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## Comparisons of phytoplankton biomass in temperate and tropical lakes

*Abstract*—Phytoplankton biomass is compared for 16 temperate and 5 tropical lakes that are sufficiently deep to develop seasonal stratification. The ratio of annual mean to maximum biomass averages 0.45 for tropical lakes and is significantly lower for temperate lakes (0.36). Seasonal (3-month peak) ratios of mean to maximum biomass (~0.7) do not differ for oligotrophic tropical and temperate lakes, but the ratios for temperate lakes fall below those of tropical lakes at higher trophic states. Tropical lakes of given trophic state have a higher minimum biomass than temperate lakes of the same trophic state; both temperate and tropical lakes show a strong increase in minimum biomass with increasing maximum biomass. The relative range of annual variation for temperate lakes is ~40% greater than for tropical lakes. Differences in the stability of layering and in the duration of seasonal mixing probably explain much of the difference in variability of biomass for tropical and temperate lakes that stratify.

A large fraction of the variation in annual average biomass among lakes can be explained by the length of the growing season, which varies with latitude. Annual primary production, a close correlate of annual mean biomass, appears to be related to latitude for this reason (Brylinsky and Mann 1973; Melack 1979). Other factors, such as water-column stability, that affect phytoplankton biomass and production are also likely to vary with latitude. Even so, latitudinal gradients have been studied very little, particularly between middle latitudes and the tropics. The weak base of information on tropical lakes has probably discouraged such comparisons.

Quantitative information on phytoplankton biomass in tropical lakes now allows some simple comparisons with temperate lakes. Three types of temperate-tropical

comparisons are made here: maximum biomass with annual and seasonal mean biomasses, maximum biomass with the annual range of variation in biomass, and mean biomass with total phosphorus at the beginning of the growing season.

A minimum duration of sampling for latitudinal biomass comparisons, given the strong seasonal variation of both temperate and tropical lakes, is 1 yr. A minimum frequency, given the need to represent all seasons with at least a few samples, is monthly. Application of these minimum requirements, with sufficient flexibility to admit a few important 10-month sample series, results in the identification of data sets for 32 tropical lakes from the published literature and a few unpublished studies. The lakes belong to four groups, each of which must be considered separately: lakes that are sufficiently deep to develop seasonal stratification, lakes that are too shallow to develop seasonal stratification, floodplain lakes, and reservoirs. The present analysis is limited to the first category, i.e. natural lakes that are sufficiently deep to stratify seasonally. Information is available for five such lakes (Table 1).

Comparative data for lakes of temperate latitude conform to the same criteria as described above for tropical lakes. Application of the screening criteria resulted in the elimination of many data sets because few temperate lakes are sampled during winter. The 16 temperate lakes listed in Table 1 all meet the screening criteria.

All five of the tropical lakes that can presently be analyzed are large. Although small tropical lakes that stratify seasonally are quite numerous, no such lakes have been studied in sufficient detail to provide the data for analysis. Because of the bias toward large lakes, an effort has been made to include as many large temperate lakes as possible for comparison.

Quantitative estimates of algal biomass

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Table 1. Stratifying tropical lakes for which phytoplankton biomass data are available over periods of 10 months or more, and of temperate lakes used in comparisons.

Lake	Location	Elevation (m)	Area* (km <sup>2</sup> )	Depth (m)	
				Mean	Max
<b>Tropical lakes</b>					
Valencia	10°N, 68°W	425	360	19	39
Lanao	8°N, 124°E	702	357	60	112
Victoria	2°S, 33°E	1,134	66,250	40	79
Titicaca	16°S, 69°W	3,800	8,100	107	281
Tanganyika	7°S, 30°E	773	34,000	700	1,470
<b>Temperate lakes</b>					
Wintergreen	53°N, 85°E	891	1	3.5	6.3
Croze Mere	54°N, 3°W	86	1	4.8	9.2
Ontario-Hamilton	43°N, 80°W	246	500	13	22
Zurich	47°N, 9°E	500	65	51	136
Leman	46°N, 6°E	400	582	153	310
Washington	48°N, 122°W	0	88	33	63
De Vila	42°N, 3°E	175	1	3.3	6.5
Ammersee	48°N, 11°E	534	48	38	83
Walensee	47°N, 9°E	500	24	100	145
Esrom	56°N, 12°E	0	1	12.3	22
Bodensee	48°N, 9°E	395	500	100	252
Attersee	48°N, 14°E	467	46	84	171
Vierwaldstattersee	47°N, 8°E	500	114	104	214
Taupo	39°S, 176°E	2,391	612	97	—
Huron	44°N, 82°W	580	59,510	76	223
Tahoe	39°N, 120°W	1,898	499	313	501

\* Shown as 1 if < 1 km<sup>2</sup>.

are used here (biovolume, Chl *a*, or algal C). Chlorophyll is adopted as the standard index of biomass; biovolume is converted to chlorophyll with a conversion factor of 0.004 mg Chl *a* per mg wet biomass. This conversion lies near the median of reported values (e.g. Bailey-Watts 1978; Gibson et al. 1971). Conversion involves inaccuracies because of variability in the ratio of chlorophyll to biomass, but the error from this source is unlikely to influence conclusions because it is a source of variation rather than of bias, and because comparisons are made over a very broad range of biomass.

If information is available for more than 1 yr, only complete years can be used in the analysis without introduction of bias. Thus an 18-month data set offers only 12 months of useful data for present purposes.

An analysis of phytoplankton biomass can be greatly facilitated by use of a scaling factor; variation within a year for a given lake can then be judged in relation to the scaling factor (cf. Smith 1990). The most useful scaling factor is the maximum phytoplankton biomass that a lake can accumulate un-

der resource-limiting conditions. Use of maximum biomass as a scaling factor can be misleading, however, if it is applied to phytoplankton communities that fail to become resource limited. With the exception of some obvious cases involving sustained high inorganic turbidity or advective losses associated with short hydraulic residence times, a strong case can be made for occurrence of resource limitation of phytoplankton at some time of the year in most lakes; it is the principle underlying quantitative relationships between nutrient loading and phytoplankton biomass.

Use of the observed maximum biomass as a scaling factor presents several serious difficulties. First, considerable stochastic variation can be expected in the observed maxima for sets of samples drawn from a given frequency distribution. Second, the observed maximum is dependent on the size of the sample series. For example, for a normal distribution the expected (mean) value for the maximum in a series of 10 samples is 1.5 standard deviations above the mean; for 20 samples it is 1.9 standard deviations

above the mean. A third problem is that the observed maximum is more likely than most other values to represent error.

A more useful way of quantifying the maximum biomass is to calculate a predetermined, high percentile that is characteristic of the underlying distribution of values for the lake. This approach is used commonly in hydrology to estimate the return frequency for high discharges (Chow 1964). This approach frees the estimate from bias associated with sample size, and it greatly reduces the influence of unrecognized sources of variation and single-sample error. For present purposes, the 95th percentile of algal biomass for a given year will be designated the maximum biomass for that year.

The form of the frequency distribution for biomass must be determined before the 95th percentile biomass can be calculated. Frequency distributions for phytoplankton biomass have not been well studied. For individual taxa, biomass frequency distributions appear to be typically skewed toward higher abundances (i.e. the mean is considerably greater than the median; Lewis 1977), but it is not obvious that this relationship would carry over to total biomass for a mixture of species. Examination of the frequency distribution of total biomass for both tropical and temperate lakes, however, typically showed skew toward higher biomass (Fig. 1). When the data show strong skew, logarithmic transformation typically normalizes the distribution.

Although detailed frequency analysis was not possible for most lakes because of the small number of data points, convergence of the mean and the median was used as an index of the success of logarithmic transformation in normalizing the biomass data. For all 5 tropical lakes and 13 of the 16 temperate lakes, logarithmic transformation resulted in convergence of the mean and the median. Data for three of the temperate lakes did not benefit from transformation and were analyzed without it (Walensee, Bodensee, and Lake Zurich).

The 95th percentiles and 5th percentiles were calculated for each lake (Table 2); the gap between these two (90% range) is used as a measure of variation. This statistic is

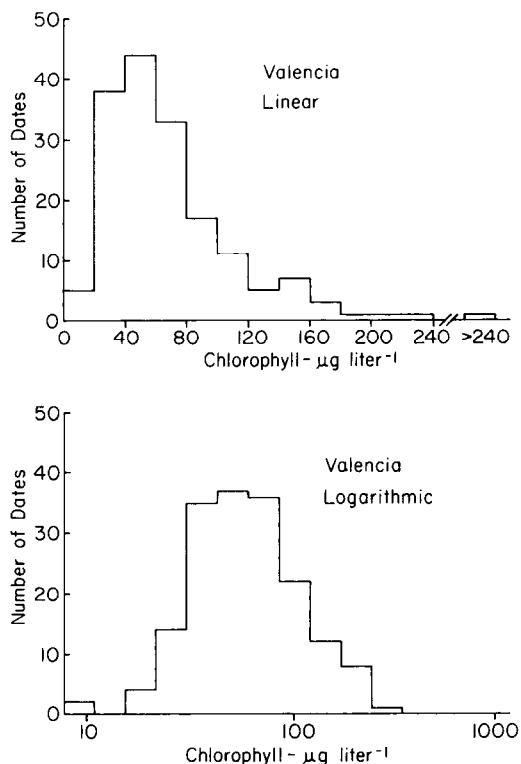


Fig. 1. Frequency histograms for phytoplankton biomass in Lake Valencia, illustrating the skew that is characteristic of untransformed phytoplankton biomass data. The lower panel shows the normalizing effect of logarithmic transformation.

superior to the observed range because it does not depend on sample size or other factors that affect the maximum as well as the minimum, i.e. it is far more stable than the observed range. The 90% range, when expressed as a percent of the mean, is an indication of relative variability for lakes of different biomass (Table 2).

The ratio of the mean biomass to the 95th percentile biomass is a measure of the constancy with which a lake can sustain its maximum biomass, which in turn is a measure of its efficiency in using nutrients: a lake with constant maximum biomass has the highest efficiency in use of nutrients. Deviations from the maximum biomass are caused by inability of the phytoplankton to retain the full inventory of nutrients in the form of biomass. If calculated on an annual basis, the ratio of mean to maximum biomass is sensitive to the length of the growing

Table 2. Phytoplankton biomass characteristics of 5 stratifying tropical lakes and 16 temperate lakes. Sources: Lewis 1974, 1986; Talling 1966; Vincent et al. 1984; Hecky and Kling 1981; Manny 1972; Reynolds 1973; Harris et al. 1980; Sommer 1986; Edmondson 1969; De Emiliani 1973; Jonasson and Kristiansen 1967; White et al. 1980; Brown and Manny 1983; Goldman 1974.

Lake	N	Mean Chl ( $\mu\text{g liter}^{-1}$ )		Percentiles		C.V. (%)	Relative 90% range (%)	Ratio of mean to max		
		Year	Season*	95th	5th			Annual	Seasonal	
Tropical lakes										
Valencia	171	75	110	170	22	76	197	0.44	0.65	
Lanao	52	6.9	11	16	2.1	60	197	0.44	0.69	
Victoria	18	3.1	4.0	5.4	1.7	33	118	0.58	0.75	
Titicaca	22	2.3	3.9	5.8	0.56	68	229	0.39	0.67	
Tanganyika	27	0.85	1.6	2.1	0.20	103	220	0.41	0.80	
Temperate lakes										
Wintergreen	45	29	67	110	2.20	122	372	0.26	0.61	
Croze Mere	144	33	49	92	6.40	97	255	0.36	0.53	
Ontario-Hamilton	50	31	35	81	8.40	53	233	0.38	0.43	
Zurich	12	7	16	18	<0.01	97	260	0.38	0.88	
Leman	20	8.2	15	40	0.48	101	483	0.20	0.38	
Washington	95	9.9	19	35	1.30	78	336	0.28	0.55	
De Vila	19	12	20	30	3.00	79	229	0.39	0.66	
Ammersee	24	4.8	12	16	0.58	118	311	0.31	0.75	
Wallensee	12	4	7.4	9.7	<0.01	87	242	0.41	0.76	
Esrom	16	4.5	5.3	12	1.00	79	253	0.36	0.44	
Bodensee	35	3.6	6.9	10.1	<0.01	111	282	0.35	0.68	
Attersee	11	2.4	4.0	6.5	0.58	74	243	0.37	0.62	
Vierwaldstattersee	12	2.1	5.0	5.2	0.41	124	231	0.40	0.96	
Taupo	12	1.5	2.5	2.8	0.65	50	147	0.52	0.88	
Huron	24	0.81	1.4	1.6	0.31	65	164	0.49	0.86	
Tahoe	82	0.22	0.42	0.68	0.03	113	300	0.32	0.62	

\* Season—the 3-month interval with highest biomass.

season and to the degree of suppression of biomass during those portions of the year that are least favorable for phytoplankton growth. A seasonal ratio can also be calculated, but there must be some common basis of calculation that allows a direct comparison between temperate and tropical lakes. For present purposes, the comparison is based on the 3-month interval of highest mean biomass during the year, as determined from 3-month running averages of biomass for each lake. Definition of the seasonal average in this way does not require a priori identification of the length of the growing season for a given category of lakes.

The seasonal ratio of mean to maximum, in contrast to the annual ratio of mean to maximum, is insensitive to suppression of biomass at times of the year when conditions are particularly unfavorable for phytoplankton. The seasonal ratio is sensitive to the ability of a lake to sustain biomass, which requires recycling of nutrients in the mixed layer. Thus comparisons of the an-

nual and seasonal ratios allow some separation of two major points of contrast for temperate and tropical lakes: the length of the growing season, and the efficiency of nutrient recycling in the upper water column during the growing season.

The coefficient of variation (C.V., ratio of standard deviation to mean, expressed as a percent), calculated from untransformed data, has been used in the past as an index of variability in phytoplankton biomass or production (e.g. Melack 1979). The C.V. when calculated in this manner is likely to be misleading because of the large and variable amount of skew in the data. The ratio of any percentile range to the mean can serve as an index of relative variability, but it should be calculated from the actual frequency distributions rather than the normal distribution, given the likelihood of skew. The C.V. was calculated for each lake in the comparison series and is reported in the data summaries but is not used in the analysis. Because of distortion caused by skew, the

Table 3. Summary of phytoplankton biomass statistics. Regression equation, both variables logarithmically transformed; the independent variable is logarithm of maximum biomass (95th percentile,  $\mu\text{g Chl } a \text{ liter}^{-1}$ ). Asterisks: \*— $P \leq 0.05$ ; \*\*— $P \leq 0.01$ .

Dependent variable	Mean (SD)	Slope (SE)	Intercept	R
Tropical lakes				
Annual mean: max	0.45(0.07)	—	—	—
Seasonal mean: max	0.71(0.05)	—	—	—
Annual min ( $\mu\text{g liter}^{-1}$ )	5.2(8)	1.00(0.00)	-0.87	0.96**
Relative 90% range (%)	192(39)	—	—	—
Temperate lakes				
Annual mean: max	0.36(0.07)	-0.077(0.038)	-0.36	0.48*
Seasonal mean: max	0.66(0.17)	-0.100(0.043)	-0.08	0.52*
Annual min ( $\mu\text{g liter}^{-1}$ )	1.6(2)	0.81(0.35)	-1.33	0.53**
Relative 90% range (%)	271(75)	—	—	—

C.V. accounts for only 30% of the variability in relative 90% range calculated from the actual frequency distributions. For present purposes, variation is expressed as relative 90% range rather than C.V.

For tropical lakes, the average ratio of mean to maximum biomass is 0.45; for temperate lakes it is lower by a quarter (Table 3; the difference in means is significant at  $P < 0.05$ ). For temperate lakes, the annual ratio declines with increasing trophic state. No statistically significant decline can be demonstrated for tropical lakes (Table 3, Fig. 2). A weak decline or a decline accompanied by considerable scatter would not be evident in the data for tropical lakes, however, because of the small number of data points. Future accumulation of data on tropical lakes could show that such a decline does exist, but the present data are not even suggestive of it.

As expected, the seasonal biomass ratios are consistently higher than the annual ratios. Temperate lakes show strongly declining ratio with increasing maximum biomass. Tropical lakes show no significant decline, although a weak decline is suggested by the data ( $P = 0.07$ ), but the slope for temperate lakes is not within the 95% C.L. for tropical lake data ( $-0.040$ , SE 0.018). For temperate lakes, decline would account for a decrease in the ratio from 0.8 to 0.5 over the trophic spectrum between 1 and 100  $\mu\text{g Chl } a \text{ liter}^{-1}$ . Tropical and temperate lakes of very low maximum biomass have essentially identical seasonal ratios ( $\sim 0.7$ ).

In more productive lakes, seasonal ratios for tropical and temperate lakes diverge; they are lower for temperate lakes.

The annual minimum biomass increases significantly as the maximum increases in both temperate and tropical lakes (Table 3). The rate of increase is much greater for tropical lakes; tropical lakes sustain biomass more readily across seasons than do temperate lakes. The relative range of variation for phytoplankton biomass is not significantly dependent on trophic state in either temperate or tropical lakes. The mean relative range of variation is 40% larger for temperate lakes than for tropical lakes ( $P < 0.05$ ).

Measurements of total P are available for only two of the five stratifying tropical lakes for which phytoplankton biomass is available. For Lake Victoria, Talling (1966) gave monthly P values for 1 yr. For Lake Valencia, 171 sets of analyses are available over a period of 5 yr. For the other three lakes, only soluble P fractions have been measured. It is possible, however, to use measurements of soluble P in conjunction with phytoplankton biomass estimates to estimate total P in the three lakes.

For Lake Tanganyika, Hecky and Kling (1981) reported total dissolved P at approximately monthly intervals over a span of 10 months. To this amount can be added P incorporated in phytoplankton biomass. A conservative estimate of the P incorporated in phytoplankton biomass is  $\sim 1\%$  of dry mass or, for simplicity, a mass equal to

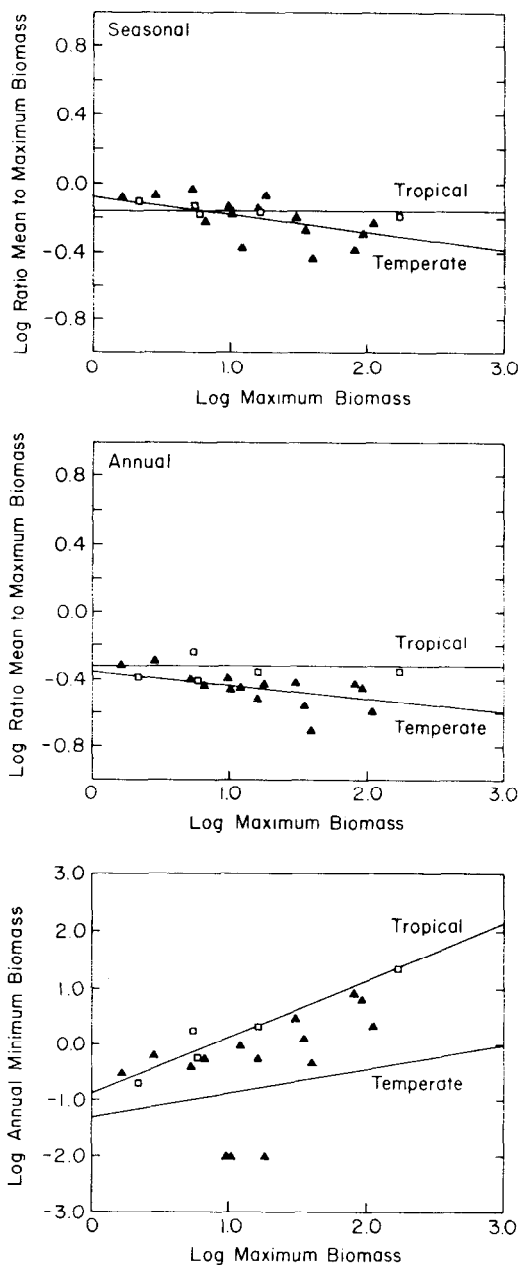


Fig. 2. Relationships of the maximum phytoplankton biomass to the annual and seasonal ratios of mean to maximum, and to the annual minimum biomass (5th percentile) of tropical ( $\square$ ) and temperate lakes ( $\blacktriangle$ ). Table 3 gives statistical information on uncertainty.

the amount of Chl *a* (Nalewajko and Lean 1980). Under some circumstances, phytoplankton may contain more than twice this much P on a weight basis.

For Lake Lanao and for Lake Titicaca, only measurements of soluble reactive P (SRP) are available. To these measurements can be added a P allowance for phytoplankton biomass equal to the amount of Chl *a* for times coinciding with P measurements. Soluble organic P is therefore omitted from these estimates.

The standard to be used here for comparison with tropical lakes is the Dillon and Rigler (1974) equation, which relates total P for the water surface in spring to average Chl *a* for the growing season. For the five tropical lakes, the 3-month interval showing maximum biomass is designated for the growing season. The P concentrations that precede the growing season are then used in the analysis; they are among the highest P concentrations in the upper water column for the entire year, as would be the case during spring mixing in temperate lakes.

Because measurements of the P fractions are incomplete in all but two cases, the estimates for three of the lakes will be lower than the true total P values. Several factors, however, reduce the significance of this deficiency in the data. In Lake Titicaca and Lake Tanganyika during periods of deep mixing, the amount of phytoplankton biomass is so low that any possible errors in estimating the P content of phytoplankton biomass are inconsequential. Also, in the two lakes for which dissolved organic P is unrepresented (Lanao and Titicaca), the amounts of SRP are sufficiently high that the inclusion of organic P would be very unlikely to change the total soluble P very much.

It seems unlikely from the data (Fig. 3) that tropical lakes will cluster above the Dillon and Rigler relationship, as might be expected given the higher efficiency of nutrient recycling indicated by the high ratio of seasonal mean to maximum for tropical lakes. This pattern may be explained by a higher incidence of N limitation in tropical lakes that stratify. Among the lakes represented in Fig. 3, Lanao, Victoria, and Titicaca frequently show  $\text{NO}_3^-$  concentrations below the detection limit ( $1-5 \mu\text{g N liter}^{-1}$  as  $\text{NO}_3^-$ ) but almost always maintain concentrations of SRP above the detection limit (i.e.  $>1-5 \mu\text{g P liter}^{-1}$  as  $\text{PO}_4^{3-}$ ). Although less in-

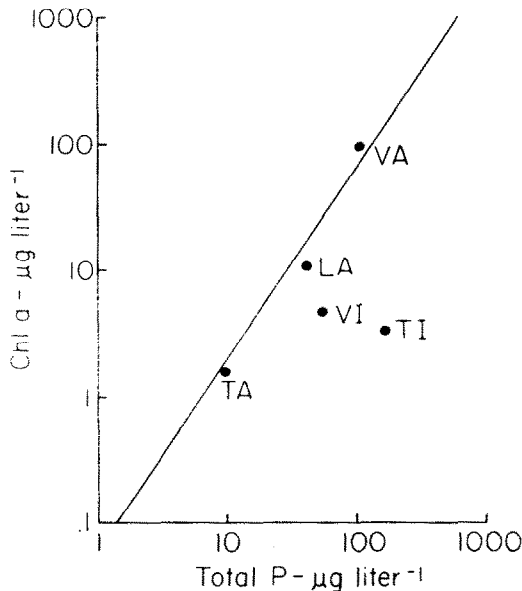


Fig. 3. Total P during mixing before the growing season in relation to mean phytoplankton biomass for the growing season (3-month period of maximum biomass) for tropical lakes shown in comparison to the line representing the Dillon and Rigler equation.

formation is available for Lake Tanganyika,  $\text{NO}_3^-$  apparently becomes completely depleted there as well (Degens et al. 1971). Lake Valencia more often shows complete depletion of  $\text{NO}_3^-$  than of SRP and responds most markedly to the addition of  $\text{NO}_3^-$  during enrichment experiments (Lewis 1986). In Lake Titicaca, experimental studies by Vincent et al. (1984) indicate N limitation;  $\text{NO}_3^-$  concentrations fall to  $<4 \mu\text{g N liter}^{-1}$  as  $\text{NO}_3^-$  for 7 months of the year concurrently with  $\text{SRP} > 30 \mu\text{g liter}^{-1}$ . Thus the circumstantial evidence for N deficiency is strong for stratifying lakes. The same may not be true of shallow, nonstratifying lakes (Melack et al. 1982; Kalff 1983). N deficiency would reduce the strength of the relationship between total P and phytoplankton biomass and would tend to cause the biomass values to cluster below the Dillon and Rigler relationship, despite more efficient P cycling mechanisms.

Seasonal mixing of tropical lakes is relatively brief (typically no more than 2 months) and is often interrupted by periods of water-column stability during which phytoplankton biomass may be regenerated

through rapid photosynthesis near the surface (Lewis 1987). Thus the brevity of the seasonal mixing and the intermittent stability that is favored by high rate of density change with heat uptake at the warm temperatures of lowland tropical lakes together ameliorate the most severe suppression of biomass that is often associated with mixing in temperate lakes. This effect contributes to the tendency of tropical lakes to have a higher minimum biomass and of the minimum biomass to increase strongly in relation to the mean biomass in tropical lakes. In addition, it is probably part of the explanation for higher ratio of annual mean to maximum in tropical lakes and for the lower relative variation in tropical lakes, although numerous other factors may also be involved.

During the growing season, a limiting nutrient is typically depleted and biomass will decline steadily if nutrients are not resupplied to the mixed layer from deeper layers or sediments. One would expect the growing season decline to be especially strong in tropical lakes, where seasonal stratification may persist over intervals as long as 9 months without complete mixing. The stability of layering in tropical lakes is far lower, however, than it is in temperate lakes during the growing season (Lewis 1987). For this reason, irregular episodes of mixed-layer thickening are more likely in tropical lakes. Irregular partial mixing brings nutrients back to the euphotic zone, where they can be used in the regeneration of biomass. This process increases the efficiency of nutrient use during the growing season in tropical lakes and is at least one cause of higher seasonal ratios of mean to maximum biomass in tropical lakes. The importance of nutrient reuse becomes progressively greater with increasing productivity, which could account for the divergence in seasonal ratios of mean to maximum biomass for temperate and tropical lakes along the trophic spectrum. Contrasts among stratifying lakes of temperate and tropical latitudes that are explained primarily by differences in the mechanisms of stratification and mixing will not apply to shallow lakes, which show substantially less seasonal variability than deep lakes (Melack 1979).

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