

Trophic state, eutrophication and nutrient criteria in streams

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Trophic state is the property of energy availability to the food web and defines the foundation of community integrity and ecosystem function. Describing trophic state in streams requires a stoichiometric (nutrient ratio) approach because carbon input rates are linked to nitrogen and phosphorus supply rates. Light determines the source of carbon. Cross system analyses, small experiments and ecosystem level manipulations have recently advanced knowledge about these linkages, but not to the point of building complex predictive models that predict all effects of nutrient pollution. Species diversity could indicate the natural distribution of stream trophic status over evolutionary time scales. Delineation of factors that control trophic state and relationships with biological community properties allows determination of goals for management of stream biotic integrity.

The importance of trophic state

Streams, like all other ecosystems, have biotic communities that rely upon carbon supply to fuel food webs and maintain the organisms that live in them. The root meaning of trophic, from the Greek ‘trophikos,’ is to nourish. Trophic state (see Glossary) is central to ecosystem structure and is inextricably linked to biotic integrity and water quality of streams. Concerns about the effects of nutrient pollution on rivers and streams have led to a recent surge in information related to factors that control trophic state. Our understanding of this basic property of stream ecosystems has expanded and in many ways draws on a holistic tradition of stream ecology to provide a new view of the role of nutrients and light, and their interactions with food webs of stream ecosystems. Baseline (reference) trophic state of a stream (flux rate of carbon into the food web in the absence of human influence) is of interest because it is the adaptive template under which stream organisms have evolved. Trophic state ranges from unproductive (oligotrophic) through intermediate productivity (mesotrophic) to highly productive (eutrophic). Eutrophication is the increase in factors that move a system toward a eutrophic state.

The concept of trophic state has been developed most extensively for lakes in large part as a result of links to water quality issues. In lakes, trophic state is functionally defined by factors related to autotrophic production, these include algal biomass, water column nutrients, and water transparency. With excessive nutrient loading, lakes

display several undesirable characteristics such as blooms of noxious algae, fish kills, and taste and odor problems. Similar concerns with water quality in streams has led to interest in factors that control trophic state [1], in particular how nutrients can be linked to trophic state and how trophic state could reflect system properties that are of interest with respect to ecosystem services. Defining trophic state in streams, however, can be more difficult than in lakes because many stream food webs are dominated by carbon inputs from land (although lakes and marine habitats also receive more carbon inputs from other systems than thought previously [2]). Thus, a complex interplay among factors that influence trophic state in streams can occur, and we have only recently erected a predictive framework to deal with this complexity.

The purposes of this review are to synthesize the definition of trophic state of streams in an ecologically meaningful framework; clarify the linkages among nutrient supply, stoichiometry (ratios of nutrients), trophic state and other ecological properties; and define a baseline trophic state while recognizing that pervasive human impacts might make finding the baseline difficult. For

Glossary

Allochthonous: from outside the system.

Autochthonous: from inside the system.

Autotrophic: inorganic carbon converted to organic carbon for metabolism and growth using energy from light (photosynthesis) or chemicals (chemosynthesis); in contrast to heterotrophic.

Autotrophic state: the relative amount of whole system primary production.

Basal energy: the initial source of energy for a food web.

Baseline trophic state: the trophic state that would be expected in absence of human influences, also referred to as reference trophic state.

Benthic: associated with the bottom of an aquatic habitat.

Biomass: the mass of living organisms.

Detritus: non-living organic material.

Eutrophic: enriched trophic state, very productive.

Heterotrophic: carbon for metabolism and growth obtained from organic carbon (in contrast to autotrophic).

Heterotrophic state: the relative amount of whole system respiration.

Mesotrophic: moderately productive, between eutrophic and oligotrophic.

Net ecosystem production: ecosystem primary production minus ecosystem respiration, an indicator of dominance of heterotrophic (negative net production) or autotrophic processes (positive net production).

Oligotrophic: low productivity.

Periphyton: algae and other microbes associated with benthic habitats.

Phytoplankton: suspended microscopic algae.

Primary production: rate of carbon production by photosynthesis.

Secondary production: production of animals that consume primary producers, other animals, or organisms that grow on detritus.

Stoichiometry: the ratio of elements (or in a broader treatment can include light).

Trophic state: the production rate of autotrophic or heterotrophic processes in an ecosystem.

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the remainder of this review, I will use the term 'stream' to signify flowing waters, including rivers.

Trophic state in streams

Streams form the essential interface between terrestrial and downstream aquatic ecosystems. As such, streams can receive a substantial amount of the basal energy for their food webs from terrestrial sources (allochthonous) of carbon, but in open canopy, clear water streams, irradiance can be sufficient to support sizeable instream production by algae and macrophytes (autochthonous). The relative importance of these carbon sources can vary seasonally in some streams (e.g. in deciduous forested streams there is a large input of leaves, followed by a lighted period when algal primary production can dominate). Given potential sources of organic carbon, trophic state of streams should include both heterotrophic and autotrophic production (i.e. heterotrophic and autotrophic state) because both can be essential sources of energy [3].

Consideration of heterotrophic state is warranted because net ecosystem production is negative (i.e. respiration exceeds gross production) in most pristine streams, even those with limited riparian (streamside vegetative) canopy [4]. A description of trophic state in streams that explicitly considers heterotrophic and autotrophic state follows one proposed a half century ago by Odum [5]. Management of trophic state and emphasis on heterotrophic processes was historically a water quality issue and was influenced by the considerable problems associated with dumping untreated sewage that contained organic carbon into rivers and streams, and subsequent problems of low dissolved oxygen. Heterotrophic state is

not commonly considered as important as autotrophic state in eutrophication management [1]; efforts of the US Environmental Protection Agency and counterparts in Canada focus primarily on nutrient criteria in streams to control autotrophic activity. In Europe, the Water Framework Directive of the European Union uses benthic algal biomass as the focal response variable. Nutrients, by extension, need to be managed to control benthic algal biomass. Thus, this review is warranted to emphasize to an applied research and basic management audience the progress made in stream ecosystem science related to trophic state.

Odum's paper [5] presents an early comprehensive view of trophic state. Some of his fundamental observations about trophic state in streams have not received as much attention and warrant renewed interest. Thus, I will discuss factors that control trophic state and how defining those factors can help us estimate natural distribution of stream trophic states.

Autotrophic and heterotrophic states are indicated by ecosystem primary production and respiration, respectively (Figure 1). Methods have been developed to measure trophic state of ecosystems by assessing whole system metabolism (Box 1). Using whole system respiration to indicate heterotrophic state means that respiration by autotrophic organisms (suspended and benthic algae and aquatic plants) as well as all other organisms (from microbes to fish) in the system contribute to heterotrophic state. Both biomass and biomass specific activity can be influenced by biotic and abiotic controlling factors. Autotrophic and heterotrophic state can be controlled by different factors. Light has a greater controlling effect on

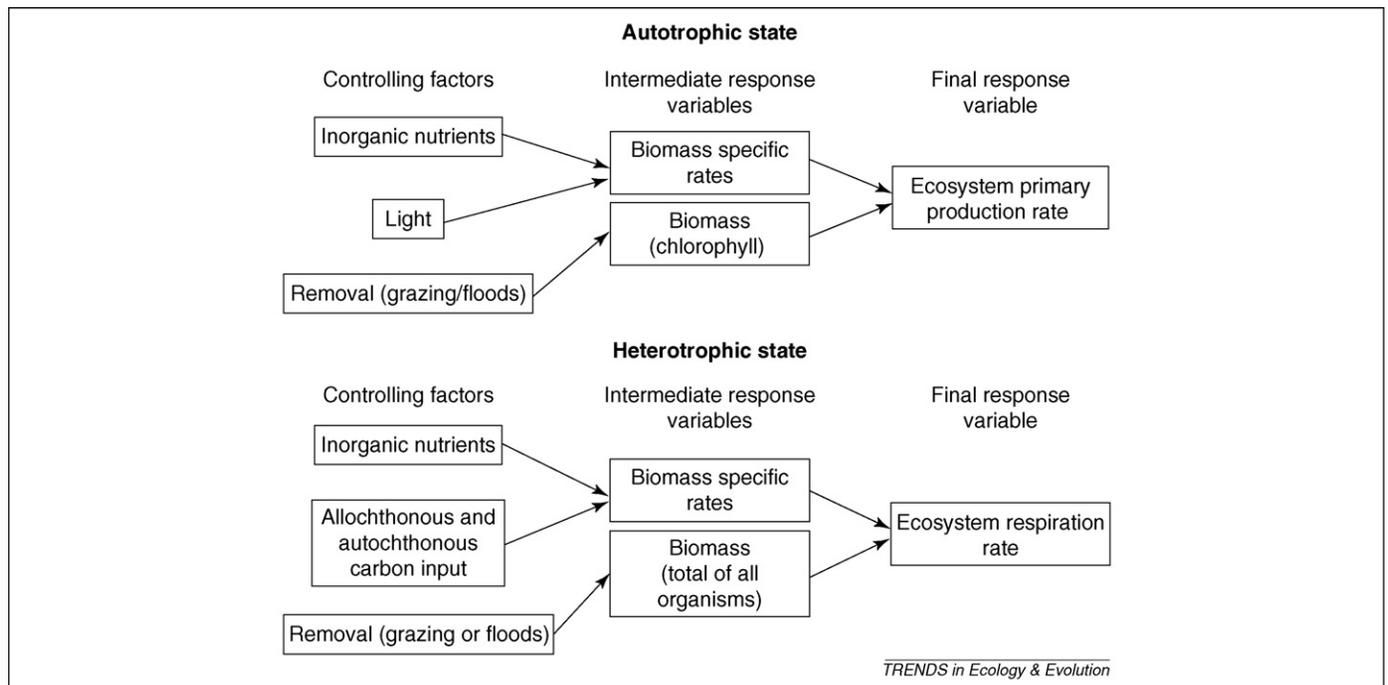
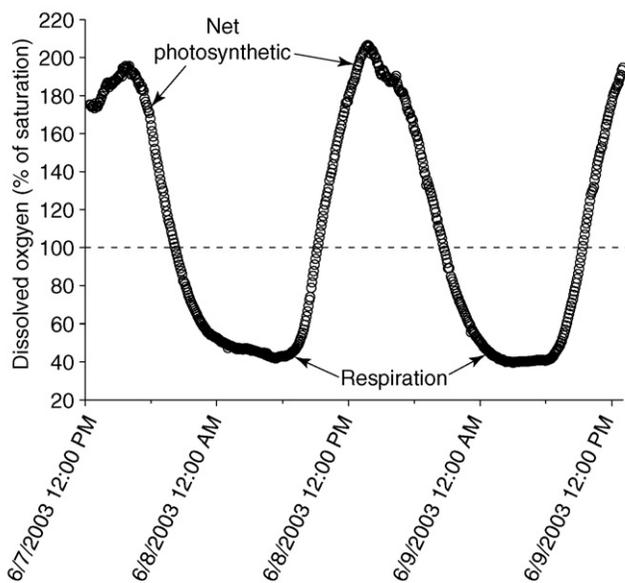


Figure 1. A simplified conceptual diagram of the relationship between trophic state, variables usually used to indicate trophic state and some potential controls on autotrophic and heterotrophic state in streams. Both autotrophic and heterotrophic states ultimately determine how much energy is available to the organisms living in the stream. Autotrophic state is dependent upon photosynthesis so is controlled by light and nutrients. Removal of photosynthetic organisms by floods or grazing also can control autotrophic state. Often biomass of primary producers (chlorophyll *a*) is used to indicate trophic state, but both biomass and activity of that biomass determine autotrophic state. By contrast, heterotrophic state is determined by organic carbon availability from both within and outside of the stream. Heterotrophic state is thus less influenced by light than autotrophic state is, and can be heavily influence by organic carbon subsidies from outside of the system (e.g. leaf input).

Box 1. Measuring trophic state in streams

Because trophic state is an indicator of energy flux to the food web, production of autotrophs and heterotrophs is most directly linked to trophic state. Production of autotrophs in streams can be measured using a variety of techniques from small scale incubations to whole system methods. The whole system methods are essentially refinements of the initial technique proposed by Odum [5], in which diurnal patterns of dissolved oxygen can be used to estimate both whole system primary production and whole system respiration (see Figure 1). Production increases dissolved oxygen, and at night respiration dominates allowing estimation of respiration rates. When exchange of dissolved oxygen with the atmosphere is accounted for, system metabolism can be estimated [4]. Much of the primary production in streams is likely to enter the food web. However, whole system respiration includes that of all organisms (plants, algae, microbes, animals) and thus includes microbial activity and respiration of primary producers in addition to carbon utilization by entire upper levels of the food web.

Autotrophic state can be characterized indirectly by considering nutrients and biomass of producers (chlorophyll *a*). Biomass of producers is positively correlated to primary production [3]. Heterotrophic state is less often characterized by biomass of heterotrophs because of a lack of easy general quantification of heterotrophic biomass. Counting and estimating activity of all fish and large invertebrates is relatively simple, but enumerating the microbes and smaller invertebrates and their activities in stream sediments remains difficult and time consuming. These small organisms can have a disproportionately large influence on system respiration rates. There are hundreds of measurements of nutrients and periphyton biomass in streams [3]. However, there are fewer whole system productivity and respiration measurements. As data-logging oxygen probes become more prevalent, reliable, and affordable, many more such measurements should become available.



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Figure 1. A diurnal trend of dissolved oxygen plotted as percent saturation. This type of curve can be used to estimate system metabolism. Photosynthesis drives the dissolved oxygen up to supersaturating levels during the day and respiration draws dissolved oxygen well below saturation at night. This trace is of data from an agriculturally influenced stream on the north side of Manhattan Kansas [37]. Dissolved oxygen levels below 50% are known to be harmful to many aquatic organisms.

autotrophic state, and allochthonous carbon input has the greatest impact on heterotrophic state. Of all factors, inorganic nutrient input and allochthonous carbon influx rates are most broadly amenable to management relative

to factors such as floods and grazing, so links between organic influx and inorganic nutrients with trophic state will be discussed. Following this discussion a more complex stoichiometric view will be presented.

Linking nutrients to trophic state and other ecosystem properties

Carbon can limit heterotrophs, given their reliance upon assimilation of organic carbon to build cells and their additional requirement for energy that must be satisfied by processing organic carbon. Alternatively, analyses of stoichiometry of food sources for heterotrophs reveals situations in which carbon is available in relative excess (such as in dead leaves) so that primary consumers can satisfy their assimilatory and metabolic carbon demand and be limited by inorganic nutrients [6]. Nutrient enrichment bioassays demonstrate that inorganic nutrients often stimulate heterotrophic and/or autotrophic activity, with nitrogen (N) and phosphorus (P) being the most important nutrients [7]. In addition, degradation rates of *in situ* leaf litter are stimulated by addition of inorganic nutrients (e.g. [8]). Thus, heterotrophic state can be a function of carbon, N or P supply rates in addition to other controls such as hydrology and consumer activity.

Benthic or suspended algal biomass can reflect autotrophic state. Several researchers [10,11,13,33] have established statistical links between water column nutrients and concentrations of benthic chlorophyll *a* (Table 1). These papers describe use of either dissolved inorganic or total nutrients to predict benthic or suspended chlorophyll *a*. In most cases, dissolved inorganic nutrients were not as strong a predictor of autotrophic biomass as were total nutrients. The poor predictive ability of dissolved inorganic nutrients (soluble reactive P and dissolved inorganic N) has been attributed to the fact that turnover rates of biologically active pools such as ammonium and phosphate can be more important than concentrations [9]. However, Biggs [10] was able to use dissolved inorganic nutrients and flow regime to predict benthic chlorophyll *a* accounting for a substantial proportion of variance. His approach is appealing because it accounts for the dynamic nature of streams. Dodds *et al.* [11] used seasonal means to smooth out variance related to shorter term hydrologic variance, but did not explicitly consider flow regime.

Far less attention has been paid to factors that control trophic state as determined by suspended chlorophyll in rivers and streams, although some research has been conducted on this topic [12]. The relationship documented between suspended chlorophyll and stream total nutrients is strong in the few papers that address this question [13,14]. In rivers and streams with low flushing rates, eutrophication could be a concern when excessive algal biomass develops in response to nutrient enrichment. For example, the Murray Darling River is subject to excessive algal blooms during low flow periods (e.g. [15]). When dilution exceeds growth rate it is difficult for substantial phytoplankton populations to become established without external sources of phytoplankton (e.g. an upstream reservoir).

An important point about whole ecosystem production related to nutrients is that a view of single nutrient

Table 1. Published relationships between nutrients, stream chlorophyll a and watershed area and days since flood^a

Dependent variable	Var 1 ^{b,c}	Var 2 ^{b,c}	N	R ²	Refs
Benthic chl a	TN		198	0.29	[11,33]
Benthic chl a	TP		254	0.13	[11,33]
Benthic chl a	TN	TP	193	0.38	[11,33]
Benthic chl a	DIN		225	0.19	[11,33]
Benthic chl a	SRP		192	0.13	[11,33]
Benthic chl a	DIN		30	0.12	[11,33]
Benthic chl a)	SRP		30	0.23	[11,33]
Benthic chl a	DIN	Days of accrual	30	0.44	[10]
Benthic chl a	SRP	Days of accrual	30	0.49	[10]
Phytoplankton chl a	TP		23	0.78	[13]
Phytoplankton chl a	TP	Watershed area	23	0.94	[13]
Phytoplankton chl a	TN		23	0.70	[13]
Mean phytoplankton chl a	TN	Watershed area	23	0.84	[13]

^aThese relationships indicate that both nitrogen and phosphorus control autotrophic state for both benthic and phytoplankton chlorophyll a across a wide variety of streams, that floods or stream size can also be important, and that total nutrients generally provide more information than dissolved inorganic nutrients.

^bVar 1 and Var 2 are the independent variables, but two variables were not used in all models. All dependent and independent variables are log-transformed in all models and are means.

^cAbbreviations: DIN, dissolved inorganic nitrogen; R², the adjusted value for the regression equation; SRP, soluble reactive phosphorus; TN, total nitrogen; TP, total phosphorus.

limitation is not warranted and both N and P need to be managed in streams. Although Liebig's Law of the Minimum and relatively low rates of P availability in many freshwaters has led to a view of P limitation predominating in freshwaters, empirical results call this view into question. Nitrogen, phosphorus, or both often limit algal biomass accrual in streams with colimitation being common [16]. Furthermore, empirical relationships between water column nutrients and algal biomass indicate that chlorophyll a yield is influenced by interactions between nutrients across a wide variety of streams ([11] Table 1). Thus, a nonequilibrium view of factors that influence trophic state with interactions between nutrients is warranted.

A stoichiometric approach that considers heterotrophy in addition to autotrophy, and relative fluxes of carbon and inorganic nutrients linked to trophic state has been justified by a string of elegant whole stream experiments in the small, forested Appalachian streams of the Coweeta Hydrologic Laboratory. These experiments used leaf litter exclusions (decreased carbon influx rates) or whole stream fertilizations to alter streams that are dominantly heterotrophic in nature owing to dense riparian canopy. Large scale exclusions of leaves and wood falling into the stream decreased secondary productivity (heterotrophic state) of the system, including slower growth rates of the top animal in the food web, the larval salamander, *Eurycea wilderae* [17]. Leaf exclusion also decreased heterotrophic microbial nutrient demand; the average distance each molecule of inorganic nutrients traveled before being taken up was longer in reaches where leaf litter was excluded [18].

Streams in this region containing the normal amount of leaves were also manipulated with chronic inorganic nutrient additions. Fertilization increased secondary production of invertebrates severalfold over expected rates [19], as well as increasing growth of larval salamanders found in the stream [20]. Because the streams are strongly heterotrophic (a closed canopy minimizes photosynthesis much of the year), inorganic nutrient stimulation of secondary production is clearly tied to stimulation of heterotrophic activity at the base of the food web. Nonetheless, the nutrient enrichment also increased autotrophic bio-

mass [21] and algal primary production is generally a more available food source than detrital pathways [22], so not all of the increase in secondary production was necessarily related to changes in heterotrophic state.

Additional evidence that heterotrophic state can be affected by nutrients is provided by analyses of black water streams in North Carolina [23]. Dissolved low oxygen conditions that could impair biotic integrity were present in several these streams. Phosphorus loading primarily and nitrogen loading secondarily stimulated problematic low oxygen conditions [23]. Taken together, the Coweeta and black water results confirm that managers need to consider carbon, nitrogen and phosphorus flux to control trophic state.

Trophic state should in part be a function of riparian condition and nutrient supply, given that the balance between heterotrophy and autotrophy in nonturbid streams seems often to be controlled primarily by overhanging tree canopy (shading and leaf input), and rates of both heterotrophic and autotrophic activities can be controlled by inorganic nutrient supply. Although other factors can control heterotrophic state, such as floods that remove leaves [24], these will not be considered in detail in this review.

A stoichiometric approach to factors that control trophic state

Trophic state can be influenced by light, external carbon source, nutrients, hydrology and food web structure. However, managers usually can only control the first three of these across broad areas, so the relative importance of light, carbon and nutrients (a stoichiometric approach) will be considered in this review. There has been a recent increase in the knowledge of stoichiometry and its influence the food web of streams [25], so a stoichiometric approach is warranted both from the perspective of understanding both ecosystem function and ecosystem structure (biotic integrity).

A stoichiometric model should consider that multiple limitations occur and that different factors can simultaneously control heterotrophic and autotrophic state (a model should include interactions among controlling vari-

ables). For example, a lighted stream still might not have high autotrophic state if nutrients are severely limiting. A model of factors that control autotrophic state could be structured empirically in the form of a multiple linear model. For example:

System production = $B_0 + (B_1 \times \text{total nitrogen}) + (B_2 \times \text{total phosphorus}) + (B_3 \times \text{light}) + (B_4 \times \text{total phosphorus} \times \text{total nitrogen}) + (B_5 \times \text{total phosphorus} \times \text{light}) + (B_6 \times \text{total nitrogen} \times \text{light}) + (B_7 \times \text{total phosphorus} \times \text{total nitrogen} \times \text{light})$.

where B_0 to B_7 are constants. Appropriate transformations are generally required to make the factors normal, most usually logarithmic transformations. In practice, such a model for chlorophyll a in lighted streams has yielded a model that includes total N and total P or the N and P interaction term (Table 1, [11]). Standard statistical techniques (e.g. regression with information criteria) can be used to determine which form of the model is empirically supported. Similar models for production instead of algal biomass are now required.

Similarly, models for heterotrophic state could be constructed and quantified if more data were available. An example model of this type would be:

System respiration = $B_0 + (B_1 \times \text{total nitrogen}) + (B_2 \times \text{total phosphorus}) + (B_3 \times \text{allochthonous and autochthonous carbon input}) + (B_4 \times \text{total phosphorus} \times \text{total nitrogen}) + (B_5 \times \text{total phosphorus} \times \text{allochthonous and autochthonous carbon input}) + (B_6 \times \text{total nitrogen} \times \text{allochthonous and autochthonous carbon input}) + (B_7 \times \text{total phosphorus} \times \text{total nitrogen} \times \text{allochthonous and autochthonous carbon input})$.

Both these models assume linear coefficients, but we know that algal biomass–nutrient relationships are non-linear and saturate at high nutrient values [11]. Similarly, primary production saturates at high light [26]. More advance models will correct for these types of saturation, although saturation of heterotrophic rates is not well established.

Given that these models do not exist yet because of lack of sufficient information to construct them, the best managers can do for now is to attempt to approximate reference or baseline conditions in streams in order to move them toward the native condition. For example, it would be appropriate to attempt to restore riparian vegetation by using native trees in areas historically dominated by temperate deciduous forests, but this management approach would be inappropriate for many prairie or desert streams. Thus, it becomes very important to delineate the baseline trophic state and baselines for factors that potentially influence trophic state.

What is the baseline trophic state of streams?

Determining baseline trophic state is necessary for understanding the adaptive template experienced by stream organisms as well as natural rates of ecosystem function. The baseline with respect to nutrients, carbon supply (as influenced by riparian vegetation) also provides a point of reference for regulation of stream water quality and biotic integrity. Our only current approach to conservation of many aquatic organisms requires reproducing the adaptive template they inhabited. A similar approach has

been taken to conservation by restoring natural flow regimes of streams [27].

The baseline approach is necessary with respect to trophic state because there is only a moderate amount of ecological information for many taxa that inhabit streams (e.g. protozoa, nematodes, rarer invertebrates, algae) with respect to their responses to stream trophic state. Thus, approximating historic trophic state that occurred before human influences is needed for conservation. Understanding the expected baseline trophic state in a region is the first step of this management approach.

Techniques used to establish the baseline trophic state of lakes are not so likely to be applicable to streams. Techniques used in lakes are based on sedimentary records to assess historical biological communities before increases in human influences. The dynamic equilibrium of a river and its floodplain gives rise to repeated episodes of erosion and deposition. Even though diatom communities (a dominant microbial primary producer in many flowing waters) of rivers and streams can be indicative of nutrients (e.g. [28]), a reliable record preserved in the sediments is difficult to obtain. Therefore, other methods are required to determine the historic trophic state of a stream before human influences. These methods require determining both external carbon input rates as well as indication of a baseline of total nutrients available.

Historic identification of riparian condition is vital for determining trophic state because the balance between heterotrophy and autotrophy in small streams is driven in large part by the presence of a riparian canopy. Tree rings and reference areas could be useful in this determination (if they are present and not all cut or removed), as well as historic photographs, early written surveys and accounts, and comparison to existing reference watersheds. Several methods have been applied to streams for determining baseline nutrient concentrations, including frequency distributions [29,30], modeling [31] and extrapolation to reference conditions [32] (Box 2).

Recent developments suggest that baseline nutrient conditions could be tied to breakpoints (thresholds) in relationships between biological variables and instream nutrient concentrations. For example, benthic chlorophyll a across a variety of streams increases with total N or total P concentration up to a point and then levels off [11,33]. The point where autotrophic state no longer changes could be a region above which primary producers have not evolved to respond to nutrient concentration. Alternatively, above this level of nutrients other factors could become limiting. In any case, nutrients are probably decoupled from autotrophic state at concentrations greater than the threshold, so management plans to achieve nutrient concentrations that are not below the threshold are unlikely to have an influence on benthic algal biomass.

Thresholds have also been demonstrated between water column nutrients and some aspects of macroinvertebrate and fish richness, with a general trend of richness decreasing as nutrient concentrations increase up to a point, after which low diversity occurs regardless of instream nutrient concentration. More specifically, Wang *et al.* [34] studied 240 wadeable streams across Wisconsin

Box 2. Determination of baseline nutrient levels in streams

Baseline nutrient conditions are important because they guide where nutrient criteria should be set. Several alternatives have been proposed to determine baseline nutrient concentration of streams. First, in regions where undisturbed watersheds are available, baseline trophic state with regard to nutrients is relatively easy to establish (with the caveat that atmospheric deposition of N could lead to increased N content). Second, the United States Environmental Protection Agency has proposed a very simple statistical approach in the absence of reference datasets, in which the value for the lower quartile of all available nutrient data is chosen [29]. This method is highly sensitive to the number and degree of nutrient-enriched sites, and does not match well with reference baseline approaches [30]. Third, a mechanistic approach has been to model expected nutrient concentration in baseline streams and account for atmospheric N deposition [31]. A fourth technique is to establish the statistical relationship between anthropogenic influences and instream nutrient concentrations and extrapolate to zero anthropogenic influence. The percentage of agricultural and urban land cover or human population in a watershed is often correlated with river and stream nutrient concentrations, and watersheds with varying land use can be used to extrapolate to reference conditions [32]. An example of this approach is illustrated for an ecoregion in the upper Midwestern USA (Figure 1).

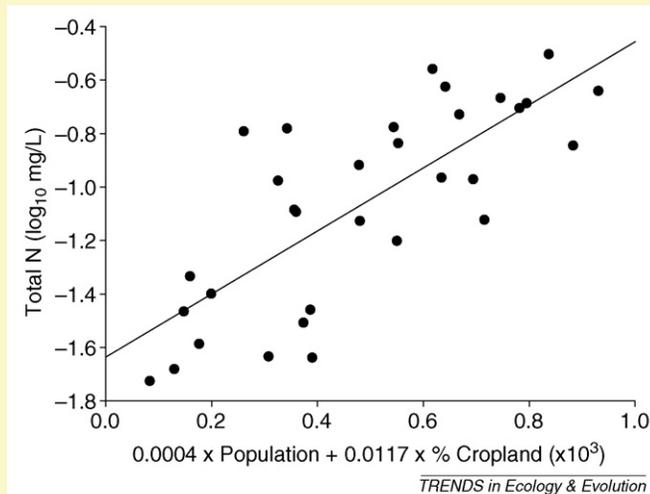


Figure 1. Illustration of extrapolation approach to estimate baseline nutrient concentration. The line crosses the y-axis at the baseline nutrient value where the effect of human population and cropland in the watersheds are removed. Data are from 32 watersheds in the Mostly Glaciated Dairy Region (upper Midwestern USA) and data collection and analyses methods are described in Ref [32].

and established thresholds for total N and P with respect to total invertebrate taxon richness. A variety of other measurements also indicated thresholds (e.g. percentage of carnivorous fishes, number of sensitive taxa), but the consistent effect on total invertebrate richness is the most compelling. This type of relationship could be explained by lack of evolutionary history of exposure to conditions that occur with greater nutrients. For example, animals that specialize in poor quality detritus could be unable to compete when ample nutrients make detritus better quality for some less specialized consumers. Further research is necessary to clarify the mechanisms for thresholds, but Wang *et al.* [34] provide an exciting glimpse into possible relationships between biotic integrity and nutrients in streams. The data could also indicate the upper bounds for nutrients in systems under baseline conditions.

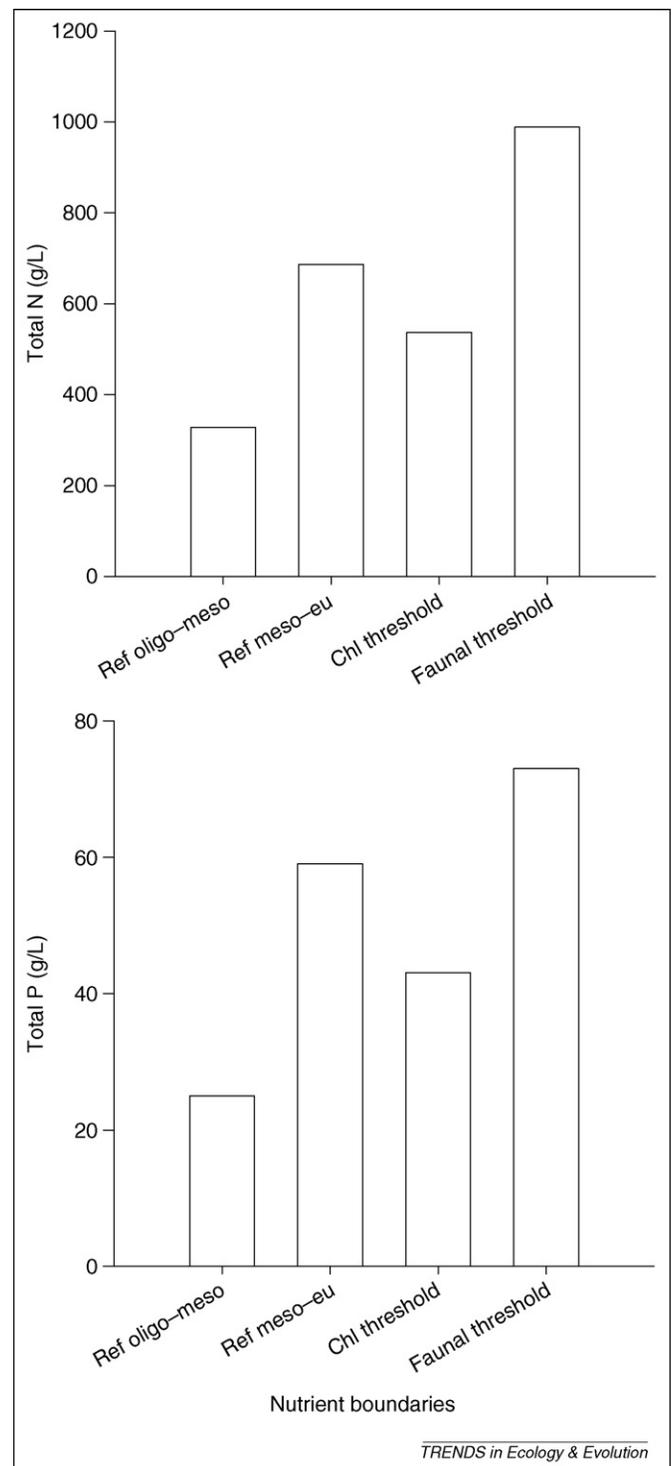


Figure 2. Suggested levels of total nitrogen and phosphorus related to trophic state boundaries and ecological thresholds. Several approaches have been suggested to classify trophic state, including estimation of nutrient regime in pristine streams and biological responses to nutrients. Values for nutrients in non-human influenced (baseline) streams have delineated broad distributions for nutrients in streams that are not impacted by humans; the lower third [oligotrophic (oligo)–mesotrophic (meso)] and upper third (mesotrophic–eutrophic (eu) boundaries) help define this distribution. Thresholds of algal biomass and nutrients can be used to indicate water column concentrations above which autotrophic state is decoupled from nutrients. Finally, thresholds in biotic integrity as indicated by species richness can be used to establish a range of trophic states that might be related to evolutionary history of the organisms found in streams. Values for nutrients were taken from Dodds [3], algal thresholds from Dodds *et al.* [11,33] and faunal (invertebrate and fish) thresholds from Wang *et al.* [34]. Abbreviations: Chl, chlorophyll a; Ref, baseline reference.

What is the natural distribution of stream trophic states?

Cumulative frequency distributions of stream trophic characteristics provide a way to create a classification system for stream trophic state. Given the traditional use of oligotrophic, mesotrophic and eutrophic states to signify categories of trophic state of ecosystems, dividing frequency distributions into lower (oligotrophic), middle (mesotrophic) and upper third (eutrophic) sections makes sense.

When trophic categories were established for baseline nutrient concentrations in US streams using cumulative frequency boundaries [31,32], median oligotrophic–mesotrophic boundaries for total N and total P were 49% and 42%, respectively, of the median mesotrophic–eutrophic boundaries [14]. The median of breakpoints in relationships of these nutrients with benthic chlorophyll *a* falls in the mesotrophic range (Figure 2). Average thresholds for fish indices and macroinvertebrate properties for total N and total P found in wadeable streams in Wisconsin [34] were somewhat greater than the upper third of expected baseline nutrient concentrations. Thus, the biological effect on stream animals occurred at a greater nutrient concentration than benthic chlorophyll *a*, but there still is a link between instream nutrients and biotic integrity. The mesotrophic–eutrophic boundaries for baseline nutrients in streams also coincide fairly roughly with lake mesotrophic–eutrophic boundaries for total N and total P of 650 and 30 µg per L, respectively [35].

Distributions of trophic state with regard to ecosystem primary production and respiration rates are less reliable, although they have been proposed [3]. There are far fewer measurements of whole system respiration and production for annual cycles than there are measurements of nutrients, so it seems somewhat preliminary to assign categories of trophic state based on metabolic characteristics. However, given links between nutrients, autotrophic and heterotrophic processes, and the role of light in determining balance between heterotrophic and autotrophic state, determining distributions of nutrients and reference riparian conditions could be sufficient for determination of baseline trophic conditions and management of trophic state. It is now up to management agencies and scientists to establish region specific distributions of trophic state.

Conclusion and recommendations for management of trophic state

Although Odum [5] recognized the importance of heterotrophy in streams, current management plans for nutrients focus primarily on autotrophic state as the response variable. The field has matured to the point where we can predict at least some aspects of baseline distributions of autotrophic and heterotrophic state of streams in a region and also can link total nutrients to biotic integrity. However, much less is known about the links between nutrients and heterotrophic state, and little about how baseline trophic state distributions change across large (e.g. continental) spatial scales. Light and nutrient stoichiometry are particularly fertile areas of recent research on trophic state and ecosystem processes [19,36].

Given what is known about factors that control trophic state, managers need to determine baseline values for nitrogen, phosphorus, external carbon supply and light. All these factors have potential for interactions. Factors can vary substantially across biomes; at the very least natural riparian vegetation can diverge. Some regions can be particularly high in inorganic turbidity, phosphorus, or nitrogen in baseline streams. It is probably not feasible to attain a trophic state that is more oligotrophic than ever occurred in a given region. We now have the tools to determine baseline trophic state, and efforts should be made to attain the baseline state if maintaining biotic integrity or conservation of native species is a priority. We are in an exciting time in stream ecological research because a fundamental and holistic understanding of the trophic state in these ecosystems is increasing rapidly and this has practical management implications as well as basic ecological value.

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