironment. *Aquatic Botany* 14: 309–324.
- Gurnell, A., 2013. Plants as river system engineers. *Earth Surface Processes and Landforms*. doi:10.1002/esp.3397.
- Helsel, D. R. & R. M. Hirsch, 2002. *Statistical Methods in Water Resources Techniques of Water-Resources Investigations of the United States Geological Survey, Book 4, Hydrologic Analysis and Interpretation, Chap. A3*. U.S. Geological Survey, Menlo Park: 524.
- Hilton, J., M. T. O'Hare, M. J. Bowes & J. I. Jones, 2006. How green is my river? A new paradigm of eutrophication in rivers. *Science of the Total Environment* 365: 66–83.
- Jensen, H. S., P. Kristensen, E. Jeppesen & A. Skytthe, 1992. Iron:phosphorus ratio in surface sediment as an indicator of phosphate release from aerobic sediments in shallow lakes. *Hydrobiologia* 235–236: 731–743.
- Jones, J. I., J. O. Young, J. W. Eaton & B. Moss, 2002. The influence of nutrient loading, dissolved inorganic carbon and higher trophic levels on the interaction between submerged plants and periphyton. *Journal of Ecology* 90: 12–24.
- Jones, J. I., A. L. Collins, P. S. Naden & D. A. Sear, 2012. The relationship between fine sediment and macrophytes in rivers. *River Research and Applications* 28: 1006–1018.
- Kaplan, Z., 2008. A taxonomic revision of *Stuckenia* (Potamogetonaceae) in Asia, with notes on the diversity and variation of the genus on a worldwide scale. *Folia Geobotanica* 43: 159–234.
- Lyons, J. B., J. H. Görres & J. A. Amador, 1998. Spatial and temporal variability of phosphorus retention in a riparian forest soil. *Journal of Environmental Quality* 27: 895–903.
- Madsen, T. V. & K. Sand-Jensen, 1991. Photosynthetic carbon assimilation in aquatic macrophytes. *Aquatic Botany* 41: 5–40.
- Madsen, J. D., P. A. Chambers, W. F. James, E. W. Koch & D. F. Westlake, 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. *Hydrobiologia* 444: 71–84.
- Marcarelli, A. M., A. T. Rugenski, H. A. Bechtold & R. S. Inouye, 2009. Nutrient limitation of biofilm biomass and metabolism in the Upper Snake River basin, southeast Idaho, USA. *Hydrobiologia* 620: 63–76.
- Maret, T. R., C. P. Konrad & A. W. Tranmer, 2010. Influence of environmental factors on biotic responses to nutrient enrichment in agricultural streams. *Journal of the American Water Resources Association* 46: 498–513.
- Munn, M. D., J. W. Frey & A. J. Tesoriero, 2010. The influence of nutrients and physical habitat in regulating algal biomass in agricultural streams. *Environmental Management* 45: 603–615.
- O'Hare, M. T., R. T. Clarke, M. J. Bowes, C. Cailles, P. Henville, N. Bissett, C. McGahey & M. Neal, 2010. Eutrophication impacts on a river macrophyte. *Aquatic Botany* 92: 173–178.
- Pelton, D. K., S. N. Levine & M. Braner, 1998. Measurements of phosphorus uptake by macrophytes and epiphytes from the LaPlatte river (VT) using <sup>32</sup>P in stream microcosms. *Freshwater Biology* 39: 285–299.
- Prairie, Y. T., 1996. Evaluating the predictive power of regression models. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 490–492.
- Rasmussen, J. J., A. Baattrup-Pedersen, T. Riis & N. Friberg, 2011. Stream ecosystem properties and processes along a temperature gradient. *Aquatic Ecology* 45: 231–242.
- Raun, A. L., J. Borum & K. Sand-Jensen, 2010. Influence of sediment organic enrichment and water alkalinity on growth of aquatic isoetid and elodeid plants. *Freshwater Biology* 55: 1891–1904.
- Riis, T. & B. J. F. Biggs, 2003. Hydrologic and hydraulic control of macrophyte establishment and performance in streams. *Limnology and Oceanography* 48: 1488–1497.
- Riis, T., K. Sand-Jensen & O. Vestergaard, 2000. Plant communities in lowland streams: species composition and environmental factors. *Aquatic Botany* 66: 255–272.
- Riis, T., A. M. Suren, B. Clausen & K. Sand-Jensen, 2008. Vegetation and flow regime in lowland streams. *Freshwater Biology* 53: 1531–1543.
- Robinson, K. L., C. Valeo, M. C. Ryan, A. Chu & M. Iwanyshyn, 2009. Modelling aquatic vegetation and dissolved oxygen after a flood event in the Bow River, Alberta, Canada. *Canadian Journal of Civil Engineering* 36: 492–503.
- Ruttenberg, K. C., 1992. Development of a sequential extraction method for different forms of phosphorus in marine sediments. *Limnology and Oceanography* 37: 1460–1482.
- Sand-Jensen, K. & J. Borum, 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany* 41: 137–175.
- Simon, N. S., D. Lynch & T. N. Gallaher, 2009. Phosphorus fractionation in sediment cores collected in 2005 before and after onset of an *Aphanizomenon flos-aquae* bloom in Upper Klamath Lake, OR, USA. *Water, Air, and Soil Pollution* 204: 139–153.
- Sosiak, A., 2002. Long-term response of periphyton and macrophytes to reduced municipal nutrient loading to the Bow

- River (Alberta, Canada). Canadian Journal of Fisheries and Aquatic Sciences 59: 987–1001.
- Squires, M. M. & L. F. W. Lesack, 2003. The relation between sediment nutrient content and macrophyte biomass and community structure along a water transparency gradient among lakes of the Mackenzie Delta. Canadian Journal of Fisheries and Aquatic Sciences 60: 333–343.
- Steffen, K., T. Becker, W. Herr & C. Leuschner, 2013. Diversity loss in the macrophyte vegetation of northwest German streams and rivers between the 1950s and 2010. Hydrobiologia 713: 1–17.
- Tesoriero, A. J., J. H. Duff, D. A. Saad, N. E. Spahr & D. M. Wolock, 2013. Vulnerability of streams to legacy nitrate sources. Environmental Science & Technology 47: 3623–3629.
- Thiébaud, G., 2008. Phosphorus and aquatic plants. Plant Ecology 7: 31–49.
- Thiébaud, G. & S. Muller, 2003. Linking phosphorus pools of water, sediment and macrophytes in running waters. Annales de Limnologie 39: 307–316.
- USEPA, 2000. Nutrient Criteria Technical Guidance Manual: Rivers and Streams. U.S. Environmental Protection Agency, Washington, DC. 253.
- von Fumetti, S., P. Nagel & B. Baltes, 2007. Where a springhead becomes a springbrook – a regional zonation of springs. Fundamental and Applied Limnology 169: 37–48.
- Waite, I. R., 2013. Development and application of an agricultural intensity index to invertebrate and algal metrics from streams at two scales. Journal of the American Water Resources Association 49: 431–448.
- Warton, D. I., 2008. Raw data graphing: an informative but under-utilized tool for the analysis of multivariate abundances. Austral Ecology 33: 290–300.
- Wersal, R. M. & J. D. Madsen, 2011. Influences of water column nutrient loading on growth characteristics of the invasive aquatic macrophyte *Myriophyllum aquaticum* (Vell.) Verdc. Hydrobiologia 665: 93–105.
- Winter, J. G. & H. C. Duthie, 2000. Stream epilithic, epipelic and epiphytic diatoms: habitat fidelity and use in biomonitoring. Aquatic Ecology 34: 345–353.
- Wright, J. C. & I. K. Mills, 1967. Productivity studies on the Madison River, Yellowstone National Park. Limnology and Oceanography 12: 568–577.