

Tropical lakes: how latitude makes a difference

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Keywords: tropical lakes, temperature, heat budgets, phytoplankton, zooplankton, trophic dynamics

Abstract

Tropical lakes are far less numerous than temperate lakes because lakes of glacial origin are rare in the tropics. Also, the mixture of lake types differs from tropical to temperate latitudes; lakes of riverine origin are probably more common than any other type in the tropics. For lakes of a given type and size, latitudinal trends can be traced mainly to latitudinal gradients in minimum monthly solar irradiance. Higher monthly minima for irradiance in the tropics are responsible for higher minimum water temperatures, higher mean temperatures for the water column, and a smaller thermal differentiation between upper and lower water column. Tropical lakes of moderate to great depth are predominantly warm monomictic, and show great regularity in seasonal mixing, which typically coincides with the hemispheric winter. Stratification is seasonally persistent, but is less stable than at higher latitudes, and the amount of heat exchange required to cause important changes in stability is also smaller than at higher latitudes. For these reasons, as well as a geostrophic factor that can magnify the variability of wind-generated mixing, tropical lakes show much more intraseasonal variation in thickness of the mixed layer than morphometrically similar temperate lakes. Episodes of mixed layer thickening alternating with subsequent restoration of a thinner mixed layer affect nutrient cycling and plankton dynamics in tropical lakes. Efficiency of nutrient cycling is high at low latitudes because of intraseasonal deep mixing combined with high mean temperatures, which support higher nutrient regeneration rates. Primary production is about twice as high on a given nutrient base as it would be at higher latitudes, primarily because of efficient nutrient cycling combined with higher mean temperatures and greater stability in solar irradiance. Nitrogen is more often a limiting element for autotrophs in the tropics than at temperate latitudes. Phytoplankton, zooplankton, and benthic communities are no more complex at low latitudes than at high latitudes, in contrast to terrestrial communities. Phytoplankton communities show broad overlap in species composition with temperate communities and have little endemism. Zooplankton also show overlap, but have more endemism, contain more taxa that are characteristically tropical, and are composed of smaller species than temperate communities. Efficiency of energy transfer appears to be low in many tropical lakes. Zooplankton fishes are neither abundant nor diverse in many tropical lakes. Zooplankton herbivores often show suppressed growth rates indicating nutritional blockage of energy transfer even when food is abundant, and transfer of energy to fishes may be intercepted or suppressed by *Chaoborus*, which is abundant and widespread in the tropics.

Introduction

The land surface of the Earth holds between 5 and 50 million lakes, as indicated by extrapolation of the frequency distribution of large lakes (Figure 1) plus scattered data on the number of lakes in

specific lake districts. The distribution function of lake areas shows that about 1500 of the largest lakes account for most of the global surface area of lakes (Figure 1, Schuiling 1977, Herdendorf 1990). These 1500 large lakes show a latitudinal distribution that reflects the abundance of large

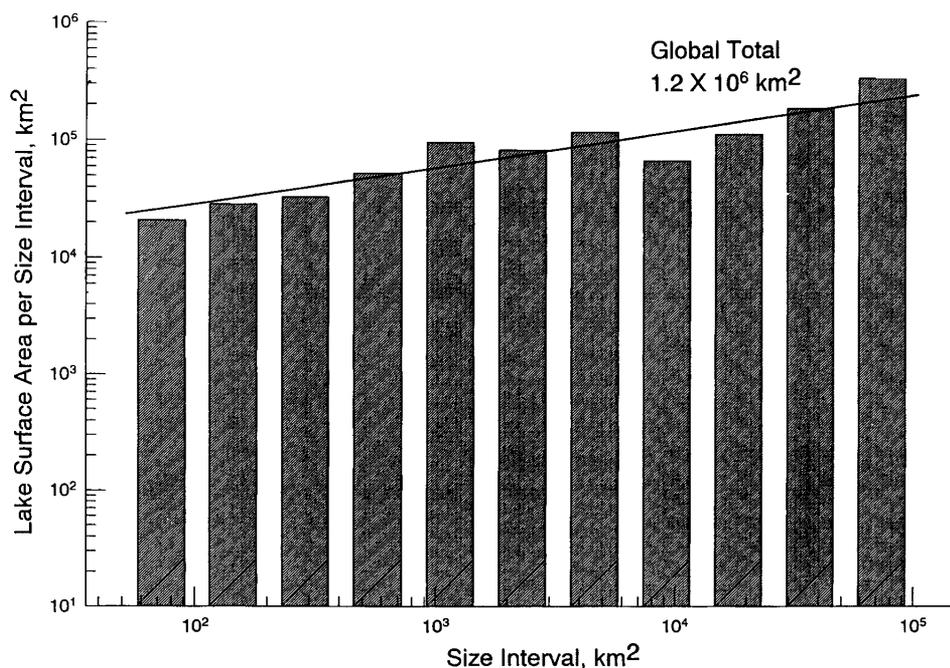


Fig. 1. Global lake surface area as a function of lake size. The raw data are from Schuiling (1977).

basins and the availability of water to fill them (Figure 2). The surface area of large lakes is lowest at latitudes coinciding with the subtropical high pressure zones and shows a small peak centered on the equator as well as a much larger peak centered at middle latitudes. The distribution of smaller lakes will not necessarily show the same pattern, however. Lakes of small to moderate size are important disproportionately to their area, but their global distribution is not known except in raw form on maps.

Random sampling from maps suggests that not more than 10% of the world's lakes are tropical. This mainly reflects the importance of glaciation in creating lakes at temperate latitudes. Lakes of glacial origin are found in the tropics, but only at the very highest elevations (Löffler 1964), and even there not in great abundance. Consequently, the mix of lake types is very different at tropical latitudes than it is at middle latitudes. Random sampling from maps suggests that at least 60% of temperate lakes are glacial, about 20% are formed by permafrost, and 20% are formed by other means, including rivers, coastal processes, and

volcanos (Figure 3). A similar rough approximation for tropical latitudes would show dominance by river lakes, and also a more even balance of several major types including lakes of volcanic, riverine, and coastal origin as well as lakes created by aeolian processes.

This review deals primarily with factors that are under climatic control; it omits any consideration of the very different mixtures of lake types that are found at different latitudes. A more complete comparison of temperate and tropical lakes would necessarily take into account the differential distribution of lake types, and especially the importance of riverine lakes in the tropics.

Latitudinal gradients in irradiance

The latitudinal climatic gradients of greatest importance in limnology are related mainly to solar irradiance. Gradients in solar irradiance are of direct relevance to photosynthesis; they also induce gradients in water temperature and in the layering and mixing of lakes. Latitudinal gradients in

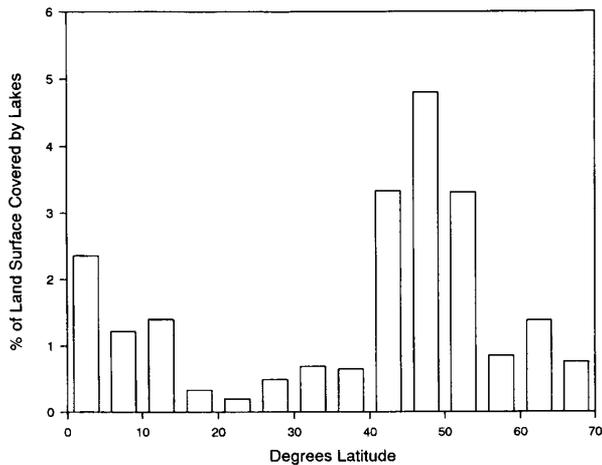


Fig. 2. Percent of land surface area covered by lakes as a function of latitude based on the distribution of the 1500 largest lakes in the world. Data are from Schuiling (1977).

irradiance result from the curvature and seasonal tilt of the Earth (Gates 1980). Standard meteorological tables (e.g. List 1951) that are calculated from these geometric factors indicate a progressive decrease in total annual solar irradiance from the equator toward higher latitudes (Figure 4). Standard tables are misleading, however, because they assume fixed attenuation of irradiance in the atmosphere. Attenuation coefficients vary greatly because of moisture and dust (Montieth 1972), and this variation is not entirely random with respect to latitude. Integration of measured solar irradiance between latitude lines over land surfaces shows that there is no distinctive downward trend in solar irradiance with latitude below 45° latitude because attenuation is high over the central tropics and decreases toward subtropical latitudes (Figure 4, Lewis 1987). Thus tropical and temperate lakes are not generically different in total annual irradiance.

Maximum daily or monthly irradiance for the annual cycle is also insensitive to latitude because changes in day length are to some extent compensatory for changes in solar angle (Figure 5). In contrast, the minimum monthly irradiance is highly sensitive to latitude, as is the annual range in solar irradiance. Thus, tropical and temperate lakes are distinguished mainly by differences in minimum annual irradiance, rather than by the mean or

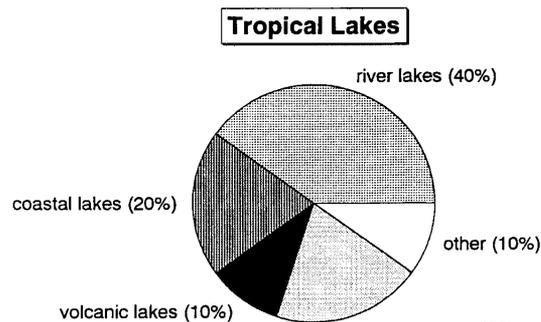
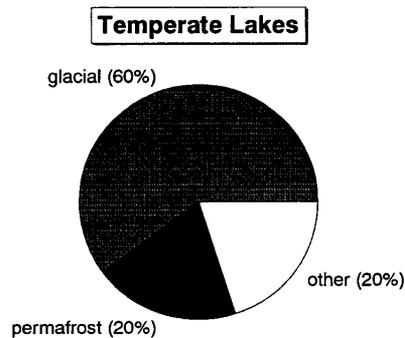


Fig. 3. Approximate proportions of lake types found at temperate and tropical latitudes, as determined by random sampling from maps.

maximum annual irradiance.

Light regulates photosynthesis, but the effect of light is moderated by temperature and nutrient supply. When multiple factors control a biological process, a more even distribution of any one of the factors over time (in this case, light) may produce higher biological yield by allowing more efficient use of other potentially limiting resources. This principle applies in several ways to the functional contrasts of tropical and temperate lakes (Lewis 1974, Vincent et al. 1986). As indicated below, it may be especially relevant to the interaction of temperature, nutrients, and photosynthesis.

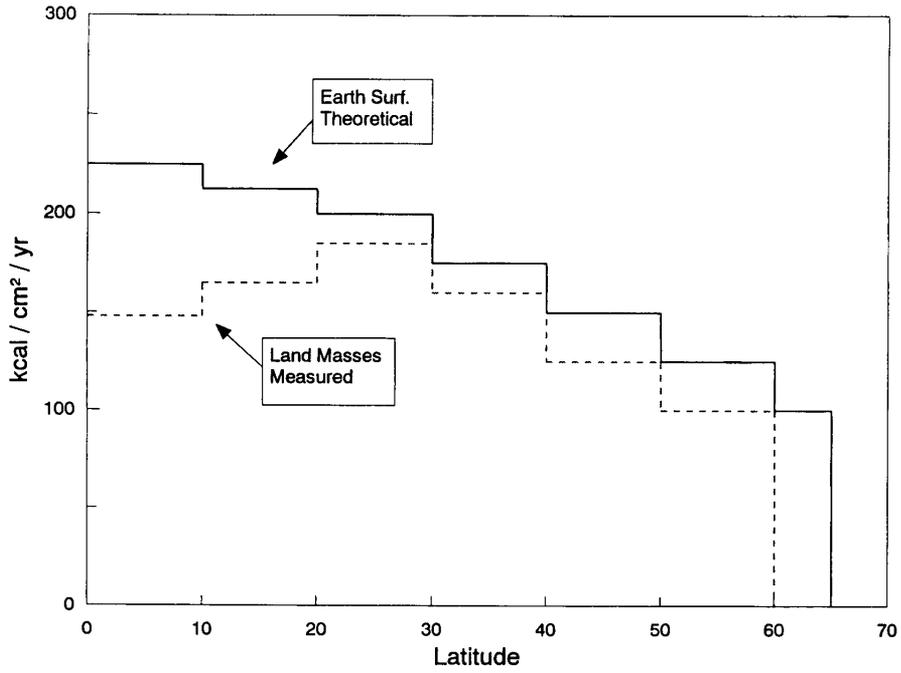


Fig. 4. Annual irradiance at the surface of the Earth as a function of latitude calculated from solar angle with a fixed attenuation coefficient (solid line) and measured (dashed line). Redrawn from Lewis 1987.

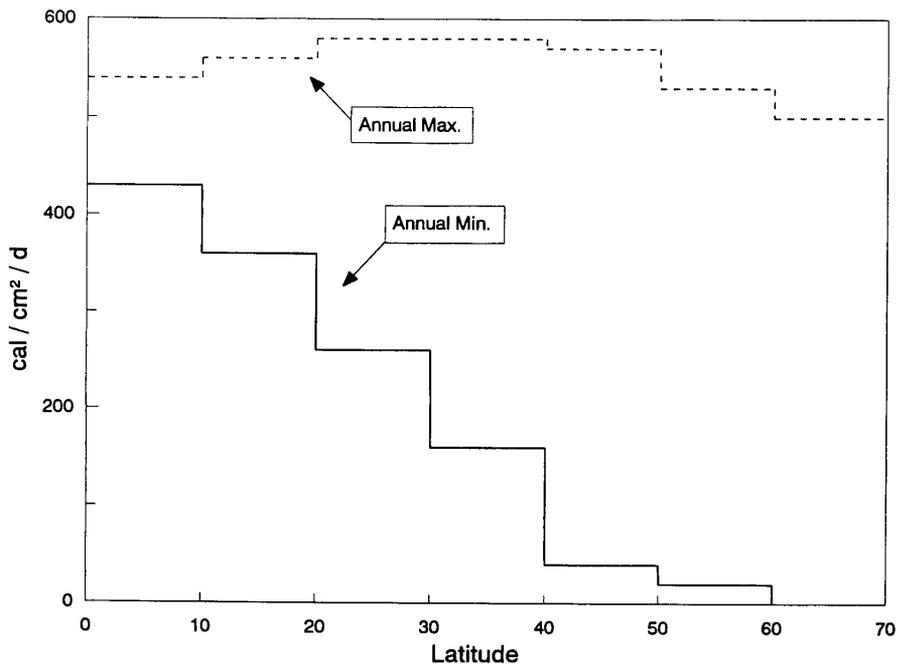


Fig. 5. Annual maximum and annual minimum irradiance as a function of latitude. Redrawn from Lewis 1987.

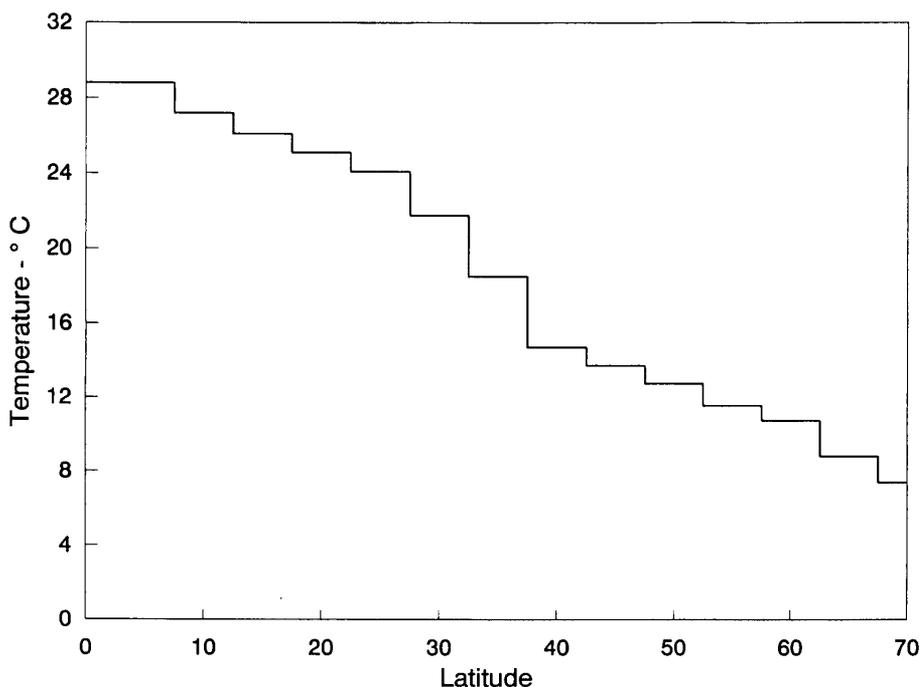


Fig. 6. Mean lake temperature as a function of latitude. Data from Lewis 1987.

Water temperature and mixing

Irradiance is connected to water temperature. Empirical data show that mean temperature declines with latitude (Figure 6). From the equator up to about 40° latitude, the decline in mean temperature is explained mainly by a steep decline in the annual minimum temperature, as reflected by temperature at the bottom of the water column during stratification (Figure 7). As might be expected from the latitudinal pattern of maximum irradiances, the annual maximum temperature is insensitive to latitude up to about 40°. Thus, tropical and temperate lakes are differentiated more strongly by minimum temperatures than by maximum temperatures.

At temperate latitudes, seasonal changes in water temperature are associated with seasonal mixing and layering of lakes. Seasonality is suppressed in the tropics, but it is by no means absent. Contrary to the earliest speculations about layering and mixing in lakes of low latitude (Hutchinson and Löffler 1956), tropical lakes that are sufficiently

deep to stratify tend to mix predictably at a particular time of year and to remain stratified for the remainder of the year (Talling 1969, Lewis 1987). In this sense they are little different from subtropical or low temperate lakes, except that the mixing season may be as short as a month or 6 weeks in the tropics. In most cases the mixing season coincides with the hemispheric winter, which implicates the steep latitudinal gradient in minimum irradiance as the major cause of seasonality. Lakes of 1-3 m depth typically are continuously polymictic (i.e., they show daily mixing; Lewis 1983a) and lakes of 3-10 m mean depth are often discontinuously polymictic (i.e., they mix irregularly, and more than once per year; Lewis 1983a).

Some lakes may show seasonal patterns that do not originate from seasonal changes in irradiance. For example, floodplain lakes can be destabilized annually by hydraulic factors (Hamilton and Lewis 1987), as are some reservoirs (Hawkins 1985, Mtada 1986, Osborne and Totome 1992), and some equatorial lakes of Africa are destabilized annually

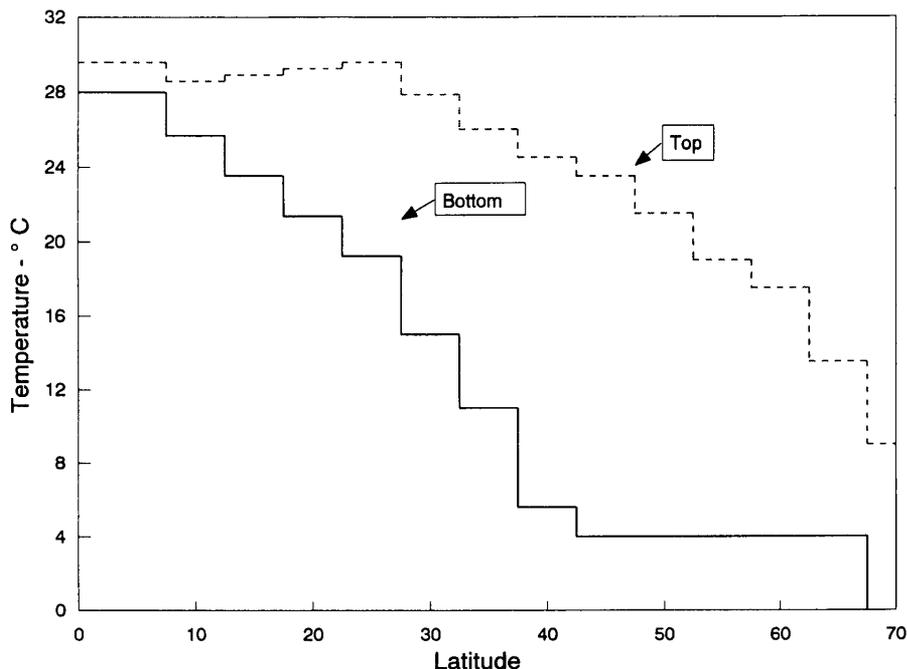


Fig. 7. Temperatures at the top (excluding transient diurnal increases) and bottom of lakes during stratification, shown as a function of latitude. Redrawn from Lewis 1987.

by seasonal winds rather than seasonal trends in solar irradiance (Talling 1969, Coulter et al. 1986, Talling 1990). The stability of layering in reservoirs with deepwater outlets may be maintained by continuous inflow of cool water (Mtada 1986).

The cause of seasonal mixing is illustrated by Figure 8, which shows surface temperature minima, reflecting minimum annual heat content, for a selection of tropical lakes. The minimum generally coincides with the hemispheric winter solstice, but is delayed slightly by the inertial nature of heat exchange between air and water.

The season of minimum temperature is usually the season of complete mixing, except for shallow lakes, which mix frequently or even daily. Although there are few long-term data sets for tropical lakes, there seems to be a strong degree of repetition in the seasonality of annual mixing in a given tropical lake. For example, Lake Valencia, Venezuela, (10°N) shows a 5-year sequence of annual mixing that is fully comparable in predictability to seasonal mixing at much higher latitude (Figure 9, Lewis 1984).

The lower water column of a tropical lake is only as cool as the annual minimum temperature for the coolest months, which is generally about 24°C at sea level (the minimum is also affected in a predictable way by elevation: Lewis 1987, Kling et al. 1990). Discounting diurnal heat gain, the top and bottom of the water column are separated by only a small temperature difference, which ranges from about 1.5°C for equatorial lakes to 5 or 6°C for lakes near the margin of the tropics (Figure 7). The high density response of water at high temperatures generates surprisingly high stability for small temperature differences in the vicinity of 24°C. For this reason, tropical lakes of moderate to great depth typically hold stratification for an entire season. Even so, the stability of layering is lower than it would be for temperate lakes of comparable shape and size. For example, the stability of stratification for a hypothetical lake of fixed dimensions increases 3-fold between mid-tropical and mid-temperate latitudes (Figure 10).

The annual heat budgets of tropical lakes are quite low (usually a few thousand calories/cm²/yr:

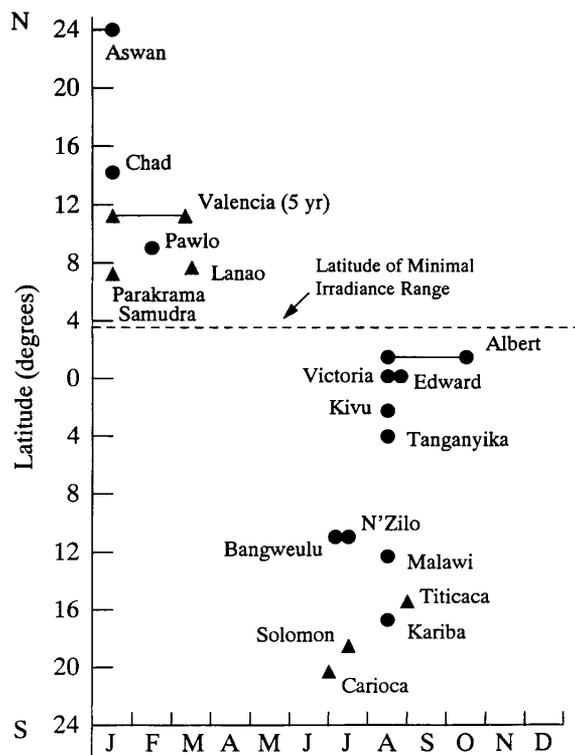


Fig. 8. Timing of the annual surface temperature minimum for a selection of tropical lakes in both hemispheres. Data represented by solid dots are from Talling 1969. Other sources are as follows: Valencia, Venezuela, Lewis 1983b, 1984; Lanao, Philippines, Lewis 1973; Parakrama Samudra, Sri Lanka, Dobesch 1983; Titicaca, Peru/Bolivia, Vincent et al. 1985; Carioca, Brazil, Henry and Barbosa 1989.

Hutchinson 1957, Lewis 1983b, Talling 1990). A few days of cloudy weather can lead to loss of a significant portion of the annual heat budget (Kittell and Richerson 1978). Episodes of non-seasonal heat loss occurring at intervals of 2 to 4 weeks in association with synoptic changes in weather (e.g. Lewis 1983, Lewis et al. 1994) can reduce stability enough to cause erosion of the thermocline and thickening of the mixed layer without causing complete mixing (the mixed layer for present purposes is defined on a 24-hour basis, i.e., disregarding transitional daytime stabilization of the upper water column). Subsequent restoration of heat gain may then lead to re-establishment of a thinner mixed layer marked by a secondary thermocline (Lewis 1973, 1983b; Richerson et al. 1977).

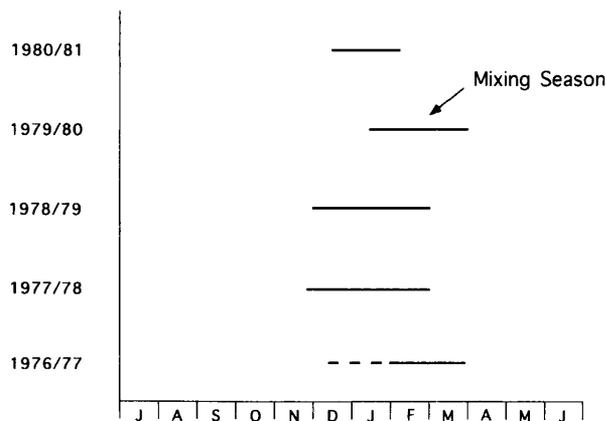


Fig. 9. Illustration of regularity in the timing of the seasonal mixing over a 5-year interval for Lake Valencia, Venezuela. Data are from Lewis 1984.

In this way, the mixed layer episodically becomes thicker and thinner, even though the water column remains stratified.

Another factor that may affect the thickness of the mixed layer is the Coriolis effect (Lewis 1987). For unconstrained water movements, the geostrophic deflection of water currents moving directly north or south, or with a significant component of movement either north or south, is quite substantial. The effect of this deflection is to reduce the water current velocity that can be generated by a given wind speed. The Coriolis effect is a function of latitude; it is negligible at the equator and highest at high latitude. Especially for lakes of moderate or great size, the Coriolis effect is a brake on current velocity, and therefore on the thickening of the mixed layer. The low Coriolis effect in the tropics will make wind more effective in establishing a mixed layer, thus reinforcing the effect of low stability in tropical water columns. The magnitude of this effect has not been studied empirically, however.

The lower stability of stratification in tropical lakes and the relationship of the Coriolis effect to latitude would, if acting alone, cause the mixed layers of tropical lakes of a given size to be thicker on the average than those of temperate lakes of the same size. Counteracting this tendency, however, is subdivision of the mixed layer in response to

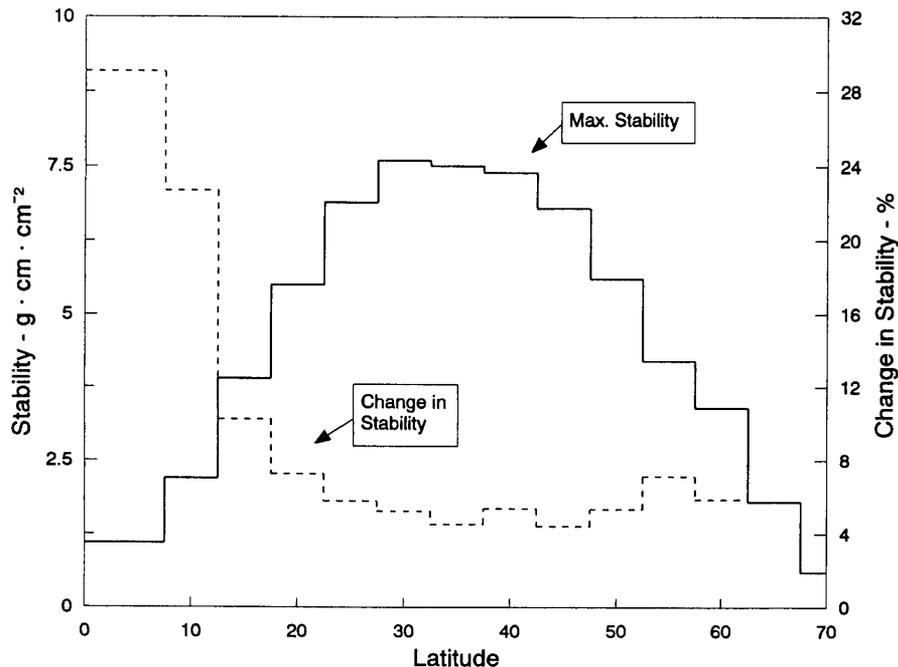


Fig. 10. Calculation of stability and change in stability for a hypothetical lake as a function of latitude. The hypothetical lake had an area of 2 km², a mixed layer 5 m thick, a maximum depth of 25 m, and a bottom area equal to 10% of the surface area. The top and bottom temperatures are as shown in Fig. 7. Change in stability is that which would result from a 0.5°C decrease in temperature of the mixed layer (250 cal/cm²). Redrawn from Lewis 1987.

relatively small heat gain because of the rapid change of density with temperature at the high base temperatures that are typical of lowland tropical lakes. Given the complexity of this combination of factors, it is difficult to calculate the expected mean and variance for mixed layer thickness as a function of latitude. Also, empirical studies have as yet produced too few careful measurements to show for certain the relative mean thickness of mixed layers in tropical and temperate lakes. Present evidence suggests that tropical lakes of a given size and wind exposure will have mixed layers that are on the average about twice as thick as at middle temperate latitudes. This is illustrated in Figure 11 by a comparison of three lakes of similar size (Constance, Valencia, and Lanao), two of which are tropical. The tropical lakes fall within the range of values that are observed in the temperate zone, but well above the mean.

At least as important as the mean thickness of mixed layers is their variability in thickness within the stratification season. The mixed layer of a

temperate lake is not fixed (Reynolds 1989), but its dimensions are in general much more stable than those of tropical lakes. A great range of variation can be expected at all latitudes, of course: small, strongly sheltered tropical lakes (e.g., Wood et al. 1984) will show much less variation than large, exposed ones, and some physical conditions of temperate lakes may greatly enhance variability (e.g., Harris and Piccinin 1980). In tropical lakes of moderate to large size, however, the mixed layer is extraordinarily dynamic because of the alternating erosion and reformation of secondary thermoclines superimposed on a seasonally stratified water column. This is illustrated by a comparison of the mixed layer thickness in Lake Constance (540 km²) and Lake Lanao (360 km²), which are approximately the same size (Figure 12): the mixed layer of Lake Lanao moves tens of meters during the stratification season.

In both tropical and temperate lakes, diurnal stratification of the upper water column may occur in calm weather. Over much of the year, diurnal

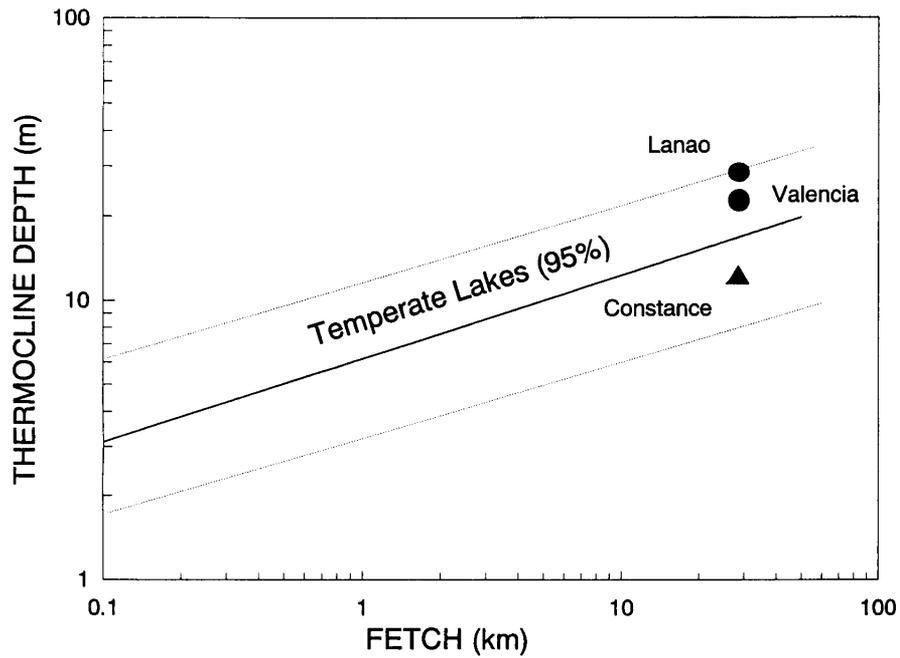


Fig. 11. A comparison of the thickness of the mixed layer in two tropical lakes (Lanao, Valencia, from Lewis 1973, 1983b) and a temperate lake (Constance, from Hollan et al. 1990) of approximately the same size, shown in relation to the range of variation in thermocline depth (which is slightly greater than the depth of the mixed layer) for a large number of temperate lakes as determined by Shuter et al. (1983).

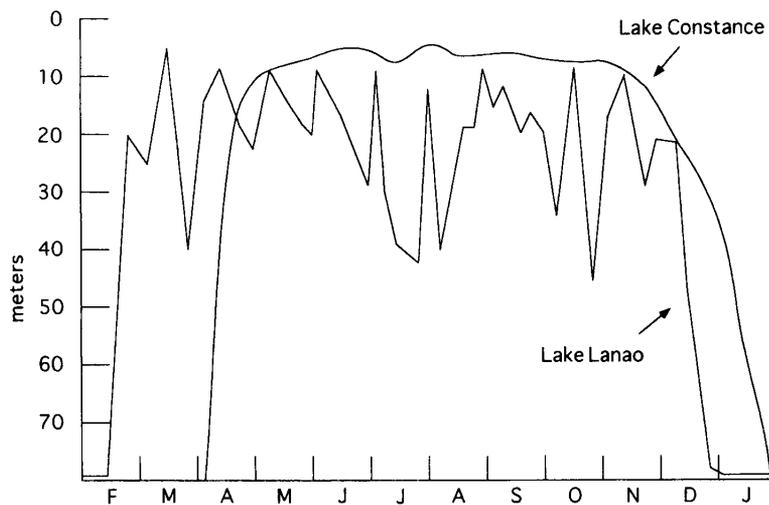


Fig. 12. A comparison of mixed layers in a tropical and a temperate lake of similar size (data from Lewis 1973, Hollan et al. 1990).

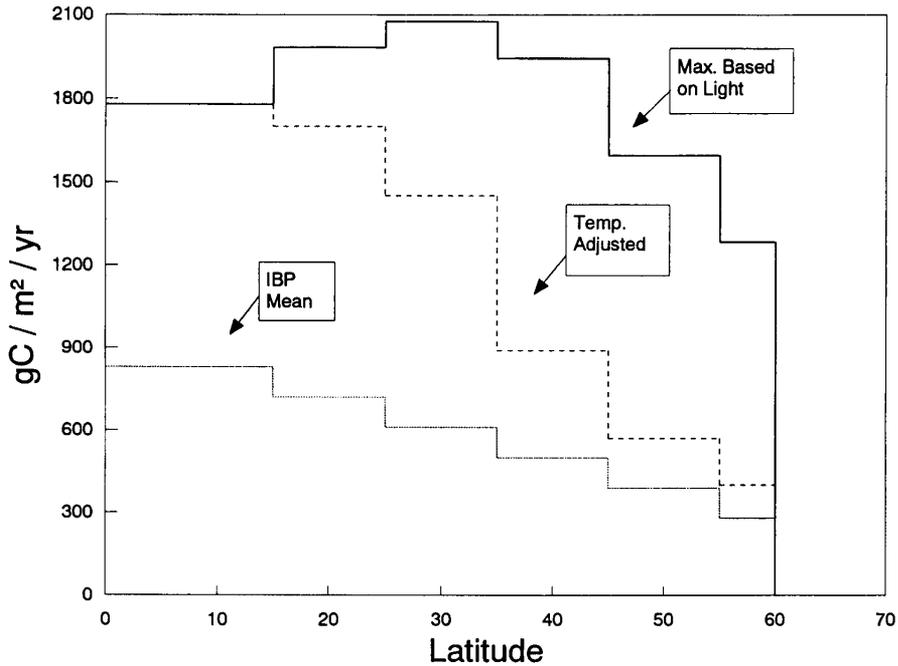


Fig. 13. Latitudinal trends in primary production. The top line shows latitudinal trends in maximum production that would be expected for nutrient-saturated conditions in the absence of any thermal effect on photosynthesis. The middle line shows the same, but with an adjustment for the thermal effect on photosynthesis under nutrient-saturated conditions. The bottom line is empirical (IBP mean). Redrawn from Lewis 1987.

stratification will be more pronounced in tropical lakes because of the more rapid change in water density with temperature at higher temperatures (Melack 1981, Bauer 1983, Ganf 1994, Talling 1990).

Overall, tropical lakes both stratify and mix more readily than temperate ones in response to changes in wind strength or reversal in heat flux. This characteristic has great significance for the efficiency of tropical lakes in recycling nutrients and in setting the successional clock for plankton communities.

Photosynthesis

Temperature and mixing affect photosynthesis. First, temperature has a direct effect on the rate of photosynthesis under nutrient-saturated conditions. There appears to be no major thermal acclimation for photosynthesis under nutrient-saturated conditions; the Q_{10} for photosynthesis is close to 2, as

would be expected for most physiological processes (Eppley 1972, Goldman and Carpenter 1974). The lower mean temperatures and lower minimum temperatures of temperate lakes are therefore a constraint on the nutrient-saturated rates of photosynthesis. The latitudinal effects can be calculated from the Q_{10} and the temperatures for lakes at different latitudes, as shown in Figure 13. The top line shows the latitudinal trend that would occur if there were no thermal gradient with latitude. The second line shows optimum photosynthesis rates adjusted for temperature; the gap between the two is a measure of the suppression of maximum photosynthetic rate caused by temperature alone. Suppression is 50-75% at middle latitudes. Thus, under conditions of continuous nutrient saturation, the effect of temperature on photosynthesis could cause annual primary production in a tropical lake to be twice or more that of a temperate counterpart. In fact this estimate appears to be reasonably accurate for highly eutrophic shallow lakes that fail to stratify

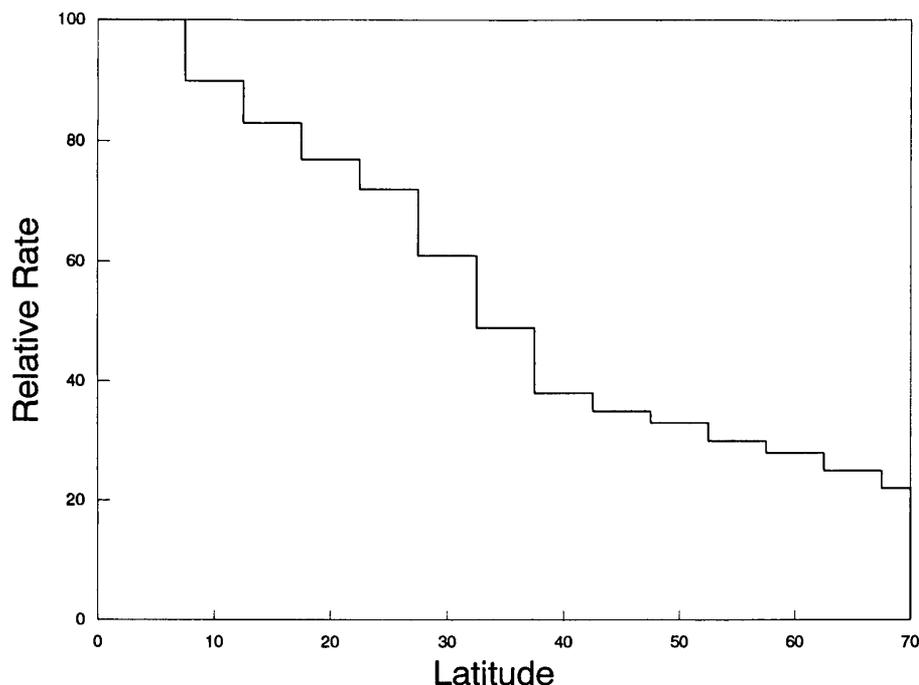


Fig. 14. Illustration of the direct temperature effect on regeneration of nutrients in a mixed layer at a Q_{10} of 2.0. Redrawn from Lewis 1987.

seasonally, as shown by the data summaries of Brylinsky (1980) and Dokulil et al. (1983). However, the phytoplankton communities of temperate and tropical lakes are often deficient in nutrients, and therefore are not fully under thermal control.

For a given nutrient load and hydraulic residence time, nutrient availability is controlled by cycling, which includes 3 major categories of processes: (1) regeneration in the mixed layer, (2) regeneration from sediment in contact with mixed layer, and (3) transfer to the mixed layer from the water column below. The first two processes are influenced by temperature and the third by mixing. As a first approximation, the temperature effect is most straightforward. Decomposition in general shows a Q_{10} of at least 2.0 if substrate quality is constant (e.g., Toerien and Cavari 1982, Morris and Lewis 1991). Latitudinal gradients in mean temperature of the mixed layer therefore can be translated into estimates of latitudinal trends in nutrient regeneration rates for the mixed layer. The thermal gradient would imply a 2- to 3-fold dif-

ference in nutrient regeneration rates from mid-temperate to mid-tropical latitudes at a Q_{10} of 2.0 (Figure 14).

Mixing is also important. There is constantly some nutrient transport into the mixed layer from below, even when the mixed layer is stable. A few estimates from empirical data suggest, however, that eddy diffusion rates are not categorically different from those of temperate lakes (Robarts and Ward 1978; Lewis 1982, 1983b). In contrast, the mixed layer is more dynamic in a tropical setting than in a temperate one. Nutrients that move from the mixed layer to deeper water are more likely to be returned, and thus reused, in tropical lakes as the mixed layer moves up and down in the water column. For this reason, tropical lakes are likely to cycle limiting nutrients more efficiently than temperate lakes not only because of their greater metabolic rate, but also because of their greater rate of nutrient return to the mixed layer from points below (Lewis 1973, 1983b).

As would be expected from higher nutrient

cycling efficiencies, tropical lakes appear to show greater primary production for a given nutrient load (Vincent et al. 1986, but see Cobelas and Rojo 1994 for a contrary conclusion), as well as greater biomass (Lewis 1990), less variation in biomass and primary production (Melack 1979, Cobelas and Rojo 1994, Lewis 1991), and weaker statistical coupling of primary production and solar irradiance (Dokulil et al. 1983, Vincent et al. 1986). Kilham and Kilham (1990a) have suggested on the basis of data from African lakes that trophic constraints derived from nutrient loading rates are fundamentally different in the tropics because of efficient nutrient cycling in the tropics. A fully satisfactory empirical verification of these predictions remains difficult because of the small number of extended studies that have been done on tropical lakes.

The IBP data on primary production (Figure 13) are a reasonable basis for latitudinal comparisons, but are weak in tropical representation. However, accumulation of data on primary production since the end of IBP seems to confirm the general latitudinal trend derived from IBP studies (Dokulil et al. 1983, Vincent et al. 1986), although Cobelas and Rojo (1994) have recently questioned the validity of the latitudinal trend. Two general points are important: (1) absolute levels of primary production are higher at tropical latitudes than at temperate ones by roughly a factor of 2; (2) the absolute deviation between actual and optimum production is higher at tropical latitudes than at temperate ones. The explanation for both of these aspects of the latitudinal trend probably has to do with nutrient cycling and not directly with temperature or solar irradiance. Trends in solar irradiance (primarily greater uniformity) and temperature (higher mean temperature) are indirectly responsible for greater nutrient recycling efficiency, but without the connection to nutrient cycling could not cause strong latitudinal trends because of the prevalence of nutrient limitation in lakes. For this reason, nutrient cycling should be a greater focus of future studies.

It is of some practical significance that more efficient nutrient cycling at tropical latitudes is not able to match fully the higher metabolic potential of algae to use nutrients at high temperatures. The

reserve potential of tropical phytoplankton populations to use additional nutrients is very high in an absolute sense, and the response of lakes to eutrophication at tropical latitudes may therefore be stronger than it is for temperate ones.

Limiting nutrients

Identity of the limiting nutrient probably shows some latitudinal trends, although it is difficult to sort them out. Silicon, which is not uncommonly limiting for diatom growth in eutrophic lakes of the temperate zone (Reynolds 1989), is in general delivered by rivers to lakes at higher concentrations in the tropics because the weathering of silicate minerals is affected by temperature (Meybeck 1979, Talling 1992, but see also Lewis and Saunders 1989). The consequences of higher Si concentrations in the supply water for lakes are not obvious, however. Higher Si concentration would seem to render Si limitation of diatom growth less likely (Talling 1992). This may not be the case, however, given that the ratio of Si to P or N is more important than the absolute concentration of Si in determining the likelihood of Si depletion. Empirical information is insufficient to show the role of Si depletion in suppressing diatom growth. Kilham and Kilham (1990b) have shown that the Si:P ratio declines with lake size in tropical Africa, suggesting that Si depletion is most likely in the largest lakes. They have also shown that *Stephanodiscus*, which has a low silica requirement, is now abundant in some locations but was dominant in many African lakes 9500 yr BP, when lake levels were higher (Kilham and Kilham 1990b). This indicates past change in the Si:P ratios in relation to climatic change.

Nitrogen and phosphorus are the key candidates for general nutrient limitation of phytoplankton. Present evidence suggests that nitrogen limitation is more important and widespread in the tropics than it seems to be in the temperate zone (Lewis 1991). Some evidence for nitrogen limitation is experimental (Kalff 1983, Lewis 1983c, Selano and Melack 1984, Fisher et al. 1988), but much is circumstantial. Tropical waters appear to have a lower ratio of dissolved inorganic nitrogen to soluble reactive phosphorus than waters of

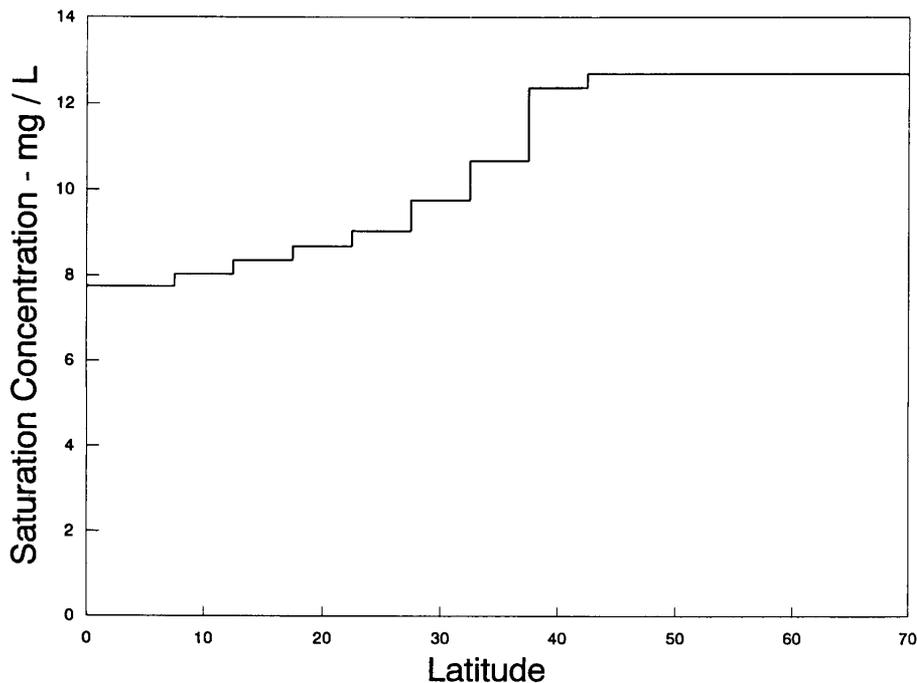


Fig. 15. Effect of latitude on the oxygen saturation capacity of lakes as calculated from surface temperatures. Redrawn from Lewis 1987.

temperate latitudes (Viner 1975). Concentrations of total phosphorus are often high (Talling 1992, Wood et al. 1984), and it is not uncommon to see soluble reactive phosphorus present in significant amounts while inorganic nitrogen is below detection limits (e.g., Lewis 1986). Abundance of nitrogen fixers is high in many tropical waters, and element ratios in biomass are often suggestive of nitrogen deficiency (Mukankomeje et al. 1993). This is not to say that phosphorus limitation is impossible in the tropics. Kalff (1983) and Peters and MacIntyre (1976) have given experimental evidence of phosphorus limitation in some African lakes, and Bootsma and Hecky (1993) have proposed that a number of the large African lakes are poised quite closely between nitrogen and phosphorus limitation.

Several factors might explain predominance of nitrogen limitation at tropical latitudes. Chemical weathering of phosphorus from parent material is more efficient at high temperatures. In addition, evapoconcentration of phosphorus will be more pronounced at low latitudes than at high ones in

general (Talling 1992, Melack and MacIntyre in press), although there is large regional variation in this factor. Finally, nitrogen losses from tropical environments are almost certainly higher than at temperate latitudes because of the high water temperatures of tropical lakes (Talling 1966, Kalff 1983). The contrast is especially strong for deep water, which may approach 4°C in a temperate lake and 24°C in a tropical one. The speed with which sediments reach low redox potential, the duration over which this redox potential is sustained, and the metabolic rate of denitrifiers in the presence of appropriate substrate all will be much higher at tropical latitudes than at temperate ones. The oxygen uptake capacity of water, and therefore the oxygen reserve of the hypolimnion, is suppressed by high hypolimnetic temperature (Figure 15). This compounds the effect of high rates of oxygen depletion at the higher deepwater temperatures of tropical lakes (Ruttner 1933). Thus nitrogen deserves especially close study in the tropics.

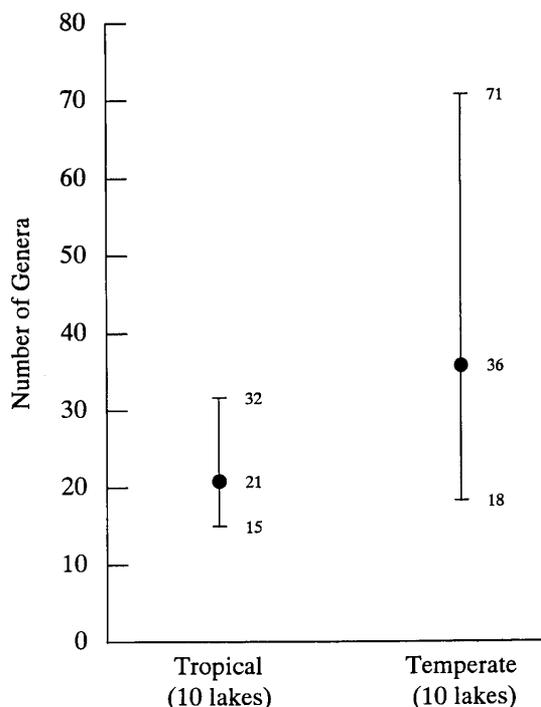


Fig. 16. Number of genera of phytoplankton in a selection of 10 tropical lakes and 10 temperate lakes (data from Lewis 1978a).

Phytoplankton

Terrestrial vascular plants show great contrasts between tropical and temperate latitudes, both with respect to composition and diversity (Cox and Moore 1985, Wilson 1988). Tropical land plant communities are far more diverse and are composed of distinctive sets of species, genera, and even families. Phytoplankton communities are quite different. The composition of communities at the level of genus, and even at the level of species, varies surprisingly little between temperate and tropical latitudes (Lewis 1978a, Kalff and Watson 1986). For example, *Melosira granulata*, which is widely distributed and abundant in Europe, North America, and other temperate locations, is also abundant and important at tropical latitudes in South America, Africa, and southeast Asia. While it remains to be seen how much genetic variation there is with latitude across different populations of a cosmopolitan morphospecies such as *Melosira*

granulata, phytoplankton appear to be surprisingly indifferent to latitude. A few important taxa of temperate latitudes, such as *Asterionella*, are either rare or excluded from the tropics, and a few important taxa such as *Cyellindrospermopsis stagnale* are characteristically tropical, but by and large it would be difficult to distinguish a phytoplankton sample as tropical without knowing the location from which it came. Endemism does occur in ancient lakes (Pollinger 1990), but only sparingly, and certainly not to the degree that is typical of vertebrates or mollusks. The evolutionary forces that shape phytoplankton speciation evidently are very weakly related to latitude. This suggests among other things that the importance of temperature in separating phytoplankton ecologically has been overestimated.

Tropical phytoplankton communities are probably no more diverse than temperate ones (Lewis 1978a, Serruya and Pollinger 1983). Most lakes contain 50 to 100 species that become sufficiently abundant to be tabulated in routine counts on an annual basis, although attention to rare species will easily extend this number. It is very difficult to make quantitative comparisons among groups of lakes because counts for individual lakes frequently involve widely varying degrees of effort in sampling, counting, and in the application of taxonomic expertise. Figure 16 shows a comparison of 10 temperate and 10 tropical lakes with respect to number of genera; this approach is more secure than a comparison of species. The comparison shows that there is extensive overlap in taxonomic richness of temperate and tropical lakes. Temperate communities might be even somewhat more diverse, but this would need to be verified by more careful study.

At temperate latitudes, there is typically a successional pattern in the development of phytoplankton communities from the beginning of the growing season to the fall mixing (Sommer 1989, Reynolds 1989). Frequently this succession involves first a predominance of diatoms, often accompanied by cryptomonads, followed by chlorophytes, and finally bluegreen algae and dinoflagellates. Individual components of the sequence may be expanded, compressed, or even

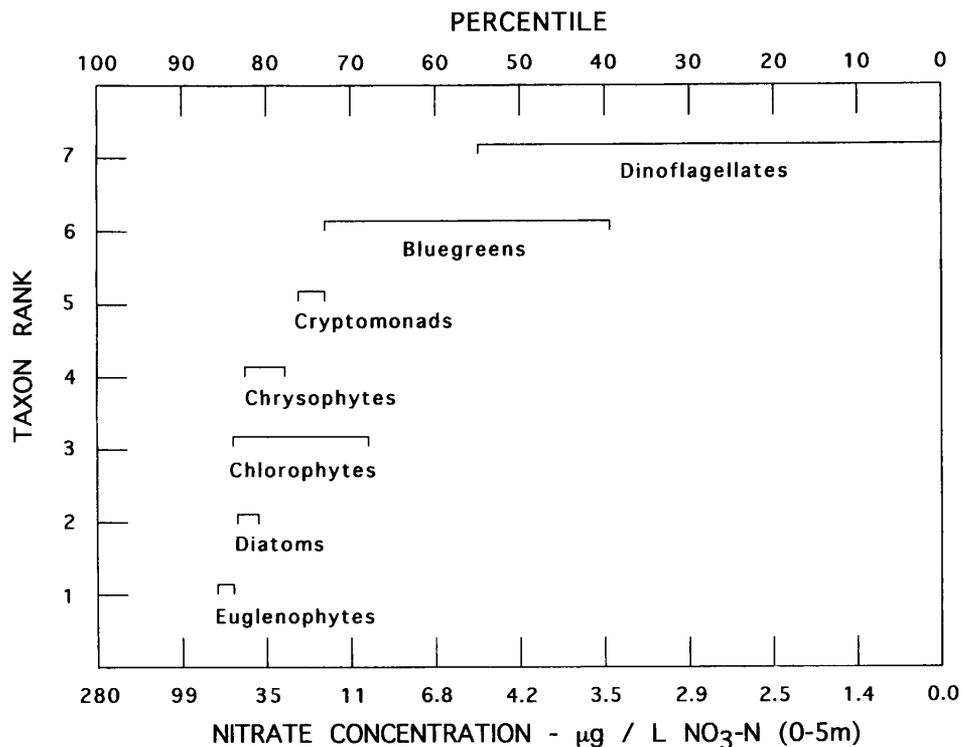


Fig. 17. Seasonal succession of phytoplankton for Lake Valencia, Venezuela, shown in terms of nitrate concentrations in the mixed layer. The nitrate concentration is a surrogate for the successional clock because nitrate concentrations decline steadily after a mixing event.

absent in individual lakes. The sequence is partly driven by physical changes from a more turbulent, thick mixed layer to a less turbulent, thinner mixed layer, by grazing, and also by autogenic processes originating with the phytoplankton themselves and mainly involving the depletion of critical nutrients as the phytoplankton community matures (Lewis 1978b,c). The temporal sequence of species in tropical lakes superficially appears to present no such order. Individual taxa seem to appear irregularly, disappear, and then reappear. Order becomes evident, however, from an analysis of species replacements following deep mixing events. The successional clock for phytoplankton communities starts to run when a mixing water column begins to stabilize. The episodic thickening of the mixed layer that occurs in many tropical lakes affects the phytoplankton much as full mixing would: it renews nutrients and increases turbulence

and transparency, thus resetting the successional clock (Lewis 1978c, 1986). With reference to mixing events, there is a clear successional pattern in tropical lakes, and in fact it is the same general pattern as in temperate lakes. Data for Lake Valencia (Lewis 1986) show how the growth of major taxa relates to surface concentration of nitrate, which declines with time since the last mixing, and therefore is a good surrogate for the successional clock (Figure 17).

While the successional sequence is fundamentally the same in tropical lakes as it is in temperate ones, there is an important contrast in the number of successional episodes per year (Lewis 1978c). In temperate lakes, the successional clock begins to run in the spring and may not be reset until significant erosion of the thermocline occurs in the fall. In tropical lakes, the successional clock is reset more frequently because of irregular

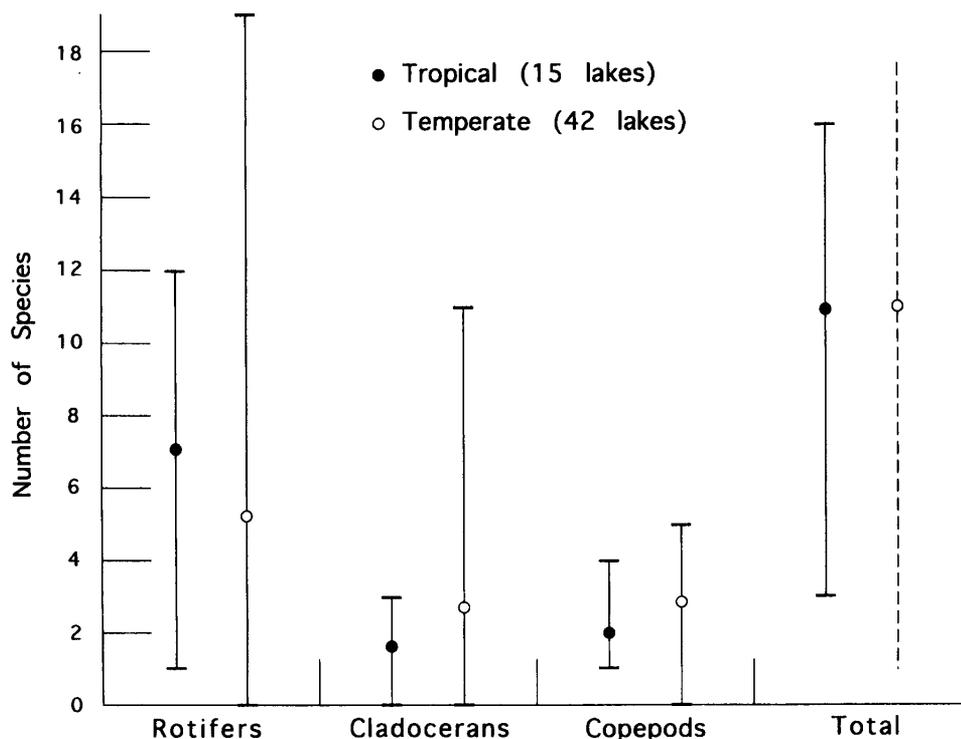


Fig. 18. Number of zooplankton species per sample for 16 tropical lakes (from Ruttner 1952) and 42 temperate lakes (from Pennak 1957).

thickening of the mixed layer, which reproduces conditions similar to those at the beginning of the growing season. In tropical lakes there are more successional episodes, but each one is briefer and may not proceed to completion. Very shallow tropical lakes are arrested in a single successional stage, which explains the greater simplicity and lower degree of seasonal variation in their phytoplankton communities.

Zooplankton

The herbivore communities of tropical lakes are also very similar in general composition to those of temperate lakes (Ruttner 1952). There is more endemism among zooplankton, particularly for calanoid copepods (e.g., Dussart 1980, Dumont and Maas 1988), than among phytoplankton, and a number of important taxa are characteristically

tropical (e.g., *Keratella tropica*, *Mesocyclops crassus*). The genus *Brachionus* is more strongly represented in tropical lakes than in temperate ones (Fernando 1980a,b). Also present are cosmopolitan species that are familiar from the temperate zone, particularly among the rotifers. *Keratella americana* and *Polyarthra vulgaris*, for example, are common in tropical lakes.

The complexity of zooplankton communities at tropical latitudes is probably no higher than at temperate latitudes. In a survey of temperate lakes, Pennak (1957) found that the limnetic zones of temperate lakes contain on a given day a mean of 2.7 copepod species 2.8 cladoceran species, and 5.5 rotifer species. Patalas (1975) obtained similar results in a survey of Ontario lakes, but also noted that very large lakes have significantly more species. Tropical lakes are very similar, both in total number of species and in distribution of species among the Copepoda, Cladocera, and

Rotifera (Lewis 1979, Arcifa 1984, Fernando 1980a,b; Figure 18). Inclusion of littoral plankton communities would double or triple the numbers of species for a given date, as would a determined search for rare species, but probably not differentially so for temperate and tropical lakes.

Tropical lakes are distinctive in the rarity of large zooplankton taxa (Fernando 1980a,b; Arcifa et al. 1992). *Daphnia*, which accounts for much of biomass of large zooplankton in temperate lakes, is seldom present in quantity in tropical lakes, and even the species that are present are of small body size (Fernando 1980a,b). Calanoids, which are often among the largest of zooplankton in temperate lakes, are absent or rare in many tropical lakes (Lewis 1979, Fernando 1980a,b). The representatives of Copepoda and Cladocera that do reach abundance in tropical lakes are small (typically <1 mm).

Reasons for differences in size structure of zooplankton communities across latitude are not yet known. Predation, which is an important influence on size structure among communities at any given latitude (Brooks 1968) appears not to explain the latitudinal trend (Fernando 1980a,b). Diversity among lakes (beta diversity) is probably lower in the tropics than at temperate latitudes (Fernando 1980a). Floodplain lakes, which are among the most abundant of tropical lakes, may have considerably higher species diversity than most other lakes (Twombly and Lewis 1987, Bozelli 1992).

Food chain efficiency and carnivory

Herbivory appears to be no more efficient in tropical plankton communities than it is in temperate ones, and may even be lower. For lowland tropical lakes there is yet no documentation of clearwater phases such as those that occur in many temperate lakes (Harris 1986). Clearwater phases indicate quantitative dominance of grazing over phytoplankton growth for at least short intervals, as one would expect in a system that shows efficient harvesting of primary production. More specific information is scarce. Because of the large amounts of data that are required to support any meaningful

insight into trophic dynamics at the herbivore level, only a few case histories present enough data to support generalizations. However, the information at hand suggests that both top-down and bottom-up controls are very important in the tropical setting (Lewis 1979, Saunders and Lewis 1988a). Herbivore populations are probably less variable in tropical lakes than in temperate ones, but they do show considerable temporal variation and in some instances may be as variable as those of temperate lakes (Saunders and Lewis 1988b).

The phantom midge, *Chaoborus*, is of exceptional importance in the tropics; suppression of herbivores by *Chaoborus* may be a major factor controlling herbivory in tropical lakes. Because of its growth over three orders of magnitude through four instars, *Chaoborus* takes essentially the entire spectrum of tropical zooplankton herbivores as its food (Lewis 1977, Hare and Carter 1987). *Chaoborus* abundance shows a strong connection with the physical and chemical characteristics of lakes. *Chaoborus* reaches only modest abundances when exposed throughout the water column to predation, but can be very abundant when an anoxic deepwater refuge is available. This phenomenon can be illustrated by studies of Lake Valencia, which show strong suppression of herbivores by *Chaoborus* predation (Figure 19; Saunders and Lewis 1988a). Suppression occurs primarily during the stratification season rather than the mixing season. During the stratification season, anoxia at the bottom of the water column provides *Chaoborus* with a refuge from fish predation, which in turn allows *Chaoborus* to become so abundant that it can suppress herbivore production. Because tropical lakes develop anoxia more quickly than temperate ones, they are more likely to provide a predation refuge over long periods of time for *Chaoborus*.

The potential effects of *Chaoborus* are two-fold: (1) *Chaoborus* in great abundance may suppress herbivory by holding herbivores at abundances that are too low to allow efficient harvesting of phytoplankton production, and (2) herbivore production consumed by *Chaoborus* must pass to fish in order to contribute to harvestable yield, and this involves an order of magnitude reduction by comparison with potential yield from a direct linkage between

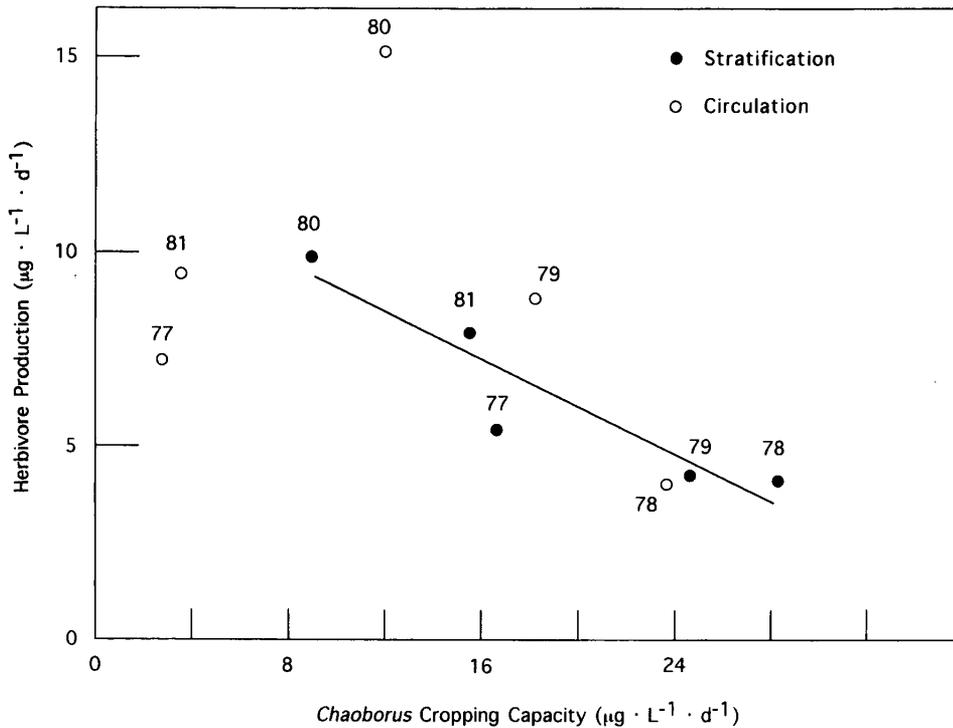


Fig. 19. Production of herbivorous zooplankton in relation to the cropping capacity of *Chaoborus* in Lake Valencia, Venezuela. The data are shown for 2 different seasons (mixing, when oxygen reaches the bottom; stratification, when the bottom is anoxic) in each of 5 years. Redrawn from Saunders and Lewis 1988a.

herbivores and fish. An interesting example of the latter point may be found in a comparison of lakes Tanganyika, Malawi, and Victoria. In Lake Tanganyika, *Chaoborus* is absent and planktivorous fish are present, and the fishery is more productive than in the other two lakes, where much production passes through *Chaoborus* before reaching fish (Hecky 1984).

Pelagic fishes can be important herbivore predators in the tropics, but the spotty distribution of truly pelagic fishes and the episodic nature of successful recruitment for many of these fishes (e.g., Unger and Lewis 1991) may reduce their overall effect on herbivores. Overall, tropical lakes are depauperate in efficient zooplanktivorous fishes (Fernando 1991a,b). Introduction of exotic zooplanktivores, and even of herbivorous fishes (cichlids) has for this reason proven to be effective in increasing yields in some cases (Fernando 1991a). A general relationship between commercial

fish yields and primary production has been shown for tropical lakes (Melack 1976), but yield may differ substantially from production (Downing et al. 1990), and this complicates latitudinal comparisons.

Bottom-up effects are easily overlooked because they are difficult to estimate. Only the studies of Lake Valencia are supported by sufficient data to allow quantitative segregation of top-down suppression of herbivory from growth suppression caused by nutritionally suboptimal food in an environment that is rich in total phytoplankton biomass. These studies showed that 51% of the deviation from maximum herbivore production could be explained by predation, 49% could be explained by suppression of individual growth rates, i.e., nutritional factors affecting herbivores (Saunders and Lewis 1988a,b). Evidence of suboptimal herbivore growth rates has also been shown by Schiemer and Duncan (1983) for Lake

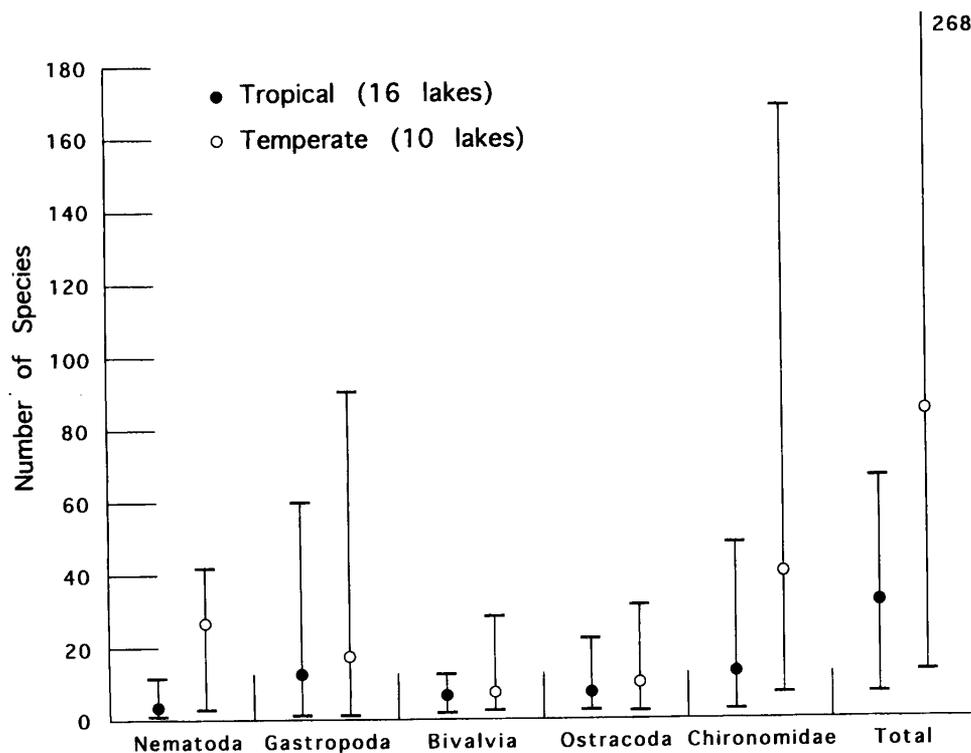


Fig. 20. Number of benthic species in 16 tropical lakes and 10 temperate lakes (data from Tudorancea et al. 1989).

Parakrama Samudra, and by Arcifa et al. (1992) for Lake Monte Alegre.

Benthos

Benthic communities show no sign of enrichment at tropical latitudes, and may even show suppressed diversity and abundance by comparison with temperate lakes (Tudorancea et al. 1989, Figure 20), although this has yet to be determined in a rigorous way. An interesting possibility is that the speed of oxygen depletion in tropical lakes has handicapped the radiation of lake benthos in tropics, and may also have suppressed the potential of benthos to support fish in tropical lakes.

Conclusion

Tropical lakes seemed almost a complete mystery as recently as 30 years ago. Present information begins to make a descriptive picture and to some extent even a mechanistic picture of tropical lakes. Similarities of lakes across latitude are surprisingly high in some respects, but differences also appear in unexpected places. Tropical lakes appear to be: (1) more efficient in producing phytoplankton biomass on a given nutrient base, (2) inclined to nitrogen rather than phosphorus limitation, (3) inefficient in passing primary production to the highest trophic levels, (4) generally similar to temperate lakes in phytoplankton and zooplankton composition, and (5) typified by strong nonseasonal variation superimposed in most cases on a seasonal cycle.

Comparisons of tropical and temperate lakes have a much potential to demonstrate the functions of lakes in general. In addition, study of tropical

lakes will be essential if tropical inland waters are to be protected and used in the wisest possible way.

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