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TROPICAL LIMNOLOGY

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INTRODUCTION

Limnology has been predominantly a science of high latitudes, despite an impressive high-water mark for tropical limnology set by Ruttner and Thienemann very early in the history of limnology (56). A large literature on tropical inland waters has now accumulated, but the thinking of limnologists and aquatic ecologists appears to have been little influenced by it. There may be little of basic interest in this literature. More likely, however, the information on tropical waters is so diffuse and fragmentary that it is difficult to use. Comprehensive or sustained studies have been few, and description rather than analysis has absorbed much of the energy of those who have worked in the tropics.

Tropical limnology would not be of extraordinary importance if tropical aquatic environments could be understood readily from the principles that apply to temperate systems. Some principles certainly do transfer across latitude very easily: The response of phytoplankton to light in a tropical lake is unlikely to differ in principle from the response of phytoplankton to light in a temperate lake. However, as recognized by Ruttner and Thienemann, trends across latitude in some of the most important variables that control the functioning of freshwater systems suggest that there must be many corresponding latitudinal trends of an ecological nature, some of which are difficult to foresee. Contrasts across latitude could thus be much more informative than continuous study in a restricted range of latitudes. For example, one might suppose (erroneously, as it turns out) that the comparative uniformity of air temperature and surface irradiance in tropical areas would create in tropical fresh waters a trend toward higher species diversity, as is the case for

forests. The possibility of dealing with questions of this scope suggests that the benefits of studying tropical fresh waters greatly exceed the mere geographic extension of limnology. This review is an attempt to identify the features of tropical freshwater systems that are likely to provide the most productive basis for comparison with waters of higher latitudes. The emphasis here is on lakes, although some principles will apply more broadly.

Only the most fundamental properties of tropical fresh waters can be dealt with here. Fundamental properties are defined here as those that would be affected if a waterbody could be moved experimentally through a latitudinal gradient free of regional and local variance. This restriction is artificial in that it fails to take into account features of tropical fresh waters that might be classified as historical or physiographic. For example, a characteristic lake of temperate latitudes, if selected on the basis of the numerical abundance, would be of glacial origin. In contrast, a characteristic lake of tropical latitudes, if chosen on a similar basis, would probably be a floodplain lake (46). Thus, some very significant latitudinal differences in the properties of fresh waters can be explained by factors other than those identified here as fundamental.

Some recent reviews cite much primary information on tropical fresh waters that cannot be specifically referenced here: Serruya & Pollinger (61), Beadle (4), and Welcomme (79, 80). In addition, Straskraba (68) gives an excellent overview of many principles underlying latitudinal trends in aquatic systems.

PRIMARY CAUSES

Fundamentally distinctive properties of tropical lakes must have their origin in one of three primary causes (shown in Figure 1). These have a limited number of important first-order effects, which are then propagated through more complex and numerous effects of higher order. An understanding of the primary causes and of the first-order effects is essential for the analysis of distinctive properties of tropical fresh waters.

Annual Solar Irradiance

Irradiance at the top of the atmosphere can be calculated from the solar constant ($1.95 \text{ cal cm}^{-2} \text{ min}^{-1}$; 47), the latitude, the day of the year, and the time of day (16). Instantaneous irradiances integrated over time in turn produce daily irradiances at the top of the atmosphere at any latitude. Tables of these values are given by List (41). Between the upper atmosphere and the surface of a waterbody, solar irradiance is reduced in relation to the optical air mass and to the attenuation coefficient, which is influenced by air itself and

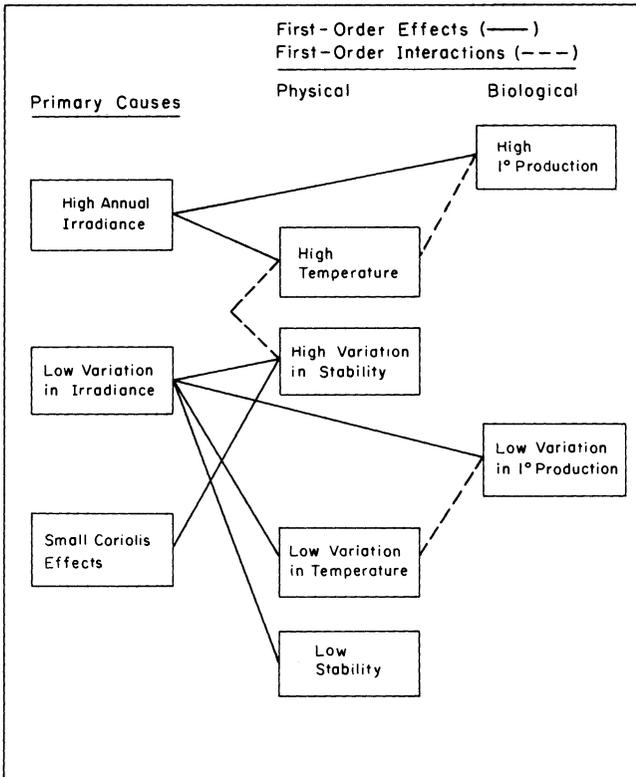


Figure 1 Diagram of the primary causes for latitudinal trends in freshwater aquatic systems and the associated first-order effects and first-order interactions.

by atmospheric moisture and particles. Although the optical air mass can be predicted from time of year, latitude, and elevation, the attenuation coefficient varies in a manner that is difficult to predict (16).

At the top of the earth's atmosphere, total annual irradiance is distributed around a maximum at 0° latitude, but the annual range of monthly irradiances is minimal at 3.4°N rather than 0° (51). Consequently, in analyzing or modelling seasonal phenomena in relation to latitude, particularly within the tropics, it may be useful to adjust the true latitude (ϕ) in relation to a "meteorological equator" at 3.4°N (40); adjusted latitude will be symbolized here as ϕ' . This meaning of "meteorological equator" differs from that of the same term when used in connection with the position of the equatorial trough, a zone of low pressure caused by convergence of tradewinds leading to formation of clouds with consequent release of latent heat (23).

Data on actual irradiances at the earth's surface have been compiled by Landsberg (27), whose map of global irradiance shows the largest amounts of annual irradiance near the margin of the tropics, rather than within the central tropics. Uneven distribution of moisture causes transmissivity of the atmosphere to be exceptionally high over subtropical land masses. Distribution of total irradiance is consequently counterintuitive in some ways. For example, a substantial portion of Amazonia receives less than $120 \text{ kcal cm}^{-2} \text{ yr}^{-1}$ ($1 \text{ kcal} = 2324 \text{ Joules}$) of total irradiance, whereas portions of the western United States, North Africa, the Middle East, and Australia beyond the tropics receive irradiance in excess of $200 \text{ kcal cm}^{-2} \text{ yr}^{-1}$. Thus, the irradiance in a portion of Amazonia is little different from the irradiance in southwestern Canada. Figure 2a shows, on the basis of the planimetry from Landsberg's maps, the observed distribution of irradiance on land masses in comparison with the distributions of irradiance outside the atmosphere and at the earth's surface, given the assumption of uniform attenuation coefficient (transmissivity = 0.8; 41).

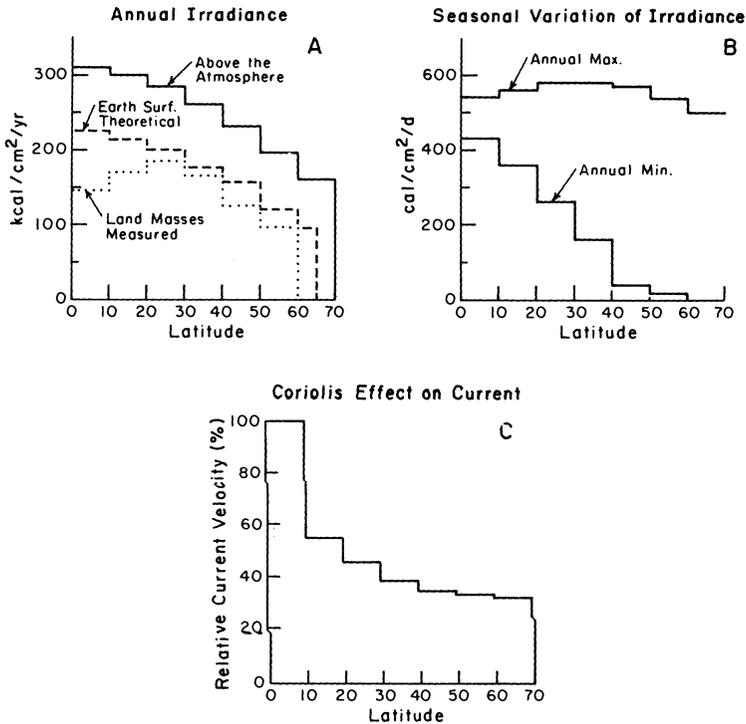


Figure 2 Trends in the primary causes of latitudinal variation.

Variation in Irradiance

At latitudes higher than 10°N or 5°S, daily irradiances, given a constant attenuation coefficient, would show a single peak near the time of the solstice. Between 10°N and 5°S, there would be one irradiance peak near the end of March and a second near the end of September. Because there are dual maxima over this range of latitudes, there are also dual minima. It is limnologically significant that these minima are not equal except at the meteorological equator; the lower of the two minima coincides with the hemispheric winter.

Very near the equator, the annual minimum daily irradiance for a constant attenuation coefficient would be approximately 85% of the annual maximum daily irradiance. The relationship of minimum to maximum at other latitudes is shown in Figure 2b for an atmospheric transmissivity of 0.7 (41) (this provides the best fit to the observed values for measured irradiance over land as shown by Figure 2a). As the figure shows, there is a substantial seasonal change in daily irradiance even within the tropics, especially above 10° lat. Outside the tropics, the seasonal amplitude of daily irradiances is even greater, but it is by no means negligible within the tropics.

Underlying the variations in daily irradiance through the year are variations in daylength. The annual range in daylength is less than 30 min at the equator, slightly over 1 hr at 10° lat, and slightly over 2 hr at 20° lat, (7). Variations in daylength may have some effects on aquatic ecosystems that are separable from the associated variations in daily total irradiance, but the main significance of changing daylength is changing total daily irradiance.

With a fixed attenuation coefficient, the annual maximum daily irradiance would increase steadily from the equator to 30°–40° lat, but the increase over this range would be less than 10% (Figure 2b). The range of minima across tropical latitudes is much more striking. The minimum daily irradiance at 30° lat is approximately 50% of the minimum at the equator (Figure 2b).

Coriolis Effects

Mass moving over the earth's surface experiences acceleration to the right of the direction of motion in the northern hemisphere and to the left of the direction of motion in the southern hemisphere. This acceleration, which is attributed as a matter of convenience to a force called the Coriolis force, is explained by change in the balance between centrifugal and gravitational forces as mass moves over the curved surface of the earth. The force is proportional not only to the speed of movement but also to $\sin \phi$, and it is therefore zero at the equator and maximum at the poles (76).

The Coriolis force affects water currents. In lakes, wind stress on the water surface is the predominant cause of water currents. The Coriolis force deflects currents created by wind stress and thus reduces the current velocity that can

be maintained by a given wind velocity, which in fact is inversely related to the square root of $\sin \phi$ (11, 48, 21).

In a waterbody that contains a vertical density gradient, such as a thermally layered lake, the depth to which mixing will be realized in response to wind is directly related to surface current velocity. For higher current velocities, greater depth of mixing will be achieved for a given density gradient. Because the Coriolis force influences the current velocity and varies with latitude, the depth of mixing in a layered waterbody that can be achieved by a given wind velocity varies inversely with latitude. For idealized systems, the effect of Coriolis force on mixing depth is quite important and can account for differences in mixing depth as much as two to threefold between low and high latitudes (48, 21).

Figure 2c shows the decline with latitude of current velocity in equilibrium with a given wind velocity for fixed conditions of water density and eddy viscosity. The notable features of Figure 2c include the large overall effect of the Coriolis force on current velocities over broad latitude ranges and the steep rate of increase in current velocities toward low latitudes. These trends carry through to hypothetical calculations of mixed layer thicknesses for given density gradients. However, calculation of the mixed layer thickness requires approximations of the vertical eddy diffusion coefficients, which are in turn dependent on the vertical distribution of densities in a lake. For reasons explained below, hypothetical calculations concerning the vertical distribution of heat as a function of latitude may be very misleading and thus may produce erroneous conclusions concerning the depth of mixing. For present purposes it is best to stop with the conclusion that winds of a given velocity working against a given density gradient will be less effective in mixing at high latitudes than at low latitudes as a result of the Coriolis force.

The potential importance of the latitudinal gradient in Coriolis force is in part influenced by lake size. In small basins, frictional forces associated with the contact between water and the boundaries of the basin are likely to be more important than the Coriolis force (64). Even so, empirical information suggests that latitudinal differences in the magnitude of the Coriolis force play a role in explaining some important differences in mixing between tropical lakes and lakes of higher latitude (29, 36).

FIRST-ORDER EFFECTS

The three primary causes of latitudinal contrasts are linked directly to six effects, designated here as first-order (Figure 1). Three important interactions between first-order effects are here designated as first-order interactions (Figure 1).

First-order effects and first-order interactions can be influenced by effects of higher order. For example, Figure 1 shows that high mean irradiance will result in high primary production at low latitudes if all other factors are equal. However, if for some reason effects of higher order caused nutrient availability to be consistently lower at low latitudes, then low nutrient availability would at least partially mask the first-order effect of irradiance on primary production.

The identification of first-order effects (as shown in Figure 1) serves two purposes: (a) it provides an initial basis for working hypotheses concerning major latitudinal trends, and (b) it allows calculation of the difference between observed latitudinal trends and those that would be expected from first-order effects; this difference is a measure of the importance of effects of higher order.

Temperature

The temperature of the upper mixed layer of a lake will vary as a function of latitude. Straskraba (68) has developed equations for the relationship between latitude and the maximum, minimum, and mean surface temperatures in IBP lakes (Figure 3a). Given the observed pattern of maximum daily irradiance between 0° and 40° lat, as shown in Figure 2b, however, the major decline in maximum water temperature with latitude below 40°, as shown in Figure 3a, seems suspect. Furthermore, the maximum surface temperature of a lake often reflects transient daytime heat accumulation and is therefore less useful than a subsurface maximum more typical of the mixed layer. For these reasons, the question of maximum temperatures for standing waters is approached here on another basis. Temperatures for running waters are subject to somewhat different constraints and are not dealt with here specifically; Ward (78) gives a good review.

Minimum water surface temperature, as determined by Straskraba (68), declines steeply with latitude; this would be expected from the decline in minimum daily irradiance with latitude (Figure 2b). Straskraba (68) used these minimum surface temperatures as an approximation of the bottom (hypolimnetic) temperatures of lakes sufficiently deep to stratify. Straskraba's equation for the relationship between latitude and bottom temperature (T_b) is $T_b = 28.1 - 0.6 \phi'$. According to this equation, bottom temperature will be close to 14°C at sea level near the margin of the tropics. This appears to be a substantial underestimate. Bottom temperatures in the range of 14°C at sea level coincide with higher latitudes, e.g. lakes of north-central Florida, $\phi' = 27^\circ$ (31); Lake Kinneret, $\phi' = 29^\circ$ (62). Near the margins of the tropics, after correction for elevation as described below, bottom temperatures are close to 19°C.

Elevation has a very strong influence on bottom temperatures in tropical

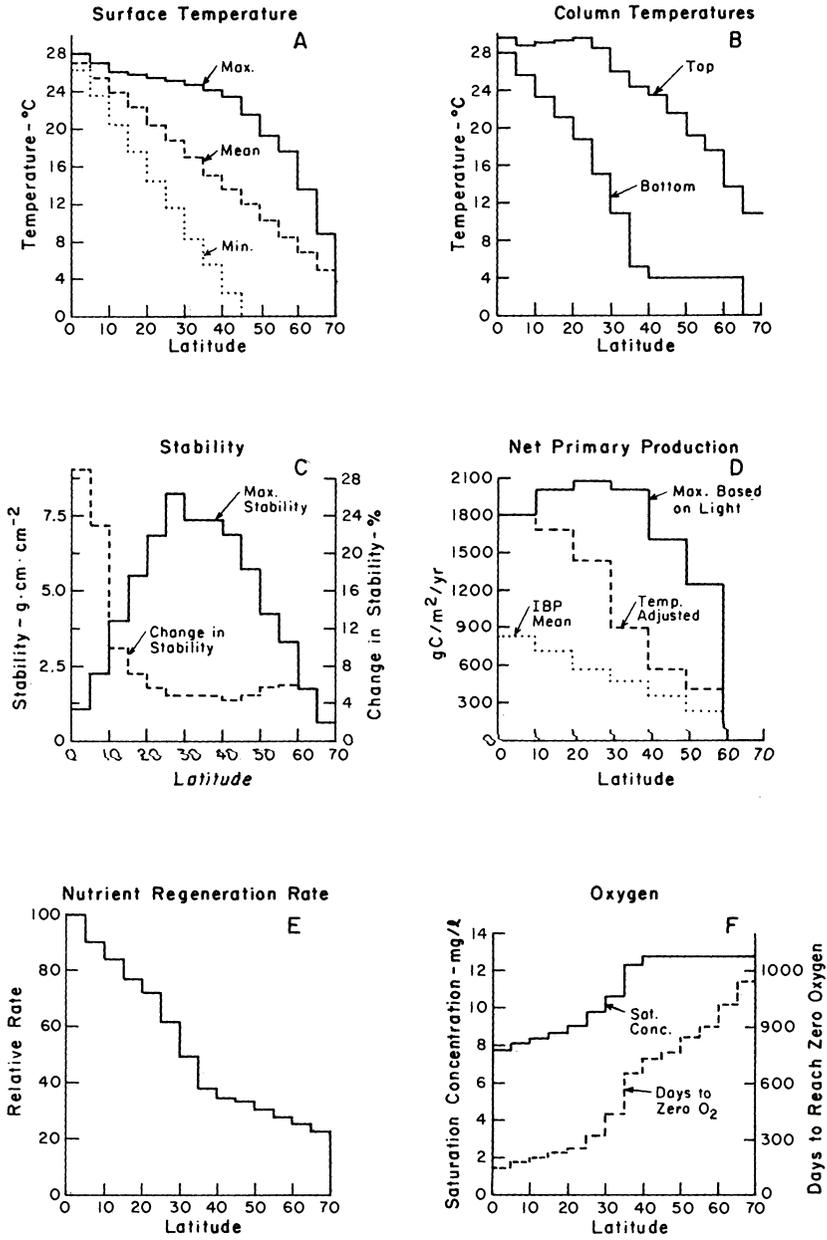


Figure 3 Trends across latitude in some important characteristics of freshwater systems.

lakes and must be considered jointly with latitude. Near the equator, bottom temperature is depressed by 4–5°C for each 1000 m of elevation (42, 43, 29, 26). Latitudinal and elevational effects have been expressed on a common basis by reference to the mean normal lapse rate, which varies from 5–10°C per 1000 m; an empirical average for a selection of tropical land-based weather stations is 6.7°C per 1000 m of elevation (29). An analysis based on this lapse rate for tropical lakes of broad altitude range and narrow latitude range produced a close relationship between bottom temperature and altitude corrected for latitude (29). For broader latitude ranges, the relationship is inaccurate and must be derived empirically rather than from the lapse rate.

The bottom temperatures, latitudes, and elevations of an earlier analysis (29) were supplemented with additional data for lakes of moderate to great depth at latitudes up to 30° (81, 1, 20, 31). The bottom temperatures were then fit by multiple regression to the two independent variables (latitude, elevation): $T_b = 28.9 - 0.43 \phi' - 0.0038 E$, where the standard errors of slopes are 0.06 for latitude (ϕ') and 0.0008 for elevation (E , meters). The equation explains 79% of variance in bottom temperatures.

The maximum range in temperature (T_r) between the bottom of a lake and the upper mixed layer, excluding temporary daily heat gain, was also analyzed empirically. Surface temperatures reported by Talling (70) for a broad latitudinal range of tropical African lakes were used as a basis for this analysis. Lake Chad was omitted because of its low mean depth. Because the surface temperatures typically overestimate the temperature of the mixed layer, the actual temperature of the mixed layer was obtained from original sources where possible or was estimated by an arbitrary correction of 1°C applied to surface temperatures in other cases. In addition, data from Lake Lanao and from Lake Valencia (29, 35, 38) were used. A plot of the maximum annual vertical temperature range (T_r) as a function of latitude indicated a strong upward trend in T_r above $\phi' = 5^\circ$, but no trend up to $\phi' = 5^\circ$. Consequently, a mean was taken of T_r between 0° and 5° lat; this mean was 1.6°C. Above $\phi' = 5^\circ$, the relationship between latitude and T_r was: $T_r = 0.50 \phi' - 0.80$. The relationship is highly significant and explains 92% of the variance in T_r .

Maximum temperatures for the mixed layer (T_m) as a function of latitude are shown in Figure 3b by addition of predicted T_r to predicted T_b at sea level between 0° and 25° latitude. There is no decrease of T_m within the tropics. In this sense the predictions are consistent with the observed solar irradiance within the tropics (Figures 2a, 2b). Above 35° lat, Straskraba's equations were used for T_m and T_b ; the average of the two relationships was used in the range 25–35° C. There is a steep decline in T_m between 30° and 40° lat. This corresponds to a steep decline in observed solar irradiance over the same range of latitudes (Figure 2a).

Stability

Stability is a measure of the amount of work required to render the water column of a lake thermally uniform (21, 22). For a lake of given shape and dimensions, stability is determined entirely by the distribution of water densities, which are related in turn to temperature.

The temperature difference between the top and bottom of a lake deep enough to stratify is lowest near the equator, reaches a peak in the vicinity of 35°–50° lat, and then declines. If the change in density were uniform across temperature, this latitudinal trend in the range of water column temperatures would be reflected in a parallel trend of water column stabilities. However, the rate of change in density with temperature increases substantially above 4°C. As recognized by the first limnologists to study tropical lakes (24, 57, 59), the uneven change in density with temperature causes the stability associated with any given temperature range to be highest at high temperatures. Consequently, latitudinal trends in stability are simultaneously influenced by the range of temperature and the mean temperature.

Latitudinal trends in stability are most easily illustrated by reference to a model lake, assumed to have a mixed-layer thickness of 5 m. This corresponds, as judged from empirical equations relating fetch to mixing depth (52, 68), to a circular lake with an area of approximately 190 ha. For purposes of calculating maximum stability, the mixed layer was assumed to have a temperature equal to the maximum shown in Figure 3b, and the rest of the lake was assumed to have a uniform temperature as indicated for lake bottoms in Figure 3b. The maximum lake depth was assumed to be 25 m, and the lake area at the bottom was assumed to be 10% of its area at the top. The lake was assumed to have the shape of a cone frustum.

Figure 3c shows the outcome of the calculation of maximum stability for the model lake; deeper lakes would show higher stability and shallower lakes would show lower stability at any given latitude. The stability first rises with latitude and then falls, in a manner that is somewhat similar to the rise and fall of temperature ranges, except that the peak for stability coincides with a lower latitude than the peak for vertical temperature range. A similar result, but with peak stability at higher latitude, was obtained by Straskraba (68) from a different set of temperatures.

Limnologists have relied almost exclusively on the annual maximum stability of a lake as an indicator of resistance to wind mixing. Little attention has been given to seasonal changes in stability. In a comparison of temperate and tropical lakes, it is essential to consider not only the annual maximum stability but also changes in stability that are likely to occur during the stratification season.

One of the most important physical contrasts between temperate and tropical lakes is their differing susceptibility to changes in stability associated with

a given gain or loss of heat. The high minimum temperatures and the small range of temperatures characteristic of tropical lakes cause any change in stability to be much greater than it is for lakes at higher latitude. For example, the model lake in figure 3c shows relative change in stability after a heat loss of 250 cal cm^{-2} , which lowers the temperature of the mixed layer by 0.5°C . A heat loss of this magnitude could easily result from a single storm or could develop gradually over two or three cloudy days (29, 37, 38). As shown by Figure 3c, the relative change in stability for tropical lakes is far higher than in temperate lakes.

Following any reduction in stability resulting from heat loss, the mixed layer of a lake tends to become thicker as the prevailing winds establish a new equilibrium between the density gradient below the mixed layer and the thickness of the mixed layer. This redistribution of heat lowers stability which is a direct function of the unevenness of heat distribution within the lake. Consequently, if winds are sufficiently strong to move the upper water column vigorously, the percent change in stability resulting from a fixed heat loss in the model lake would be even greater than that indicated in Figure 3c, especially at low latitudes.

The significance of fixed heat loss varies according to the size of a lake. A fixed heat loss is least significant in large, deep lakes because they have the highest heat budgets (18). However, for a lake of any given size, the stability will be much more variable over the short term in tropical than in temperate lakes. This variation of stability is reciprocal, i.e. a period of sunny weather causing a net heat gain of given magnitude results in a greater relative increase in stability in a tropical than in a temperate lake. A latitudinal contrast in stability is also likely in lakes that do not stratify seasonally, although it may not be so profound as the one that applies to lakes of moderate to great depth. Because of the high mean temperature of the water column, shallow tropical lakes will have an especially strong tendency to develop diurnal stratification resulting from daytime heat uptake. The resulting alternation of daytime stability with nighttime mixing is extremely important to the metabolism of many shallow lakes and may be especially important at low latitudes (3, 77, 15, 72, 73).

Annual Primary Production

Figure 1 shows a first-order effect of annual irradiance on annual primary production and a first-order interaction between temperature and annual primary production. These are best explored by means of calculations involving the model lake used in the calculation of stabilities in relation to latitude. As before, the thickness of the mixed layer is assumed to be 5 m. Estimates are based on net rather than gross phytoplankton production; some of the same principles would apply to rooted aquatic plants.

The size of the first-order effect of annual surface irradiance on primary production is calculated for the model lake at different latitudes under conditions of nutrient sufficiency for the primary producers. Deferring a consideration of the importance of water temperature, we assume that photosynthesis will occur at rates corresponding to the highest water temperatures (0–5° lat, Figure 3b). Under the most favorable conditions of nutrients and light, natural phytoplankton populations can be expected to have an efficiency close to 0.06 moles of CO₂ per Einstein of photosynthetically active radiation (PAR) absorbed by the cells (50, 2).

The amount of light intercepted by phytoplankton cells in the model lake can be approximated from the amount of PAR entering the water column, the extinction of light by phytoplankton in the water column, and the extinction of light by other means in the water column. PAR entering the water column is estimated as total irradiance \times 0.46 after correction for a 10% surface loss (71). For maximum production, the amount of chlorophyll in the mixed layer should be sufficient, when combined with other factors causing light absorption in the water column, to result in the absorption of approximately 99% of the PAR between the top and the bottom of the mixed layer. Higher stocks of algae will result in higher production near the surface, but this is offset by respiratory losses in the darker part of the mixed layer. Lower stocks of algae will have lower production because of the absorption of a higher proportion of irradiance by factors other than algae.

The extinction coefficient (disregarding spectral changes) that corresponds to removal of 99% of PAR within the top 5 meters is 0.92. Over the 5-m thickness of the mixed layer, pure water would account for a mean extinction coefficient for PAR of approximately 0.1 (65). Extinction by other substances varies widely with no evident relationship to latitude; a value in the midrange for productive fresh waters that can be used for present purposes would be 0.5. Consequently, the extinction accounted for by algae in the model lake should be $0.92 - 0.5 - 0.1$, or 0.32. Chlorophyll corresponding to this amount of extinction depends upon the value of n : $n = k_c/c$, where c is chlorophyll concentration (mg m^{-3}), k_c is the extinction coefficient for chlorophyll, and n has units $\text{m}^2 \text{mg}^{-1}$. As shown by Kirk (25), n varies with a number of factors, including size and morphology of phytoplankton cells or colonies. However, since there is no reason to expect a latitudinal trend in n , it is again reasonable to work with a midrange value. Surveys of laboratory and field data for n (71, 25, 10) show that such a value is $0.015 \text{ m}^2 \text{mg}^{-1}$. With this value of n , the chlorophyll required to cause 99% extinction of PAR in the water column of the model lake is $21 \mu\text{g l}^{-1}$.

Although the thickness of the mixed layer is held constant for purposes of the calculation, maximum possible production does vary with the thickness of the mixed layer. In general, under nutrient-sufficient conditions, lakes with

thinner mixed layers (e.g. small lakes or very shallow lakes) can have a higher net production because biomass is more concentrated, which allows higher proportional absorption of PAR by the phytoplankton. The relationship between thickness of the mixed layer and maximum production has been explored by Uhlmann (75). According to Uhlmann's calculation of the empirical relationship, maximum potential production would be, if other factors were equal, 25% less for a lake with mixed layer thickness of 10 m and 40% greater for a mixed layer thickness of 2.5 m than in a lake with a mixed layer thickness of 5 m. For the model lake with a mixed layer thickness of 5 m and a chlorophyll concentration of $21 \mu\text{g l}^{-1}$, approximately 35% of the irradiance within the mixed layer is absorbed by algae, and 65% is absorbed by other means.

One additional important consideration is the light saturation of photosynthesis, which occurs at relatively low light intensities for phytoplankton. Saturating intensities vary according to a large number of factors, but a median value would be in the vicinity of $120 \mu\text{Einst m}^{-2} \text{sec}^{-1}$ PAR (19). Except in the winter at high latitudes, surface PAR irradiances can be expected to average as much as $1500 \mu\text{Einst m}^{-2} \text{sec}^{-1}$ over approximately two thirds of the day ($1 \text{ cal cm}^{-2} \text{min}^{-1} \text{PAR} = 3170 \mu\text{Einst m}^{-2} \text{sec}^{-1} \text{PAR}$: 67). For this reason, light in the uppermost portion of the mixed layer will typically exceed the saturating irradiances. To avoid complications that arise from curvature of the photosynthesis-irradiance response curve in the vicinity of the saturating irradiance, the photosynthesis response is assumed to flatten exactly at I_k ; this leads to an underestimate of photosynthesis just above I_k , but also to a compensating overestimate just below I_k .

To discount the absorption of light by phytoplankton in excess of the saturating irradiance, it is convenient to define an effective absorption efficiency (not to be confused with the many other efficiencies used in modelling photosynthesis, as described by Parsons et al—50). This efficiency is the proportion of PAR at any depth absorbed by phytoplankton up to the threshold of the saturating irradiance. For the model lake, this efficiency reaches a maximum of 35% below the depth corresponding to the saturating irradiance and a minimum of approximately 7.5% just at the water surface over the middle portion of the day. Inhibition at high irradiances, which would further reduce this efficiency near the water surface, is ignored because it probably does not play a large role in natural populations (19). *Integration of the efficiencies* across depth and time at latitudes that combine minimum cloud cover and low variation in daylength (20° – 30° lat) indicates a composite annual efficiency close to 20% for the model lake. The efficiency is higher at other latitudes, where surface irradiance is suppressed by cloudiness or by longer intervals of low irradiance at certain times of the year. Examples from various latitudes indicate a 0.4% increase in annual average efficiency for

each $10 \text{ kcal cm}^{-2} \text{ yr}^{-1}$ decrease in total annual irradiance over the range of annual irradiances shown in Figure 2a; this relationship is used in the calculation of production in relation to latitude.

Figure 3d shows the hypothetical maximum production based on nutrient-sufficient conditions and optimal temperature in the model lake. The hypothetical maximum production does not begin to decline significantly until latitudes exceed 40° .

In accounting for the effect of temperature on primary production under nutrient-sufficient conditions, it is necessary to set a temperature for the mixed layer at each latitude (a monthly schedule of temperatures would be more realistic but is unnecessarily complex for present purposes) and to specify a relationship between maximum growth rate and temperature. The temperature of the mixed layer is set midway between the annual maximum temperature of the mixed layer and the temperature of the lake bottom during stratification, as shown in Figure 3b. Some data for specific lakes show that this provides a reasonably close but slightly low estimate of mean annual temperature in the mixed layer. The temperature effect on production can be calculated from the mean temperature and a Q_{10} for phytoplankton growth. Work by Eppley (12) and Goldman & Carpenter (17) shows that the Q_{10} for growth rate of phytoplankton under nutrient-sufficient conditions at optimal irradiance is close to 2.0.

Figure 3d shows the result of calculations that correct primary production for temperature. The correction results in a steep decrease of maximum production with latitude. Figure 3d also shows the mean net annual primary production as a function of latitude for IBP lakes (6). The deviation between the temperature-adjusted maximum primary production and the IBP mean represents the average influence of effects of higher order on primary production. The scatter around the IBP mean extends above the mean by a factor of approximately 2, which corresponds very closely to the calculated temperature-adjusted maximum annual production in nutrient-sufficient populations, as would be expected if the calculations are reasonable.

The possible major causes for deviation between the IBP mean production and the temperature-adjusted maximum are two: (a) nutrient supply, and (b) factors that remove biomass (sedimentation, grazing, dilution). It would be difficult to make a case, for lakes of any latitude, that the removal of biomass has dominant effects on the mean abundance of phytoplankton. However, grazers can suppress biomass if nutrients are already limiting or can affect the species composition of phytoplankton by selective feeding (54). In contrast, much direct and indirect evidence suggests that nutrients have a dominant influence on the mean abundance of phytoplankton at any given latitude (60, 49). Consequently, we attribute to nutrients most of the deviation in Figure 3d

between the mean and the temperature-adjusted maximum primary production, although biomass removal must also contribute something to this deviation.

Table 1 summarizes the latitudinal variation in magnitude of controls on primary production, including the effect of nutrients, which is deduced by subtraction of the first-order effects from the observed trends in primary production with latitude. For purposes of broad comparison, lakes of latitude 0–20° are compared with lakes of latitude 30–60°. The first set of comparisons lists the causes of deviation from the global maximum primary production, which is taken to be the production under nutrient-sufficient conditions at maximum temperature for maximum incident irradiance, which occurs at 20°–30° lat (Figure 3d). In tropical lakes, cloudiness accounts for a slight suppression from the theoretical maximum. At temperate latitudes a combination of cloudiness and changes in daylength suppresses production from the theoretical maximum by as much as 20%. The temperature effect is quite small in tropical lakes and very large in temperate lakes, where it even exceeds the irradiance effect. The proportion of total suppression accounted for by nutrients is 5 times as high at low latitudes as at high latitudes, but the total suppression from the theoretical maximum is still significantly greater at high latitudes, primarily because of the temperature effect.

The second set of comparisons shows the deviation from the latitudinal maximum (taking temperature and observed surface irradiance into account) caused by nutrients. The effect of nutrients viewed from this perspective is still half again as strong in tropical lakes as in temperate lakes. The table also shows the nutrient renewal rate of phytoplankton biomass in the model lake, defined as the number of times the average nutrient inventory in biomass is replaced in the course of a year in order to sustain the observed mean

Table 1 Control of primary production in tropical (0–20° latitude) and temperate (30–60° lat) lakes. See text for details.

	Tropical lakes (0–20°)	Temperate lakes (30–60°)
Causes of deviation from global maximum		
Incident irradiance (%)	6	20
Temperature (%)	7	49
Nutrients (%)	48	10
Total (%)	61	79
Trends in nutrient effects		
As a cause of deviation from latitudinal production maximum (%)	55	35
Biomass nutrient renewal, yr ⁻¹	147	74

production for the IBP lake series. If the mixed-layer inventory of the critical nutrient (typically phosphorus or nitrogen) is tied up mostly in the form of biomass, which is the case in many lakes, the nutrient renewal rate in biomass will approach the nutrient turnover rate for the mixed layer. If the nutrient pool is not mostly tied up in biomass, the nutrient turnover rate of the mixed layer will be lower than the nutrient renewal rate for biomass. The table indicates that nutrient renewal rates for biomass will be approximately twice as high in tropical as in temperate lakes. Because most phytoplankton communities are nutrient-limited over a significant portion of the year at any latitude, the implication of the table is that tropical lakes must have more efficient nutrient recycling systems in order to sustain their observed production. The explanation for these more efficient recycling systems should be sought in effects of higher order that provide nutrient feedback to primary production.

Variation in Primary Production

Lakes that are deep enough to stratify show a pervasive tendency to mix deeply once per year (or twice per year for lakes that develop ice cover) on a predictable seasonal basis. This principle applies to lakes of low latitude, except possibly for small lakes within a very few degrees of the meteorological equator (37). Within the tropics, the mixing season typically coincides with the hemispheric winter (70) and is mainly caused by loss of stability resulting from cooling of the upper water column. The duration of the mixing season has not been well studied in relation to latitude, but it appears to last between one and three months in the tropics.

At any latitude, the occurrence of deep mixing or complete mixing in a lake of moderate to great depth is likely to reduce net primary production to negligible levels by reducing the light that can be absorbed by the average phytoplankton cell to such an extent that maintenance costs approach or exceed the rate of photosynthesis. Consequently, the most probable annual minimum net production for such lakes at any latitude is effectively zero. The annual amplitude of variation in net production is thus determined exclusively by the maximum production, which is related to latitude by mechanisms similar to those already explained for mean annual production. Because the maximum daily irradiance does not change greatly between 0° and 60° lat (Figure 2b), the maximum potential daily production for nutrient-sufficient populations is mainly controlled by the temperature of the mixed layer. In practice, however, the modifying effect of nutrient availability during the season of maximum production, when temperatures differ least across latitude, is so great that the temperature effect may be of secondary importance to the effects of higher order that regulate nutrient supply within the mixed layer.

EFFECTS OF HIGHER ORDER

The first-order effects (Figure 1) are connected to many effects of higher order. Some of these have been explored empirically, others are merely suspected, and still others may yet be unknown. Although a complete discussion is not possible here, the importance and nature of some of these higher order effects can be illustrated by use of existing information on four lake properties: (a) thickness of the mixed layer, (b) nutrient regeneration efficiency, (c) oxygen depletion in deep water, and (d) species diversity.

Thickness of the Mixed Layer

Oceanographers think of the upper water column as a mixed layer, whereas limnologists think of it as an epilimnion. The oceanographic concept is less confusing and easier to apply, especially in the analysis of tropical lakes. The epilimnion has been defined in various ways (21), some of which would lead to an overestimate of the amount of water that is mixing actively under the influence of the wind on a daily basis. Identification of the epilimnion from a vertical temperature profile is extremely difficult in relation to tropical lakes, in which the vertical temperature gradient is typically small. On the other hand, the mixed layer can be defined very simply as the portion of the water column that is of uniform temperature near sunrise, before the daytime uptake of heat (29, 36). The thickness of the mixed layer can also be estimated from thermal profiles taken after daytime heat accumulation has begun, but this is difficult at low latitudes where the daytime warming can account for a significant portion of the total vertical temperature range. Unfortunately, interpretation of layering and mixing in tropical lakes has often been confused by this difficulty.

It is tempting to predict the thickness of the mixed layer as a function of latitude for a model lake on the basis of a simple mixing model incorporating the wind velocity, the Coriolis force, and the density profile (68). Such a prediction would show that the thickness of the mixed layer increases toward low latitude as the Coriolis force and the maximum stability of layering decrease. However, empirical information on tropical lakes suggests that this approach is too simple.

For temperate lakes, the traditional concept has been that the mixed layer is of nearly constant thickness until a gradual but steady thickening occurs as a result of the erosion of the thermocline during the cooling season. Thermal data for temperate lakes show that this concept is basically accurate, although it may gloss over some functionally important temporary changes in the mixed layer associated with irregular variations in wind strength. However, such a concept is highly inaccurate for tropical lakes. Tropical lakes are far

more sensitive than temperate lakes to changes in wind stress and changes in heat content. The reasons for this include the minimal Coriolis effect, the low maximum stability, and the high response of stability to changes in heat content in tropical lakes. In understanding how these factors influence the thickness of the mixed layer in tropical lakes, it is important to think of the range, rather than the average, for wind velocity and net heat gain or loss.

During especially windy weather, thickening of the mixed layer in tropical lakes can occur to an extent that would be improbable or impossible during even the most severe storms over temperate lakes. Because of the sensitivity of the stability of tropical lakes to heat loss, thickening of the mixed layer by wind can be especially pronounced if strong winds are accompanied by cloudy weather, as is often the case. During calm and sunny weather, and particularly following an episode of cooling that results in thickening of the mixed layer, heat may be taken up without being efficiently distributed. Inefficient heat distribution is promoted by the thickness of the mixed layer and the high stability that can be induced in the upper part of the water column by a relatively small heat gain. The result is likely to be a new and thinner mixed layer superimposed on the old mixed layer (29, 36, 55).

Convection caused by nocturnal heat loss may be greatest at low latitudes because higher density changes accompany a given heat loss when water temperature is high. However, both theoretical considerations (13) and data from tropical lakes (36, 45) show that mixing caused by convection alone is likely to be superficial; mixed layers of no more than a few meters can be retained in large tropical lakes for extended intervals during calm weather.

The thickness of the mixed layer in tropical lakes is likely to be much more variable than that in temperate lakes. Even so, it is not obvious whether the average thickness of the mixed layer changes with latitude. After observing extreme variations in the thickness of the mixed layer in Lake Lanao, Lewis (29) concluded that mixed layers in tropical lakes must be consistently thicker on the average than those in temperate lakes of similar size and exposure. However, subsequent studies of Lake Valencia (45) showed that the mean thickness of the mixed layer did not deviate significantly from that predicted for a comparable temperate lake, even though the range of thicknesses was far greater than would have been expected for a temperate lake. The issue of mean thickness should be considered unresolved until careful year-round measurements have been made of mixed layer thicknesses in more tropical lakes, including particularly smaller lakes, so that statistically valid comparisons can be made of lakes at different latitudes. In any event, latitudinal trends in mean thickness of the mixed layer are surely secondary in importance to the great latitudinal contrasts in irregular variation of mixed layer thicknesses.

Higher variability in the thickness of the mixed layer at low latitudes has numerous important implications for latitudinal trends in physical, chemical, and biological characteristics of lakes. For example, a major increase in the thickness of the mixed layer in a tropical lake will be accompanied by (a) a change in light availability associated with dilution of biomass and movement of plankton to greater mean depths, and (b) a change in nutrient availability caused by entrainment of nutrients into the mixed layer from deep water. These changes will be reflected in the species composition and productivity of primary producers, which may in turn affect higher trophic levels (39, 30, 32, 33, 35, 69, 74). Because of large, unpredictable, and biotically potent changes in the mixed layer, tropical lakes should be viewed as less stable in some respects than temperate lakes, and especially so in relation to plankton. This is contrary to what one might suppose from the apparent uniformity of surface irradiance and water temperature at low latitudes.

Nutrient Cycling Efficiencies

Trends in primary production with latitude, when analyzed together with trends in other factors that vary with latitude, indicate more efficient recycling of nutrients at lower latitudes (Table 1). Two of the most important factors influencing recycling efficiency in lakes are: (a) the speed with which a limiting nutrient is released from nonliving organic matter in a form that can be reabsorbed by primary producers, and (b) the rate at which nutrients are resupplied to the growth zone from deeper water or sediments to offset sedimentation losses. Both factors contribute to an explanation of higher nutrient cycling efficiency in tropical lakes.

The regeneration of nutrients in usable form in the mixed layer through decomposition is largely a function of metabolic rates of decomposer organisms. From the mean temperature of the mixed layer in relation to latitude, as developed in connection with the analysis of production, it is possible to estimate the latitudinal trend in nutrient regeneration rates on the assumption that the Q_{10} for decomposition is near 2.0. The estimated rate (Figure 3e) varies almost fivefold with latitude.

A stratified lake experiences loss of nutrient inventory in the mixed layer during the growing season as a result of sedimentation of nutrients to deeper water. The speed with which this influences primary production is highly variable according to the physical properties of the lake, the size of the initial nutrient inventory, and nutrient demand. However, if all other factors are equal, the potential production during the growing season for a lake that experiences nutrient limitation will be directly related to the rate of return of nutrients from deep water. In temperate lakes, the return of nutrients from deep water is small because the upper mixed layer does not usually mix with

deeper water until seasonal thickening of the mixed layer occurs. There is a small amount of transfer by turbulence at the boundary between layers, and the upwelling of seiches, although unusual, may also enrich the epilimnion. In general, however, nutrient depletion commonly proceeds steadily without return of major amounts of nutrients from deeper water. In tropical lakes, the situation can be very different because of large changes in the thickness of the mixed layer. A period of growth in a relatively shallow mixed layer may lead to severe nutrient depletion. However, subsequent thickening of the mixed layer coincident with cool, windy weather returns nutrients from deep water to the mixed layer, thus allowing higher rates of production to be reestablished near the surface. It is not yet possible to estimate the size of this effect. However, case studies (69, 30, 39) show that variations in the thickness of the mixed layer could easily magnify the primary production of tropical lakes by a factor of two or more in comparison to the productivity of physically similar lakes at higher latitudes.

Bottom Oxygen Depletion

Because of biochemical oxygen demand, the deep waters of lakes experience oxygen depletion during the season of stratification, when oxygen cannot be renewed either by photosynthesis or by mixing. For temperate lakes, the bottom oxygen at the end of the stratification season is related to oxygen concentration at the time of stratification, lake productivity, and lake depth (21). These factors will also influence oxygen concentrations in the deep water of tropical lakes. In addition, however, two factors will be responsible for latitudinal trends in the occurrence of oxygen depletion in deep water: (a) the effect of temperature on the saturation concentration of oxygen in water, and (b) the sensitivity of biochemical oxygen demand to temperature. It is possible to estimate latitudinal trends in oxygen depletion resulting from the combined action of these two factors.

As an index of oxygen depletion, the areal hypolimnetic oxygen deficit is most convenient (AHOD: 28). The AHOD is named in a misleading way because it is really a measure of the rate of oxygen depletion per unit area of hypolimnion, rather than a measure of the actual deficit at a point in time. Although the AHOD varies widely, the data of Cornett & Rigler (9) indicate that the model lake, if located at high latitude and if producing at average rates, would have an AHOD at or above $500 \text{ mg O}_2 \text{ m}^{-2} \text{ d}^{-1}$. To calculate latitudinal effects, we use this number. The AHOD can then be adjusted to the higher bottom temperatures at low latitudes according to the pattern shown in Figure 3b. This adjustment is made with the assumption that the Q_{10} is 2.0 for decomposers, and it also assumes that decomposers do not exhaust the organic matter that is the basis of their oxygen consumption. Because of the lower concentrations of oxygen held by water at high temperatures, the initial

oxygen concentration in deep water at the beginning of stratification will be consistently lower at low than at high latitudes for lakes that achieve full oxygen saturation at the time of mixing (Figure 3f). The lower initial oxygen content will reinforce the effect of higher AHOD in leading to more rapid exhaustion of oxygen in deep water. The combined effects are illustrated for the model lake in Figure 3f.

The trend toward lower oxygen concentrations in deep water at lower latitudes, as shown in Figure 3f for the model lake, is magnified by three other factors that are not reflected in the figure and that have yet been scarcely explored. First, the duration of the stratification season in tropical lakes may be longer than in temperate lakes of similar size and shape. This would lead to a longer interval of oxygen depletion and result in more extreme seasonal oxygen depletion in deep water. Second, the productivity of tropical lakes for a given amount of nutrient is almost certainly greater than that of temperate lakes. This could magnify the amount of oxygen demand in deep water for tropical lakes generally, although the effect is offset to an unknown degree by the greater tendency in warmer lakes for organic matter to decompose before reaching deep water (58). Third, tropical lakes may less readily achieve oxygen saturation during the mixing season than temperate lakes. For a given oxygen concentration at the start of mixing, tropical lakes will deviate less from the saturating concentration and thus will take up oxygen less rapidly. Even more importantly, the oxygen demand in the water of a tropical lake continues at very high levels during seasonal mixing because of the high temperatures during mixing, and this may partially offset oxygen uptake at the surface.

As foreseen by Ruttner (57), oxygen depletion will be much more likely in tropical than in temperate lakes. This trend may have profoundly affected the exploitation of deep water by benthos and fishes and may even have influenced the evolution and diversification of these groups in tropical waters. Furthermore, because low oxygen concentrations are accompanied by large changes in the chemistry of natural waters, especially near the sediment-water interface, latitudinal trends in the chemistry of hypolimnetic waters can also be expected.

Species Diversity

In moist terrestrial environments, there is a striking and much discussed increase of species diversity at low latitudes (8, 20). This trend culminates in the remarkably high species diversity of tropical moist forests. There is no corresponding trend in the species diversity of freshwater plankton communities. Phytoplankton communities show no marked latitudinal trends in species diversity (34); there may even be a minor trend toward lower diversity at low latitudes, although this remains to be confirmed from a larger data base.

Zooplankton communities also seem to be of similar complexity across latitude (14, 35, 61).

The tropical terrestrial communities that are so extraordinarily diverse are marked by great abiotic stability and probably also by continuous minor disturbance sufficient to maintain habitat diversity (8, 66). The open waters of lakes at any latitude are much less likely than are forests to offer a spatial mosaic of abiotic conditions sufficiently persistent through time to support exceptional diversity. Diversity in plankton communities is probably maintained by continual temporal change rather than physical heterogeneity. Whereas tropical forest communities appear to approach equilibrium in community composition, plankton communities of lakes appear to be almost continually in succession. Succession is probably the main mechanism by which diversity is maintained in plankton communities.

Thickening of the mixed layer can be viewed as a disturbance that resets the successional clock in plankton communities (33, 53, 54, 63). Some empirical evidence indicates that the plankton communities of tropical lakes experience more frequent disturbances, and consequently more numerous discrete successional episodes, than do the plankton communities of temperate lakes (32, 39). Sequences of taxa in tropical lakes can even be predicted in some cases a priori from the abiotic changes accompanying succession; these sequences are surprisingly similar in temperate and tropical lakes (39). More numerous successional episodes will produce greater irregularity in the abundance of individual taxa but will not necessarily broaden the range of taxa because there is a strong element of repetition in separate successional episodes. In fact, frequent truncation of succession by initiation of new episodes may reduce diversity somewhat because it prevents the occurrence of taxa that are specialized for late stages of succession. Consequently, it seems quite reasonable, in view of latitudinal trends in abiotic factors and the diversity regulation mechanisms for plankton, that there should be no major trends in diversity with latitude for plankton.

A study of latitudinal trends in the diversity of higher organisms, such as benthos and fish, might be especially informative given the absence of trends in freshwater plankton communities. Unfortunately, there is at present no good basis for these latitudinal comparisons. Apparently, no careful study has ever been done of latitudinal trends in the diversity of benthic communities in freshwaters. Had a striking trend existed, it would almost certainly have been subjected to analysis; the literature on specific lakes suggests that there is no increase in the diversity of lacustrine benthos toward lower latitudes. An interesting possibility is that benthic communities in the tropics have been handicapped by pervasive anoxia in benthic environments at low latitudes, and this has suppressed the diversification of benthic faunas, especially in deep water.

For fish communities, the latitudinal trends are also unclear, although the raw information is available to support comparisons. Lowe-McConnell (44) concluded from an extensive survey of tropical fish communities that there is a trend toward higher diversity at lower latitudes. However, this idea has not been put to any kind of statistical test, and that may be essential for satisfactory proof because of the complicating effects of drainage basin size on species richness of fish faunas. Welcomme (80) shows a clear relationship between basin size and diversity across all latitudes. It is interesting that at any given basin size, Welcomme's plot of individual drainage basins shows no indication of an assortment of basins by latitude. Also, the exceptionally diverse endemic faunas of ancient lakes (5) must be discounted as a complicating factor in broad latitudinal comparisons. Thus any quantitative trend in species diversity of fish communities with latitude remains to be explored.

CONCLUSIONS

A sound basis already exists for understanding the primary causes, the first-order effects, and the first-order interactions of factors controlling latitudinal trends in aquatic ecosystems. This foundation supports a number of general conclusions about latitudinal trends. The supply of energy and nutrients to autotrophs as well as some important physical and chemical regulatory mechanisms varies with latitude. These variations are often not intuitively obvious, nor do they conform to some preconceived notions that might be derived from analogies with terrestrial communities. In addition, many effects of higher order resulting from fundamental differences in tropical and temperate freshwater systems are still to be studied. These include such basic phenomena as nutrient regeneration mechanisms, propagation of short-term irregular variation in critical environmental variables through food chains, successional responses of higher trophic levels to environmental variation, and contrasts in adaptive strategies for organisms occupying environments that have very different ratios of predictable to unpredictable variation. Because of some provocative contrasts in the trends of species diversity in aquatic and terrestrial systems, latitudinal comparisons in aquatic systems also offer the prospect of insight into the mechanisms that govern biotic diversity.

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