Nutrients and the "dead zone": the link between nutrient ratios and dissolved oxygen in the northern Gulf of Mexico

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The "dead zone", an area with reduced concentrations of dissolved oxygen, forms every year off the mouth of the Mississippi River in the northern Gulf of Mexico. Some marine animals are stressed or killed by the hypoxic conditions, with negative consequences for this large and economically important marine fishery. In the past, the dead zone has been linked to nitrogen (N) input from the Mississippi River, but recent analyses suggest that phosphorus (P) also plays a role. It has therefore been proposed that controlling both the N and P entering the Gulf may be required to minimize hypoxia. However, the use of elemental ratios (stoichiometric analysis) of dissolved inorganic nutrients to reach this conclusion is scientifically tenuous. Stoichiometric analyses of total N and P and the results of several nutrient enrichment growth bioassays also suggest the importance of both N and P, but offer less evidence for a P effect, providing a stronger scientific basis for management.

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The "dead zone" is a large area of decreased dissolved oxygen concentration in bottom waters that forms each summer in the northern Gulf of Mexico. This hypoxic zone (HZ) is formally defined as an area where the dissolved oxygen falls below 2 mg O_2 per liter. Low dissolved oxygen potentially stresses or kills marine life and could lead to shifts in community structure and ecosystem dynamics in one of the most important recreational and commercial fisheries in the near coastal zone of the conterminous United States. The HZ has been expanding in size since the 1950s, as greater amounts of nutrients from human activities are loaded into the Gulf of Mexico via the Mississippi and Atchafalaya Rivers (Rabalais *et al.* 2002).

The excess nutrients stimulate phytoplankton blooms (large populations of suspended algae). Once the phytoplankton cells sink to depths where light does not penetrate, they are decomposed by the microbial community that concomitantly consumes dissolved oxygen. Stimulation of phytoplankton growth increases the flux of organic material from surface waters and fuels microbial decomposition and dissolved oxygen consumption. The lower dissolved oxygen levels in bottom waters lead to increased mortality among organisms sensitive to hypoxic conditions.

Excess nitrogen (N), derived from agricultural activities in the Mississippi River drainage basin and entering the Gulf of Mexico, was thought to be the primary factor in the formation of the HZ. About 90% of the total freshwater-derived nutrient load to the Gulf of Mexico comes from the Mississippi (about 70%) and the Atchafalaya Rivers (Rabalais *et al.* 2002). The area of the HZ exceeded 20 000 km^2 in 2001, the largest since Rabalais began measurements in 1985 (Rabalais *et al.* 2002). It is thought that the larger the HZ, the greater the potential for environmental damage; consequently, remedies are being sought.

A recent controversy erupted over the idea that phosphorus (P) alone could potentially stimulate phytoplankton in the Gulf, therefore ultimately controlling hypoxia (Ferber 2004; Boesch 2004). This suggestion was based in part on a well-publicized analysis of trends of dissolved inorganic N and P stoichiometry (ratios of dissolved inorganic N to dissolved inorganic P) in the Mississippi River. This report, while not officially released or peer reviewed, was circulated broadly. The analysis stimulated interest because it could be interpreted to mean that control of P, rather than N, would be necessary to manage Gulf eutrophication. In my opinion, the report contained some common errors and assumptions that probably

In a nutshell:

- Control of both total nitrogen (N) and phosphorus (P) entering the Gulf of Mexico could be necessary to minimize adverse ecological impacts of nutrient runoff from the Mississippi River drainage basin, because ratios of total N to P entering the Gulf suggest that both nutrients may be important
- Nutrients actively cycle in ecosystems, and basing management decisions on flux rates and dynamics may lead to better management decisions than those based only on concentrations of inorganic nutrients
- Suitable analyses of long-term monitoring data of total N and P, coupled with appropriate bioassay experiments, could help in decisions related to the management of environmental problems in the Gulf of Mexico

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Table 1. Statistical relationships between nutrient ratios at sites in the Mississippi River basin, representative of nutrient loading to the Gulf of Mexico

Site	*Dependent*	*Independent*	*Intercept*	*Slope*	R^2	*P*	*N*
Mississippi River at Belle Chasse, LA	TN/TP	DIN/SRP	15.79	0.28	0.13	<0.003	116
Mississippi River at Belle Chasse, LA	TN/TP	DIN/TP	8.63	0.98	0.81	<0.000	139
Lower Atchafalaya at Morgan City, LA	TN/TP	DIN/SRP	21.0	0.231	0.09	0.0028	97
Lower Atchafalaya at Morgan City, LA	TN/TP	DIN/TP	8.74	1.23	0.77	<0.000	115

See Alexander *et al.* (1998) for description of data sources.

would have been corrected had it been subjected to scientific review before release. Ultimately, following extensive peer review and public comment, the US Environmental Protection Agency decided not to complete the analysis because it would not contribute substantially to the resolution of the problem (www.epa.gov/msbasin/taskforce/peer_review.htm). However, the fact that the report received so much attention indicates a need to explore potential misconceptions surrounding nutrient dynamics in aquatic ecosystems. This controversy brought to the forefront the widespread practice of using ratios of dissolved inorganic N to P to indicate factors that limit phytoplankton production.

Resolving this question is important because of the potential environmental and financial costs associated with controlling N and P sources throughout the Mississippi River drainage basin. The situation also illustrates potential problems with release of unreviewed science in high-stakes environmental management issues, regardless of whether or not the release is intentional. Controversy surrounding cultural eutrophication (stimulation of algal blooms caused by nutrients derived from human activities) is not new to ecological science; in past decades, intense battles occurred over the importance of carbon (C) relative to P in lakes, and commonly involved scientists, the public, politicians, and managers (Edmondson 1991). There are now debates regarding nutrient control in streams, lakes, and coastal marine areas across the globe (Smith 2003). With denser human populations worldwide, more fertilizer will be needed to produce crops to feed people, and watershed disturbances and nutrient pollution will likely intensify (Carpenter *et al.* 1998). Since there are considerable economic impacts involved, debate over such issues will only increase, in part because uncertainty can benefit people both for and against eutrophication control. Solid science will minimize such uncertainty.

Interest in nutrient pollution has stimulated extensive research on nutrient dynamics and ecological stoichiometry, and their relevance to primary production. Much of this research has focused on freshwater systems. However, no physiological characteristic of phytoplankton, particularly with respect to stoichiometric analysis, has been demonstrated to clearly separate marine and freshwater systems (Guildford and Hecky 2000). The purpose of the analysis presented here is to describe how stoichiometric characterization of nutrient loading (the relative amounts of nutrients entering the Gulf) and water column nutrient dynamics can be applied to assess how nutrient pollution is related to Gulf hypoxia. Additional issues that are clearly important (Howarth 1988; NRC 2000), such as the influence of the benthic zone on nutrient cycling, stratification and mixing of Gulf waters, and shifts in algal communities, will not be discussed in depth here. Rather, this analysis will evaluate the fundamental approaches for estimating nutrient loading and discuss which nutrients might control (limit) phytoplankton growth in the northern Gulf, as well as the reasons that ratios of inorganic N to inorganic P are inadequate for assessing nutrient limitation.

Viability of existing analyses of nutrient loading in the northern Gulf

Extensive data exist on nitrate and soluble reactive phosphorus (SRP) concentrations in the Mississippi River, because chemical determination of these forms of N and P is relatively easy. Total N (TN) is composed of inorganic N (ammonium, nitrite, and nitrate) and dissolved and particulate organic N. Total P (TP) is composed of particulate and dissolved organic P, in addition to SRP (inorganic P and some chemically reactive organic P forms). Given the abundance of data on inorganic N and P concentrations, figures for nitrate loading are often used to indicate total N loading (eg Rabalais *et al.* 1999 used nitrate because of a longer record set and the bioavailability of nitrate) and phosphate inputs are also reported in some instances (Knecht 2000). However, researchers studying lakes have found that total N and P loadings are generally much better predictors of algal biomass and production than nitrate or SRP loadings (Ryding and Rast 1989). The advantage of using total nutrient amounts to predict algal biomass is presumably because nitrate or SRP loadings do not completely characterize the total amount of nutrient available to primary producers. The attempt to use nitrate and SRP to determine nutrient loading leads to the question: how well do nitrate and SRP loadings to the northern Gulf reflect total N and P loadings?

Analysis of nutrient data from the United States Geological Survey (USGS) station located on the Mississippi River approximately 15 km below New Orleans reveals that nitrate predicts TN moderately well;

nitrate concentration is linearly related to TN and explains 80% of the variance between the two. Nitrate values are about 0.5 mg L^{-1} less than TN values (Figure 1). However, only 30% of the variance in TP is predicted by SRP, which underestimates TP by about 0.05 mg L^{-1} in a TP:SRP range of 1–6. These data suggest that total N and P should be used to provide direct estimates of nutrient loading to the northern Gulf, and leads to an assessment of using ratios of dissolved inorganic nutrients to indicate nutrient limitation.

What nutrients limit primary production in the northern Gulf?

The ultimate aim with respect to the HZ is to assess the limitation of net ecosystem production in the surface waters of the Gulf. However, in practice, most experiments assess the relative limitation of growth of extant phytoplankton populations (Howarth 1988). In typical nutrient enrichment bioassays, replicate samples of the natural water, including phytoplankton, are treated with various combinations of nutrients. After a suitable incubation period under the appropriate light and temperature conditions, phytoplankton growth is measured. Nutrient enrichment bioassays can provide evidence of nutrient limitation (which nutrient or nutrients control algal growth), although caution should be used in experimental design and interpretation of results (O'Brien 1972). A series of bioassays conducted by Smith and Hitchcock (1994) demonstrated that N, P, or both can stimulate primary production in a region close to the Mississippi River delta where the HZ forms. Their experiments also documented some spatial and seasonal variation in the degree of N and P nutrient limitation. The results of these bioassays should be viewed with caution, because they used a short-term ^{14}C method that may be subject to distortion (Lean and Pick 1981), few bioassays were carried out, and the area where the bioassays were conducted did not exactly match the area where the HZ forms.

Others have attempted to use ratios of dissolved inorganic N to P to indicate the relative degree of N or P limitation in the Gulf of Mexico. For example, Rabalais *et al.* (1999) used ratios of dissolved inorganic N (DIN; nitrate + nitrite + ammonium) to TP to indicate nutrient limitation. A more recent, unreviewed EPA report (as described by Ferber 2004, and now withdrawn) relied upon DIN-to-SRP ratios to assess factors controlling algal growth, as have several other near-coastal marine studies (see Howarth 1988; Fisher *et al.* 1992). It is interesting to note that a recent report by the National Research Council (NRC 2000) suggests that marine studies "add credence to the application of bioassay data and inorganic nutrient data in assessing whether nitrogen or phosphorus is more limiting in estuaries".

Approaches using inorganic nutrient ratios ultimately stem from early papers by Redfield (1958), who noted that algae in the open ocean had molar ratios of N to P and C that were similar to ratios of the same elements dissolved in the water column in inorganic form. He hypothesized that the similarities were due to phytoplankton control of these ratios over very large spatial (global oceans) and temporal (global biogeochemical turnover times) scales; phytoplankton cells exhibit similar ratios under balanced growth conditions when they are nutrient-replete. This idea has subsequently been reversed and applied to smaller-scale, non-equilibrium systems, to suggest that inorganic nutrient ratios can be used to assess limitation.

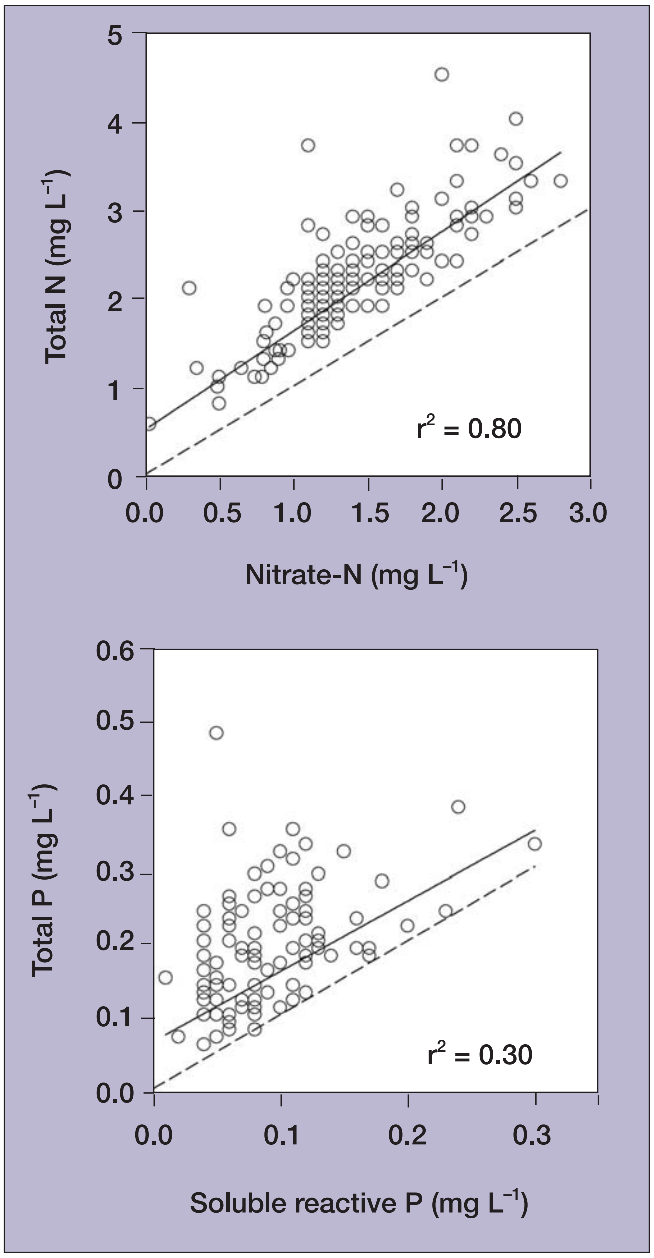

Figure 1. *Total and dissolved inorganic N and P concentrations in the Mississippi River immediately before the waters enter the Northern Geological Gulf of Mexico. The data are from the United States Geological Survey and are described by Alexander* et al. *(1998). Dashed line = 1:1 relationship (perfect correspondence between dissolved inorganic and total nutrient concentration); solid line = the best fit relationship.*

Using inorganic nutrient ratios to indicate nutrient limitation is based on one key assumption: that the concentration of a dissolved inorganic nutrient is reflective of the rate of its supply. The responses of growth-based bioassays of Smith and Hitchcock (1994) from the northern Gulf did not reliably correspond to inorganic nutrient ratios of water samples (as is often true with nutrient bioassays in coastal waters). Further consideration to determine what can reliably be inferred from inorganic nutrient levels and ratios is warranted.

Problems with using inorganic nutrient ratios to assess nutrient limitation

There are several trails of evidence suggesting that ratios of inorganic N to P are not reliable indicators of nutrient availability (Dodds 2003). The assumption that relative concentrations (standing stocks) of inorganic nutrients can be used to determine relative supply rates (availability) to primary producers is based upon two principal fallacies.

First, it is incorrect to assume that SRP concentrations are the same as phosphate concentrations. The SRP assays include forms of phosphorus in addition to phosphate, so that when SRP concentrations are in parts per billion, phosphate concentrations are often in parts per trillion (eg Hudson *et al.* 2000). Soluble reactive P is a poorly defined chemical fraction (Dodds 2003), and the phosphate to SRP ratio decreases as the intensity of P limitation increases (Dodds 1995). SRP is also a poor indicator of TP, with SRP:TP being extremely variable across aquatic ecosystems (Dodds 2003). There is no clear way to relate SRP to physiological characteristics (eg uptake kinetic constants) across aquatic systems because SRP is a chemically, not biologically, defined quantity.

Second, it is not necessarily true that the size of a dissolved nutrient pool is directly proportional to the rate at which it can be used. Even though phosphate concentrations can be miniscule, uptake rates can be rapid because of very high uptake efficiency at low nutrient concentrations and high rates of mineralization (Dodds *et al.* 1989).

Nutrient pools are highly dynamic, and turnover rate, as well as absolute concentration, is important (Dodds 1993). For example, in highly eutrophic systems, amounts of dissolved inorganic nutrients can approach zero when algal demand is high. These considerations suggest that using ratios of dissolved inorganic nutrients may give a misleading picture of nutrient limitation in any aquatic ecosystem.

The dynamic nature of nutrient uptake and how it may be decoupled from absolute concentrations of dissolved inorganic nutrients can be illustrated with a simple budgeting approach:

$$\text{net uptake} = \text{gross uptake} - \text{mineralization}$$

Net uptake is the rate of decrease of nutrient concentration in the water, assuming that dilution or external sources are negligible. Gross uptake is the demand by organisms (mostly algae and bacteria), and mineralization is the release of inorganic nutrients from organisms (excretion and death). In planktonic systems, the gross dilution or enrichment from outside a particular parcel of water is often relatively small over short time periods (eg hours to days) compared with the gross uptake and mineralization (eg Dodds *et al.* 1989). Even in streams, where dilution rates are very high over each unit area of water column, uptake and mineralization control ambient concentrations (Dodds *et al.* 2002). Gross uptake rate becomes constant at high nutrient concentrations because organisms can only use nutrients at some maximal rate. Gross uptake must be zero when nutrient concentration is zero. Thus, an asymptotic curve typically describes the relationship between gross uptake and nutrient concentration. Gross uptake is a function of concentration below some saturating level, but mineralization is not (again, over short periods, this is generally true).

An important feature of this budgeting approach is that it predicts steady state inorganic nutrient concentration. At concentrations in excess of the steady state concentration, net uptake is positive (gross uptake exceeds mineralization) and at concentrations less than the steady state concentration, net uptake is negative (gross uptake is less than mineralization). Many aquatic ecosystems, from freshwater to marine, are approximately at equilibrium with regard to gross uptake and mineralization (Dodds 1993).

An additional feature of this budgeting approach is that gross uptake rate (eg the rate of nutrient uptake by suspended algae) can vary widely and yield exactly the same steady state nutrient concentration if mineralization rate varies as well (Figure 2). Stated differently, a planktonic community can be twice as productive, yet still exhibit the same steady state inorganic nutrient concentration as a corresponding community that is half as productive. The budgeting approach illustrates why it is unwise to assume that standing stocks of inorganic nutrients will necessarily reflect biological productivity in equilibrium systems. In non-equilibrium systems, the correlation between standing stocks and availability may be even more tenuous; a short-term dilution event may make even the most nutrient-rich ecosystem seem nutrient depleted, as a spike may make a generally nutrient-poor environment seem more replete than it is. Therefore, if standing stocks of dissolved inorganic nutrient concentrations give ambiguous information about nutrient limitation and availability, what can be inferred from the data on nutrient loading as related to nutrient availability?

Nutrient loading and limitation in the northern Gulf of Mexico

Assays for inorganic nutrients cannot indicate supply rates when nutrient concentrations are low. If concentrations are high, however (eg milligrams per liter of soluble reactive phosphorus or nitrate), amounts are ample for substantial phytoplankton growth. For example, algal blooms are common in lakes and estuaries with limited inorganic turbidity when *total* N exceeds 1 mg L^{-1}, and total P exceeds 0.05 mg L^{-1}. Concentrations of dissolved inorganic nutrients make up a portion of total nutrient concentrations, so if dissolved inorganic N and P exceed 1 and 0.05 mg L^{-1}, respectively, then even higher total nutrient concentrations – and subsequent phytoplankton blooms – are more likely.

Probably neither N nor P are limiting as the waters of the Mississippi enters the northern Gulf of Mexico, because the absolute concentrations of dissolved inorganic N and P are so high. Mean values from the USGS data collected in the 1980s from the lower Mississippi River station Belle Chasse, just downstream of New Orleans, were 1.50 and 0.09 mg L^{-1} for DIN and SRP, respectively. These values are often large enough that phytoplankton are unable to take up nutrients at a greater rate with additional increases in concentration (eg Dodds *et al.* 1989), and are also typical of lakes where algal blooms are common. The relatively large concentrations of DIN and SRP suggest that some other factor (eg light) limits productivity. Turbidity is high in "the big muddy" Mississippi, so light is in short supply in the marine waters at the mouth of the river. Once the turbidity settles or is diluted by the clearer waters of the Gulf, the nutrients can stimulate productivity until they are taken up by phytoplankton or become diluted with lower nutrient, higher salinity water from the Gulf.

The TN:TP ratios in river water entering the northern Gulf can be used to characterize nutrient limitation (Figure 3), assuming that the Mississippi River is the major source of nutrients to the area where the HZ occurs. Balanced algal growth occurs at an N:P molar ratio of approximately 16:1. The total N and P data from the Mississippi River have values above and below this point, with a mean of 26, suggesting that both N and P limitation can occur. It is broadly assumed that N is the primary limiting nutrient in the high salinity (low river influence) regions of the northern Gulf of Mexico, but this assumption is based mainly on the correlation of primary production with nitrate loading (eg Lohrenz *et al.* 1997). Assuming that the bulk of the waters in the Gulf of Mexico are deficient in N, as water from the Mississippi River is diluted, N limitation will eventually dominate.

The DIN:SRP poorly represents TN:TP that is entering the northern Gulf (Figure 3). The broad scatter in the relationship between DIN:SRP and TN:TP, and the lack of a 1:1 fit with TN:TP, indicate that TN and TP data should be used where available. Given that DIN:SRP leads to N:P ratio estimates that are much greater than TN:TP, DIN:SRP should overpredict the degree of P limitation caused by nutrient loading from the Mississippi River. The mean DIN:SRP and TN:TP ratios for the Mississippi and Atchafalaya Rivers data are 45 and 26, and 51 and 29, respectively. DIN to TP values are considerably closer to TN:TP values, and DIN:TP tends to consistently underpredict true values of TN:TP by about 5 (Figure 3). This underprediction could lead to the conclusion that the system is more N limited than it is. These data suggest that, when possible, TN:TP should be used to characterize stoichiometry of nutrient loading, but that, with appropriate corrections, DIN:TP can serve as a more reliable surrogate for TN:TP than can DIN:SRP. Such considerations may be important if the historical record of SRP and DIN data is much better than that for TN and TP.

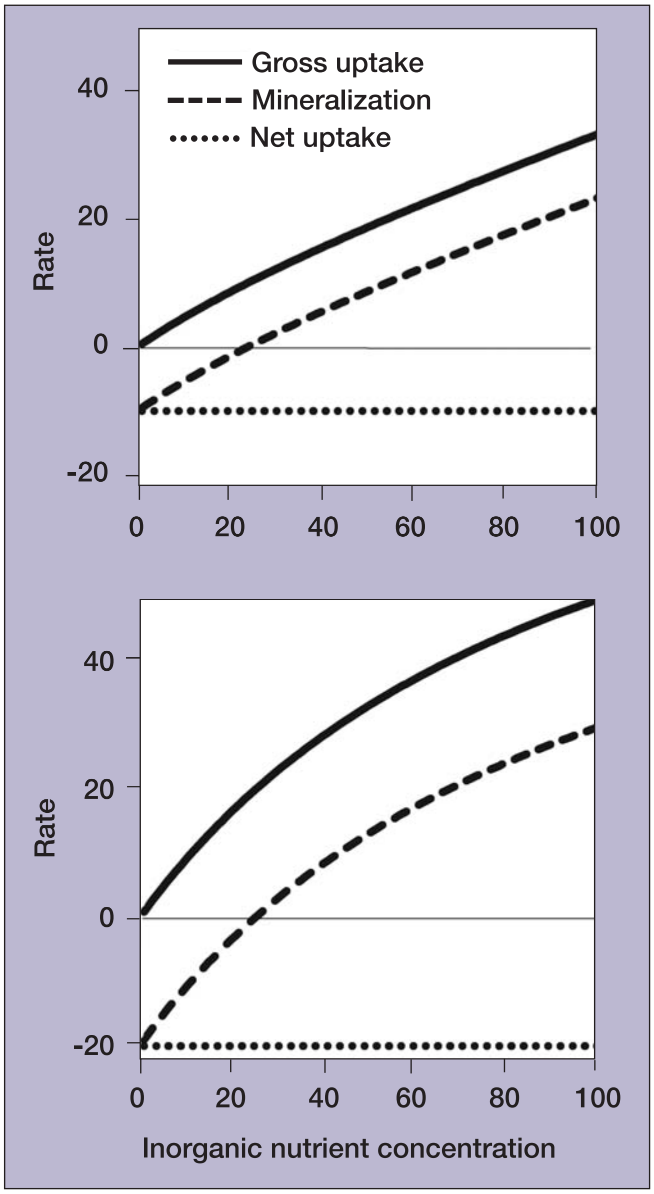

Figure 2. *Relationships between nutrient concentration, net uptake, gross uptake, and mineralization. These graphs indicate that the stable inorganic nutrient concentration occurs where the line for net uptake crosses the origin of the y-axis. These curves also illustrate how a biological assemblage can be twice as active, yet have exactly the same stable inorganic nutrient concentration.*

Uncertainties and conclusions

A major question that remains unanswered is how much of the nutrient loading from the mouth of the Mississippi

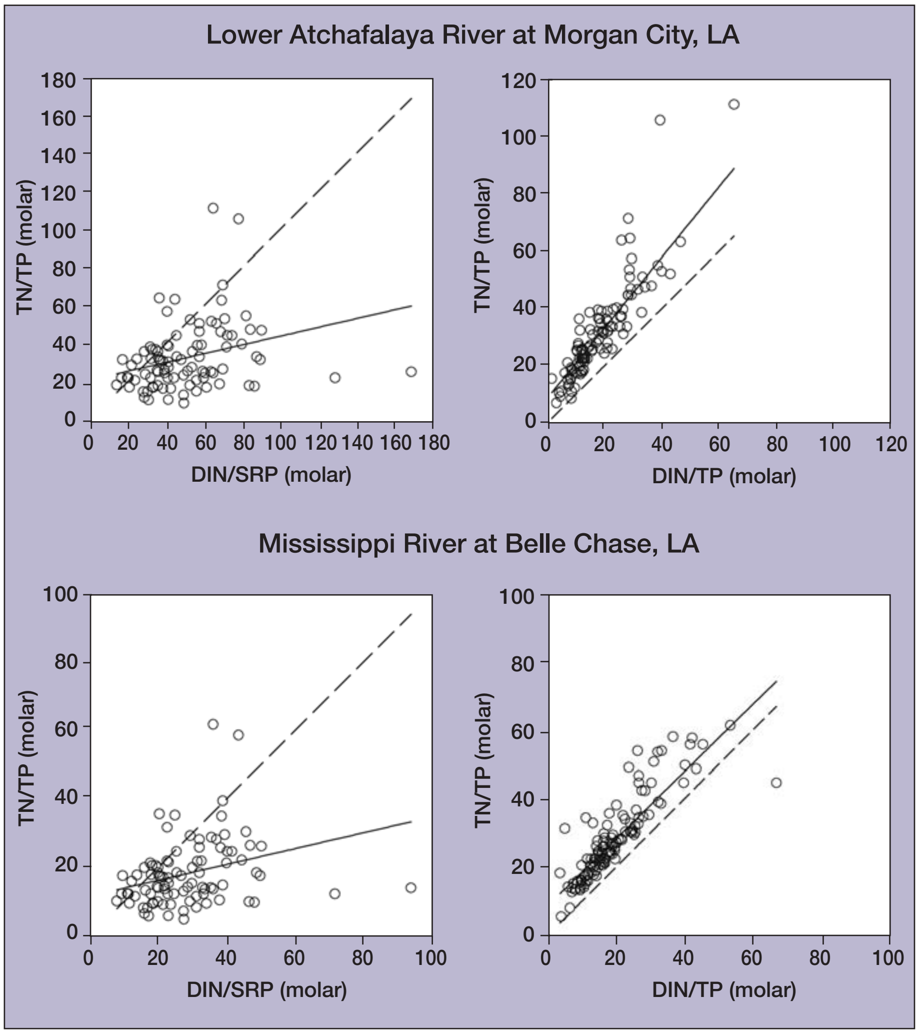

Figure 3. *Relationships between the nutrient ratios at the river sites that are most important in nutrient loading into the northern Gulf of Mexico. All data were taken from USGS reports, as described by Alexander* et al. *(1998) from the Mississippi River at Belle Chase and the Atchafalaya River at Morgan City. Only sampling events were included in which data for DIN, SRP, TN, and TP were all available. Dashed line = 1:1 relationship; solid line = the relationship described with the equations in Table 1.*

River is directly responsible for stimulation of the phytoplankton blooms that ultimately lead to hypoxia. If P is associated with suspended sediments, then some of it may settle. Sulfur is more abundant in the marine waters and will bind with iron in the sediments, allowing release of P into the water column (Blomqvist *et al.* 2004). The gradient of iron binding is not well established for the area where the HZ occurs, although progress has been made on this front (Sutula *et al.* 2004).

Denitrification (leading to loss of dissolved N) should increase with hypoxia; more extensive anoxic zones will occur in benthic sediments, and anoxic conditions will form more readily in microbial consortia associated with aggregates of suspended particles (Paerl and Pinckney 1996). Thus, hypoxia may induce conditions that increase rates of denitrification. Decreases of P could lead to more N being transported farther into the Gulf. In the Neuse River Estuary, management to control P decreases N retention by algae, causing N to move further out into the marine environment (Paerl *et al.* 2004). It is an open question whether such an effect would intensify or lessen hypoxia near the Gulf coast. Finally, the relative importance of nutrient inputs from the deeper waters of the Gulf could be better characterized. The case has been made that nitrogen inputs from deep waters are relatively unimportant (Rabalais *et al.* 1999, 2002), but such analyses for P have not been published. A detailed understanding of nutrient dynamics, hydrology, and biological responses is necessary to address these questions; gaining this understanding will require additional study.

Maintaining conditions as close as possible to those over recent evolutionary time (native or pristine) minimizes the probability of environmental damage in any ecosystem. A rational approach is therefore to allow only the human impacts that can be verified as not causing harmful environmental effects, and to control all potential impacts until it can be demonstrated that they are harmless. The burden of proof should be on the polluter. Given this philosophy, it would be prudent to decrease total N and P loadings via the Mississippi drainage to the northern Gulf. Increased N loading has been established as a culprit in hypoxia problems in the Gulf. The philosophy of minimizing damage, and the knowledge that disruptions of stoichiometry of nutrient inputs as well as amounts of individual nutrients can alter ecosystem structure and function, attempts to control both N and P would provide the most protective approach unless it can be established scientifically that there is no ecological effect of increased loading of P to the northern Gulf of Mexico.

Ecological stoichiometry is a powerful tool to assess nutrient limitation of phytoplankton. If incorrectly applied, however, erroneous conclusions can be reached with regard to relative nutrient limitation and effects of nutrient loading into sensitive aquatic ecosystems. The available data on the ratios of total N and P nutrient loading to the northern Gulf, and the few nutrient bioassays that have been published for the region, indicate that neither N nor P pollution from humans can be ruled out as causes of hypoxia in the Gulf of Mexico. Thus, an effort to control inputs of both nutrients to the Mississippi River and its tributaries might be necessary to minimize the potential damage caused by the annual formation of a "dead zone".

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