

MINI-REVIEW

# Nutrient Cycling in Lakes and Streams: Insights from a Comparative Analysis

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## ABSTRACT

Understanding of general ecosystem principles may be improved by comparing disparate ecosystems. We compared nutrient cycling in lakes and streams to evaluate whether contrasts in hydrologic properties lead to different controls and different rates of internal nutrient cycling. Our primary focus was nutrient cycling that results in increased productivity, so we quantified nutrient cycling by defining the recycling ratio ( $\rho$ ) as the number of times a nutrient molecule is sequestered by producers before export. An analytic model of nutrient cycling predicted that in lakes  $\rho$  is governed by the processes that promote the mineralization and retard the sedimentation of particulate-bound nutrients, whereas in streams,  $\rho$  is governed by processes that promote the uptake and retard the export of dissolved nutrients. These differences were the consequence of contrast between lakes and streams in the mass-specific export rates (mass exported  $\cdot$  standing stock<sup>-1</sup>  $\cdot$  time<sup>-1</sup>) of

dissolved and particulate nutrients. Although  $\rho$  is calculated from readily measured ecosystem variables, we found very few published data sets that provided the necessary data for a given ecosystem. We calculated and compared  $\rho$  in two well-studied P-limited ecosystems, Peter Lake and West Fork Walker Branch (WFWB). When ecosystems were scaled so that water residence time was equal between these two ecosystems,  $\rho$  was three orders of magnitude greater in WFWB. However, when we scaled by P residence time,  $\rho$  was nearly equal between these two ecosystems. This suggests broad similarities in  $\rho$  across ecosystem types when ecosystem boundaries are defined so that turnover times of limiting nutrients are the same.

**Key words:** ecosystem; lakes; streams; nutrient cycling; lotic; lentic; comparative analysis; ecosystem models.

## INTRODUCTION

Cycling of limiting nutrients is an important property of ecosystems (forest, Vitousek and Sanford 1986; ocean, Eppley and Peterson 1979; grassland, McNaughton and others 1988; lake, Fee 1979; stream, Elwood and others 1982). For many ecosystems, internal nutrient cycling is the dominant

source of nutrients for primary producers (for example, Levine and Schindler 1980; Tripathi and Singh 1994), so there is tight coupling between the rate of nutrient cycling and primary productivity. Consumers thereby can control primary productivity by altering the rate of nutrient remineralization and subsequent uptake (Kitchell and others 1979). Furthermore, the magnitude of nutrient cycling has important effects on ecosystem resistance and recovery from disturbance (DeAngelis and others 1989). For these reasons, processes governing the rate of

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cycling have received considerable attention from ecologists. However, studies tend to be conducted within a single ecosystem or ecosystem type, and there have been few attempts to derive generalized hypotheses about the processes governing nutrient cycling across ecosystems. Comparative analysis of nutrient cycling may be able to provide such generalizations (Pace 1991), and the broadest generalizations may be generated by comparisons of very different types of ecosystems (Fisher and Grimm 1991).

Freshwater ecosystems provide a large contrast in physical properties, defined in part by contrasts in water flow and hydrologic flushing rate. At one end of this continuum are streams (unidirectional flow and high flushing rate), and at the other end are lakes (turbulent mixing and low flushing rate). These ecosystems are further distinguished by the relative importance of benthic (streams) versus pelagic (lakes) productivity. Perhaps because of these differences, nutrient cycling in lakes and streams has been studied with markedly different paradigms. A comparative analysis that addresses how differences in nutrient cycling between lakes and streams are a consequence of the contrasts in physical environments may lead to a broader understanding of nutrient cycling in aquatic ecosystems.

Because nutrient cycling in aquatic ecosystems is governed in part by hydrologic processes, one may expect markedly different controls on recycling and also different amounts of internal nutrient cycling in lakes and streams. The main goal of this article is to assess these expectations. We focus on cycling that ultimately results in the uptake of limiting nutrients by producers and therefore quantify internal nutrient cycling by considering the number of times nutrient molecules are sequestered by producers before export. We use a generalized model of nutrient cycling to evaluate how differences in hydrology cause the controls of nutrient cycling to differ between lakes and streams. We then quantify and compare the amount of internal nutrient cycling between a lake and stream ecosystem to evaluate whether markedly different physical environments lead to different amounts of recycling.

### Nutrient Cycling in Lentic Systems

Much research on lake nutrient cycling has focused on lake epilimnetic zones, most likely because this region has clearly defined boundaries and the majority of primary production often occurs there. The majority of epilimnetic primary production often is fueled by recycled nutrients (Fee 1979; Levine and Schindler 1980; Caraco and others 1992), so that internal processes that mediate the rate of nutrient

cycling have large effects on lake productivity. For example, lake morphometric features that reduce nutrient losses can enhance nutrient cycling and thereby enhance primary production (Fee 1979; Fee and others 1992, 1994). Also, excretion by zooplankton (Barlow and Bishop 1965; Andersson and others 1988; Urabe and others 1995) and fish (Kraft 1992; Schindler 1992; Schindler and others 1993; Vanni 1996) can be important sources of nutrients for phytoplankton. Enhanced algal growth in response to nutrient release by zooplankton may compensate for or even exceed losses due to grazing (Lehman and Sandgren 1985; Sterner 1986; Sterner and others 1995). However, *Daphnia* grazing also can reduce nutrient cycling by increasing nutrient export via sedimentation of fecal material (Bossard and Uehlinger 1993; Elser and others 1995).

### Nutrient Cycling in Lotic Systems

Because nutrient cycling in streams has a downstream vector, nutrient cycling resembles a downstream "spiral" (Webster and Patten 1979; Elwood and others 1982). Thus, stream ecologists often quantify nutrient cycling by measuring spiralling length ( $S$ ), which is the downstream distance a nutrient molecule travels while cycling from a dissolved form to particulate form and back to dissolved form. Nutrient transport may occur in the particulate or dissolved form, but because much of this transport occurs in the dissolved form, many investigators focus on the dissolved component of spiralling length, called the uptake length (Stream Solute Workshop 1990). Uptake length varies substantially among streams. Streams with extensive hyporheic (subsurface) flow have shorter uptake lengths (Mulholland and others 1997) and therefore have higher rates of nutrient cycling. Substrate composition and channel type also affect uptake length, but the manner by which these attributes affect uptake length may be site specific and depend on complex interactions between light availability and channel morphology (Munn and Meyer 1990; Martí and Sabater 1996). Consumers may affect spiralling length by reducing recycling of nutrients within periphyton mats (Mulholland and others 1991, 1994), and by increasing the particulate transport of nutrients (Wallace and others 1982; Grimm 1988). Disturbances, such as floods, create a temporal pattern of nutrient cycling wherein spiralling lengths are long immediately after floods and gradually shorten over successional time (Martí and others 1997; Fisher and others 1998).

## A COMMON CURRENCY OF NUTRIENT CYCLING

Lake ecologists often quantify nutrient cycling by calculating the portion of primary production supported by recycled nutrients (Caraco and others 1992), the ratio of “new” primary production to recycled production (*F* ratio; Eppley and Peterson 1979), or the increase in compartment transfers that results from cycling (Finn 1976; Richey and others 1978). In contrast, stream ecologists quantify nutrient cycling by calculating spiralling or uptake length. A synthesis of ideas begins with a common metric to quantify nutrient cycling in both ecosystem types. One way to arrive at such a metric is to consider the fundamental processes that control cycling rates. In the broadest sense, the amount of internal nutrient cycling is determined by the rate at which nutrients are sequestered and the rate at which nutrients are lost from the ecosystem. These two processes can be combined by considering the average number of times nutrient molecules are used before being exported from the system (Poister and others 1994). We refer to this measure as the recycling ratio ( $\rho$ , which can be calculated as the ratio of uptake rate (*U*; mass/time) to export rate (*E*; mass/ time):

$$\rho = \frac{U}{E}. \quad (1)$$

Thus,  $\rho$  is a dimensionless number with a straightforward interpretation that can be applied to all ecosystem types. Moreover,  $\rho$  can be derived from parameters often measured in both lakes and streams. For example, in streams  $\rho$  equals stream length (*L*) divided by the spiralling length (Newbold and others 1982), and in lakes  $\rho$  equals the inverse of the export ratio (proportion of sequestered nutrients that is exported; Baines and Pace 1994; Elser and others 1995).

## A CONCEPTUAL MODEL FOR NUTRIENT CYCLING IN LAKES AND STREAMS

A generalized model must suppress the idiosyncrasies of individual ecosystems and highlight common processes. We derived such a model from the premise that nutrient cycling is controlled by the uptake rate of dissolved nutrients, the rate of nutrient release from particulates, and the rate of nutrient export from the ecosystem (Figure 1). We define the dissolved pool as consisting of both inorganic (available) and organic (unavailable) forms and consider the consequences of this aggregation later (see Discussion). We define the particulate component

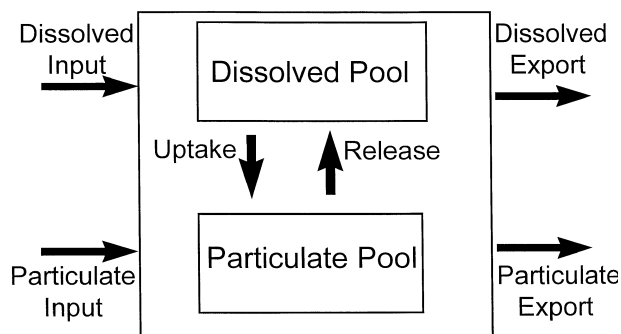


Figure 1. Schematic representation of conceptual model. Arrows represent fluxes of nutrients, and boxes represent nutrient pools.

as any ecosystem component that is capable of active uptake of dissolved nutrients (for example, phytoplankton, periphyton, and microbes). Nutrients may leave the system directly from the dissolved pool (hydrologic flushing) or via the particulate pool (sedimentation, downstream transport). The nutrient release component encompasses the entire flux of nutrients through the producer pool that results in nutrients being transferred to the dissolved pool. This includes consumer-mediated remineralization. However, the fraction of consumed nutrients that is sequestered into consumer tissues (consumer sinks; Andersen 1997) can be considered a nutrient export because at short time scales, these nutrients are not available for production.

The model provides a framework to evaluate the ways in which lakes and streams differ. Although it is not clear whether uptake or release rates differ between these ecosystems, there is evidence that the route of export does. Within lake epilimnetic zones, particulates are suspended in a medium that has low flushing rates (high hydraulic residence times), such that sedimentary losses are often more important than hydrologic losses (Frisk and others 1980). Furthermore, any hydrologic loss that occurs is comprised of both suspended particulate and dissolved components. Thus, particulate-bound nutrients should have a higher mass-specific export rate (mass exported  $\cdot$  standing stock<sup>-1</sup>  $\cdot$  time<sup>-1</sup>) than dissolved nutrients. In low-order streams, particulates are largely attached to the stream bed so that they have high residence time, whereas the residence time of water is much shorter. Thus, dissolved nutrients should have a higher mass-specific export rate than particulate-bound nutrients. We propose that an important distinction between lakes and streams is the relative magnitude of mass-specific export rate for particulate (denoted  $e_p$ ; higher in

**Table 1.** Comparison of Percentages of Hydrologic versus Sedimentary Export for Lakes

	Hydrologic (%)	Sedimentation (%)	Reference
Nitrogen			
Kinneret	69	31	Smith and others 1989
Horw Bay	21	79	Bloesch and others 1977
Rotsee	34	66	Bloesch and others 1977
Phosphorus			
Kinneret	9	91	Smith and others 1989
Mendota	21	79	Lathrop and others 1998
Mirror	2	98	Caraco and others 1992
Horw Bay	15	85	Bloesch and others 1977
Rotsee	54	46	Bloesch and others 1977
Paul	14	86	S.R. Carpenter unpublished
Peter	8	92	S.R. Carpenter unpublished
West Long	3	97	S.R. Carpenter unpublished

lakes) and dissolved (denoted  $e_d$ ; higher in streams) nutrients.

To test this idea, we gathered published data on N and P export for lake epilimnetic zones and for C, N, and P transport for streams. The literature typically reports total export, that is, mass-specific export · standing stock, but not standing stock. Thus, comparisons of  $e_d$  and  $e_y$  require addition information or assumptions.

For lakes, nutrients can be exported via either hydrologic flushing or sedimentation. Sedimentation consists only of particulate nutrients, but hydrologic losses consist of both dissolved and particulate nutrients. Thus, if all nutrient export is via sedimentation, then  $e_y \gg e_d$ , and if all nutrient export is via hydrologic losses and all particulates are suspended, then  $e_y = e_d$ . The assumption that nutrients in attached (for example, benthos) particulates can be ignored is reasonable for large, deep lakes with limited littoral zones and extensive pelagic zones. Shallow lakes with extensive littoral production may have  $e_d > e_y$ .

We compiled data on hydrologic and sedimentary losses for lakes where the pelagic zone comprised at least 50% of the epilimnetic area (Table 1). In most

cases, sedimentation losses exceeded hydrologic losses, indicating  $e_y \gg e_d$ . Even in lakes where hydrologic losses exceed those for sedimentation (Kinneret for N, Rotsee for P), hydrologic losses likely include some particulates and  $e_y$  may exceed  $e_d$ . Furthermore, it was not uncommon for investigators to ignore hydrologic losses when constructing N budgets (for example, Hama and others 1990). Thus, data in Table 1 suggest that  $e_y$  generally exceeds  $e_d$  for lakes. Data were not available for C because most investigators assert that C loss via hydrologic processes is negligible and therefore rarely measure it (for example, Forsberg 1985; Baines and Pace 1991).

For streams, there is no sedimentation loss because benthos is contained within the ecosystem. We therefore require an alternative means to discern the relative magnitudes of mass-specific exports. One approach derives from the observation that the majority of nutrients are bound to particulates. For example, Hall and others (1998) report that 85% of N standing stock is particulate (seston, benthos) in Hugh White Creek. Peterson and others (1986) estimate that the dissolved C concentration in Kuparak River averages only  $10.1 \text{ g m}^{-3}$ , compared with a benthic particulate C standing stock of  $56.1 \text{ g m}^{-2}$  (Harvey and others 1997). Similarly, Fisher (1977) estimated that particulate organic matter comprised 96.5% of the total detrital organic matter. Finally, Newbold and others (1983) estimate that 99.5% of P standing stock in West Fork Walker Branch was particulate.

Because particulate standing stock  $\gg$  dissolved standing stock, nutrient export should be overwhelmingly dominated by particulate-bound nutrients if the mass-specific export of dissolved and particulate nutrients were the same ( $e_d = e_y$ ). However, published data on streams indicate that nutrient export is not dominated by particulates, and that dissolved export is commonly the dominant route of export (Table 2). For organic C, dissolved transport represented as much as 95% of transport (mean = 64%; Table 2). Differences in the route of N transport were more striking, with dissolved transport averaging 88% of total transport, except for Hugh White Creek that had a very high (85%) particulate export rate (Table 2). Fewer data were available for P. Newbold and others (1983) and Mulholland and others (1985) indicated that, during baseflow conditions, P is dissolved for the majority of its travel distance (Table 2), and most subsequent studies only have measured P uptake length. However, over long time periods (greater than 1 year), Meyer and Likens (1979) and Peterson and others (1992) noted large amounts of particulate P transport. Most

**Table 2.** Comparison of Dissolved versus Particulate Nutrient Transport for Streams

	Dissolved (%)	Particulate (%)	Reference
Organic carbon			
Rattlesnake Springs	68	32	Cushing 1997
Bear Brook	23	77	Findlay and others 1997
Fort River	76	24	Fisher 1977
Kings Creek	94	6	Gray 1997
Kuparak River	92	8	Harvey and others 1997
Monument Creek	93	7	Irons and Oswood 1997
Sycamore Creek	98	2	Jones and others 1997
Breitenbach	96	4	Marxsen and others 1997
Canada Stream	21	79	McKnight and Tate 1997
Ogeechee River	96	4	Meyer and others 1997
Creeping Swamp	95	5	Mulholland 1981
West Fork Walker Branch	32	68	Mulholland 1997
White Clay Creek	33	67	Newbold and others 1997
Buzzards Branch	74	26	Smock 1997
Keppel Creek	47	53	Treadwell and others 1997
Satellite Branch	33	67	Wallace and others 1997
Hugh White Creek	29	71	Webster and others 1997
Phosphorus			
Bear Brook	21	78	Meyer and Likens 1979
West Fork Walker Branch	86	14	Newbold and others 1983
Kuparak River	49	51	Peterson and others 1992
Nitrogen			
Sycamore Creek	95	5	Grimm 1987
Fryxcell Stream	90	10	Howard-Williams and others 1989
Bear Brook	96	4	Meyer and others 1981
Beaver Creek	82	18	Naiman and Melillo 1984
Hugh White Creek	15	85	Hall and others 1998
Watershed 10	78	23	Triska and others 1984

of this particulate transport occurred during short-lived floods, when large amounts of particulate matter are scoured from the stream bed. However, during baseflow conditions, particulate export is much less than dissolved export (Meyer and Likens 1979; Mulholland and others 1985). Data from 213 streams from the United States Geological Survey National Water Quality Assessment Program provide similar results; the mean dissolved N and P export from these streams was 80% and 66%, respectively (see <http://www.rvares.er.usgs.gov/nawqa>). Only 14 of these streams had less than 50% dissolved P export, and only one stream had less than 50% dissolved N export.

Combining data on standing stocks and export rates provides estimates of the relative magnitudes of  $e_d$  and  $e_p$ . For N in Hugh White Creek (Hall and others 1998), the ratio  $e_d/e_p$  (denoted  $\gamma$ ) is 4.2, indicating that a nutrient molecule is four times more likely to be transported when in the dissolved than when in the particulate state. For C in Fort

River (Fisher 1977), the ratio of mass-specific export rates is more than an order of magnitude greater ( $\gamma = 87$ ). The most extreme estimate of  $\gamma$  comes from P transport in Walker Branch creek, where we estimate that the ratio of mass-specific exports is  $\gamma = 1200$ . Thus, published data from streams support the contention that mass-specific export of dissolved nutrients exceeds that of particulate nutrients.

### EVALUATING THE CONSEQUENCES OF NUTRIENT EXPORT: A MATHEMATICAL MODEL OF NUTRIENT CYCLING

We developed a mathematical model of nutrient dynamics to evaluate how the sensitivity of  $\rho$  to uptake and release rates depends on the relative magnitudes of dissolved and particulate mass-specific export. We adopted a mathematical approach commonly used in models of stream (Newbold and others 1982, 1983; Stream Solute

Workshop 1990) and lake (DeAngelis 1992) ecosystems, in that we assumed linear, donor-controlled transfers of nutrients between compartments. Although globally the assumption of linearity is false, it is a reasonable approximation of nutrient dynamics under some conditions (DeAngelis 1992). Also, donor-control of nutrient transfers is not a reasonable assumption over all state space, because nutrient uptake can be independent of dissolved nutrient concentration when nutrient concentrations are high (Hart and others 1992) or when particulate biomass is low (Mulholland and others 1990). Thus, the following model approximates uptake kinetics when dissolved nutrients are in limiting supply relative to nutrient demands of the biota.

Nutrient uptake by producers is described by the nutrient uptake coefficient,  $u$  (time<sup>-1</sup>), which indicates the fraction of the dissolved pool ( $D$ ; mass) that flows into the particulate pool ( $Y$ ; mass) per unit time. Similarly, nutrients are released from the particulate pool back into the dissolved pool at a rate described by the nutrient release coefficient ( $r$ ; time<sup>-1</sup>) and the particulate standing stock. The release coefficient encompasses the entire flux of nutrients through the producer pool that results in nutrients being released. Exports of nutrients via the dissolved and particulate pools are also donor controlled and are described by the mass-specific export parameters  $e_d$  (time<sup>-1</sup>) for dissolved nutrient losses and  $e_y$  (time<sup>-1</sup>) for particulate nutrient losses.

Under these assumptions, nutrient dynamics can be described by the expressions:

$$\frac{dD}{dt} = I + rY - uD - e_d D \quad (1a)$$

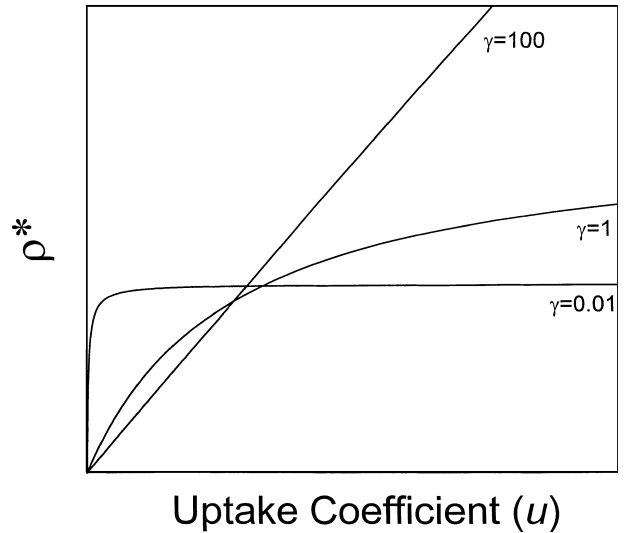
$$\frac{dY}{dt} = uD - rY - e_y Y, \quad (1b)$$

where  $I$  represents the input rate of dissolved nutrients (mass/time). For mathematical convenience, we did not include particulate inputs, but this simplification did not change the qualitative results of our model (see below). At steady state, the standing stocks are given by:

$$D^* = \frac{I(e_y + r)}{e_d e_y + e_d r + u e_y} \quad (2a)$$

$$Y^* = \frac{Iu}{e_d e_y + e_d r + u e_y}. \quad (2b)$$

We used these expressions to calculate  $\rho$  as a function of  $r$ ,  $u$ ,  $e_y$ , and  $e_d$ . At steady state,  $\rho$  equals  $uD^*$  (uptake rate) divided by  $e_d D^* + e_y Y^*$  (export



**Figure 2.** Effect of export route ( $\gamma$ ; dissolved:particulate export coefficients) and uptake coefficient ( $u$ ) on  $\rho^*$ .  $\rho^*$  is a linear function of  $u$  when  $\gamma$  is large (dissolved > particulate),  $\rho^*$  is independent of  $u$  when  $\gamma$  is small (particulate > dissolved), and  $\rho^*$  is an asymptotic function of  $u$  for intermediate values of  $\gamma$ .

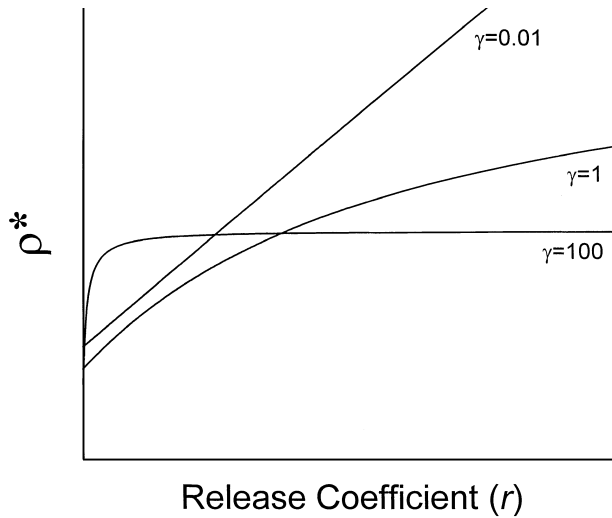
rate). This expression simplifies to give the steady state recycling ratio ( $\rho^*$ ):

$$\rho^* = \frac{u(e_y + r)}{e_d e_y + e_d r + u e_y}. \quad (3)$$

We can use this model to evaluate the sensitivity of  $\rho^*$  to changes in the release or uptake coefficient under different assumptions about the importance of dissolved versus particulate export. We define the parameter  $\gamma$  as the ratio of mass-specific export coefficients ( $e_d/e_y$ ) and rearrange Eq. (3) as:

$$\rho^* = \frac{\gamma(e_y + r)}{e_d} \left( \frac{u}{u + \gamma(e_y + r)} \right). \quad (4)$$

We first consider how  $\gamma$  affects the sensitivity of  $\rho^*$  to the uptake coefficient ( $u$ ). Eq. (4) indicates that  $\rho^*$  is an asymptotic function of  $u$ , with a maximum  $\rho^*$  equal to  $\gamma(e_y+r)/e_d$ .  $\rho^*$  is half this maximum value when  $u = \gamma(e_y+r)$ . When  $\gamma$  is large ( $\gamma = 100$ ; dissolved > particulate export), both the asymptote and the half-saturation value are large so that over a broad range of  $u$ , the function  $\rho$  is approximately a linear function of  $u$  (Figure 2). When  $\gamma$  is small ( $\gamma = 0.01$ ; particulate > dissolved export), both the half-saturation value and the asymptote are low, such that over most values of  $u$ ,  $\rho^*$  is independent of  $u$  (Figure 2). At intermediate values of  $\gamma$  ( $\gamma = 1$ ),  $\rho^*$  is an asymptotic function of  $u$ , indicating that  $\rho^*$  is sensitive to  $u$  when  $u$  is small but independent of  $u$



**Figure 3.** Effect of export route ( $\gamma$ ; dissolved:particulate export coefficients) and release coefficient ( $r$ ) on  $\rho^*$ .  $\rho^*$  is a linear function of  $r$  when  $\gamma$  is small (particulate > dissolved),  $\rho^*$  is independent of  $r$  when  $\gamma$  is large (dissolved > particulate), and  $\rho^*$  is an asymptotic function of  $r$  for intermediate values of  $\gamma$ .

at higher values because other processes become limiting (Figure 2).

Analogous results were obtained for the sensitivity of  $\rho^*$  to the release coefficient ( $r$ ). When  $\gamma$  is small,  $\rho^*$  increases approximately linearly with  $r$  (Figure 3). When  $\gamma$  is large,  $\rho$  is approximately independent of  $r$  because the asymptote and half-saturation value are very low (Figure 3). Like the relationship between  $\rho^*$  and  $u$ ,  $\rho^*$  is an asymptotic function of  $r$  for intermediate values of  $\gamma$  (Figure 3). In summary, the relative magnitude of the mass-specific dissolved and particulate export rates dictates the extent to which uptake processes or release processes limit the rate of internal nutrient cycling.

We also can evaluate the sensitivity of  $\rho^*$  to uptake and release parameters by considering approximations of Eq. (3) for extreme values of  $\gamma$  (for example, when export is almost entirely in either the dissolved or the particulate form). When  $\gamma$  is very large, we can approximate Eq. (3) by setting  $e_y = 0$ :

$$\rho^* = \frac{u}{e_d}. \quad (5)$$

When  $\gamma$  is very small, we can approximate Eq. (3) by setting  $e_d = 0$ , such that Eq. (3) simplifies to:

$$\rho^* = 1 + \frac{r}{e_y}. \quad (6)$$

These approximations indicate that the processes governing cycling may be markedly different between lakes (small  $\gamma$ ) and streams (large  $\gamma$ ). When  $\gamma$  is large (streams),  $\rho$  is governed by the uptake and dissolved export coefficients. Importantly, this result leads to the same model structure outlined in the Stream Solute Workshop (1990) (where  $u = k_s$  in the Stream Solute Workshop notation). Specifically, if all nutrient transport is in the dissolved form, then the approximation of  $\rho^*$  [Eq. (5)] is equivalent to uptake length divided by stream length. When  $\gamma$  is very small (lakes),  $\rho$  is governed by the tendency for nutrients in the particulate pool to be released into the dissolved pool versus being exported from the system ( $r/e_y$ ). This result is equivalent to the model of lake epilimnetic nutrient dynamics presented by Elser and others (1995).

These results imply that the mechanisms by which consumers affect nutrient cycling may be fundamentally different in lakes and streams. In streams, consumers affect  $\rho$  by modifying the fate of dissolved nutrients (uptake versus export;  $u/e_d$ ). The primary way that consumers affect this ratio is by altering the transient water storage within periphyton mats (Mulholland and others 1994; Steinman and others 1995). These storage zones are important because they promote high rates of cycling within algal mats (Paul and Duthie 1989). Consequently, by reducing periphyton biomass, periphyton grazers may increase uptake length and thereby decrease  $\rho$  (Mulholland and others 1994). In contrast, the model predicts that consumers in lakes affect  $\rho$  by affecting the fate of particulate nutrients (release or export;  $r/e_y$ ). Thus, zooplankton may alter productivity by increasing nutrient release rates via the consumption and excretion of nutrients (Barlow and Bishop 1965; Lehman 1980; Lehman and Sandgren 1985; Sterner 1986), or by affecting nutrient sedimentation rates (Bossard and Uehlinger 1993; Elser and others 1995). Zooplankton stoichiometry (Elser and others 1996) controls the ratio of nutrients released to nutrients incorporated into body tissues, and thereby affects  $\rho$ .

Eq. (6) shows that when release ( $r$ ) is zero,  $\rho^* = 1$ . This is due to the assumption that nutrient inputs enter the dissolved pool. All nutrients need to be sequestered at least once because they have to enter the particulate pool to be exported. If nutrient inputs are in particulate form, the approximation for  $\rho^*$  in lakes equals  $r/e_y$ . The approximation for  $\rho^*$  for streams does not depend on the route of nutrient import. Thus, these approximations are robust to the route of nutrient input into the ecosystem.

## THE RECYCLING RATIO: A STREAM-LAKE COMPARISON

A broad comparison of  $\rho$  across many lakes and streams would provide great insight into the similarities and contrasts between lakes and streams. This may appear to be a simple task, because  $\rho$  is calculated from readily measured ecosystem variables. In lakes, nutrient export rates often are measured in nutrient budgets, and uptake rates can be estimated from primary production and C:P ratios of producers. Remarkably, there were few instances where these parameters were measured and/or reported concurrently (but see Levine and Schindler 1980; Caraco and others 1992; Poister and others 1994; Elser and others 1995). In streams, calculating  $\rho$  from spiralling length is straightforward, but as described below, additional data needed to make useful comparisons are typically lacking (for example, nutrient standing stock).

As an alternative to a broad comparison, we calculated  $\rho$  for two well-studied, P-limited ecosystems where extensive data are available: West Fork of Walker Branch (WFWB) and Peter Lake. These sites were chosen because data on nutrient dynamics in both of these systems are among the most detailed available. WFWB is a first-order woodland stream located at the Oak Ridge National Laboratory (Tennessee, USA) and has been the site of extensive research on P dynamics (Newbold and others 1981, 1983; Mulholland and others 1985). Peter Lake is a small (2.2 ha) oligotrophic kettle lake located at the University of Notre Dame Environmental Research Station (near Land O' Lakes, Wisconsin, USA) and has been the focus of whole-lake experiments since 1951, including experimental P enrichment since 1993 (Carpenter and Kitchell 1993; Carpenter and others 1996).

We calculated  $\rho$  for the pelagic epilimnion of Peter Lake over the summer stratified periods of 1991–96. Nutrient uptake rate (g/d) was calculated from estimates of primary production (Carpenter and others 1996) and the C:P ratio of phytoplankton. The latter estimates were derived from empirical regressions of seston C:P and epilimnion total P (TP) concentration (Sterner and others 1997; J. Elser personal communication) and were corroborated by direct measurements of C:P in 1994 (N. Caraco, unpublished data). Nutrient export rates (g/d) were calculated as the P loss rate necessary to balance the inputs and weekly changes in P standing stock. Weekly P standing stock was estimated from measurements of TP (mg/m<sup>3</sup>) sampled at various depths, and estimates of epilimnetic volume derived were from hypsometric data. When the thermocline deep-

ened, we considered this to be an input of new nutrients equal to the volume of water added times the TP at the depth immediately below the thermocline the previous week. P inputs were estimated from the known P enrichment rates and from estimated background P inputs (Houser 1997).

We calculated  $\rho$  for WFWB from data in Newbold and others (1983) and Mulholland and others (1985) by using the relationship that  $\rho$  equals the length ( $L$ ) of stream reach divided by the spiralling length ( $S$ ). This derivation of  $\rho$  is scale dependent, however, being a function of the reach length. One way to circumvent this difficulty is to define the stream reach length such that WFWB is comparable to Peter Lake. In other words, we defined ecosystem boundaries in a way that allowed us to make a useful comparison between ecosystems, recognizing that these boundaries may not represent delineations of adjacent ecosystems (Likens 1998). We chose two metrics with which to scale WFWB: water residence time and P residence time. To standardize by water residence time, we calculated the stream length required for WFWB to have the same water residence time as the epilimnion of Peter Lake (200 days; Cole and Pace 1998) assuming discharge = 3 L/s, width = 2.0 m, and water depth = 0.05 m (Newbold and others 1983). This calculation yielded a standardized length of 518 km, which is approximately three orders of magnitude longer than the actual length of WFWB (less than 400 m; Newbold and others 1983). To standardize by P residence time, we calculated Peter Lake P residence time from yearly mean P standing stocks and estimated P export rates (see above) and used the mean of the 6 years considered in this study (mean = 25.6 days). We then calculated stream length necessary so that WFWB had a comparable P residence time assuming that the P standing stock = 63.7 mg/m<sup>2</sup> (exchangeable P), and downstream P flux rate = 0.0168 mg P/s (Newbold and others 1983). This yielded a standardized length of 292 m. For all WFWB calculations, we used the mean of four estimates of  $S$  (mean = 67.5 m; Mulholland and others 1985).

Over years 1991–96,  $\rho$  in Peter Lake ranged from 2.3 to 6.5 and averaged 3.2. For WFWB,  $\rho$  varied widely depending on the scaling factor used. When scaling by water residence time, the recycling ratio of WFWB was 7674, over three orders of magnitude greater than  $\rho$  of Peter Lake. However, when scaling by P residence time, the recycling ratio of WFWB equaled 4.32. Thus, when the two systems were scaled by P residence time, there was little difference in the amount of internal nutrient cycling between Peter Lake and WFWB.



These results beg the question whether scaling by nutrient residence time necessarily yields more similar recycling ratios, or whether this result is unique to the two ecosystems compared here. To address this question, we revisit the derivation of the recycling ratio.  $\rho$  is defined as the ratio of nutrient uptake rate ( $U$ ; mass/time) divided by nutrient export rate ( $E$ ; mass/time). Using the notation defined for Eq. (1), we can express  $\rho$  as

$$\rho = \frac{U}{De_d + Ye_y}. \quad (7)$$

This expression allows us to evaluate how the two scaling metrics affect  $\rho$ . Scaling ecosystems by water residence time ( $R_d$ ) is equivalent to scaling by  $1/e_d$ , so that Eq. (7) simplifies to

$$\rho = \frac{U\gamma R_d}{D\gamma + Y}. \quad (8)$$

Thus,  $\rho$  is a linear function of water residence time, where the slope increases asymptotically with  $\gamma$  (Figure 4). Consequently, the large differences in  $\rho$  between Peter Lake and WFWB is largely attributable to the very different routes of P export (Tables 1 and 2). In contrast, standardizing by nutrient residence time ( $R_i$ ; time) implies that the ratio of total nutrient standing stock ( $D + Y$ ) to export rate ( $E$ ) is constant, so Eq. (7) simplifies to:

$$\rho = \frac{R_i U}{D + Y}. \quad (9)$$

Eq. (9) shows that  $\rho$  is a linear function of nutrient residence time whose slope does not depend on the route of export (Figure 4) but instead depends on the ratio of uptake rate to total nutrient standing stock. Thus, the similarity in  $\rho$  between Peter Lake and WFWB indicates the uptake rates per total nutrient standing stock were roughly equivalent.

## DISCUSSION

We used  $\rho$  as a metric with a simple ecosystem model to evaluate its sensitivity to broad ecological processes, such as uptake and remineralization rate. This exercise suggested that the controls on nutrient cycling in lakes and streams are very different, and that these differences are attributable to contrasts in the residence times of water and particulates. In streams, the export coefficient of dissolved nutrients exceeds that of particulate nutrients, so that cycling is controlled by the ability of particulates to sequester nutrients and by the tendency of dissolved

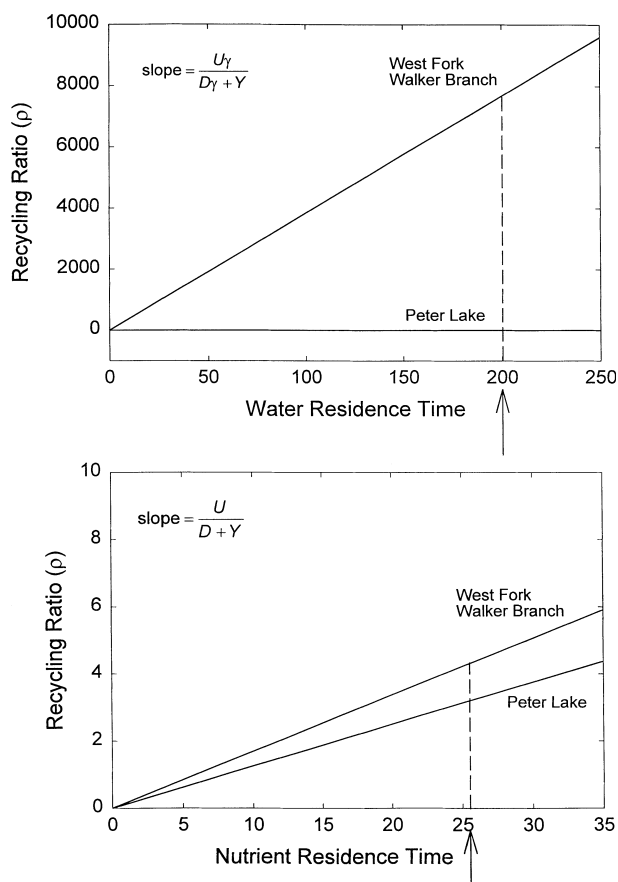


Figure 4. Comparison of how scaling factors used to define stream reach length affects the comparison between West Fork Walker Branch (WFWB) and Peter Lake. The recycling ratio ( $\rho$ ) is a linear function of water residence time, where the slope depends on the ratio of dissolved to particulate export coefficients ( $\gamma$ ). Because  $\gamma$  is much larger in WFWB, scaling by water residence time yields a very large recycling ratio in WFWB. In contrast, the estimate of  $\rho$  obtained by scaling WFWB by nutrient residence time does not depend on  $\gamma$ , and therefore  $\rho$  is very similar between Peter Lake and WFWB.

nutrients to travel downstream. In lakes, the export coefficient of particulate nutrients is far greater than that of dissolved nutrients, so that cycling is controlled by processes that promote the remineralization and retard the sedimentation of particulate-bound nutrients. An important implication of these results is that consumers should have very different roles in regulating nutrient cycling in these two systems. In lakes, consumers alter nutrient cycling by affecting the rate of nutrient remineralization from particulates and the rate of particulate export. In contrast, consumers in streams alter nutrient cycling by reducing cycling within algal mats, which likely affects both the uptake and export coefficients.

We expected a priori that  $\rho$  would be driven by hydrology and therefore would be very different between lakes and streams. This was true when ecosystem boundaries were scaled by a hydrologic metric (water residence time), but  $\rho$  was very similar when ecosystems were scaled so that the turnover times of limiting nutrients were the same. This similarity is surprising given that the controls on nutrient cycling are markedly different between lakes and streams. The similarity in  $\rho$  suggests broad similarities across very different ecosystems may exist when ecosystem boundaries are adjusted to standardize nutrient residence times.

A comparison of  $\rho$  from other lakes and spiralling lengths of other streams confirms that the observed similarity between Peter Lake and West Fork Walker Branch was not merely coincidental. Poister and others (1994) report recycling ratios of 3.7, 6.6, and 7.6 for three lakes in Northern Wisconsin. Elser and others (1995) document seasonal variation in  $\rho$  ranging from 1.5 to 4 in Lake 110 and 0.8–2 in Lake 240 at the Experimental Lakes Area, Manitoba, Canada. Furthermore,  $\rho$  calculated for Paul Lake, Wisconsin, during 1991–96 averaged 2.0 (T.E. Essington unpublished analysis). Thus, the recycling ratio of Peter Lake may be typical for North temperate lakes. Furthermore, the range of spiralling lengths for West Fork Walker Branch (22–97 m; Mulholland and others 1985) is similar to that measured for other streams. Munn and Meyer (1990) report P uptake lengths ranging from 32 to 188 m in Hugh White Creek, North Carolina, and from 188–666 m in Watershed 2, Oregon. Martí and Sabater (1996) document P uptake lengths ranging from 10 to 250 m in La Solana, Spain, and 20 to 400 m in Riera Major, Spain. Similar ranges of P uptake lengths are reported in D'Angelo and Webster (1991) and Martí and others (1997). Unfortunately none of these studies reported the P standing stock and downstream flux rate required to standardize these systems by P residence time. However, this comparison indicates that spiralling length of WFWB is not atypical. Provided that the P flux and standing stock are not drastically different, recycling ratios scaled by nutrient resident time should be similar to that estimated for WFWB.

Conclusions regarding the amount of internal nutrient recycling and the primary processes that govern nutrient cycling are largely dependent on the spatial and temporal scales of the analysis. We defined the spatial scale of Peter Lake as the pelagic epilimnion, because this region has clearly defined boundaries across which nutrient fluxes can easily be measured, and because the bulk of primary production occurs there. Very different conclusions

may be drawn if one considers the nutrient cycling in the entire lake. Clearly, expanding the spatial extent of the ecosystem will increase nutrient residence time, and thereby increase  $\rho$ . However, estimating whole-lake residence time can be difficult owing to difficulties in estimating nutrient exchange and storage in sediments. Defining spatial extent of stream ecosystems is even more problematic, a difficulty long recognized by stream ecologists. Our analysis only considered nutrient cycling within the stream channel and only considered small-order streams. Very different conclusions may be drawn by considering broader spatial extents. For example, defining a stream ecosystem as the entire drainage from headwaters to ocean would yield a very different perspective regarding the relative importance of dissolved versus particulate export. Furthermore, broadening the spatial extent of the stream to include lateral fluxes and processing of nutrients in riparian zones would lead to larger estimates of  $\rho$  than considering only the longitudinal flux of nutrients.

The majority of published research on freshwater ecosystems derives from temperate lakes and streams, but as noted by Dodds (1997), these do not represent the majority of ecosystem types. Our sensitivity analysis of  $\rho$  to  $\gamma$  provides some expectations concerning less well-studied systems. Shallow lakes may have a higher  $e_d$  than deep lakes and therefore may more closely resemble streams. Similarly, reservoirs that have high hydrologic flushing may be considered intermediate between the stream and lakes considered here. Finally, large rivers may have extensive particulate transport and therefore may more closely resemble lakes than smaller streams.

Our model did not distinguish between organic and inorganic dissolved nutrients, yet organic nutrients may comprise a substantial portion of the dissolved nutrient pool (Webster and Meyer 1997). The general predictions of our model are robust to this simplification. The distinction between available and unavailable nutrients can be generalized in the parameter  $u$ , which reflects the fraction of the dissolved pool taken up by particulates. When organic nutrients dominate the dissolved nutrient pool,  $u$  should be fairly small. In lakes, this will affect the rate of primary production but have little effect on the amount of nutrient cycling [Eq. (6)]. In streams, this should drastically affect both primary production and nutrient cycling because  $\rho$  is highly sensitive to the uptake coefficient when  $e_d$  is large. [Eq. (5)].

Comparative analyses of disparate ecosystems are challenging tasks. As we show here, choosing an

appropriate temporal and spatial scale for comparative analyses is not a trivial exercise, and the results of any such analyses are likely to be dependent on the scales chosen. An equally difficult challenge is overcoming differences in terminology and identifying useful parameters for making cross-ecosystem comparison. The recycling ratio was a useful parameter for our comparison of lakes and streams, because it has an intuitive and straightforward interpretation. However, this parameter is not ideal for stream ecosystems because its inherent dependence on stream reach length. Thus, comparative parameters may be considered compromises much in the way that Fisher and Grimm (1991) describe cross-ecosystem comparisons as an optimization problem, where the adequacy of controls declines but generality of conclusions increases with more disparate ecosystems. Comparative parameters similarly may be less appropriate for individual ecosystem types but may allow evaluation of more general ecosystem properties.

Perhaps the most important point of this study is that much can be gained from viewing two systems by using a common conceptual framework. Several insights were derived about each ecosystem simply by generating a simple model and evaluating how lakes and streams were contrasted within this framework. Moreover, the model served as a basis from which comparisons between the two ecosystems could be made and was useful for generating hypotheses concerning how the two systems differ. Comparative analyses of these sort (for example, Wagners and others 1998) are likely to be more effective than simply recognizing differences and similarities between systems because these analyses recognize that the processes that generate differences may be shared.

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