

# Basis for the protection and management of tropical lakes

William M. Lewis, Jr

Center for Limnology, Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder,  
Colorado 80309-0216, USA

## Abstract

Management of lakes for the protection of water quality, aquatic life and other uses must be approached somewhat differently in the tropics from how it is approached at temperate latitudes. More than half of all tropical lakes are accounted for by natural river lakes or reservoirs. Therefore, degradation of water quality in rivers will have direct negative effects on the majority of lakes in the tropics. Also, regulation of rivers, which is one result of river impoundment, is a potential cause of damage to river lakes. Tropical lakes are more sensitive than temperate lakes to increases in nutrient supply and show higher proportionate changes in water quality and biotic communities in response to eutrophication. Tropical lakes are especially prone to loss of deep-water oxygen, and in order to maintain ecological stasis therefore require more stringent regulation of organic and nutrient loading than temperate lakes. Nutrient containment must be more strongly oriented toward nitrogen, the most probable limiting nutrient in tropical lakes, than has been the case at temperate latitudes. However, phosphorus control is also important. Nitrogen management may be more feasible in the tropics because of high temperature, which is one of the critical conditions for efficient denitrification. Planktonic and benthic communities of the tropics bear a close resemblance, both in composition and diversity, to those of temperate latitudes; there is no parallel to the latitudinal gradient in biodiversity that is characteristic of terrestrial ecosystems. Foci of biodiversity, which require special attention, include the endemic species of ancient lakes and the diverse fish communities of very large rivers. The latter are an especially valuable untapped economic resource, but face severe impairment due to hydrological regulation and pollution of rivers. Effective management programs for tropical lakes will focus on interception of nutrients, protection of aquatic habitats from invasive species, and minimization of hydrological changes in rivers to which lakes are connected. In the absence of protective management, tropical lakes will decline greatly in their utility for water supply, production of commercially useful species, and recreation.

## Key words

**aquatic communities, eutrophication, tropical lakes, water quality.**

## INTRODUCTION

Lakes throughout the temperate latitudes have been drastically altered as a result of increases in population density, economic growth, and changes in land cover. Within the last 30 years, limnologists have developed a scientific basis for diagnosing and anticipating changes that occur in temperate lakes as waters and watersheds are used more intensively by humans. This knowledge is now the foundation of protective regulations for lakes in many countries. Furthermore, where lakes have been most profoundly altered and have lost much of their value, scientific understanding of lakes is being used in prescribing restoration methods (e.g. de Bernardi

*et al.* 1996; Hosper 1997; Scheffer 1998). The future for applied limnology involves even more extensive efforts to protect and restore lakes.

Limnology in the tropics has only recently developed past the stage of exploration (Melack 1996; Talling & Lemoalle 1998), but the need for application of limnological knowledge is as pressing at tropical latitudes as it is in the temperate zones. However, the extent to which the limnology of temperate latitudes can be applied in the tropics is not always clear. General limnological principles are often transferable across latitude. For example, the growth of algae in a lake at any latitude is likely to be limited by the availability of one or more key nutrients; an increase in the supply of these nutrients by humans is likely to change many of the characteristics of the lake. On the other hand, some limnological principles are not so easily applicable across latitude. For

example, we know that temperate dimictic lakes have a growing season that coincides with the warm months. Do tropical lakes have a growing season or not?

The purpose of this paper is to summarize some of the ways in which tropical and temperate lakes differ. Where differences can be identified, the implications for management and protection of tropical lakes are interpreted in light of the differences.

## TWO KINDS OF LATITUDINAL CONTRASTS

There are two very different kinds of latitudinal contrasts among lakes: physiographic and climatic. Physiographic contrasts relate to the relative abundance of lakes per unit of land mass, and to the proportions of different kinds of lakes. Climatic contrasts relate to the fundamental climatic variables associated with latitude.

Globally, lakes cover approximately 1% of land surface area (Herdendorf 1990). The distribution of lake area with latitude is uneven, as shown by Fig. 1. The total lake surface area is small in the subtropics because of low precipitation, which coincides with zones of persistently high pressure (subtropical highs; McGregor & Nieuwolt 1998), and the scarcity of glacial basins at these latitudes. Lake surface area is highest at temperate latitudes and moderate at tropical latitudes.

For purposes of lake protection and management, Fig. 1 can be quite deceptive. Approximately 90% of lake surface area is accounted for by the 250 largest lakes in the world

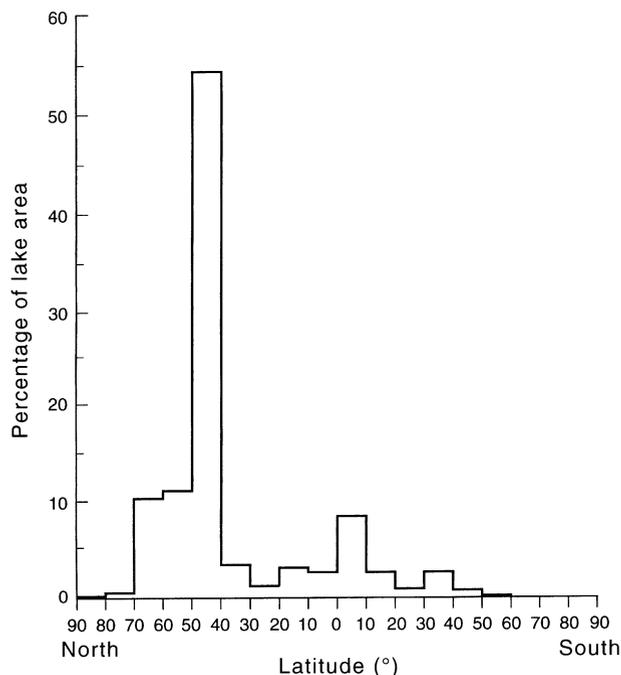


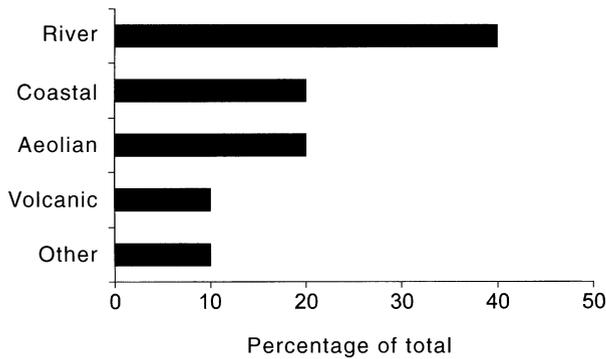
Fig. 1. Latitudinal distribution of lake surface area (from the data of Herdendorf 1990).

(Herdendorf 1990). Therefore, Fig. 1 primarily reflects the distribution of only 250 lakes. There are approximately 10 million lakes on the earth (Wetzel 1992), very few of which are large. Protection and management of the world's largest lakes presents a difficult and exceedingly important problem to which limnologists working at tropical latitudes must make a contribution. However, many regions and even entire nations are remote from any of the largest lakes. In such cases, lakes of small to moderate size are of paramount importance. Therefore, many practical questions in applied limnology relate to the abundance, distribution, and typology of lakes that are of small to moderate size. These lakes do not make a significant contribution to the global surface area as represented in Fig. 1, but are of critical importance to human populations throughout the tropics.

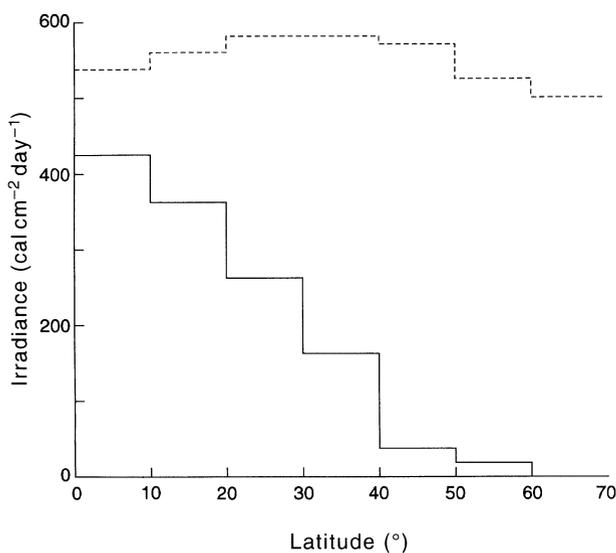
At present, we have no comprehensive estimate of the number of lakes as a function of latitude. A provisional estimate was developed by Lewis (1996) through random sampling based on maps. According to this approach, more than 90% of lakes are located at temperate latitudes. In other words, the number of lakes per unit surface area is far larger in the temperate zones as a whole than it is in the tropics as a whole. Of course, this generalization does not apply to certain regions, such as temperate arid regions where surface waters are scarce, or selected tropical lake districts where lakes are quite abundant.

Economic development and population growth require stable water and hydroelectric power supplies. Therefore, we can expect that tropical peoples, some of whom have been constructing reservoirs for centuries (Fernando & Indrasena 1969), will construct reservoirs in parallel with their economic development. Furthermore, because of the relative scarcity of natural lakes, reservoirs will be the predominant lake type in many regions. This leads to the conclusion that in the tropics as a whole, limnology must be more strongly oriented towards reservoirs than it has been at temperate latitudes, to some extent, this orientation is already evident in the literature (Tundisi 1994). This is not to say that lakes of natural origin should be ignored. In fact, one could argue that natural lakes deserve special attention in the tropics because of their relative scarcity.

The proportional abundance of lake types appears to vary greatly with latitude, but we have no comprehensive statistics on this subject. Random sampling from maps led Lewis (1996) to conclude that river lakes are the most abundant type at tropical latitudes (Fig. 2), whereas the lakes that predominate at temperate latitudes owe their origins to ice. Coastal and aeolian lakes are also numerically important in the tropics. Other lake types can be important in specific regions, but less so overall. For example, lakes of volcanic origin are abundant in parts of Central America and



**Fig. 2.** Proportions of natural lake types in the tropics, as estimated by Lewis (1996).



**Fig. 3.** Latitudinal trends in (---) maximum and (—) annual minimum irradiance (adapted from Lewis 1987). 1 cal = 4.1855 J.

Indonesia. Nevertheless, we conclude from Fig. 2 that tropical limnology, at least as it relates to the management and protection of natural lakes, must emphasize non-glacier lakes, and especially river lakes.

The special importance of reservoirs and river lakes in the tropics raises a practical issue of very great importance for tropical limnology. Reservoirs and river lakes often receive water from large areas (river drainages) relative to their size. Therefore, reservoirs and river lakes are especially vulnerable to changes in the hydrology or water quality of rivers. Because of the importance of reservoirs and river lakes, the welfare of lakes in the tropics is even more closely related to the welfare of rivers than it is at temperate latitudes.

### CONTRASTS RELATED TO CLIMATE

Climate varies with latitude, but some important latitudinal trends are obscured by variations among individual lakes and variations in climate within regions at a given latitude.

As a means of clarifying the latitudinal component of variation related to climate, one can imagine a hypothetical lake of fixed size, depth, and water quality that can be moved across a latitudinal gradient (Lewis 1996). In this way it is possible to separate latitudinal trends from the specific characteristics of an individual lake or aspects of climate that are not explained by a latitudinal trend.

It is well known that the mean annual solar irradiance at tropical latitudes exceeds that of temperate latitudes, and is more uniform across the months of the year. Of greatest direct importance for limnological contrasts, however, are the latitudinal trends in maximum and minimum irradiance over an annual cycle at a given location. The maximum and minimum annual irradiance are determined in a large part by the seasonal tilting of the Earth, but also to some degree by regional variations in the attenuation coefficient of the atmosphere (as determined by moisture or dust for example). Figure 3 shows only the component of variation that is determined by the seasonal tilt of the Earth, and assumes a fixed attenuation coefficient. Figure 3 explains the single-most important basis for understanding latitudinal trends in lakes. As shown by the figure, the main contrast between temperate and tropical lakes lies in the season of minimal irradiance (hemispheric winter). The season of maximum irradiance (hemispheric summer) differs much more modestly across latitude.

As shown by Fig. 3, an identifiable season of negative heat budgets is characteristic of tropical lakes. Furthermore, the timing of this annual season of negative heat budgets is predictable. Except in rare instances, it coincides with the hemispheric winter. Even very near the equator, where dual minima may occur, the minimum that is most extreme coincides with hemispheric winter.

The important features of Fig. 3 include not only the minimum irradiance for a given latitude, but also the deviation between the minimum and the maximum for a given latitude. The minimum irradiance is related to the timing and duration of seasonal mixing, whereas the difference between the minimum and the maximum is related to the stability of the water column during the season of stratification.

### SEASONALITY IN TROPICAL LAKES

One of the most useful ways of classifying lakes is by the frequency of complete mixing. Lakes in temperate latitudes are most often dimictic, that is, they have a seasonal period of ice cover, fall and spring mixing, and a season of stable stratification coinciding with maximum heat content. Although the dimictic status of temperate lakes is fundamental, it is not universal. For example, very shallow lakes, even though they have the characteristic ice cover, in some instances can be insufficiently deep to stratify, and therefore

must be classified as cold polymictic (Lewis 1983). Lakes near the low-latitude margin of the temperate zone can be warm monomictic (no ice cover; single annual mixing), or have intermittent ice cover.

Tropical lakes are fundamentally warm monomictic in the same sense that temperate lakes are fundamentally dimictic. The occurrence of a cool season coinciding with the hemispheric winter ensures that a mixing season at that time is very likely. The difference in temperature between the top and the bottom of the water column is relatively small (approximately 2°C, discounting diurnal heat gain). However, because water density responds most markedly to changes in temperature when the temperature is high (Fig. 4), there is sufficient density difference between the top and bottom of tropical lakes to sustain seasonal stratification, except in lakes that are shallow in relation to their area.

Deviations from the fundamental mixing type occur in the tropics, as they do at temperate latitudes. Lakes that have low relative depth may show intermittent mixing throughout the year rather than seasonal mixing, that is, they are warm polymictic for the same reasons that shallow temperate lakes are cold polymictic (Fig. 5). Polymixis will be continuous (i.e., daily) for very shallow lakes or discontinuous (multiple but not daily mixing events) for lakes with a mean depth of 5–10 m, depending on area (Fig. 6).

In principle, on the basis of morphometric variables, it should be possible to predict the distinction between monomictic and polymictic conditions for tropical lakes. One handicap in making the distinction is the lack of extended temperature records for tropical lakes. From what is known of tropical lakes, Figs 5 and 6 show the approximate conditions of distinction for the monomictic and polymictic conditions in tropical lakes.

The deepest tropical lakes show the characteristic tropical seasonality, that is, deep mixing on a seasonal cycle. However, wind strength may be insufficient to move the entire water mass. This is also the case for the deepest temperate lakes. In this sense, the deepest tropical and temperate lakes represent a variant of the fundamental type, that is, there is a strong tendency toward seasonal mixing but without a penetration of mixing to the greatest depths. Such lakes verge on meromixis (failure to mix completely), but strong vertical exchange during the cool season prevents most of them from having the chemocline that is characteristic of truly meromictic lakes (Lewis 1983). Truly meromictic lakes are found occasionally in the tropics, as they are at temperate latitudes.

Although the patterns shown in Figs 5 and 6 are relatively well documented, there is still much confusion about the seasonality of mixing cycles in tropical lakes. This confusion can be traced to a global analysis of lake typology based on

mixing as described by Hutchinson and Löffler (1956). As shown by subsequent extended studies, which were unavailable to Hutchinson and Löffler, the typology was fundamentally erroneous for tropical lakes. Unfortunately, the

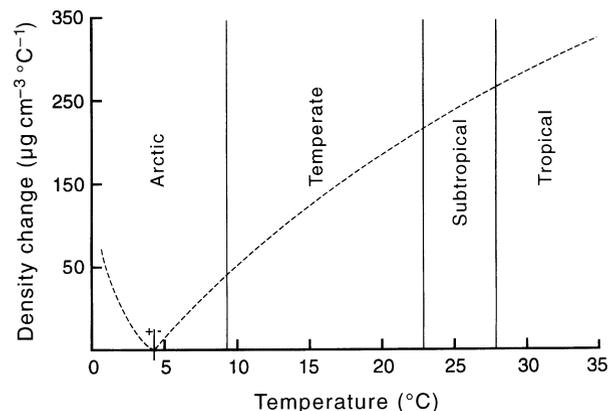


Fig. 4. Change in the density of water that accompanies a change in temperature of 1°C.

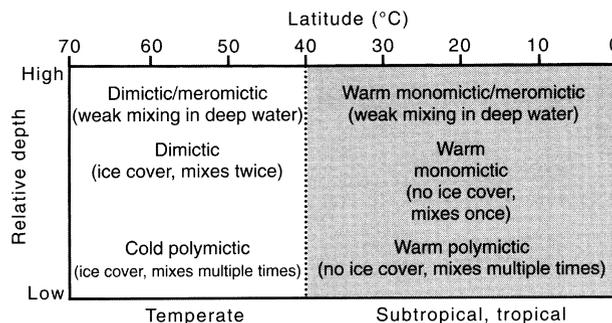


Fig. 5. Illustration of the latitudinal distribution of lake types based on mixing.

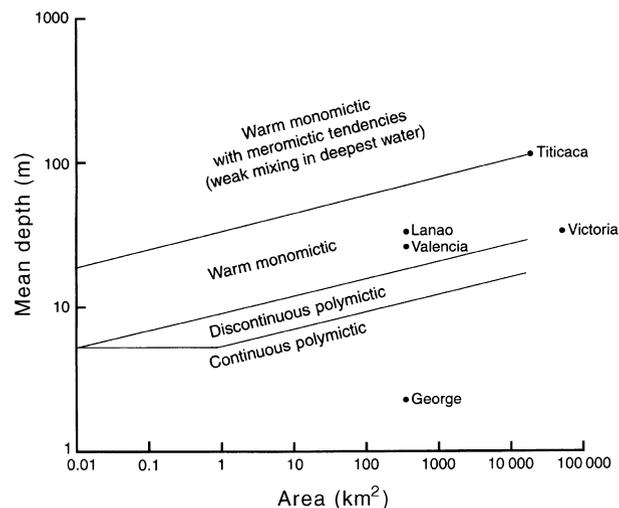


Fig. 6. Approximate relationship between mean depth, surface area, and mixing patterns in tropical lakes. Five well documented examples are shown on the figure.

synthetic diagram put forth by Hutchinson and Löffler has perpetuated the idea that tropical lakes are fundamentally either polymictic or oligomictic. Tropical lakes are fundamentally monomictic, with variations toward polymixis where the relative depth is low, and variations towards meromixis where the relative depth is high.

Because reservoirs and river lakes are of special concern in the tropics, their mixing patterns should be considered here in relation to other kinds of lakes. Tropical reservoirs will typically show strongly developed warm monomictic patterns (Tundisi 1994). In some cases, however, a continuous supply of cool river water in large amounts may stabilize stratification, thus preventing seasonal mixing of the entire water column (Mtada 1986; Tundisi 1994). Also, as in reservoirs of the temperate zones, shallow reservoirs with large amounts of throughflow may show confusing, irregular patterns of mixing and stratification caused by disruption of the fundamental pattern through passage of large amounts of river water.

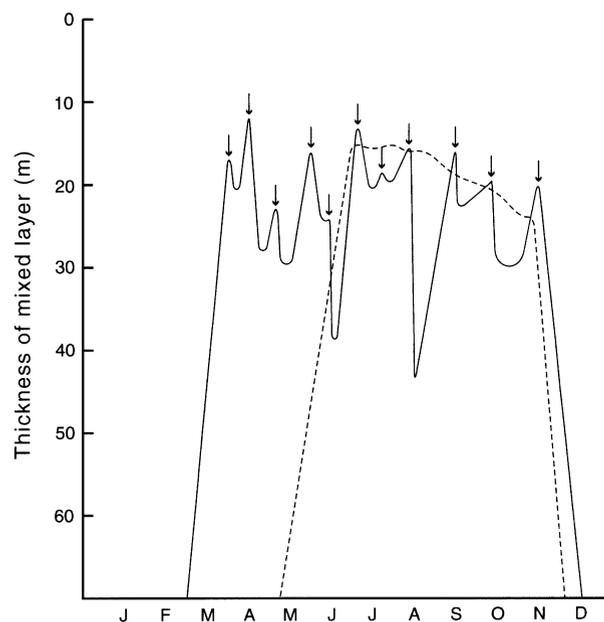
The seasonality of a river lake is influenced very strongly by the seasonal hydrologic cycle of the river to which it is connected (Hamilton & Lewis 1987; Furch & Junk 1997). Most importantly, the depth of such lakes changes greatly on a seasonal basis. For example, a typical floodplain lake along the Orinoco River might change in mean depth from approximately 1 m at the end of the dry season to 6 m or more during high water (Hamilton & Lewis 1987). Lakes of the Amazon várzea show a similarly broad range of seasonal changes in depth, but generally are deeper than those of the Orinoco. MacIntyre and Melack (1988) have shown how the seasonal change in depth of such a lake also changes the possibility for sustained stratification: at low water, a floodplain lake may be insufficiently deep to support stratification, whereas a seasonal flood increases the water depth so that it is sufficient to allow stable stratification. Therefore, for tropical river lakes there is not only a seasonal trend in the tendency toward gain or loss of heat, as for other kinds of lakes, but also a seasonal change in the water depth and amount of throughflow, either of which could affect stratification.

#### LATITUDINAL VARIATIONS IN PHYSICAL DYNAMICS OF THE MIXED LAYER

Even though tropical lakes are fundamentally warm monomictic, and therefore stratify seasonally unless they have a low relative depth, there are some important contrasts with temperate lakes in the characteristics of the mixed layer during stratification. The stability of layering in a temperate lake is much higher than that in a tropical lake with the same morphometric characteristics, even though both lakes may have well-developed seasonal stratification. The practical

significance of the latitudinal difference in stability has to do with short-term variations in the heat content of lakes. During the season of maximum heat content, the dimensions of the mixed layer of a temperate lake are quite stable. There are some exceptions, such as the occurrence of hypolimnetic upwelling, which can occur on large lakes in response to internal seiches of high amplitude (Imberger & Patterson 1989). However, in general, temperate lakes will show stability in the thickness of the mixed layer until seasonal heat loss begins in the autumn. In other words, the absolute stability of layering in temperate lakes is so high that frontal events causing alternating loss and gain of heat from the water column do not change the stability enough to lead to changes in the dimensions of the mixed layer (Fig. 7).

The response of tropical lakes to frontal systems on the scale of days to weeks is very different from that of temperate lakes. A typical event, which may cause heat loss of  $800\text{--}1300\text{ J cm}^{-2}$ , results in a loss of stability as high as 25% in a tropical lake (Lewis 1987), whereas the corresponding percentage for a similar event in a temperate lake would be only approximately 5%. With a loss of stability reaching 25% in the presence of even moderately strong winds, there will be a readjustment in the thickness of the mixed layer: the



**Fig. 7.** Hypothetical illustration of the difference in the dynamics of the mixed layer in a (---) temperate and (—) tropical lake. The temperate lake has a shorter stratification season and the mixed layer is marked by a much greater temporal stability in thickness. The tropical lake has a longer season of stratification and is marked by recurrent changes in the thickness of the mixed layer reflecting repeated cycles of gain and loss in the heat content of the upper water column.

metalimnion will erode until the mixed layer has thickened to the point where turbulence induced by water movement under the influence of wind is counterbalanced by the magnitude of the density gradient (as indicated by the Richardson number at the interface of water masses of different densities). The water column will then stabilize until there is a reversal in heat budget associated with calm, sunny weather that is favorable for net heat uptake. Under these conditions, the newly gained heat will accumulate toward the uppermost portion of the mixed layer, and will induce a density difference that is quite large relative to the small amount of heat gained. The result often is the development of a secondary thermocline within the mixed layer. Thus a new mixed layer is established, which is thinner than the previous one.

A repeated cycle of thickening and thinning of the mixed layer under the influence of alternating loss and gain of heat is characteristic for tropical lakes. The result is a stepped thermal structure that reflects past changes in the thickness of the mixed layer (Fig. 8).

Alternate thinning and thickening of the mixed layer with recurrence intervals of a few weeks has numerous implications for the functioning of tropical lakes. For example, tropical lakes may show great short-term variation in the amount of phytoplankton biomass, primary production, and even zooplankton biomass because of episodic changes in the mixed layer (Lewis 1996). Thus, an understanding of the special nature of physical dynamics in the mixed layer leads to explanations of events in the plankton communities of tropical lakes.

The dynamic condition of the mixed layer in tropical lakes promotes the accelerated recycling of nutrients. If the mixed layer of a lake is quite stable, as it typically is in temperate

lakes (Fig. 7), nutrients lost from the epilimnion cannot be used again by primary producers until the autumn mixing, except for small quantities that are transferred by eddy diffusion from the metalimnion into the mixed layer. In contrast, tropical lakes can recapture a large quantity of nutrients lost from the mixed layer simply through thickening of the mixed layer. Thus the potential for production of phytoplankton biomass on a given nutrient base is higher in tropical lakes than it is in temperate lakes (Lewis 1974). This means that tropical lakes may be more responsive to eutrophication than temperate lakes.

## TEMPERATURE

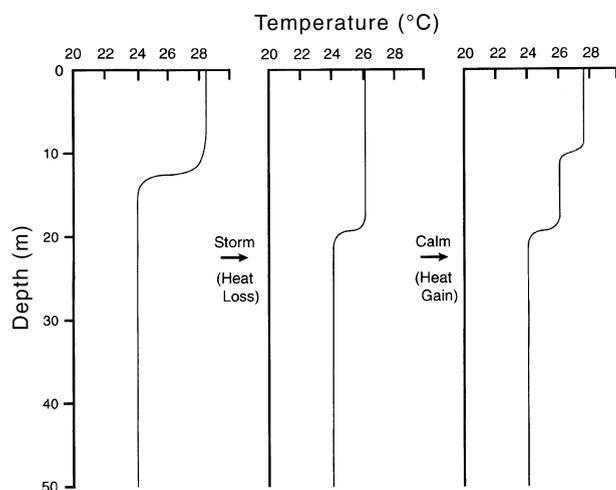
Water temperature affects both the anabolic and catabolic processes of lakes. In general, the relationship between temperature and metabolism can be described by a  $Q_{10}$  of approximately 2.0, that is, metabolic rates are likely to double with a  $10^{\circ}\text{C}$  increase in temperature, provided that some other factor is not strongly suppressing the rate (Eppley 1972; Toerien and Cavari 1982).

During summer, the upper water column of temperate lakes at low elevation reaches temperatures that approach those typical of the tropics. This is not surprising, given the relatively low sensitivity of maximum irradiance to latitude (Fig. 3). The annual average temperature of the mixed layer, however, is much lower for a temperate than for a tropical lake. Therefore, metabolic processes that are dependent on temperature tend to be steadier and of higher rate in the upper mixed layers of tropical lakes. Consequently, the nutrient cycling caused by regeneration of inorganic nutrients through microbes in the mixed layer will occur more rapidly in the upper zones of tropical lakes during stratification. For a given nutrient supply, photosynthesis will also be more rapid. The consequences for primary production and phytoplankton biomass will be discussed below.

A second consideration is the temperature of the hypolimnion, which presents an even more significant latitudinal contrast than temperature in the upper water column. The temperature of the hypolimnion in a tropical lake is only as low as the seasonal minimum air temperature, that is, in the vicinity of  $24^{\circ}\text{C}$  for lakes located within  $10^{\circ}$  of the equator at low elevation. Such high temperatures sustain high rates of microbial metabolism. Nutrients are likely to be regenerated more rapidly and completely, and oxygen is removed much more rapidly than would be the case at the lower temperatures that are characteristic of temperate lakes.

## OXYGEN

Oxygen in the deep water of tropical lakes is a critical matter for their protection and management. Three factors



**Fig. 8.** Illustration of a sequence of changes in mixed-layer thickness for a tropical lake through a period of heat loss and heat gain.

work against the retention of oxygen in the deep waters of tropical lakes: i) the long duration of stratification in tropical lakes, which will typically last 10–11 months rather than 6–9 months, as in temperate lakes (Fig. 7); ii) the poorer ability of water to hold oxygen at high temperatures than at low temperatures (approximately  $8 \text{ mg L}^{-1}$  tropical vs.  $12 \text{ mg L}^{-1}$  at  $45^\circ$  latitude during mixing, when the hypolimnetic concentrations are set by contact of the entire water mass with the surface); and iii) higher rates of microbial metabolism at the high temperatures characteristic of the deep waters of tropical lakes. Together, these three factors magnify the influence of any organic enrichment of deep waters. Therefore, undesirable effects associated with anoxia caused by eutrophication or direct organic enrichment of waters will be more serious and more quickly realized in tropical lakes than temperate lakes. A corollary of this is that any tropical lake that sustains oxygen in deep waters as a natural condition should be protected with special care if deep-water oxygen is to be preserved, because small increases in oxygen demand can lead to the elimination of deep-water oxygen in a tropical lake. Even for lakes that are naturally anoxic in deep water, an extension of the duration, severity, or spatial distribution of the anoxia within the hypolimnetic zone may have strong negative consequences for the biota and for the usefulness of the lake as a water supply or fishery. Thus, oxygen conservation is an even more important management principle for tropical lakes than it has been for temperate lakes.

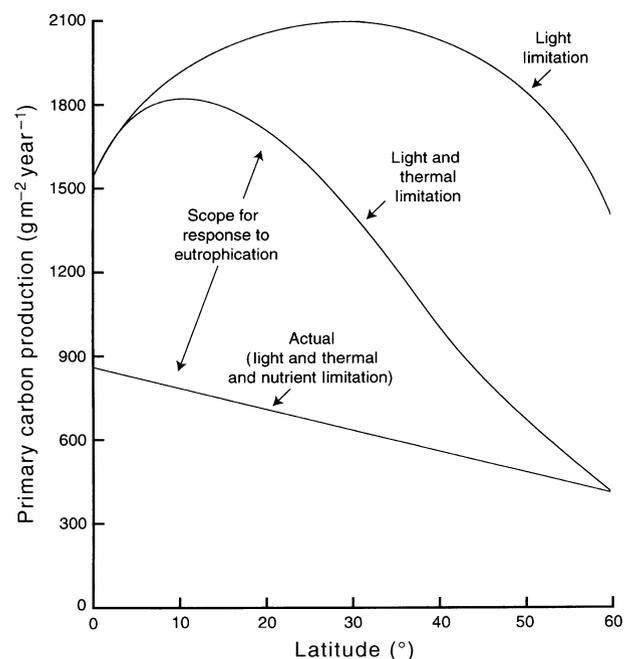
### PRIMARY PRODUCTION AND PHOTOSYNTHESIS

If primary production were exclusively under the control of solar irradiance, it would show a slight suppression near the equator caused by high humidity (cloudiness) and a steady decline beyond  $30^\circ$  caused by short days (Fig. 9). However, primary production also is influenced by temperature. If the effect of temperature is superimposed on the effect of solar irradiance, the expected latitudinal trend would be even more striking (Fig. 9).

Primary production is influenced not only by solar irradiance and temperature, but also by the availability of nutrients, which is more difficult to predict than solar irradiance or temperature. In fact, persistent nutrient depletion could nullify the effects of temperature and irradiance; a nutrient-limited tropical lake would sustain no more net primary production than a temperate lake with a similar degree of nutrient limitation. The International Biological Programme studies showed, however, that primary production does decrease as a function of latitude (Fig. 9). Although these studies were not focussed on tropical lakes, subsequent measurements of the production of tropical lakes have verified

the general trend, that is, that annual primary production is highest at low latitudes (Lewis 1996). The implication is that tropical lakes are favored not only by high solar irradiance and high temperature, but also by high efficiency of nutrient use, which allows primary production to reflect the favorable irradiance and temperature.

The foregoing discussion of the seasonality and dynamics of the mixed layer explains why primary production can be highest at low latitudes, even though nutrient limitation occurs in tropical lakes. Under nutrient-limiting conditions, the ability of a lake to sustain primary production is determined by recycling mechanisms. Recycling mechanisms within the mixed layer occur more rapidly at low latitude because of sustained high temperature. Furthermore, nutrients lost from the upper mixed layer are much more likely to be returned to the euphotic zone of a tropical lake within a given stratification season because of the dynamic nature of the mixed layer. Therefore, a functional explanation is available for a latitudinal trend in nutrient-use efficiency, as is necessary to explain higher production in tropical lakes. Thus, on the basis of nutrient-cycling efficiency alone, tropical lakes should be considered more sensitive to eutrophication than temperate lakes, that is, the potential for eutrophication to degrade water quality (phytoplankton biomass, deep-water oxygen, etc.) is highest at tropical latitudes (Fig. 9).



**Fig. 9.** Latitudinal trends in annual net primary production of lakes under three conditions: optimal solar irradiance with optimal temperature and nutrient saturation (top line), optimal solar irradiance with actual temperature (middle line), and observed rates (i.e. reflecting actual solar irradiance, temperature, and nutrient limitation).

**Table 1.** Summary of some characteristic features of tropical lakes, with their consequences for the functioning of tropical lakes, and management implications

Features of tropical lakes	Consequences	Implications
Natural lakes not abundant	Reservoirs of high relative importance	Management of reservoirs is of high priority
Glacier lakes scarce among natural lakes	River lakes are the predominant natural type	Status of rivers dictates welfare of most lakes
Predominantly warm monomictic	Predictable annual mixing season except in shallow lakes	Seasonal anoxia likely in deep water; seasonal cycle in water quality
High hypolimnetic temperature, long stratification season	High probability of hypolimnetic oxygen depletion	High vulnerability to eutrophication or organic loading
Recurrent changes in thickness of mixed layer	Recurrent nutrient enrichment of mixed layer	High efficiency of nutrient use; strong response to anthropogenic nutrient loading
Nitrogen limitation of autotrophs predominate over phosphorus limitation	Nitrogen pollution especially problematic	Denitrification of waste critical; phosphorus removal also important
Invertebrate predators favoured by anoxia	Herbivores consumed mostly by invertebrate predators	Low fish production per unit primary production; eutrophication may lower fish production
Planktonic and benthic biodiversity similar to those of temperate lakes	Analogies with temperate lakes closer than for terrestrial environments	Biodiversity protection challenging but less so than in terrestrial tropics

Beyond the efficiency of recycling, which magnifies the severity of eutrophication at tropical latitudes, Fig. 9 shows why symptoms of eutrophication will be more severe under high nutrient-loading conditions in the tropics. The potential magnitude of the response to eutrophication is higher in the tropics than in the temperate latitudes, as represented by the large distance between the line for actual and potential production in Fig. 9. Eutrophication can occur more easily, produce more severe symptoms, and be more prolonged as a proportion of the annual cycle at tropical latitudes.

## NUTRIENTS

Although phytoplankton, attached algae and macrophytes require 20 or more elements for the synthesis of protoplasm, the growth rate of a given species population at a particular time will be either unresponsive (unlimited by nutrients) or responsive (limited by nutrients) to the addition of nutrients. If the population is not responsive to the addition of nutrients, it is growing under conditions of nutrient sufficiency, that is, it is either growing at a maximum rate, temporarily unchecked by environmental factors, or it is limited by some other factor (e.g. light). Often, however, the addition of nutrients causes a growth response. The response to the addition of a mixture of nutrients can be traced exclusively or primarily to a single nutrient in the mixture (the limiting nutrient). This is the so-called limiting-nutrient principle, or Liebig's law of the minimum (Hutchinson 1973; Talling

1979). A complication occurs when different species are limited by different nutrients, but usually the community responds as if limited by one nutrient.

Basic principles and field evidence both indicate that tropical lakes, like temperate lakes, will often show nutrient limitation of autotrophs. There may be latitudinal trends, however, in the persistence or frequency of nutrient limitation. As at temperate latitudes, tropical lakes that stratify seasonally are likely to show the most severe nutrient limitation. Such lakes, whether tropical or temperate, show a progressive seasonal separation of nutrient supply from nutrient demand as free nutrients accumulate in the lower water column, while growth is limited primarily to the upper water column. Tropical lakes can be expected to stratify for a larger proportion of the year than temperate lakes, for reasons already explained. Therefore, it would seem that the extent and intensity of nutrient limitation in tropical lakes would be high, given that stratification promotes nutrient limitation, especially for phytoplankton. This expectation is false, however, because of intraseasonal variation in the thickness of the mixed layer within tropical lakes. Repeated thickening of the mixed layer fertilizes the upper water column as nutrients that accumulate in deeper water are returned to the growth zone. As already explained, recurring cycling of nutrients between the growth zone and deeper water allows tropical lakes to be more efficient in the use of nutrients than temperate lakes. High temperatures in

deep water enhance this effect by rapidly regenerating the available forms of nutrients from the unavailable forms of nutrients through microbial action.

A second potential point of comparison across latitudes has to do with the identity of the limiting nutrient. Experience with the inland waters of temperate latitudes makes a strong case for the significance of phosphorus and nitrogen as limiting nutrients for autotrophs (Welch 1992). Other macronutrients (i.e. essential elements present in  $\mu\text{g L}^{-1}$  quantities or more) seem to be present almost universally in amounts sufficient to satisfy the needs of autotrophs. Only inorganic carbon and silicon stand out as possible causes of limitation in addition to nitrogen and phosphorus. Evidence that trace elements have an important role remains unconvincing, except perhaps in very special circumstances.

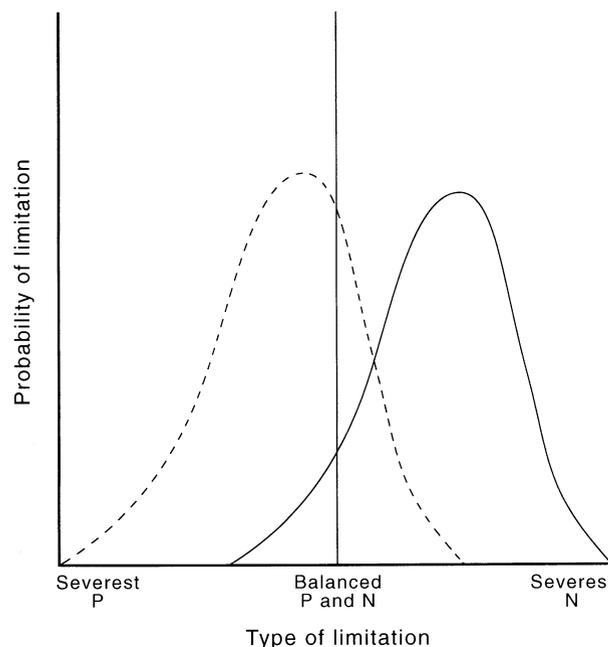
Limitation by inorganic carbon is fundamentally different from that of nitrogen and phosphorus, insofar as it can occur only when photosynthesis rates are very high, that is, only under full sun, and only in lakes rich in autotrophs (Talling 1976). The atmospheric  $\text{CO}_2$  pool relieves any incipient inorganic carbon limitation in most situations. Likewise, a silicon limitation is of much narrower significance than limitation by phosphorus and nitrogen. It affects only diatoms, and possibly to a few less-common taxa with silicious attachments. Furthermore, silicon limitation may be less likely in the tropics than at temperate latitudes because of higher rates of rock weathering in the tropics (Talling 1992), although tropical lakes with very low flushing rates may show silicon deficiency affecting diatoms (Kilham & Kilham 1990).

The literature on tropical lakes supports the conclusion that nutrient limitation in tropical lakes centers on deficiencies of phosphorus or nitrogen, as is the case in temperate latitudes. A more subtle question, which is more difficult to resolve, has to do with the relative frequencies of nitrogen and phosphorus limitation for tropical autotrophs. Phosphorus is widely considered to be the dominant limiting nutrient for lakes in temperate latitudes (Welch 1992). While phosphorus limitation is a common occurrence in temperate lakes, attention to nitrogen limitation has probably been insufficient. Phosphorus and nitrogen limitation are rather closely balanced in temperate waters that are not subject to anthropogenic waste disposal. In fact, alternation between phosphorus and nitrogen limitation has been documented for some lakes (Morris & Lewis 1988).

The available empirical information, while by no means comprehensive, suggests that nitrogen limitation is more important at tropical latitudes than it is at temperate latitudes (Talling & Lemoalle 1998). Phosphorus limitation does occur in some lakes, and in other cases the balance between

phosphorus and nitrogen limitation seems to be rather close, as it is for many natural waters at temperate latitudes. On the whole, however, there are more instances of clear nitrogen limitation than of clear phosphorus limitation for tropical lakes that have been studied by use of bioassay or other methods. Circumstantial evidence also supports this conclusion. For example, nitrogen-fixing bluegreen algae appear to be more widespread in unpolluted waters of the tropics than in unpolluted lakes of temperate latitudes, and tropical waters are much more likely than temperate lakes to show significant amounts of soluble reactive phosphorus combined with negligible amounts of inorganic nitrogen. As shown by Fig. 10, the probability that a given phytoplankton community will be strongly limited by nitrogen or phosphorus (i.e. with a wide margin between a primary and secondary limitation) differs between tropical and temperate lakes.

There are reasons to expect that nitrogen will be more important in the tropics than at temperate latitudes. Natural phosphorus supply can be traced to the chemical weathering of rock. This process is thermally sensitive, and will



**Fig. 10.** Diagrammatic illustration of the differing probabilities for type and severity of nutrient limitation at (—) tropical and (---) temperate latitudes. For the temperate lakes sampled randomly during the growing season, the frequency distribution for nutrient limitation is most heavily weighted toward phosphorus, although some lakes under some conditions will be limited by nitrogen or closely balanced between phosphorus and nitrogen limitation. For tropical lakes, the frequency distribution is shifted toward a predominance of nitrogen limitation, although some phosphorus limitation can also be found.

occur at considerably higher rates for a given rock type and geochemical setting where the temperature is higher (Meybeck 1979). Thus it is expected that the primary supply of inorganic phosphorus to inland waters of the tropics will be richer. As at temperate latitudes, most of the nitrogen reaching tropical lakes comes from soils. It might seem that nitrogen fixation, which also benefits from high temperature at tropical latitudes, would occur so rapidly as to dominate the nitrogen budgets of at least some tropical lakes, and thus reduce the likelihood of nitrogen limitation in tropical lakes. The light requirements of nitrogen fixation are so high, however, that nitrogen fixers, while widespread in the tropics, are unlikely to provide more than a small proportion of the total nitrogen budget for a tropical lake (Lewis & Levine 1984).

Perhaps even more important to the balance between nitrogen and phosphorus in temperate lakes is denitrification. This process is stimulated by anoxia and by high temperatures in sediments. Anoxia is more likely to occur and be more persistent in tropical lakes than in temperate ones, and sediment temperatures are higher. Although it has not yet been demonstrated, tropical lakes probably lose a much larger proportion of their total inorganic nitrogen to denitrification than do temperate lakes. There is no comparable latitudinally sensitive factor affecting phosphorus.

The management implications of nutrient limitation dominated by nitrogen are more complex than one might expect. A high likelihood of nitrogen limitation for tropical lakes suggests that human disposal or mobilization of inorganic nitrogen is more perilous in the tropics than it is at temperate latitudes, that is, it is likely to provoke a trophic response even in the absence of additional phosphorus loading. At the same time, phosphorus control will be essential in the tropics, as it is in temperate latitudes. While a single nutrient tends to be limiting at any given time, waste disposal is typically such a potent source of nutrients that the initial limitation (in this case likely that of nitrogen) is quickly relieved, and progression to further water-quality deterioration is determined by the availability of the secondary limiting nutrient, which in this case is most likely phosphorus. Therefore, control of eutrophication requires management of phosphorus as well as nitrogen.

At temperate latitudes, phosphorus control has proven more feasible than nitrogen control. Phosphorus can be precipitated by relatively cheap chemical agents (e.g. alum), and in this way reduced from concentrations exceeding  $1 \text{ mg L}^{-1}$  in typical secondary effluent to as little as  $0.02 \text{ mg L}^{-1}$  in effluent treated by additional procedures designed to remove phosphorus. Removal of phosphorus will be critical to the maintenance of beneficial uses for tropical lakes. Nitrogen

removal may prove more feasible at tropical latitudes than it has at temperate latitudes. Nitrogen removal is typically accomplished by processes that facilitate denitrification in waste-water treatment plants. One major handicap for the efficiency of these processes is low temperature (Metcalf & Eddy 1991). Tropical latitudes have the advantage of constantly high temperatures, except at the highest elevations, and therefore may get more benefit from denitrification facilities than would be typical for temperate latitudes.

Because tropical lakes are especially prone to eutrophication and loss of hypolimnetic oxygen, nutrient containment has an even higher priority than it does at temperate latitudes. Containment of both nitrogen and phosphorus should be incorporated into waste-water treatment plans for the tropics. The importance of this principle is magnified by the high likelihood of connections between tropical rivers and the dominant types of tropical lakes, which include reservoirs and river lakes. Widespread nutrient pollution of running water in the tropics will have undesirable effects on the usefulness of tropical lakes.

## BIODIVERSITY

Terrestrial environments of the tropics are impressive repositories of global biodiversity. For example, a random sample of 1000 trees would yield approximately five species in a northern boreal forest, 20 species in a temperate deciduous forest, and 120 species in a tropical forest (Hubbell 1979). Furthermore, species with restricted distributions are commonplace in terrestrial habitats in the tropics. For these reasons, the global consequences for the loss of terrestrial biodiversity are much more profound at tropical latitudes than at temperate latitudes.

The ancient lakes of the tropics are centres of biodiversity for both aquatic vertebrates and invertebrates (Serruya & Pollinger 1983). Some individual lakes of the African rift valley, for example, support hundreds of fish taxa, the vast majority of which are endemic (Lodge 1998). The great attention that these irreplaceable laboratories of evolution have received may give the impression that tropical inland waters, like tropical forests, are categorically different from temperate inland waters in their biodiversity.

Aside from ancient lakes, which number very few, the composition and diversity of lacustrine biotas in tropical lakes appear to be similar to those of temperate lakes (Lewis 1996). For example, the morphotaxa of phytoplankton are largely cosmopolitan, although we must reserve judgement on genetic differences that may not be evident from morphology. Many of the dominant species that occupy tropical lakes are indistinguishable, even to the practiced eye, from the taxa that are dominant in temperate lakes. There are

some exceptions. For example, *Cylindrospermopsis stagnale* (Wolosz.) is common in tropical lakes but not so in temperate ones; *Asterionella* is a common component of temperate phytoplankton assemblages, but not so in the tropics. Even so, endemism is very weak in the phytoplankton generally, and the tropics are no exception. While a few endemic taxa have been described from ancient lakes (perhaps because these lakes invite special taxonomic scrutiny), phytoplankton are broadly distributed in the tropics, as they are at temperate latitudes.

The diversity of individual phytoplankton communities appears to be no greater than it is at temperate latitudes (Lewis 1987). Proportional representation of taxa is also very similar, although tropical latitudes may show a higher proportion of bluegreen algae and a lower proportion of golden brown algae. Thus, latitudinal differences are subtle, and by no means comparable in scale to those observed in terrestrial communities.

The zooplankton communities of tropical lakes are also very similar across latitudes (Lewis 1987). Cladocerans, copepods, and rotifers all make major contributions, and constitute approximately the same proportion of biomass, productivity, and species diversity at tropical and temperate latitudes, although individual lakes vary a great deal at any given latitude. There is little endemism among the zooplankton. The calanoids show the greatest amount of endemism (Hutchinson 1967); this tendency shows no latitudinal trend that has yet been documented. Many important taxa cross latitudinal zones (e.g. *Polyarthra vulgaris* Carlin), although some do not (e.g. *Thermocyclops decipiens* (Kiefer)). As with the phytoplankton, there are signs of subtle but potentially important trends in community composition. For example, large cladocerans are much less abundant at tropical than at temperate latitudes (Fernando 1980a,b). Overall, however, the tropical and temperate zooplankton are similar.

Benthic communities appear to differ little across latitude with respect to diversity (Lewis 1996), although species composition varies more latitudinally than it does for phytoplankton or zooplankton. Benthic communities of lakes may in fact be depauperate in the tropics because of the strong tendency toward deep-water anoxia at tropical latitudes.

Fish faunas, which are subject to much more endemism than the communities already mentioned, are more difficult to characterize latitudinally, but clearly do not present such striking latitudinal contrasts as do terrestrial plants, the impressive and very special biodiversity of fishes in ancient lakes notwithstanding. The diversity of fishes in river systems bears a quantitative relationship to the size of their

drainage basins (Welcomme 1979); this trend complicates the interpretation of latitudinal trends. According to Welcomme (1979) and Lowe-McConnell (1975), tropical fish faunas are more diverse, but Welcomme's data show that watershed area explains more than two orders of magnitude in variation, whereas other factors (including latitude) account for about half an order of magnitude for any given range of drainage areas.

The fish faunas of tropical lakes are more likely than those of temperate lakes to have a strong affiliation with riverine fish faunas. The glaciated regions of temperate latitudes provide immense habitat space, much of which is only remotely connected to large rivers. In contrast, the dominant lake types of the tropics lie astride or beside large rivers. Therefore, the welfare of tropical lacustrine fish faunas is very sensitive to the welfare of rivers, which makes the protection of these faunas especially difficult.

The biodiversity of tropical lake communities raises only a few issues that are latitudinally special. In many cases, the lessons for management, many of which are drawn from unfavorable experience, can be transferred with some confidence from the temperate zones. Tropical aquatic faunas, like temperate ones, are subject to disruption by the introduction of invasive species, which often lead to reduced human benefits from lakes (e.g. the East African lakes; Johnson and Odada 1996; Fryer 1991).

Implications for the management of biodiversity include transferability of lessons from temperate latitudes, special attention to centres of biodiversity (ancient lakes and the largest river basins), and special efforts to protect riverine fish faunas for the benefit of lakes. As in the temperate zones, the introduction of species, while often well-intentioned can be ecologically disastrous.

## PRODUCTION OF CONSUMERS

Because primary production is likely to be higher on a given nutrient base in the tropics than it is at temperate latitudes, one might anticipate that the production of invertebrate and vertebrate consumers would be proportionately higher as well (Downing *et al.* 1990), or perhaps that the production of consumers would be several-fold higher because of the compounding effect of high efficiency across trophic levels. Field evidence, however, is inconclusive.

Melack (1976) studied the fish yields of tropical lakes in comparison to primary production, and concluded that yields of tropical fisheries are directly related to gross primary production. It is difficult to generalize about consumer production from studies of fisheries, however, because fisheries typically focus on specific portions of the fauna, and often leave a large amount of fish production unharvested. For

example, Bailey (1989) showed that the fisheries of the Amazon floodplain (*várzea*) take only approximately 3% of total annual fish production.

Although yields in fisheries are a poor indicator of production, there is a persistent view among those who have analyzed fishery yields that the lacustrine fisheries of the tropics are much less productive than might be expected. Fernando and Holčík (1991; see also Fernando *et al.* 1998) have advanced the hypothesis that lacustrine fisheries in the tropics (especially in reservoirs) are handicapped by the weak adaptation of tropical fish faunas to lacustrine conditions. With the exception of ancient lakes, where specialized fishes have adapted extensively to lacustrine conditions, tropical lakes often contain fishes that have strong riverine affinities. If the Fernando/Holčík hypothesis is correct, the inability of tropical lacustrine fish communities to be high producers may be due in part to the poor representation of taxa capable of making an efficient conversion of planktonic foods to fish biomass.

Because there are few measurements of consumer production in tropical lakes other than fish harvest, there is little basis for an overall evaluation of consumer production in tropical lakes, but some case studies indicate the range of possible outcomes. River lakes, which are an integral component of floodplains, may have provided some of the greatest opportunities for adaptation of tropical fish faunas to lacustrine conditions. In an intensive study of the trophic relations involving fish in the Amazon *várzea*, Bailey concluded that total fish production per unit area was very high (1% of primary production); so high, in fact, that it could not be explained by presumed food sources. In contrast, Saunders and Lewis (1988) and Unger and Lewis (1991) showed for Lake Valencia, Venezuela, that the low production of pelagic fishes (0.03% of primary production) was explained by the presence of large populations of *Chaoborus*, which intercepted zooplankton biomass very efficiently and yet were not highly vulnerable to the fish. Furthermore, the same study showed that the foodchain efficiency of the lake was much higher during seasons when oxygen was available throughout the water column than when the deep water was free of oxygen.

There may be an important and widespread relationship between *Chaoborus*, fish production, and anoxia in tropical lakes that are deep enough to stratify seasonally. When deep waters become anoxic, *Chaoborus* is much less vulnerable to fish predation because fishes are unable to reach *Chaoborus* populations that are resting within the anoxic zone during the daylight hours. As *Chaoborus* becomes increasingly abundant, it consumes the production of herbivorous zooplankton, which is the largest energy source for

fishes. Thus, many tropical lakes may show low efficiency of consumer production because of deep-water anoxia. Eutrophication will magnify this tendency.

Managers of tropical lakes should be aware that the greatest potential for increasing indigenous or sustained commercial yields of fisheries often lies in the adjustment of fishing practices, which are slow to change because of cultural inertia (Bailey 1989). The increase of primary production, as might occur through eutrophication, is less likely to magnify the production of harvestable consumers because the connection between primary production and harvest is indirect and difficult to manipulate. Furthermore, eutrophication is likely to have the undesirable consequence of increasing the population density of the widespread invertebrate *Chaoborus*, which intercepts primary production before it can reach fish populations, thus potentially reducing fish production by as much as 90%.

## CONCLUSIONS

Challenges to the ecological integrity and usefulness of lakes are very much the same at tropical latitudes as at temperate latitudes: eutrophication, organic loading, invasive species, and hydrographic changes in rivers that affect river lakes. Intensification of these challenges for individual lakes can be traced to waste disposal, changes in land use, and diversion or impoundment of water. However, the effects of some of these environmental challenges will differ considerably between tropical and temperate lakes. Tropical lakes are likely to show a higher degree of adverse response to eutrophication or organic loading than would occur in temperate lakes. Nitrogen will probably play a larger role in eutrophication than it has at temperate latitudes, and hydrographic changes in rivers will be more important because of the greater proportional importance of river lakes in the tropics. A strong degradation in the ecological integrity and economic value of lakes can be expected in the absence of management plans that anticipate and offset or minimize the negative effects of growing human populations on tropical lakes.

## ACKNOWLEDGEMENTS

I thank Professor W. D. Williams for urging me to prepare this paper. I acknowledge the US National Science Foundation for supporting my work in the tropics, and numerous scientists of tropical countries for working with me and helping me over the years.

## REFERENCES

- Bailey P. B. (1989) Aquatic environments in the Amazon Basin, with an analysis of carbon sources, fish production, and yield. In: Dodge D. P. (ed.) *Proceedings of the*

- International Large Rivers Symposium (LARS)*. Canadian Special Publication in Fisheries and Aquatic Sciences, 106, Ottawa, pp. 399–408.
- de Bernardi R., Calderoni A. & Mosello R. (1996) Environmental problems in Italian lakes, and lakes Maggiore and Orta as successful examples of correct management leading to restoration. *Verh. Internat. Verein. Limnol.* **26**, 123–138.
- Downing J. A., Plante C. & Lalonde S. (1990) Fish production correlated with primary productivity, not the morphoedaphic index. *Can. J. Fish. Aquat. Sci.* **47**, 1929–1936.
- Eppley R. W. (1972) Temperature and phytoplankton growth in the sea. *Fishery Bull.* **70**, 1063–1085.
- Fernando C. H. (1980a) The species and size composition of tropical freshwater zooplankton with special reference to the oriental region (South East Asia). *Int. Revue Ges. Hydrobiol.* **76**, 149–167.
- Fernando C. H. (1980b) The freshwater zooplankton of Sri Lanka, with a discussion of tropical freshwater zooplankton composition. *Int. Review Ges. Hydrobiol.* **65**, 85–125.
- Fernando C. H., Gurgel J. J. S. & Moyo N. A. G. (1998) A global view of reservoir fisheries. *Int. Rev. Hydrobiol.* (Special Issue) **83**, 31–42.
- Fernando C. H. & Holčík J. (1991) Fish in reservoirs. *Int. Rev. Ges. Hydrobiol.* **76**, 149–167.
- Fernando C. H. & Indrasena H. H. A. (1969) The freshwater fisheries of Ceylon. *Bull. Fish. Res. Stn.* **20**, 101–134.
- Fryer G. (1991) Biological invasions in the tropics: Hypotheses versus reality. In: Ramakrishnan P. S. (ed.). *Ecology of Biological Invasion in the Tropics*. International Scientific Publications, New Delhi, pp. 87–101.
- Furch K. & Junk W. J. (1997) Physicochemical conditions in floodplains. In: Junk W. J. (ed.). *The Central Amazon Floodplain: Ecology of a Pulsing System*. Springer-Verlag, Berlin, pp. 69–108.
- Hamilton S. K. & Lewis Jr W. M. (1987) Causes of seasonality in the chemistry of a lake on the Orinoco River floodplain, Venezuela. *Limnol. Oceanogr.* **32**, 1277–90.
- Herdendorf C. E. (1990) Distribution of the world's large lakes. In: Tilzer M. M. & Serruya C. (eds). *Large Lakes: Ecological Structure and Function*. Springer-Verlag, New York, pp. 3–38.
- Hosper H. (1997) *Clearing Lakes*. Ministry of Transport, Public Works and Water Management, Institute for Inland Water Management and Waste Water Treatment, Lelystad, The Netherlands.
- Hubbell S. P. (1979) Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* **203**, 1299–1309.
- Hutchinson G. E. (1967) *A Treatise on Limnology* Volume II: *Introduction to Lake Biology and the Limnoplankton*. John Wiley and Sons, New York.
- Hutchinson G. E. (1973) Eutrophication: The scientific background of a contemporary practical problem. *Am. Scient.* **61**, 269–279.
- Hutchinson G. E. & Löffler H. (1956) The thermal classification of lakes. *Proc. Nat. Acad. Sci.* **42**, 84–96.
- Imberger J. & Patterson J. C. (1989) In: Hutchinson J. W. & Wu T. Y. (eds). *Advances in Applied Mechanics*. Academic Press, Cambridge, pp. 303–475.
- Johnson T. C. & Odada E. (eds) (1996) *Limnology, Climatology and Paleoclimatology of the East African Lakes*. Gordon and Breach, Toronto.
- Kilham S. S. & Kilham P. (1990) Tropical limnology: Do African lakes violate the 'first law' of limnology? *Verh. Internat. Verein. Limnol.* **24**, 68–72.
- Lewis Jr W. M. (1974) Primary production in the plankton community of a tropical lake. *Ecol. Monogr.* **44**, 377–409.
- Lewis Jr W. M. (1983) A revised classification of lakes based on mixing. *Can. Jour. Fish. Aquat. Sci.* **40**, 1779–1787.
- Lewis Jr W. M. (1987) Tropical limnology. *Ann. Rev. Ecol. Syst.* **18**, 159–184.
- Lewis Jr W. M. (1996) Tropical lakes: How latitude makes a difference. In: Schiemer F. & Boland K. T. (eds). *Perspectives in Tropical Limnology*. SPB Academic Publishers, Amsterdam, pp. 43–64.
- Lewis Jr W. M. & Levine S. N. (1984) The light response of nitrogen fixation in Lake Valencia, Venezuela. *Limnol. Oceanogr.* **29**, 894–900.
- Lodge D. M. (1998) Responses of lake biodiversity to global changes. In: Sala O. E., Chapin F. S. & Huber-Sannwald E. (eds). *Future Scenarios of Global Biodiversity*. Springer-Verlag, New York.
- Lowe-McConnell R. H. (1975) *Fish Communities in Tropical Freshwaters*. Longman, London.
- McGregor G. R. & Nieuwolt S. (1998) *Tropical Climatology*. John Wiley and Sons, Chichester.
- MacIntyre S. & Melack J. M. (1988) Frequency and depth of vertical mixing in an Amazon floodplain lake (L. Calado, Brazil). *Verh. Internat. Verein. Limnol.* **23**, 80–85.
- Melack J. M. (1976) Primary production and fish yield in tropical lakes. *Trans. Amer. Fish. Soc.* **105**, 575–580.
- Melack J. M. (1996) Recent developments in tropical limnology. *Verh. Internat. Verein. Limnol.* **26**, 211–217.
- Metcalf & Eddy Inc. (1991) *Wastewater Engineering: Treatment, Disposal, and Reuse*. 3rd Edition. McGraw-Hill Publishing Company, New York.

- Meybeck M. (1979) Concentrations des eaux fluviales en elements majeurs et apports en solution aux oceans. *Rev. Geol. Dyn. Geogr. Phys.* **21**, 215–246.
- Morris D. P. & Lewis Jr W. M. (1988) Phytoplankton nutrient limitation in Colorado mountain lakes. *Freshw. Biol.* **20**, 315–327.
- Mtada O. S. M. (1986) Thermal stratification in a tropical African reservoir (the Guma Dam, Sierra Leone). *Arch. Hydrobiol.* **107**, 183–96.
- Saunders III J. F. & Lewis Jr W. M. (1988) Dynamics and control mechanisms in a tropical zooplankton community (Lake Valencia, Venezuela). *Ecol. Monogr.* **48**, 337–353.
- Scheffer M. (1998) *Ecology of Shallow Lakes*. Chapman and Hall, London.
- Serruya C. & Pollinger U. (1983) *Lakes of the Warm Belt*. Cambridge University Press, Cambridge.
- Talling J. F. (1976) The depletion of carbon dioxide from lake water by phytoplankton. *J. Ecol.* **64**, 79–121.
- Talling J. F. (1979) Factor interactions and implications for the prediction of lake metabolism. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **13**, 96–109.
- Talling J. F. (1992) Environmental regulation in African shallow lakes and wetlands. *Hydrobiol. Trop.* **25**, 87–144.
- Talling J. F. & Lemoalle J. (1998) *Ecological Dynamics of Tropical Inland Waters*. University Press, Cambridge.
- Toerien D. F. & Cavari B. (1982) Effect of temperature on heterotrophic glucose uptake, mineralization, and turnover rates in lake sediments. *Appl. Environ. Microbiol.* **43**, 1–5.
- Tundisi J. G. (1994) Tropical South America: Present and perspectives. In: Margalef R. (ed). *Limnology Now: A Paradigm of Planetary Problems*. Elsevier, Amsterdam.
- Unger P. A. & Lewis Jr W. M. (1990) Population ecology of the pelagic fish, *Xenomelaniris venezuelae* (Atherinidae), in Lake Valencia. *Ecology* **72**, 440–56.
- Welch E. B. (1992) *Ecological Effects of Wastewater*. Chapman and Hall, London.
- Welcomme R. L. (1979) *Fisheries Ecology of Floodplain Rivers*. Longman, New York.
- Wetzel R. G. (1992) Gradient-dominated ecosystems: Sources and regulatory functions of dissolved organic matter in freshwater ecosystems. *Hydrobiologia* **229**, 181–198.