

Nitrogen, phosphorus, and eutrophication in streams

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Abstract

Flowing waters receive substantial nutrient inputs, including both nitrogen (N) and phosphorus (P), in many parts of the world. Eutrophication science for rivers and streams has unfortunately lagged behind that for lakes, and results from lakes might inform those interested in stream eutrophication. A key controversy in lake eutrophication science is the relative importance of controlling P and N in water quality management, and we are interested how the science of this controversy transfers to flowing waters. A literature review indicates (1) stream benthic chlorophyll is significantly correlated to both total N and total P in the water column, with both nutrients explaining more variance than either considered alone; (2) nutrients have increased substantially in many rivers and streams of the United States over reference conditions, and strong shifts in N and P stoichiometry have occurred as well; (3) bioassays often indicate N responses alone or in concert with P responses for autotrophic (primary production and chlorophyll) and heterotrophic (respiration) responses; (4) both heterotrophic and autotrophic processes are influenced by the availability of N and P; and (5) N-fixing cyanobacteria usually do not seem to be able to fully satisfy N limitations in rivers and streams when P is present in excess of N. These data suggest both N and P control should be considered in the eutrophication management of streams.

Key words: eutrophication, nitrogen, phosphorus, streams

Introduction

There have been strong anthropogenic effects on rivers and streams of the world (Smith et al. 1999), including substantial increases in nutrients in many of them (Meybeck 1982, 1993, Meybeck and Helmer 1989, Alan 2004). Concerns about stream eutrophication have been raised as the United States and other countries have started to adopt nutrient control in management of streams (Dodds and Welch 2000). River and stream eutrophication science has lagged behind that for lakes, however, and it is important to know how well our knowledge transfers from lentic to lotic ecosystems.

Considerable controversy has occurred over the relative roles of nitrogen (N) and phosphorus (P) in controlling the eutrophication of lakes. This controversy primarily stems from differences of opinion regarding a general paradigm developed more than 3 decades ago

suggesting that P mainly limits freshwaters, N mainly limits marine waters, and estuarine habitats may be transitional (Hecky and Kilham 1988). The evolution of this view is rooted in historical battles over nutrient limitation and eutrophication and subsequent experimental demonstration by Schindler (1974) that inorganic carbon supplies were not growth-limiting to phytoplankton blooms (Fisher et al. 1995, Sterner 2008). More recently, however, the view that P alone limits algal production in lakes has been challenged by researchers who argue that N also plays an important role (Howarth and Paerl 2008, Lewis and Wurtsbaugh 2008, Paerl 2009), whereas others contend that P loading control alone is sufficient to control eutrophication (Schindler and Hecky 2008, Schindler et al. 2008, Schindler 2012).

The argument for N as well as P being an important factor controlling phytoplankton biomass is based on more than 50 years of bioassays indicating the presence of

N limitation, or of N and P co-limitation (Morris and Lewis 1992, Dodds et al. 1989, Elser et al. 1990, 2007). Empirically, it has been broadly confirmed that more algal biomass is produced per unit total P in the water column when total N to total P ratios (TN:TP) are high, based on analyses of summer means from the epilimnia of lakes (e.g., Smith 1982, Prairie et al. 1989). Moreover, although the biogeochemistry of P does not have a significant gaseous component, dissolved inorganic N can be lost in the form of N_2 via microbial denitrification, thus reducing N availability in the water column of both rivers and lakes (Hill 1979, Paerl et al. 2014).

The counterarguments in favor of an ultimate primacy of P limitation in lakes are that (1) N fixation should ultimately compensate for N deficiencies in phytoplankton communities; (2) the responses of bioassays often widely diverge from those of whole-lake because of the unnatural conditions that exist within the closed bioassay enclosures and because bioassays are typically run only for short periods (hours, days, or weeks), whereas the phytoplankton communities of whole lakes respond over multiple years; and (3) N-loading control could incur unnecessary expense in eutrophication control (Schindler 1974, Schindler and Hecky 2008, Schindler et al. 2008, Schindler 2012).

Our aim was to explore the issue of N and P as pollutants in streams and determine whether the water quality management arguments proposed by lake scientists also may apply to streams. To approach this question we first discuss how lake-based approaches can be applied to streams with respect to algal biomass and then assess the degree to which nutrients and nutrient ratios have changed over time in the United States. We then consider the idea that community responses other than biomass accumulation might be important in assessing the effects of nutrients on trophic state in streams. Results from small-scale bioassays, whole-stream nutrient additions, and analyses of other components of fluvial food webs are placed in context with N and P enrichment. Finally, we consider the degree to which N fixation can potentially compensate for N deficiencies in stream ecosystems.

Correlations among nutrients and algal biomass in flowing waters

A key advance in eutrophication science was the development of statistical relationships between epilimnetic algal biomass and water column concentrations of TP (Sakamoto 1966, Dillon and Rigler 1974, Vollenweider 1976, Cooke et al. 2005). Quantitative estimates of in-lake TP concentrations are then predicted from nutrient inputs from the surrounding watershed and

airshed, and a plan for nutrient loading-based eutrophication control is constructed. A parallel empirical approach was taken by Lohman et al. (1992) to link benthic algal biomass and total water column nutrients for streams in Missouri. This approach was subsequently broadened to (predominantly temperate zone) streams located throughout the world (Dodds et al. 2002, 2006), and several key findings emerged. In these studies, TN and TP were found to be correlated with benthic algal biomass up to a point, but these relationships leveled off at high P or N concentrations. As in lakes (Smith 1982, Prairie et al. 1989), N and P together described benthic algal biomass better than either alone, and more P means more chlorophyll with per unit N and vice versa (Fig. 1). This

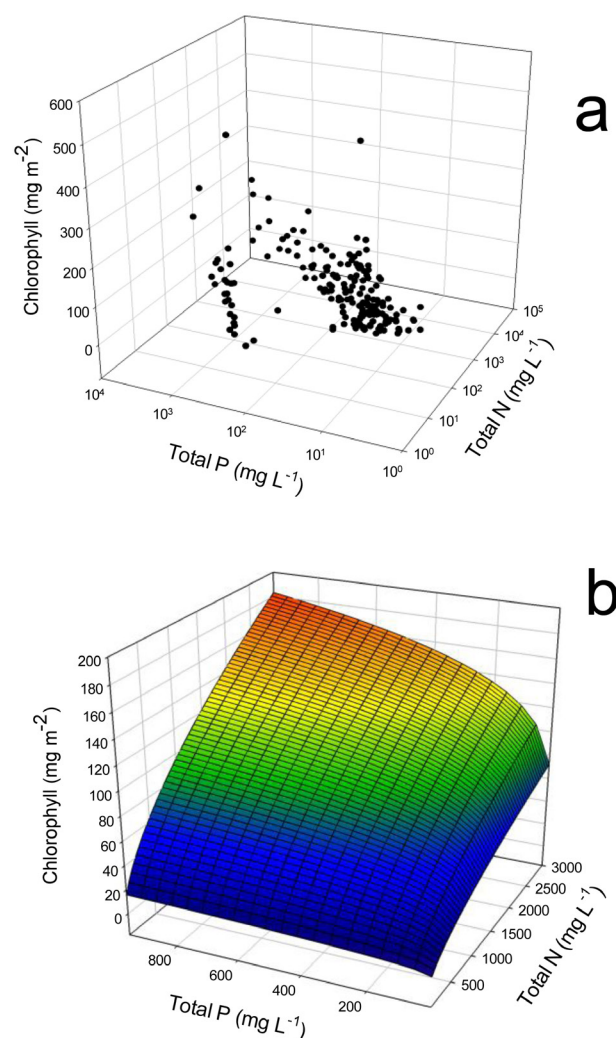


Fig. 1. (a) Summer mean benthic chlorophyll concentrations from streams worldwide as a function of summer mean concentrations of total P and total N in the water column. (b) Response surface derived from multiple regression analyses of the data shown in Figure 1a. Data from Dodds et al. (2006).

relationship was used to guide nutrient control efforts in the Clark Fork River of Montana (Dodds et al. 1997), and it was later demonstrated that benthic algal biomass declined as predicted in regions of the watershed where nutrient loading was controlled (Suplee et al. 2012).

The above evidence suggests that both N and P jointly play a role in the stimulation of benthic algal productivity in streams. Just as Smith (1982) showed for lakes, less algal biomass is expected if both N and P are lowered; however, these are just correlations. One problematic issue with the lake data is that high algal biomass must lead to more N and P because the cells of phytoplankton are made up of these elements. At least for rivers and streams, suspended algae in the water column are distinct from benthic algal biomass, with the planktonic biomass forming a minor amount of total algal biomass in any but the slowest and largest lentic systems. This spatial separation of primary productivity could be one reason the chlorophyll/nutrient relationships are much weaker in streams than in lakes, but other factors could increase variability, including flooding (e.g., Biggs 1995), herbivory, and light attenuation by riparian vegetation.

In a study of modestly impacted streams in the foothills and mountains of Colorado, Lewis and McCutchan (2010) found no evidence for correlation of periphyton biomass correlation with any form of P and a weak but significant correlation with dissolved inorganic N concentrations. They suggested that greater concentration increases could be necessary to increase benthic algal biomass; that invertebrate grazing cannot explain their observed patterns; and that other factors, such as algal biomass at start of growing season, length of growing season, and water temperature, explained more of the variation of periphyton biomass in these nutrient-poor to modestly enriched streams.

Planktonic algal biomass in rivers is also strongly linked to concentrations of TP in the water column. Van Nieuwenhuysse and Jones (1996) observed a similar leveling off of chlorophyll at high P resembling that of Dodds et al. (2002), but, presumably because TN measurements were not available, Van Nieuwenhuysse and Jones (1996) did not test whether the inclusion of total N improved their regression relationship for suspended chlorophyll *a* in streams. Further analyses might reveal similar results, with river phytoplankton biomass being dependent on the concentrations of both TN and TP in the water column, but such multivariate regression analyses have not yet been attempted or published to our knowledge.

In general, we conclude a strong statistical link exists between both N and P and algal biomass in streams (at least benthic algal biomass); thus, at least one piece of

evidence suggests that both nutrients should be considered in eutrophication management efforts for flowing waters. If nutrient pollution of streams is not a widespread problem, however, then eutrophication issues would be unimportant in rivers and streams. As we demonstrate, there is strong evidence that anthropogenic N and P enrichment has influenced eutrophication-related water quality in fluvial ecosystems.

How much nutrient enrichment has occurred in US rivers, and how have N:P ratios changed?

A key issue in eutrophication science is determining the baseline conditions that existed before large-scale anthropogenic modification of landscapes and the advent of nutrient losses from modern agriculture and increased rates of atmospheric nutrient deposition. Several approaches have been suggested for local determination of reference nutrient levels, with the best approach involving comparisons of present conditions to reference or slightly modified systems. Unfortunately, however, many areas of the United States do not currently contain reference-quality streams because nutrient exports have remained unaltered since European colonization in only a small number of relatively isolated watersheds. In addition, widespread atmospheric deposition of both N and P makes finding a watershed that can be used as a reference even more unlikely.

The initial approach developed to define reference nutrient concentrations delineated areas expected to naturally have higher or lower concentrations of nutrients. This spatial delineation led to the idea of nutrient ecoregions (Omernik 1987, 1995); however, some US ecoregions (e.g., the Corn Belt) were defined without available true natural reference conditions. Given these uncertainties, 2 approaches have since been used to estimate baseline pre-European settlement nutrient concentrations across the United States. Smith et al. (2003) used the Sparrow model to model expected streamwater nutrient concentrations across the country. Dodds and Oakes (2004) later linked stream nutrient concentrations to land-use/land-cover data (a multivariate approach similar to that used previously by Omernik 1987) and used these relationships to factor out the anthropogenic influence (i.e., by extrapolating to zero anthropogenic effect using multiple regression methods). The conclusions from these 2 independent approaches agreed broadly.

Subsequently, the predicted baseline nutrients were compared to river surveys by the Environmental Protection Agency (using nationwide data filtered to remove bias, mostly from the 1990s) to estimate the

degree of enrichment in US streams (Dodds et al. 2009). These data revealed that median values of TN and TP have increased over time in most of the ecoregions of the United States, in many cases dramatically (Fig. 2). We thus conclude that the nutrient enrichment of flowing waters in the United States is a common and real problem.

Data from US rivers collected by the United States Geological Survey (Alexander et al. 1996) reveal a wide range of TN and TP in the water column of US rivers (Fig. 3a). As noted in the previous section, the observed range of TN and TP concentrations predicts N limitation of algal growth in some stream and river ecosystems and

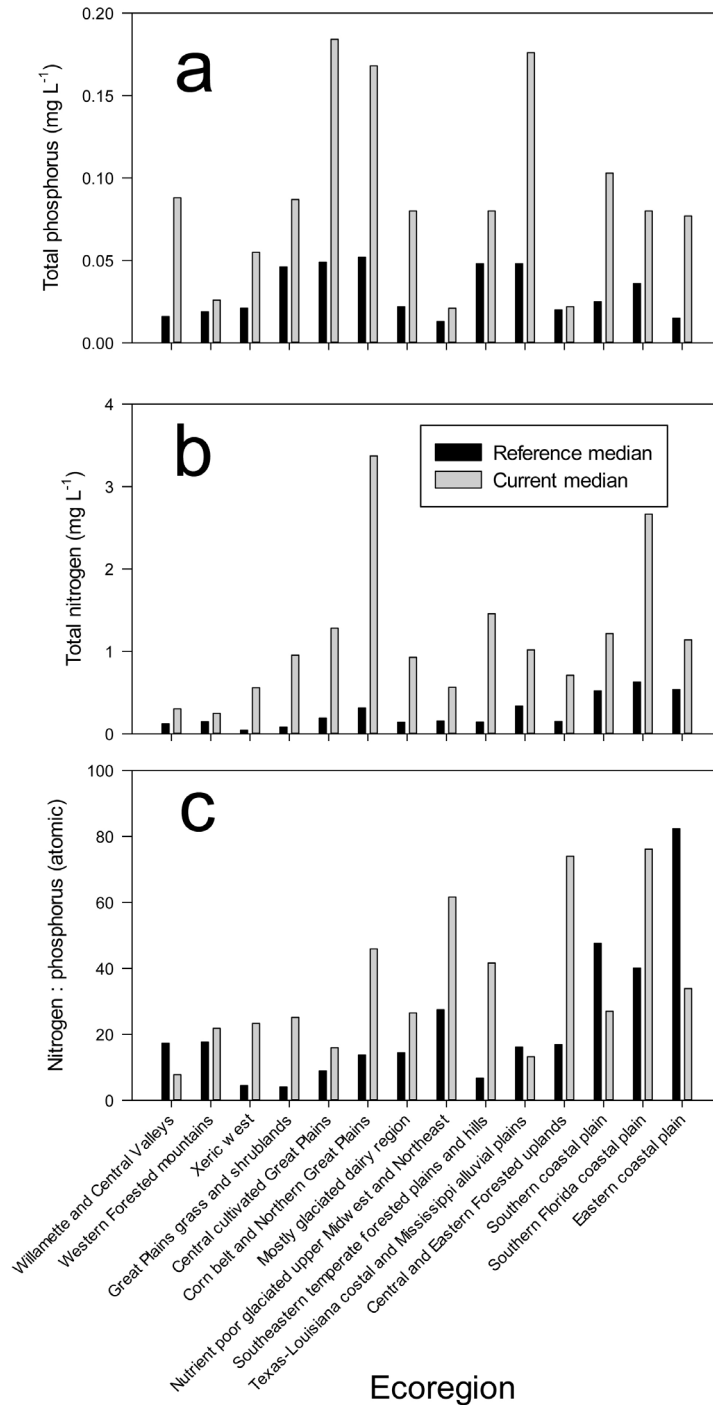


Fig. 2. Reference and current (1990s) median (a) total phosphorus, (b) total nitrogen, and (c) atomic nitrogen to phosphorus ratios by nutrient ecoregion across the United States. Data replotted from Dodds et al. (2009).

Table 1. Suggested trophic boundaries for rivers and streams (from Dodds et al. 1998). Note these were based on current nutrient distributions in the United States at the time, not corrected for anthropogenic influence (an unknown proportion of the sites used to create these distributions were true reference sites).

Variable (units)	Oligotrophic	Mesotrophic	Eutrophic
mean benthic chlorophyll (mg m^{-2})	<20	20–70	>70
maximum benthic chlorophyll (mg m^{-2})	<60	60–200	>200
suspended chlorophyll ($\mu\text{g L}^{-1}$)	<10	10–30	>30
Total N ($\mu\text{g L}^{-1}$)	<700	700–1500	>1500
Total P ($\mu\text{g L}^{-1}$)	<25	25–75	>75

P limitation in others. A Redfield ratio N:P of 16:1 by moles in general indicates a roughly balanced supply of N and P, and algae assemblages tend to mirror this ratio fairly closely when growing under balanced growth conditions (Hillebrand and Sommer 1999). Many TN:TP ratios observed in US rivers and streams greatly exceed the Redfield ratio; however, many others are far lower than 16:1 (Fig. 3b).

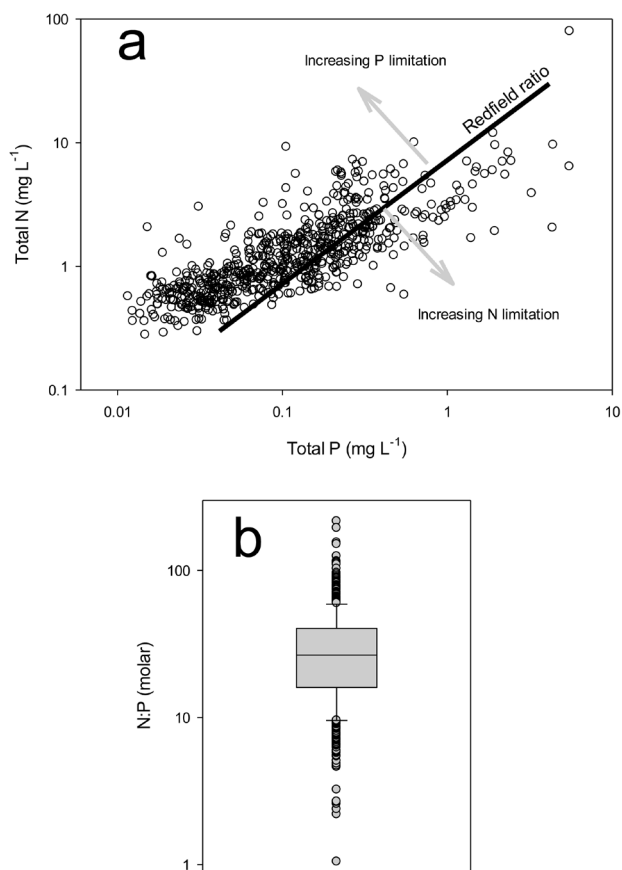


Fig. 3. Total N and total P values from (a) 658 US rivers with 10 or more data collections from 1973–1995 (Alexander et al. 1996). Line indicates a molar ratio of 16:1. (b) Distribution of N:P molar ratios in the same dataset. Median is middle box, and top and bottom of box are the 75th and 25th percentiles respectively; whiskers denote the 5th and 95th percentile of the data.

The median values of the reference and current values for data from Dodds et al. (2009) can also be used to estimate how nutrient stoichiometry changes in response to nutrient enrichment. The increases in N and P concentrations have not been proportional, and therefore the degree of N or P limitation in streams could have shifted with anthropogenic inputs; however, this change is not consistent among nutrient ecoregions (Fig. 2). Although an increase in TN:TP is more common across ecoregions, the sampling protocol for these data is not proportional to the actual number of streams in each ecoregion, and ecoregions vary considerably in total area and drainage density within the ecoregion. Sampling weighted among and within ecoregions also may be important because N:P ratios depend on flow paths in each individual watershed (Green et al. 2007).

These changes in nutrient stoichiometry also can influence both community structure in rivers and streams and the proportion of different elements transported downstream (Justić et al. 1995). By extension, changes in stoichiometry may change trophic state and food web pathways in rivers and streams (discussed briefly below).

The concept of trophic state in streams

Although stream researchers have long recognized that carbon sources for stream organisms can originate both from within (autochthonous) or outside (allochthonous) the system (Vanotte et al. 1980), this important distinction has less recently transferred to the traditional concept of trophic states. Traditionally, the trophic state of lakes has been based on phytoplankton biomass concentration, which was thought to represent the main food source for consumers in the food web. Thus, eutrophication science has historically been focused on nutrient stimulation of algal productivity (with biomass serving as a proxy for production). The role of allochthonous materials in food webs of lakes and oceans, however, is now recognized as substantial, and their contribution can at times be greater than autochthonous production (Dodds and Cole 2007). A new view of eutrophication, based on the Greek root of the word *eutrophia* for food, is therefore necessary to

capture the full ecological consequences of nutrient enrichment in streams because nutrient availability can influence the processing of detritus as well as the quality of algal food sources for consumer organisms. This view adds more complexity to trophic state assessment approaches based on measured concentrations of nutrients and chlorophyll alone (e.g., Table 1).

Dividing the concept of trophic state into autotrophic and heterotrophic facets makes clear that both internal and external sources of carbon to stream food webs should be considered to best understand energy flows through these ecosystems (Dodds 2007). The classic definition of trophic state based on phytoplankton for lakes was initially transferred directly to benthic algal biomass in streams, and the links between algal biomass and nutrient additions were the only factors considered to respond to nutrient enrichment. Many heterotrophic processes, such as carbon cycling, however, can potentially be limited by the supply rates of inorganic nutrients because many sources of detritus are carbon-rich and N- and P-poor (e.g., Ferreira et al. 2015).

Several reviewers have considered bioassays in streams (e.g., Francoeur 2001), typically based on the use of nutrient-diffusing substrata such as permeable clay pots (Pringle and Bowers 1984) or plastic containers with permeable tops (Tank and Webster 1998) filled with nutrient-enriched agar and placed in streams. After an *in situ* colonization and incubation period of several weeks, these substrata are removed and analyzed for attached

chlorophyll density on the solid surfaces. In general, early chlorophyll-based bioassays demonstrated that responses could be found to N alone, P alone, N+P, or neither nutrient (e.g., Francoeur 2001, Elser et al. 2007). Although no response was fairly common, growth responses to N alone or N+P were also frequently observed. These data suggest that, at least in the short-term, benthic algal biomass production in streams can be limited by factors other than N and P alone.

Additional twists to enrichment bioassays include adding a diffusing substrate made of thin wood (Tank and Webster 1998) to simulate natural detrital surfaces. Researchers have also started to measure variables in addition to chlorophyll, including measurements of ergosterol content for fungal biomass response (Tank and Dodds 2003) and analyses of gross primary production and respiration (Johnson et al. 2009). Johnson et al. (2009) explored nutrient responses using both inert substrata (porous glass) and wood veneers. They monitored respiration, gross primary production, and chlorophyll as the response variables (Fig. 4) from 62 sites in reference, agricultural, and urban settings across the United States and found several interesting patterns: (1) the chlorophyll response varied across substrata, but N limitation and N and P co-limitation were indicated as for prior bioassays; (2) the primary production and respiration responses could be stimulated by factors other than P alone, and the 2 responses could vary at the same site (i.e., heterotrophic and autotrophic responses did not always match); and (3) responses varied on wood and glass substrata, indicating that the carbon in the wood or physical differences in the 2 substrata led to the development of different biofilm communities that in turn responded differently to nutrient enrichment.

Given the observed diversity of responses to nutrient enrichment, stream bioassays unfortunately tend to leave us in much the same position as in lakes. What if, as Schindler (2012) claims, short-term bioassay results are simply not indicative of long-term responses? Whole-stream nutrient enrichment experiments for streams are far less common than for lakes; some studies have reported increases in algal production, but not all of these responses are completely attributable to P enrichment alone (e.g., Stockner and Shortreed 1978, Perrin et al. 1987, Peterson et al. 1993, Borchardt 1996).

More recently, some interesting results have indicated that both nutrients can be important, not only to whole-ecosystem algal biomass but also to whole-ecosystem carbon processing and transport (e.g., Gulis and Suberkropp 2003, Ferreira et al. 2006). For example, a series of whole-stream nutrient additions in the US Adirondacks was recently performed at varied N:P ratios, and multiple response variables including rates of

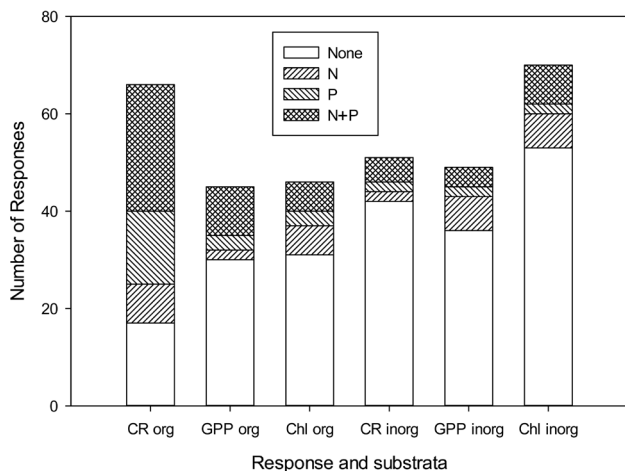


Fig. 4. Bioassays of biofilm limitations from 65 streams across the United States with different response variables (CR = community respiration, GPP = gross primary production, Chl = chlorophyll) on different surfaces for biofilm development (org = wood veneer, inorg = porous glass) with total number of statistically significant responses (None is no response, N is response to N addition alone, P is response to P addition alone, and N+P is either co-limitation or primary response to one with a secondary response to another). Data replotted from Johnson et al. (2009).

litter breakdown were followed. In that study, both N and P played a role in stimulating leaf decomposition and altering the rate of carbon retention (Rosemond et al. 2015).

Additional information indicates that nutrients can alter biotic properties of stream animal communities, perhaps independent of more traditional influences on algal productivity and litter breakdown rates. The data of Wang et al. (2007) suggest that increased N levels as well as P levels can decrease the diversity of key groups of fishes as well as invertebrates (Wang et al. 2007). In a similar study, Evans-White et al. (2009) found that invertebrate primary consumer diversity decreased steeply with increasing P, eventually leveling out to relatively low diversity. Evans-White et al. (2009) hypothesized that these responses were a result of altered food quality mediated through eutrophication-related changes in the stoichiometry of the consumers' food resources. The weaker relationship for predators (who eat other invertebrates with more constrained stoichiometric compositions than basal food sources) than for primary consumers was considered to be correlative evidence for this argument. Stoichiometric shifts in food quality are documented to have negative impacts on grazers and higher trophic levels in lakes (Hessen 2013), and there is no reason to assume similarly mechanisms related to stoichiometric shifts would not apply in streams as well (e.g., Frost et al. 2002).

Broadening the view of trophic state in streams beyond considering only stimulatory effects on autotrophs opens more avenues for both N and P to be important system drivers. The concept of heterotrophic state in addition to autotrophic state (Dodds 2006) is also encapsulated in the terrestrial literature by the recent concept of green and brown food webs (e.g., Wu et al. 2011). Understanding the importance of the brown food webs has been clear in stream ecology for canopy-covered systems as well as turbid large rivers (Vanotte et al. 1980). Data considered under this broadened view suggest that N as well as P, or N+P, are important determinants of system activities in streams, and thus eutrophication by both N and P deserves consideration.

Cyanobacteria and N fixation in streams

Cyanobacteria are widespread in the world's flowing waters (Scott and Marcarelli 2012), and slow-moving, nutrient-enriched rivers and streams have been observed to develop planktonic blooms of potentially harmful cyanobacteria (CynoHABs) analogous to those found in lakes (e.g., Murray River, Australia: Baker and Humpage 1994; Neuse River: Affourtit et al. 2001). Where water clarity permits the formation of benthic growth, however, stream algal biomass is more frequently dominated by

substrate-attached cyanobacteria when these organisms are present. Nitrogen-fixing, heterocystous cyanobacteria observed in the benthic habitats of streams include *Rivularia*, *Nostoc*, *Scytonema*, *Calothrix*, and *Gleotrichia*. Additionally, *Epipithemia* containing N-fixing endosymbionts is common in some streams (e.g., Richardson et al. 2009). Heterocystous genera of benthic algae, however, are seldom found in highly enriched waters, although some dominate in naturally high P–low N waters (e.g., *Nostoc*; Dodds and Castenholz 1988). Landcare Research, 1 of 7 Crown Research Institutes in New Zealand, view heterocystous species of cyanobacteria as mostly occurring in high-quality New Zealand streams (<http://www.landcareresearch.co.nz/resources/identification/algae/identification-guide>, accessed 2 July 2015).

A key issue in eutrophication science is the potential for N-fixing cyanobacteria to compensate for any deficiency in biologically available N. Can heterocystous cyanobacteria dominate N cycling, and will the local ecosystem retain this new N once it is fixed? Unfortunately, N fixation is much less frequently measured than other N-cycling rates (e.g., nitrate and ammonium uptake and denitrification), and reviews of N budgets for flowing waters suggest that N-fixation rates are rarely measured in rivers and streams (Marcarelli et al. 2008). In stream studies that measured both N uptake and fixation, the rates of N fixation have rarely been observed to equal or exceed rates of dissolved inorganic N uptake (Marcarelli et al. 2008); however, advective N fluxes and frequent seasonal scouring of biofilms transport much of the newly fixed N out of the local system. In contrast to lakes, where retention times may be months or years, stream networks often have retention times on the order of days, making it unlikely that the slow process of N fixation can ultimately satisfy total biological demands for inorganic N. We note in the experimental stream study by Stelzer and Lamberti (2001) in which nutrients were manipulated for a month, low N:P supply ratios did not lead to a shift to cyanobacterial dominance, in direct contrast to the expected response of lake phytoplankton. Scott and Marcarelli (2012) considered grazing and scouring more important determinants of benthic cyanobacterial dominance in streams than nutrient conditions. Moreover, because streams are dominated by benthic habitats, the potential for denitrification is high (Mulholland et al. 2008), perhaps leading to greater proportional N losses in the N budgets of streams relative to lakes. We provisionally conclude that the probability that N fixation can eventually compensate for N-limited conditions induced by excess P loading is much lower in streams than it is in lakes, but this hypothesis should be directly tested.

Conclusions

Although eutrophication science in fluvial ecosystems lags well behind that for lakes, major advances are being made. Here we present broad, multiple lines of evidence that note the importance of both N and P in stream trophic state. This evidence includes statistical correlations, small scale bioassays, and whole-stream enrichment experiments. Both autotrophs and heterotrophs seem to be influenced by changes of nutrients. Both N and P pollution are common in the United States (and elsewhere), and the relative increases are spatially distinct. Any view of nutrient limitation that focuses on P alone in streams will miss much of the nuance of nutrient limitation for primary producers as well as for detritivores and other heterotrophs higher in the food web. We thus urge further research on the impacts of nutrient enrichment on fluvial ecosystems.

We also stress that multiyear nutrient water quality databases exist for large numbers of rivers and streams located worldwide and that comparative analyses of these data are likely to provide important new insights. In particular, we urge our colleagues to perform studies that parallel Minaudo et al. (2015), who analyzed 30 years of data documenting the recovery of the Loire River (France) from eutrophication. It will be crucial to examine the speed with which eutrophic flowing waters respond to N and P loading controls and the degree to which hysteresis effects can be expected to occur during the eutrophication recovery process (Jarvie et al. 2013).

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