Causes for the high frequency of nitrogen limitation in tropical lakes

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Introduction

Nitrogen limitation of phytoplankton appears to be very common in tropical lakes (reviewed by LEWIS 1996, TALLING & LEMOALLE 1998). The evidence for the widespread occurrence of nitrogen limitation in tropical lakes is mostly circumstantial rather than experimental, but involves several kinds of indicators that are known to correlate well with experimental evidence. These indicators include the persistence of significant concentrations of soluble reactive phosphorus over extended intervals when inorganic nitrogen is depleted to negligible levels, sustained occurrence of heterocystous blue–green algae in lakes of widely varying trophic status, and low ratios of inorganic nitrogen to inorganic phosphorus or of soluble nitrogen to soluble phosphorus.

The apparently widespread occurrence of nitrogen limitation in tropical lakes raises questions about latitudinal differences in components of the nitrogen cycle that might explain the greater likelihood of nitrogen deficiency in tropical lakes. Two general types of explanations are possible: (1) low external supply of nitrogen in tropical lakes, and (2) high internal loss of nitrogen from tropical lakes. Latitudinal differences in the external supply of nitrogen from watersheds to lakes seem unlikely, in view of recent studies which indicate that nitrogen yield from undisturbed watersheds, although quite sensitive to amount of annual runoff, is unrelated to latitude (LEWIS et al. 1999, LEWIS 2002). Thus, attention can be focused on internal losses. The most obvious mechanism of internal loss is denitrification, which has the potential to alter N/P ratios in lakes (SEITZINGER 1988).

Denitrification is the reduction of nitrate- or nitrite-nitrogen to N_2, and encompasses intermediate steps that can produce byproducts, including N_2O (BROCK & MADIGAN 1994). The main end-product of denitrification under aquatic conditions is N_2 (SEITZINGER 1988), and the chief significance of denitrification from the present perspective is the conversion of biologically available nitrogen to biologically unavailable nitrogen in the form of N_2.

Denitrification may occur in lake sediments even when the overlying water contains oxygen. Under such conditions, however, the effect of denitrification on the nitrate content of overlying water may be minimal because denitrification in the sediments is driven by nitrification, which converts ammonium to nitrate at oxic microsites, and denitrification, which converts nitrate to N_2 at nearby anoxic microsites (SEITZINGER 1988). Major changes in the nitrate content of the hypolimnion are most likely when anoxia occurs in the hypolimnion. Under these conditions, surficial sediments lose nitrate rapidly, and planktonic denitrification also occurs (e.g. VINCENT et al. 1985). There appears to be little lag time between the development of anoxia and the onset of rapid denitrification, presumably because denitrification is a facultative characteristic of many microbes (ZUMFT 1997). Denitrification accompanying anoxia characteristically brings nitrate concentrations in the anoxic portion of the hypolimnion virtually to zero, thus reducing the amount of inorganic nitrogen that will be present in the water column at the time of the next mixing. In this way, denitrification may restrict the nitrogen supply to autotrophs.

Conditions favorable to denitrification may be more probable in tropical lakes than in temperate lakes (VINCENT et al. 1985, LEWIS 1996). The purpose of this paper is to demonstrate the degree to which tropical and temperate lakes differ with respect to their potential for significant loss of nitrogen to denitrification.

Methods

The method for analysis of denitrification potential across latitudes is an extension of latitudinal comparisons developed previously for other purposes (LEWIS 1987). The initial premise of the analysis is that hypolimnetic conditions will determine the denitrification potential of lakes, and that these conditions can be defined as a function of latitude through information that is available from the literature and simple calculations applicable to latitudinal gradients.

The initial step of the analysis is the identification of hypolimnetic temperatures for lakes as a function

of latitude. This information, which is based on field observations, is taken from LEWIS (1987). A second step in the analysis is the estimation of the amount of time required for anoxia to develop in lakes of different latitudes. Because the individual characteristics of lakes, including in particular productivity, morphometry, and elevation, have an influence on the rate of hypolimnetic oxygen depletion, the latitudinal factor is best analyzed through consideration of a hypothetical lake having fixed characteristics. For the purposes of the present study, and following studies of oxygen depletion developed elsewhere by LEWIS (1987), the hypothetical lake will be assumed to lie at sea level, to have an area of approximately 200 ha, and to consist of a cone frustum whose bottom has an area 10% of the size of the surface area of the lake. This lake will have a mixed layer thickness of approximately 5 m, a maximum depth of 25 m, and a hypolimnetic volume approximately equal to the epilimnetic volume.

For calculation of the expected rate of oxygen depletion in the hypothetical lake at various latitudes, an oxygen demand factor must be used. Present estimates are based on areal hypolimnetic oxygen deficits (AHOD, as mg O_2 m^{-2} day^{-1}) for temperate lakes that have low (100), moderate (300), and high (1000) respiration rates, as given by CORNETT & RIGLER (1980). The estimation of time required for complete anoxia to develop in the hypolimnion requires calculation of the oxygen-holding capacity of the hypolimnion, which is taken from the expected bottom temperatures for lakes at various latitudes. Bottom temperatures are assumed to reflect the temperature of the water at the time of complete (seasonal) mixing. The hypothetical lake is assumed to reach saturation for the appropriate temperature during mixing. The concentration of oxygen for the hypolimnion thus estimated for all latitudes leads, along with morphometric information on the hypothetical lake, to an estimate of the total oxygen content of the hypolimnion. The rate of oxygen depletion per unit area of hypolimnetic surface, as specified by the AHOD data from CORNETT & RIGLER (1980), is assumed to be applicable to lakes having hypolimnetic temperatures of 4 °C, and to be correspondingly higher, reflecting accelerated rates of microbial respiration, at the higher temperatures that are characteristic of lower latitudes. The rate of depletion is scaled up from a base level defined at 4 °C by use of a Q_{10} of 2.0 (doubling for a 10 °C rise in temperature). The volume of oxygen in the hypolimnion at each latitude, combined with the expected rate of oxygen depletion at each latitude, leads to a prediction of the amount of time required to exhaust all of the oxygen in the hypolimnion at any given latitude.

Estimates were also made of differences in the rates of nitrate disappearance following anoxia in lakes across different latitudes. For the purposes of this estimation, it was assumed that significant disappearance of nitrate from the water column caused by denitrification does not occur until the onset of anoxia, but the rate of respiration, and thus the demand for oxidizing power, is essentially the same with anoxia as without anoxia, so long as nitrate is present, and that denitrification shows a Q_{10} of approximately 2.0. These assumptions, although only approximate, seem generally consistent with data reviewed by SEITZINGER (1988) for temperate lakes. Consumption of nitrate is based on the observation that nitrate is a very efficient oxidizer and is used by a wide variety of bacteria. The molar ratio of nitrogen used to carbon oxidized during denitrification is ~1.25 (SCHINDLER 1985).

Results

Bottom temperatures are expected to be within the vicinity of 4 °C from the highest latitudes down to a latitude of approximately 40°, at which point they begin to rise steadily to a maximum of 24–28 °C in the equatorial region (Fig. 1). There is a corresponding reduction in the oxygen-holding capacity of water, which is highest near 4 °C (about 13 mg/L), and lowest near the equator (just under 8 mg/L, Fig. 2). Metabolic rates for hypolimnetic microbes, assuming sufficient organic carbon supplies, are approximately four times higher in the hypolimnion of tropical lakes than in the hypolimnion of lakes above 30° latitude (Fig. 2). At tropical latitudes, the combination
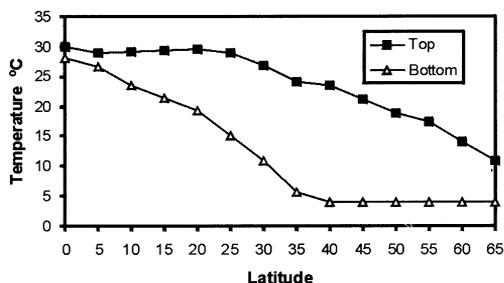

Fig. 1. Characteristic surface and bottom temperatures for stratified lakes at various latitudes (from LEWIS 1987).
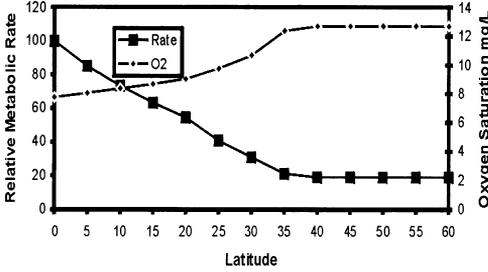
Fig. 2. Relative metabolic rate (arbitrary scale) and saturation concentration for oxygen (sea level) based on calculations explained in the text.
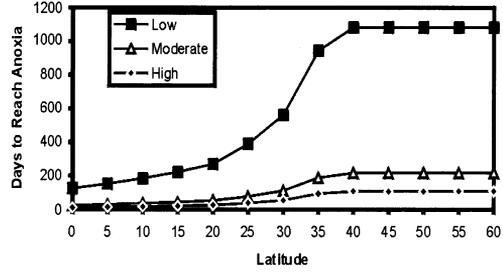

Fig. 3. Days required for the hypolimnion of a stratified lake to become completely anoxic at various latitudes under three levels of respiratory oxygen demand (low, 100 mg m^{-2} day^{-1}; moderate, 300 mg m^{-2} day^{-1}; high, 1000 mg m^{-2} day^{-1}).

of lower oxygen inventory in the hypolimnion and higher oxygen consumption rates, leads to a substantially lower expected duration of the persistence of oxygen in the hypolimnion at a given latitude, for a given value of AHOD, than in temperate lakes (Fig. 3). The rate of decline of nitrate concentrations after anoxia follows a similar pattern (Fig. 4).

Discussion

A latitudinal gradient in hypolimnetic temperatures is the primary cause of major differences in denitrification potential. The low temperature of temperate lakes during spring mixing allows maximum storage of oxygen during mixing and, as reflected in hypolimnetic temperatures during stratification, suppresses the rates of both oxygen use and denitrification. It is clear that tropical lakes of moderate to high productivity with a hypolimnetic volume more or less equal to eplimnetic volume have virtually no possibility of retaining oxygen in the hypolimnion throughout the stratification season. Even tropical lakes of low productivity will be likely to enter anoxia during extended stratification (Fig. 3).

Figure 3 should be interpreted in light of the duration of the stratification season at various latitudes, and also with respect to lake morphometry. For lakes in the upper portion of temperate latitudes, the duration of the summer stratification season is as little as 5 or 6 months (e.g. Lake Mendota, 43° N, ~140 days
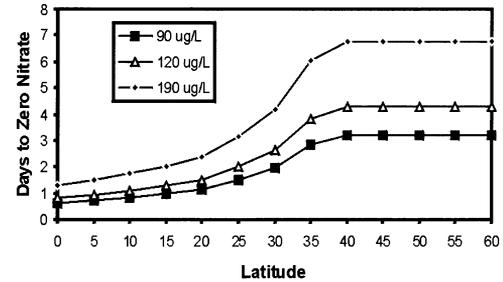

Fig. 4. Days required for elimination of nitrate in a model lake hypolimnion following the onset of hypolimnetic anoxia at various latitudes. Three initial nitrate-nitrogen concentrations are represented in the figures: 90, 120, and 190 µg/L; oxygen demand is 300 mg m^{-2} day^{-1}.

of stratification; BROCK 1985). Tropical lakes are typically stratified for 9–10 months each year (LEWIS 2000), and lakes of low temperate to high tropical latitudes are likely to be intermediate in this respect. Thus, tropical lakes not only show more rapid progression toward anoxia, but also have more time to develop anoxia because of their prolonged seasonal stratification.

The hypothetical lake that was used in performing the calculations leading to Figs. 2 and 3 has specific morphometric characteristics that influence the rate of progression toward anoxia. A deeper lake of the same size would store more

oxygen at a given latitude, and thus would progress more slowly toward anoxia, whereas a shallower lake, unless too shallow to stratify at all, would show the opposite tendency at any given latitude. Only lakes with high relative depth and low productivity could be expected to retain oxygen near the bottom in the lowland tropics. Even these lakes might tend to be anoxic in the deeper layers, however, because of the likelihood that small lakes of high relative depth will not be completely mixed, or will be completely mixed only in certain years of especially cool weather.

Under the assumptions that are used here for modelling, the time required for total depletion of oxygen is much greater than the subsequent time required for total depletion of nitrate at any given latitude (Figs. 3 and 4). The time is shorter in all cases simply because nitrate concentrations are assumed to be within the natural range (90–190 µg/L NO_3^--N, LEWIS et al. 1999), and these concentrations are much lower than concentrations of oxygen. Even if the use of nitrate were slowed several-fold by the inefficiencies of microbes using nitrate rather than oxygen, the nitrate depletion phase following anoxia would not last very long except at the highest latitudes. Although water pollution could boost concentrations of nitrate as much as 10-fold, the time required for elimination of even this additional nitrate through denitrification, under the assumptions used here for modelling, would still be considerably less than for the preceding depletion of oxygen. Thus, it seems likely that the key control on potential for denitrification is the amount of time required for loss of oxygen from the hypolimnion rather than the amount of time required for loss of nitrate following the onset of anoxia.

In conclusion, latitudinal trends in hypolimnetic metabolic rates, hypolimnetic oxygen holding capacity and duration of stratification cause a steep latitudinal gradient in the potential for denitrification. Except for very shallow lakes that fail to stratify, virtually all stratified lakes at low latitude can be expected to lose a substantial portion of their nitrogen inventory on an annual basis through denitrification, and thus have greater likelihood of nitrogen depletion by phytoplankton growing in the upper water column.

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