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Nutrient dynamics in streams and the role of *J-NABS*

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Abstract. Nutrient dynamics in streams has been an important topic of research since the 1960s. Here we review this topic and the significant role played by *J-NABS* in its development. We limit this review almost exclusively to studies of N and P because these elements have been shown to limit productivity in streams. We use the expression *nutrient dynamics* for studies that included some measures of biological processes occurring within streams. Prior to the 1970s, instream biological processes were little studied, but through 1985 conceptual advances were made, and 4 types of studies made important contributions to our understanding of instream processes: 1) evidence of increased plant production and decomposition in response to nutrient addition, 2) studies showing a downstream decrease in nutrient concentrations, 3) studies using radioisotopes, and 4) budget studies. Beginning with the first paper printed in its first issue, *J-NABS* has been the outlet for key papers advancing our understanding of rates and controls of nutrient dynamics in streams. In the first few years, an important review and a conceptual model for conducting experiments to study nutrient dynamics in streams were published in *J-NABS*. In the 1990s, *J-NABS* published a number of papers on nutrient recycling within algal communities, the role of the hyporheic zone, the role of spawning fish, and the coupling of data from field ^{15}N additions and a N-cycling model to provide a synoptic view of N dynamics in streams. Since 2000, *J-NABS* has published influential studies on nutrient criteria for streams, rates of and controls on nitrification and denitrification, uptake of stream nutrients by riparian vegetation, and nutrient dynamics in urban streams. Nutrient dynamics will certainly continue to be an important topic in *J-NABS*. Topics needing further study include techniques for studying nutrient dynamics, nutrient dynamics in larger streams and rivers, the ultimate fate of nutrients taken up by plants and microbes in streams, ecological stoichiometry, the effects of climate change, and the role of streams and rivers in nutrient transformation and retention at the landscape scale.

Key words: nutrient dynamics, nutrient cycling, streams, nitrogen, phosphorus.

> "A lifeless river would have a very different chemical regime" (Hynes 1970, p. 52)

Streams carry many dissolved chemicals, but only a few are biologically important, and only N and P have been shown to limit productivity in streams. Other elements, such as K, Ca, S, Fe, Si, and Mb might be critical to some organisms at some times, but they have not been well studied. However, studies of some of these less important chemicals have made significant contributions to our understanding of stream processes (e.g., Pringle et al. 1986). Some other chemicals, such as Al and Se, might be important in streams because of negative effects on organisms. We are limiting our review almost exclusively to studies of N and P, and we are using the expression *nutrient dynamics* for studies that included some measures of biological processes occurring within streams (Table 1). Other reviews in this special issue, including those on geomorphology and hydrology (**Poole 2010**[3]), organic matter dynamics and ecosystem metabolism (**Tank et al. 2010**), and groundwater–surface water interactions (**Boulton et al. 2010**) are related to the review of nutrient dynamics we present here.

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[3] Boldface indicates paper was published in *J-NABS*

TABLE 1. Components of nutrient dynamics in streams. DIn = dissolved inorganic nutrient, DOM = dissolved organic matter, POM = particulate organic matter.

Sources
Geologic weathering
Precipitation (direct channel interception)
Diffuse inputs (nonpoint sources)
Point sources (natural, e.g., springs, and anthropogenic)
Fertilization
Indirect
Leaf (and other allochthonous organic matter)
Sediment
Gas (source for N_2 fixation)
Upstream migration from other lake and marine ecosystems
DIn removal from water
To benthic substrate
Chemical precipitation
Adsorption
To hyporheic zone
Adsorption
Microbial immobilization
To plants
Vascular plant uptake
Periphyton uptake
Potamoplankton uptake
Heterotrophic microbial immobilization
Complexation with DOM
Adsorption with POM
Instream production of DIn
Plant leaching
Vascular plants
Periphyton
Plankton
Heterotrophic microbial mineralization
Consumer excretion
Invertebrates
Fish
Losses
Downstream transport to lakes and marine ecosystems
Denitrification
Insect emergence
Downstream migration to lakes and marine ecosystems

Studies of Nutrient Dynamics Prior to *J-NABS*

Early papers made little mention of instream nutrient processes

Before the 1970s, there were a number of studies of chemical concentrations in streams and how these were related to sources. A notable example was Gibbs' (1970) study of major ions in world rivers and their relation to geological and precipitation sources and modification by instream evaporation and chemical precipitation. Bond's (1979) study of a Utah stream showed how terrestrial processes in an undisturbed watershed affected stream nutrient concentrations. Many studies illustrated how anthropogenic changes to watershed vegetation modified stream chemistry (e.g., Bormann et al. 1968, Brown et al. 1973, Johnson and Swank 1973, Vitousek and Reiners 1975). Also, many studies documented eutrophication of streams caused by nutrient inputs (summarized by Hynes 1960).

Various reviews at that time made almost no mention of instream biological processes. Hynes (1960, p. 68) showed a diagram with a decrease in nutrient concentrations downstream from a pollution source and wrote, "… if the river is long enough and receives enough extra water from tributaries and surface run-off, it can 're-purify' itself." However, in another chapter (p. 122), he noted that in addition to dilution, nutrients might be "used up," clearly anticipating the significance of biological processes expressed in his later book (Hynes 1970). The summary by Owens et al. (1972) dealt mostly with sources of nutrients, although they did mention that low NO_3^- concentrations in summer could be because of plant uptake, denitrification, or NH_4^+ volatilization. The book edited by Allen and Kramer (1972) was titled *Nutrients in Natural Waters*, but streams were only briefly mentioned in one chapter with no mention of nutrient processes in streams. Stream studies clearly lagged behind lake and marine research in this regard. Golterman (1975) made no mention of instream processes in his review of river chemistry and attributed seasonal and longitudinal chemical variations to terrestrial factors. This failure to mention instream nutrient processes was not an oversight on the part of these and other authors, but rather it reflected the lack of study of nutrient dynamics at that time. Hynes' (1970) chapter on chemical characteristics of flowing waters was primarily a discussion of chemical sources, distribution, and chemical reactions. He stated (p. 46), "To my knowledge nobody has ever demonstrated or suggested that any of them [K, N, or P] is a limiting factor of plant growth in a natural stream." In his review of P in streams, Keup (1968) mentioned biological growth as a potentially important removal process. Similarly, Casey and Newton (1972, 1973) mentioned plant and microbial uptake of nutrients but concluded that N and P were generally in excess in English streams. They found evidence of significant plant uptake of P in only one stream. Westlake (1975) suggested that N and P and perhaps K were insufficient for optimum vascular plant growth in oligotrophic English streams. Hynes (1970, p. 52) clearly recognized the potential importance of instream biological processes and concluded his chapter on stream chemistry with, "A lifeless river would have a very different chemical regime."

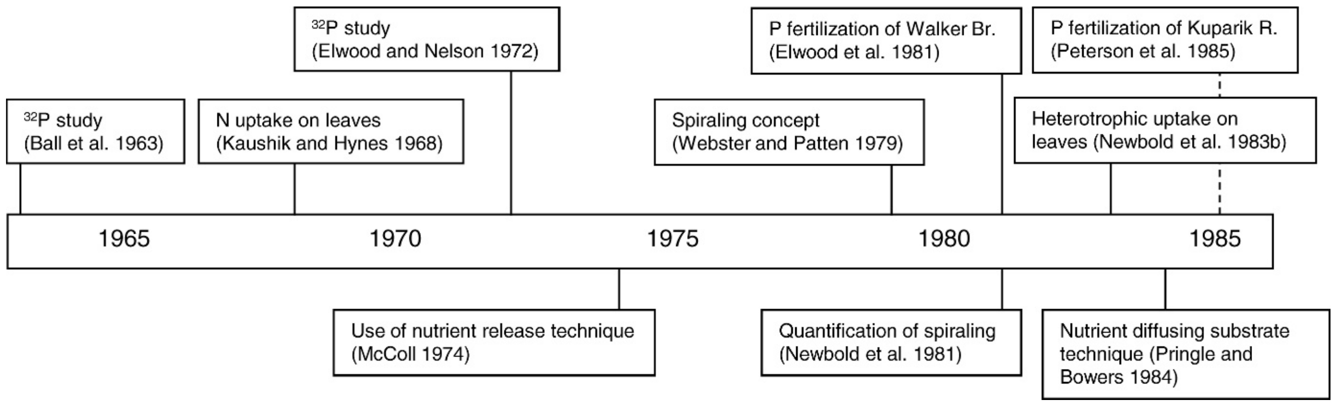

FIG. 1. A timeline of significant papers contributing to our understanding of stream nutrient dynamics before *J-NABS* was established. Details of these contributions are presented in the text. Dashed lines are used for clarity when a connecting line passes behind a box.

Instream processes modify nutrient concentrations

Four types of studies were primarily responsible for contributing to an early understanding of the role of instream processes: 1) evidence of increased plant production and decomposition in response to nutrient addition, 2) studies showing a downstream decrease in nutrient concentrations, 3) studies using radioisotopes, and 4) budget studies.

Nutrient addition studies.—In 1948, Huntsman found that placing bags of fertilizer in and adjacent to a nutrient-poor stream in Nova Scotia resulted in luxuriant algal growth, more invertebrates, and greater fish abundance. However, Warren et al. (1964) observed that simply adding sucrose to Berry Creek, Oregon, resulted in increased trout production, and Wuhrmann and Eichenberger (1975) noted that adding N and P to stream channels had no effect on productivity, although adding dilute sewage did. Similarly, Traaen (1978) found that addition of sewage increased gross primary production. In one of the early demonstrations of nutrient limitation in streams, Stockner and Shortreed (1976, 1978) observed that P fertilization in streamside channels increased algal growth. Elwood et al. (1981; Fig. 1) demonstrated that P addition to Walker Branch, Tennessee, accelerated leaf decomposition and increased primary production, and Peterson et al. (1985; Fig. 1) observed extensive changes to a tundra stream resulting from P fertilization. Bothwell (1985) found that P concentration limited algal production in the Thompson River, British Columbia, but that concentrations of only 3 to 4 μg/L were sufficient to saturate growth rates. In contrast, Triska and Sedell (1976) and Newbold et al. (1983a) observed that N addition to streams had little measurable effect on stream processes.

Observations of longitudinal declines in nutrient concentrations.—As early as 1951, Neal observed relatively high concentrations of P in the headwater springs of Boone Creek, Kentucky, and suggested that this P was "consumed" downstream. Talling (1958) described longitudinal nutrient patterns in the White Nile but attributed these changes primarily to tributary inputs and depletion of plant nutrients in swamps and reservoirs. Edwards (1974) measured Si depletion in English rivers, apparently because of diatom uptake, and Hill (1979) attributed a significant decline in N in Duffin Creek, Ontario, to uptake by algae and macrophytes and to denitrification in the sediments. Aiba and Ohtake (1977) developed a model of P in a river flowing through Tokyo that included biotic assimilation of P and biological mineralization.

Radiotracer studies.—The first use of radioisotope tracers in streams was published by Ball and Hooper (1963) but lagged behind similar studies in lakes by 15 y (Hutchinson and Bowen 1947). In their seminal study, Ball and Hooper (1963) released ^{32}P into a Michigan stream and demonstrated considerable annual and longitudinal variation in P uptake. Nelson et al. (1969) and Elwood and Nelson (1972; Fig. 1) also used stream additions of ^{32}P to measure periphyton uptake and turnover of P. Other researchers made use of contaminant releases of radionuclides to demonstrate biological uptake of nutrients (e.g., Davis and Foster 1958, Kevern 1964, Gardner and Skulberg 1966, Cushing 1967, Cushing and Rose 1970). Whitford and Schumacher (1961, 1964) studied algal P uptake with ^{32}P in flowing-water mesocosms, and Webster and Patten (1979; Fig. 1) used radioisotopes to measure consumer nutrient turnover in streams.

Budget studies of nutrients.—Budget studies provide limited information on instream processes; however, they can provide suggestions as to the significance of instream processes, especially when combined with direct process measurements. Crisp (1970) made a very careful budget of nutrients crossing a watercress bed in England and documented nutrient uptake by the harvested watercress and net input of P from the fertilized cress bed to the stream. Hall (1972) estimated a P budget for New Hope Creek, North Carolina, and found that inputs and outputs were small relative to storage and that the stream was in approximate steady state. The combination of budget data and instream process measurements led Webster and Patten (1979) to describe the spiraling of nutrients, although the process was implicit in the diagram of stream P dynamics presented by Elwood and Nelson (1972). Meyer and Likens (1979) used a budget approach to study P in Bear Brook, New Hampshire, and inferred instream processes from differences in forms of input and output.

Other studies documenting instream nutrient dynamics

These 4 types of studies (nutrient addition, longitudinal decrease in nutrient concentrations, radioisotopes studies, and budget estimations) provided clear evidence that instream process can modify nutrient concentrations. A variety of other studies documented the importance of specific instream processes. Stake (1968) found that aquatic plants in a polluted stream in Sweden accumulated P, and he noted that rooted plants might get nutrients from the sediments. Kaushik and Hynes (1968; Fig. 1) and Mathews and Kowalczewski (1969) found heterotrophic immobilization of N during leaf decomposition. Gregory (1978) used a ^{32}P release to demonstrate heterotrophic immobilization in an Oregon stream. The importance of nutrient uptake by microbes associated with decaying leaves became recognized as one of the most significant nutrient processes in streams (e.g., Newbold et al. 1983b; Fig. 1).

Nutrient uptake by autotrophic and heterotrophic processes is now measured fairly routinely with low-concentration additions of nutrients, a technique first used by McColl (1974; Fig. 1), but measurement of the opposing process, mineralization, has been much more limited. Hynes (1975) noted that very little was known about N release back into the water. Leaf decomposition studies showed immobilization of nutrients but also suggested that, at some point, net mineralization of nutrients must occur.

Another valuable technique was the use of nutrient diffusing substrates (Pringle and Bowers 1984 [Fig. 1], Fairchild et al. 1985). This technique made it possible to compare potential nutrient limitation among various streams.

Woodall and Wallace (1975) noted the importance of detritivores to the release of chemicals from decomposing leaves, and various radiotracer studies have measured nutrient mineralization by consumers (e.g., Webster and Patten 1979). Detritivores also can influence nutrient uptake rates by heterotrophic microbes indirectly by their effects on detritus standing stocks. Mulholland et al. (1985) found that snails reduced nutrient uptake by accelerating leaf decomposition.

Another way by which consumers might contribute to stream nutrient dynamics is by translocation of nutrients. Juday et al. (1932) found that migrating salmon moved significant amounts of nutrients upstream. After their ^{32}P release into a stream, Ball et al. (1963; Fig. 1) found that some of the radiotracer moved upstream. They hypothesized that this upstream movement was probably the result of upstream movement by consumers. Fittkau (1970) suggested that caimans in Amazonian rivers might function like bears in Alaska by feeding on migrating fish and mineralizing the fish-carried nutrients. Hall (1972) suggested that migrating fish might influence stream P budgets, and Durbin et al. (1979) found that nutrient mineralization by alewife migrating upstream to spawn significantly increased respiration on leaves.

The processes of N fixation and denitrification are input and output processes that are unique to the N cycle. Denitrification was suggested to be important in steams by Hill (1979) but was not actually measured until Duff et al. (1984) used the acetylene block technique in large chambers containing undisrupted periphyton communities and found that denitrification during the night could be a considerable sink for NO_3^- in a N-rich stream. Gray (1951) noted the presence of N-fixing bacteria in an English chalk stream, and Horne and Carniggelt (1975) first measured N fixation by the cyanobacterium *Nostoc* in a California stream. Few other studies have demonstrated that stream N fixation is an important process (but see **Marcarelli et al. 2008**).

One study done before 1986 stands out as providing a comprehensive view of nutrient dynamics in streams. Using results of P radiotracer studies, Newbold et al. (1983a) developed and calibrated a quantitative, mass-balance model that included the simultaneous processes of cycling and transport of P in streams. This model was based on the spiraling concept of Webster and Patten (1979) and used the spiraling measurement techniques developed by

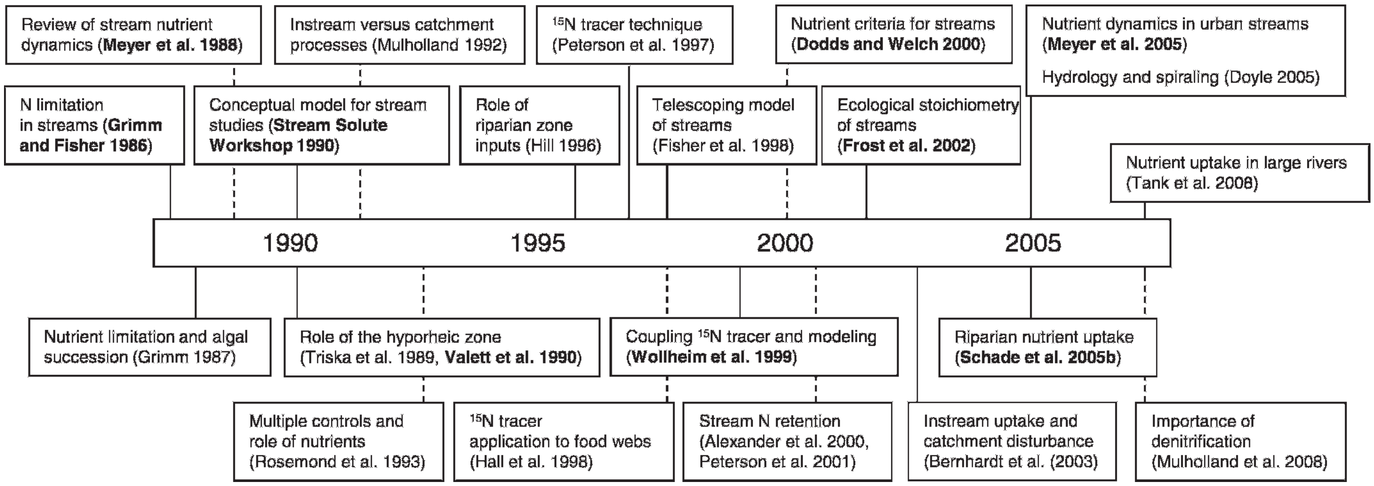

FIG. 2. A timeline of significant papers contributing to our understanding of stream nutrient dynamics after *J-NABS* was established. Details of these contributions are presented in the text. Dashed lines are used for clarity when a connecting line passes behind a box. Boldface indicates paper was published in *J-NABS*.

Newbold et al. (1981; Fig. 1). Because suitable radiotracers for N do not exist, a similarly comprehensive understanding of stream N dynamics did not occur for another decade when routine and relatively inexpensive mass spectrophotometry made the use of ^{15}N tracers possible.

Advances in Nutrient Dynamics since 1986 and the Role of *J-NABS*

Beginning in the 1980s and continuing to the present, many papers have addressed patterns and controls of nutrient dynamics in streams, and these studies have considerably advanced our understanding of this aspect of stream ecology. *J-NABS* has played an influential role in this development. Two papers on nutrient limitation of stream algae were published in the first volume of *J-NABS* (**Grimm and Fisher 1986** [Fig. 2], **Lowe et al. 1986**). Since 1990, an average of 5.3 papers/y on nutrient dynamics in streams have appeared in *J-NABS* (representing 8–12% of all papers in *J-NABS*) with a significant increase during the last few years (Fig. 3A, B). Here we discuss some of the most important developments and the role that *J-NABS* has played.

Nutrient dynamics and further development of the spiraling concept

Two papers, both published in *J-NABS* and both products of workshops, were arguably the most significant papers on nutrient dynamics in streams since the introduction of the spiraling concept and the

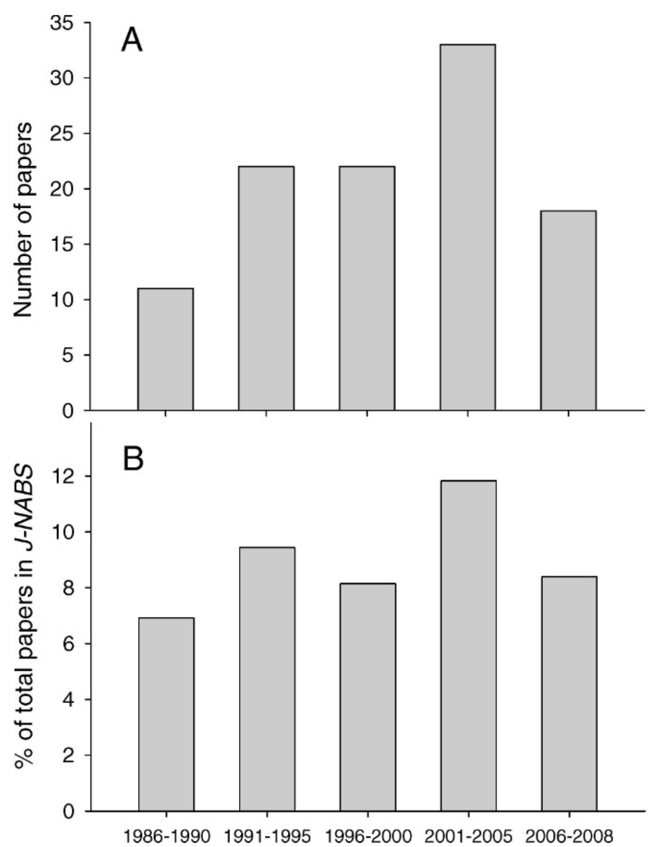

FIG. 3. Frequency distribution of papers on stream nutrient dynamics appearing in *J-NABS* as total number of papers per interval (A) and as a percentage of all *J-NABS* papers published during that interval (B). Note the last interval is only 3 y.

development of field indices to quantify spiraling. Meyer et al. (**1988**; Fig. 2) was a product of a meeting in April 1987 at the Flathead Lake Biological Station. The authors explored gaps in our understanding of elemental dynamics in streams and focused on landscape-level processes and the relative importance of upstream, riparian, and instream controls. Meyer et al. (**1988**) advocated a number of future research directions, including studying critical stream ecotones, such as biofilms, hyporheic zones, and floodplains, and emphasized the potential contributions of whole-stream manipulations supplemented by intensive studies of key processes and variables. Also, Meyer et al. (**1988**) advocated a network of experimental streams that laid the foundation for several large cross-site experiments (see *Nutrient dynamics* below).

Stream Solute Workshop (**1990**; Fig. 2) was the product of a meeting organized by Nick Aumen and held at the University of Mississippi in early 1989. The authors used the spiraling concept as a basis from which to produce a conceptual model for studies of stream nutrients and other solutes that integrated physical, chemical, and biological processes. They also identified advantages and limitations of various methods for studying solute dynamics and recommended short-term nutrient injection experiments as a more practical substitute for isotopic tracer approaches to quantify nutrient uptake lengths in streams. This paper showed how the new transient storage model approach to stream hydrodynamics developed by Bencala and others (e.g., Bencala and Walters 1983) could be used with the spiraling approach to develop a more holistic understanding of the physical controls on nutrient dynamics. Uptake velocity, sometimes called the mass transfer coefficient (in units of length/time), was introduced as a useful stream nutrient dynamics metric for relating uptake rate to nutrient concentration in water. In more recent years, this parameter has been used to scale nutrient dynamics to entire drainage networks (e.g., Wollheim et al. 2006, **Poole 2010**).

Several other significant papers have helped to refine application of the spiraling concept over the past 2 decades, although most of these papers have appeared in other journals. In an influential concept paper, Fisher et al. (1998; Fig. 2) considered the stream corridor as a hydrologically connected set of subsystems from riparian zones to the stream channel and showed how the spiraling concept could be applied to the broader stream corridor to quantify resistance to and recovery from flood disturbances. Doyle (2005; Fig. 2) incorporated hydrologic variability into spiraling theory by proposing a new metric, functionally equivalent discharge, which is "the single discharge that will reproduce the magnitude of nutrient retention generated by the full hydrologic frequency distribution when all discharge takes place at that rate" (p. G01003).

Several methodological advances have occurred recently. Payn et al. (2005) found a solution to the problem identified by Mulholland et al. (**2002**) when using the nutrient-addition approach rather than tracer additions to compare uptake lengths and rates among streams. Payn and colleagues showed how multiple nutrient-addition experiments could be used to determine uptake lengths comparable to those determined by tracer approaches. Runkel (2007) has suggested a transport-based approach for the analysis of time-series and steady-state data during tracer addition experiments that involves fitting a transient storage model that includes uptake terms to identify uptake rate coefficients for both the main channel and storage zones. This approach does not require steady-state tracer additions and might allow the use of pulse-type additions. Tank et al. (2008; Fig. 2) conducted a pulse-type N addition in a large river (Upper Snake River, Wyoming) and applied the transport-based approach recommended by Runkel (2007). Tank et al. (2008) reported that NH_4^+ and NO_3^- uptake velocities were similar to those in smaller streams in the same drainage. This paper was important because it suggested that nutrient uptake in large rivers could be as high as in small streams and because it provided a method for determining nutrient uptake in streams and rivers that are too large to use the steady-state addition approach.

Nutrient limitation and uptake

Nutrient limitation of algae was thought to be less common in streams than in lakes or the ocean because the continuous flow of water in streams was expected to replenish nutrient supplies to biota (Hynes 1969). This view began to change in the late 1970s and early 1980s with publication of several pioneering papers on P limitation of stream algae. Nutrient limitation studies in streams became more common during the mid to late 1980s, and many of the most important papers on this topic were published in *J-NABS*. In fact, the very first paper in *J-NABS* was written by Grimm and Fisher (**1986**), who dealt with N limitation of algae in Sycamore Creek in the Sonoran Desert of Arizona. Their paper was one of the first to demonstrate N limitation in streams and showed that, in some regions, such as the southwestern US, N rather than P is often the limiting nutrient. Subsequently, Hill and Knight (1988) demonstrated N limitation of periphyton in a northern California stream, Lohman et al. (**1991**) reported N limitation of periphyton in an Ozark stream, and Wold and Hershey (**1999**) found colimitation by both N and P in a Lake Superior tributary stream. Together these papers expanded the regional extent of N limitation or colimitation. More recently, Francoeur (**2001**) did a meta-analysis of 237 stream nutrient-addition experiments and found that colimitation by N and P was more common than limitation by either nutrient alone. Rosemond (**1994**) showed how nutrients, light, and herbivory all limited algal production at different times of the year in a forested stream (see also Rosemond et al. 1993 [Fig. 2], 2000). Interaction between light and nutrient limitation also was demonstrated by Sabater et al. (**2000**), who reported that P uptake increased >2× in response to riparian deforestation along a Mediterranean stream, and by Hill and Fanta (2008), who showed that P and light could colimit stream periphyton growth simultaneously. Mulholland and Rosemond (**1992**) demonstrated the spatial effects of nutrient limitation in streams and showed that stream periphyton became increasingly P limited with distance downstream from nutrient inputs because of upstream uptake and retention of P.

Fine-scale nutrient recycling also is an important nutrient source for stream algae. Peterson and Grimm (**1992**), building from the seminal paper of Grimm (1987; Fig. 2) on algal succession, biomass development, and nutrient limitation, showed how internal N recycling became more important for meeting nutrient demand during the later stages of succession when large biomass accumulations reduced the availability of water-column nutrients. Similarly, Steinman et al. (**1995**), building on earlier work by Mulholland et al. (1991), showed that nutrient recycling within dense algal mats that developed in the absence of grazers was a significant nutrient source for P-limited stream periphyton.

In the last decade, work has focused on the relationship between nutrient uptake, algal biomass, and nutrient concentration. In a study of New Zealand streams, Biggs (**2000**) showed that variation in nutrient concentration explained up to ⅓ of the variation in benthic chlorophyll *a* across streams. Dodds and Welch (**2000**; Fig. 2) argued that nutrient criteria were the most effective way of preventing nuisance levels of algal biomass, and Dodds (**2003**) argued that total N and total P, rather than the dissolved inorganic forms of these nutrients, should be used to define nutrient status and establish nutrient criteria in streams. Dodds et al. (**2002**) showed that nutrient uptake was controlled by biological kinetics responding to nutrient concentration, but that nutrient uptake did not necessarily saturate at high concentration in streams. However, Newbold et al. (**2006**) found that uptake of NH_4^+ and PO_4^{3-} in streams draining into New York City's drinking-water reservoirs could be described by Michaelis–Menten kinetics with half-saturation concentrations of ~1 mg N/L and 12 μg P/L, respectively.

Nutrient uptake by heterotrophic organisms, particularly bacteria and fungi associated with decomposing leaves, also is important in streams (e.g., Tank et al. 2000, Webster et al. 2003, Mulholland 2004). At some times, particularly in autumn and winter in forested streams, it can be the dominant mechanism for nutrient uptake.

Role of hyporheic and riparian zones

Among the most significant new developments in stream nutrient dynamics during the past 25 y was identification of the importance of nutrient uptake and recycling in hyporheic and riparian zones. This development broadened the view of stream ecosystems to include more than surface water and benthic surfaces (reviewed in **Boulton et al. 2010**).

Among the most influential early papers on the role of the hyporheic zone in nutrient cycling was a series of studies by Triska and coworkers (Triska et al. 1989 [Fig. 2], 1990, 1993, Duff and Triska 1990). These papers showed that the hyporheic zone could be both a NO_3^- source (via nitrification) and sink (via denitrification), depending on the rate of hydrological exchange with surface water, which controlled NO_3^- supply and redox conditions in the hyporheic zone. Triska et al. (1989) were particularly influential in providing a hydrologic definition of the hyporheic zone (≥10% surface water) and a conceptual model of the role of the hyporheic zone in nutrient cycling. Two excellent short reviews in the mid-1990s (Findlay 1995, Jones and Holmes 1996) and a book shortly thereafter (Jones and Mulholland 2000) helped to stimulate additional work focusing on hydrologic exchange rate and residence time in hyporheic nutrient and organic C cycling and its role in stream nutrient dynamics.

J-NABS played an important role in our understanding of stream nutrient cycling and the hyporheic zone beginning with the paper of Valett et al. (**1990**; Fig. 2). Valett and colleagues showed that the hyporheic zone was a significant source of nutrients to surface water in Sycamore Creek, Arizona, as mediated by the spatial distribution of hydraulic head (upwelling vs downwelling), which controlled dissolved O_2 inputs and mineralization in the hyporheic zone. In the first issue of 1993, *J-NABS* published a series of papers on various hyporheic zone perspectives organized by Valett, Hakenkamp, and Boulton (**Valett et al. 1993**). This collection included a paper by Bencala (**1993**) that presented a catchment perspective on hyporheic zone hydrology and solute dynamics. Papers by Stanford and Ward (**1993**), Hendricks (**1993**), and Palmer (**1993**) touched on the topic of nutrient dynamics, but focused mostly on hydrology and organisms.

A series of 5 *J-NABS* papers focused specifically on hyporheic N dynamics. In a pair of studies in Sycamore Creek, Holmes et al. (**1994**) and Jones et al. (**1995**) showed that the parafluvial (hyporheic zone lateral to the stream channel) and hyporheic zones were sources of NO_3^- to surface water as a result of mineralization of organic N, nitrification, and flow paths that transported materials from these zones to surface water. Wondzell and Swanson (**1996**) reported similar findings for a stream in Oregon. Dent et al. (**2001**) showed that patchy geomorphic features produced characteristic spatial variability in hydrodynamics (upwelling and downwelling) and surface-water nutrient concentrations at scales ranging from a few meters to several kilometers in Sycamore Creek. Last, in an Antarctic stream study published in *J-NABS*, McKnight et al. (**2004**) reported that the hyporheic zone beneath seasonal glacial meltwater streams can act as either a NO_3^- source to benthic algal mats via mineralization or a NO_3^- sink via denitrification depending on the direction and rate of subsurface flow.

The effect of riparian zones on stream nutrient dynamics has not received much attention in *J-NABS*. A number of studies published in other journals have shown that the riparian zone can be an important sink for NO_3^- in groundwater before entering streams (e.g., Peterjohn and Correll 1984, Lowrance et al. 1984, McDowell et al. 1992, Hill 1996 [Fig. 2]). However, Schade et al. (**2005b**; Fig. 2) showed that the effect can be in the other direction, as well—riparian-zone vegetation can be a significant sink for streamwater N along water flowpaths from the stream to adjacent riparian zones.

N dynamics

In the past decade, studies on the rates and controls on N uptake and retention have become an important part of stream nutrient research. Concern about eutrophication of estuaries and coastal oceans (e.g., seasonal development of dead zones in the Gulf of Mexico, harmful algal blooms in North Carolina estuaries, loss of benthic macrophyte beds in the Chesapeake Bay) and the role of streams as N filters or sinks has driven much of this work.

Several studies in which traditional techniques, such as mass balance, uptake of added nutrients, and nitrapyrin addition (nitrification) or acetylene block (denitrification), were used to explore stream N dynamics were published in *J-NABS*. Kemp and Dodds (**2001**) showed how stream algae stimulated nitrification rates via dissolved O_2 production, and Strauss et al. (**2004**) showed that O_2 penetration into sediments controls nitrification rates in the Upper Mississippi River. In a study of N fluxes associated with epilithon communities in the River Garonne, France, Teissier et al. (**2007**) reported a biomass threshold between net N assimilation by autotrophs and net mineralization by heterotrophs at epilithon biomass levels of 23 g ash-free dry mass (AFDM)/m^2. In a recent paper, Hoellein et al. (**2009**) used substratum-specific and whole-stream NO_3^- addition experiments to show the importance of streambed composition on seasonal variability in reach-scale uptake and the important role of epilithic biofilms for NO_3^- uptake in forested streams.

A series of papers on denitrification using the acetylene block technique on sediments demonstrated the importance of NO_3^- concentration and, secondarily, temperature as controlling factors (**Martin et al. 2001**, **Schaller et al. 2004**, **Strauss et al. 2006**). Teissier et al. (**2007**) also showed that denitrification rates increased with biomass, but only in the dark when O_2 was not being produced by the autotrophic component of the biofilm. Ruehl et al. (**2007**) presented an interesting approach that combined measurements of longitudinal changes in NO_3^- concentration and stable N and O isotope enrichment factors to evaluate NO_3^- uptake rates and the role of denitrification (which results in isotopic enrichment of NO_3^-) in the Pajaro River, California.

One of the most important advances in the study of N dynamics in streams was the development of a field tracer ^{15}N addition approach. This approach was first used in a study of NH_4^+ uptake in the Kuparuk River (Peterson et al. 1997; Fig. 2). Wollheim et al. (**1999**; Fig. 2) showed how data from field ^{15}N experiments could be coupled with a model to provide a more synoptic view of N cycling in streams, and Hall et al. (1998; Fig. 2) showed how the ^{15}N approach could be used to trace N cycling in stream food webs. Others then used the tracer ^{15}N additions to examine foodweb linkages (**Mulholland et al. 2000**), preferential use of the upper layer of epilithon by grazers (**Rezanka and Hershey 2003**), and the relative importance of autochthonous versus allochthonous N in stream food webs (**Hamilton et al. 2004**).

The ^{15}N addition approach was the basis of a large cross-site study known as the Lotic Intersite Nitrogen Experiment (LINX). In summary papers from the LINX study, Peterson et al. (2001; Fig. 2) and Webster et al. (2003) used experimentally measured average rates of N cycling (gross N uptake and remineralization) to show that instream uptake could reduce N concentrations and flux by an average of ⅔ over a 1-km distance in a 1st-order stream. Mulholland et al. (2004) adapted the ^{15}N addition approach to measure reach-scale NO_3^- uptake and denitrification in streams, and in a 2nd cross-site study (LINX II), Mulholland and colleagues used it to compare NO_3^- dynamics in 72 streams draining different land uses across the US (Mulholland et al. 2008 [Fig. 2], 2009a, Hall et al. 2009).

In recent years, several studies have attempted to put stream N uptake into a landscape and even global context by defining the role of streams in N retention in large river basins. This work has resulted in somewhat conflicting views regarding where within the drainage network N retention is most important. Some authors suggest that small streams (generally $\leq$3rd–4th-order) might control N exports from river networks because of their high surface area to volume ratios and large contribution to total network stream length (Alexander et al. 2000 [Fig. 2], Peterson et al. 2001). Other studies indicate that larger streams and rivers might dominate N removal in drainage networks because of their longer water residence times and transport distances (Seitzinger et al. 2002, Wollheim et al. 2006, Ensign and Doyle 2006). Mulholland et al. (2008) offered an explanation for these conflicting views based on their observation that NO_3^- uptake and denitrification rates are strongly related to NO_3^- concentration across many biomes and landuse types. Mulholland et al. (2008) developed a model that used this relationship to predict N retention in a large river basin and showed that the relative significance of small vs large streams is a function of NO_3^- loading, with the importance of larger streams increasing at high loading rates as the capacity for uptake in smaller streams becomes saturated and a larger fraction of the NO_3^- load is exported downstream. More recently, Alexander et al. (2009) showed how interactions among N loading, instream denitrification rates, and hydrological factors controlled seasonal as well as spatial variation in N retention within river networks. These landscape or globally oriented stream and river N-uptake papers have not appeared in *J-NABS*, probably because of the attempt of the authors to reach a broader audience.

Role of consumers in stream nutrient dynamics

The role of anadromous fish migrations as nutrient subsidies enhancing nutrient availability and cycling in streams has been a valuable area of research. Early studies by Richey et al. (1975) and Sugai and Burrell (1984) and more recent studies (e.g., Wipfli et al. 1998, 1999, Johnston et al. 2004) have reported greater primary productivity or epilithic biomass in streams with spawning salmon runs or when salmon carcasses were experimentally added to streams than in streams without salmon, presumably because of the nutrient subsidy provided by salmon. Natural abundance ^{15}N studies have shown that marine-derived N is incorporated into food webs and cycled within stream ecosystems (Kline et al. 1990, Bilby et al. 1996). However, some studies found no effect of spawning fish carcasses on periphyton (Minshall et al. 1991, Rand et al. 1992). A recent study in southeast Alaska streams indicated that salmon clearly increased nutrient concentrations, but responses by epilithon were variable because of factors, such as light limitation and hydrologic disturbance (Mitchell and Lamberti 2006). In a related study focusing on the aquatic insect communities of these Alaskan streams, Lessard and Merritt (2006) found that the positive effect of marine-derived N on abundance and biomass was limited to certain taxa, primarily chironomid midges.

J-NABS has played a modest role as an outlet for work in this area of research. Schuldt and Hershey (**1995**) used both comparative and experimental approaches to examine the effect of salmon carcass decomposition on Lake Superior tributary streams and found higher P concentrations and periphyton biomass with than without salmon. Schuldt and Hershey (**1995**) also reported ^{15}N evidence that salmon-derived N cycled through the stream food web. Minakawa et al. (**2002**) reported increased biomass and growth rate of stream insects with experimentally added salmon carcasses in a Washington stream, primarily as a result of direct consumption of the carcasses by insects. In contrast, Ambrose et al. (**2004**) reported that salmon carcass additions to northern California streams had no effect on periphyton biomass or primary production, possibly because of light limitation. However, Peterson and Matthews (**2009**) reported higher periphyton biomass and significant uptake of salmon-derived nutrients by periphyton, bryophytes, and decomposing leaves when salmon carcasses were added to laboratory streams. Summarizing work to date, it appears that spawning runs of salmon and other anadromous fish can provide nutrient subsidies and enhance nutrient uptake in stream ecosystems through both direct feeding by consumers on carcasses and bottom-up enhancement of periphyton productivity by nutrients released during carcass decomposition, but the latter mechanism might be confined to those streams in which light levels are high and nutrients are strongly limiting.

Nutrient retention in urban streams

Recent interest in nutrient cycling and retention in urban streams appears to be driven largely by rapid urbanization and the need for better understanding of nutrient cycling and its controls in urban streams to mitigate or minimize effects of urbanization on stream ecosystem function and basin-scale nutrient retention. Historically, the focus of research on the effects of urbanization on stream nutrient dynamics has been on point-source nutrient inputs from wastewater treatment plants and other facilities. Some studies, including 2 in *J-NABS* (**Meals et al. 1999**, **Haggard et al. 2005**) examined nutrient uptake below wastewater treatment plant effluents.

Much of the recent work on nutrient dynamics in urban streams has been more comprehensive and has evaluated how structural and functional changes caused by urbanization affect nutrient uptake and cycling. In a review of urban streams, Paul and Meyer (2001) noted that ecosystem processes were understudied and nutrient uptake and retention largely ignored, and that urban streams provide opportunities to test stream concepts and to understand and manage ecosystems that include humans. Perhaps in response to the challenges laid out by Paul and Meyer (2001), a special series of papers from a symposium held in Melbourne, Australia, in December 2003 was published in *J-NABS* Volume 24, Issue 3 (**Feminella and Walsh 2005**). Several of these papers focused on nutrient dynamics in urban streams. Meyer et al. (**2005**; Fig. 2) showed that NH_4^+ and soluble reactive P (SRP) uptake rates decreased with the proportion of urbanized area in the catchment and that this effect appeared to be related to declines in sediment organic matter and the biotic demand for nutrients associated with this material. Groffman et al. (**2005**) also reported that denitrification could be a significant sink for streamwater NO_3^- in urban streams, but that denitrification in these geomorphologically unstable systems is limited by the paucity of debris accumulations that provide the conditions necessary for denitrification. Grimm et al. (**2005**) suggested that some urban modifications to stream networks, such as detention basins and artificial lakes in the Phoenix, Arizona, area could enhance nutrient uptake and retention.

Last, several recent papers have compared N dynamics among urban, agricultural, and forested streams in the same region. O'Brien et al. (2007) used ^{15}N additions to compare NO_3^-uptake among 9 streams of contrasting land use in Kansas and found that NO_3^- concentration rather than land use per se was the most important factor controlling uptake and denitrification rates. Perhaps somewhat surprisingly, O'Brien and colleagues also reported that uptake rates did not appear to saturate with increasing NO_3^- concentration when comparing among streams, a finding confirmed in the full LINX II study (Mulholland et al. 2008). Arango and Tank (**2008**) compared nitrification and denitrification rates among 18 agricultural and urban streams in southwestern Michigan and found that both were positively related to sediment C content, which was not related to land use. However, denitrification was also positively related to NO_3^- concentration which tended to be higher in agricultural than in urban streams. In a whole-stream ^{15}N addition study conducted in forested, agricultural, and urban streams in northeastern Spain, von Schiller et al. (2009) reported highest rates of NO_3^- uptake and denitrification in the agricultural stream and intermediate rates in the urban stream, a result that probably reflected the higher NO_3^- concentrations compared to the forested stream. Epilithon largely accounted for the higher NO_3^- uptake rates in the agricultural stream, probably because the streambed was largely cobble, and epilithon were more productive under higher NO_3^- concentration.

Importance of instream uptake for catchment nutrient budgets

An important advance in the understanding of stream nutrient dynamics was the appreciation that nutrient concentrations and flux in streams are not necessarily reflective of the biogeochemistry of the terrestrial ecosystems they drain. The development of the small-catchment approach to terrestrial biogeochemistry with the seminal studies of Likens and Bormann (e.g., Likens et al. 1977) used stream chemistry as the spatial integrator of the net effects of the forest in processing atmospheric inputs, internal cycling of nutrients, and the biogeochemical response to disturbances. Although never explicitly stated, and despite the early recognition by Hynes (1970) that streams affect nutrient concentrations, the underlying assumption (at least by some) was that instream processes would not appreciably alter the signals from terrestrial processes (i.e., streams were largely drainage pipes).

Gradually this view began to change, beginning with papers by Meyer and Likens (1979), Grimm (1987), Munn and Meyer (1990), Mulholland (1992; Fig. 2), and Burns (1998) that showed substantial uptake of N and P within streams. Mulholland used an inverse modeling approach to show that distinct seasonal patterns in NO_3^- and SRP concentrations were related to instream processes rather than to seasonal changes in the forest (Mulholland and Hill 1997, Mulholland 2004). Peterson et al. (2001) used a model of stream nutrient dynamics and data from cross-site field ^{15}N addition experiments to show that instream processes could remove most of the N entering streams in groundwater within 1 km of its entry. Bernhardt et al. (2003; Fig. 2) showed that the increases in NO_3^- concentrations commonly observed in response to forest disturbance were highly dampened by instream uptake of NO_3^- after a severe ice storm that caused extensive forest damage at Hubbard Brook Experimental Forest. In a subsequent paper, Bernhardt et al. (2005) argued that the unexplained long-term decline in NO_3^- outputs from New England catchments might be caused, in part, by increased uptake in streams as forests have aged and debris dams and organic matter storage in streams has increased. While assimilatory uptake is probably not a long-term sink for N, it might enhance denitrification rates by providing the organic-rich sediments conducive to development of anoxic hotspots for tightly coupled processes of mineralization and denitrification (sensu Seitzinger et al. 2006).

Building on past work in Walker Branch, Roberts and Mulholland (2007) used a mass-balance approach to show that high rates of instream inorganic N retention are related to seasonal peaks of primary production during early spring and of heterotrophic respiration associated with leaf decomposition in autumn. Hall and Tank (2003) also showed tight coupling of NO_3^- uptake with primary production in streams (see also **Tank et al. 2010**). Goodale et al. (2009) reported very low stream NO_3^- concentrations after leaffall in autumn, a pattern increasingly being reported for streams draining deciduous forests and resulting from high rates of instream uptake by heterotrophic microbes during leaf decomposition. A revised concept of catchment nutrient dynamics that includes the active role of stream processes in controlling exports has been nicely summarized by Hall (2003). However, Brookshire et al. (2009) argued that most streams are in longitudinal steady state with no net uptake of nutrients, and thus, stream chemistry can be used as an integrated measure of terrestrial outputs. Clearly, more work is needed on this subject.

Where to Now?

Nutrient dynamics in streams and the role of streams in nutrient retention will remain an important and exciting area of future research. One significant and unresolved issue is the role of streams as landscape nutrient filters at regional and continental scales and what stream properties control this role. Several papers have been published recently on this topic (Alexander et al. 2000, Peterson et al. 2001, Mulholland et al. 2008), but more work is needed. This issue is central to topics, such as the preservation or reestablishment of riparian buffer zones and designing stream restorations. For example, Roberts et al. (**2007**) demonstrated the importance of woody debris additions for enhancing nutrient uptake in stream restorations.

A better understanding is needed of the rates and controls on nutrient dynamics in larger streams and rivers. Few empirical studies of nutrient dynamics have been done in rivers, but recent modeling efforts have suggested that rivers play a considerable role in nutrient retention at the scale of large drainage basins (Seitzinger et al. 2002, Wollheim et al. 2006). Methodological constraints have limited empirical studies in large rivers (e.g., constant rate ^{15}N addition techniques might be difficult at high discharge), so clever new approaches are needed.

The ultimate fate of nutrients removed from water by benthic organisms in streams and rivers is an important issue for long-term nutrient retention and prevention of eutrophication. Are these nutrients simply released back to the water at or near the location of uptake; transported downstream in particulate organic form during periods of high flow (storms) and deposited in sediments of floodplains, lakes, reservoirs, estuaries, and coastal oceans; or further transformed (e.g., to dissolved organic form) and potentially lost (e.g., denitrification) from the system? What are the factors controlling these fates? These questions must be addressed to provide a full understanding of the role of streams and rivers in landscape nutrient budgets and the eutrophication of lakes, reservoirs, and coastal ecosystems downstream.

Before 1986, stream nutrient studies were mostly about P, and more recent studies have focused more on N. Studies that have considered N and P simultaneously are rare. Ecological stoichiometry (Sterner and Elser 2002) addresses how elemental composition of producers, consumers, and their interactions drive changes in N and P availability and alter nutrient limitation of biotic processes. Ecological stoichiometry has been applied in streams (e.g., **Frost et al. 2002** [Fig. 2], Cross et al. 2003, 2005, Dodds et al. 2004, Schade et al. 2005a, **Rothlisberger et al. 2008**), and we foresee continued advances in our understanding of stream nutrient dynamics coming from additional stoichiometric studies of stream processes.

Climate change and its impacts on stream nutrient dynamics will also be an important area of future research. Stream nutrient dynamics will undoubtedly change as climate changes in the future because the input and cycling of nutrients are strongly influenced by climate (temperature and seasonality, precipitation and runoff). Climate change might influence stream nutrient dynamics as much via indirect effects (e.g., changes in riparian vegetation and light availability, quantity and quality of organic matter inputs; e.g., Mulholland et al. 2009b) as via direct effects. Understanding how climate change is likely to affect stream nutrient dynamics will be critical as we plan how to manage or restore streams to adjust to those changes.

Last, advances in measurement technologies hold exciting promise for future research on nutrient dynamics in streams. Battery-powered in situ sensors with datalogging capabilities that allow unattended field measurement of some nutrients (PO_4^{3-}, NH_4^+, NO_3^-) at high frequency (e.g., min–h) have recently become available. Such in situ, high-frequency measurements should allow observation of signals of ecosystem responses (e.g., diurnal, storm-related, disturbance) that have been difficult to detect by manual sampling and that should enhance our understanding of patterns and controls on nutrient dynamics. These measurements also might enhance the use of stream chemistry as a monitoring tool to provide a spatially integrated signal of catchment biogeochemistry. In situ mass spectrometers capable of measuring the stable isotope content of nutrients in water (e.g., ^{13}C, ^{15}N, ^{18}O of dissolved organic and inorganic forms of N and P) are another technology that might not be far off. Stable isotope studies have been influential in understanding nutrient sources and transformations in streams, but the need to sample and process water and organic matter manually has limited the scope and temporal resolution of this information.

Methodological advancements and breakthroughs are often the drivers for major advances in ecosystem science and allow us to ask new questions and view systems with entirely new perspectives. Development of radiotracer techniques, use of stable isotopes, nutrient releases, and nutrient diffusion substrates all contributed significantly to our understanding of stream nutrient dynamics. Future research should benefit greatly from new measurement technologies over the next decade.

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