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Comparative transparency, depth of mixing, and stability of stratification in lakes of Cameroon, West Africa[1]

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Abstract

Morphometry, oxygen concentration, temperature, and transparency were studied in 39 natural lakes in Cameroon, West Africa. Thermal profiles from 31 of the lakes and data from published studies were used to calculate stability of thermal stratification and evaluate morphological correlates of mixing depth. Twenty-six lakes showed some degree of stratification and 17 had distinct thermoclines and well-developed, anoxic hypolimnia. Total stability of the water column ranged from 0 to 5,784 J m^{-2}. The high values were similar to or greater than those of other tropical and temperate lakes. Lake depth seems to exert a stronger influence on stability than does lake area, but depth or stability measures alone provide little information about heat distribution or mixing regime. A strong positive relationship between water transparency and thermocline depth in both tropical and temperate lakes suggests that reductions in buoyant resistance to vertical mixing, caused by deeper penetration of solar radiation, are important in establishing mixing depths in various lakes. Comparisons of persistent thermocline depth in tropical vs. temperate lakes, regardless of size, indicate that mixing depths in tropical lakes are often greater than those in their temperate counterparts. This difference is caused in part by the narrow ranges of temperature and smaller absolute density gradients in these tropical lakes, against which the mixed layer is deepened.

Knowledge concerning the formation and maintainence of the upper mixed layer in oceans and lakes has expanded greatly in recent years (Phillips 1977; Imberger 1985). Entrainment of deeper, denser water into the base of the epilimnion is the primary mechanism of mixed-layer thickening. The turbulent kinetic energy required has been shown to come from stirring processes such as wind mixing or penetrative convection (Kraus and Turner 1967; Foster 1971; Woods and Barkmann 1986) and from shear production within boundary layers of the epilimnion (Pollard et al. 1973; Dillon and Powell 1979; Price et al. 1986). When coupled with water transparency and meteorological data, these mechanistic approaches can be used to model and predict the vertical transport of heat and momentum on both diurnal and seasonal time scales (Holloway 1980; Woods 1980; Spigel et al. 1986). Morphological features may also influence the integrated response of mixed layers to climate, as shown by the positive correlation in temperate lakes between summer thermocline depth and lake fetch or area (Gorham and Boyce pers. comm.; Patalas 1984).

Given these advances in understanding of the structure and energetics of mixed layers, it is surprising that in tropical lakes even the most fundamental information, such as persistent thermocline depth and stability of stratification, is so limited (Lewis 1984). In Lake Titicaca heat transfers have been found to dominate diurnal mixing (Vincent et al. 1984), and Henderson-Sellers (1984) showed that horizontal advection controlled mixing depths in a subtropical reservoir. MacIntyre and Melack (in press) discussed the frequent, nonseasonal mixing of shallow Amazon floodplain lakes, and Wood et al. (1976) presented a climatological study of seasonal mixing and stratification in several Ethiopian crater lakes. Finally, Lewis (1973, 1983) suggested that the small density differences across narrow temperature ranges, typically found in tropical lakes, plus small Coriolis effects, could explain the deep and variable mixing depths in lakes Lanao and Valencia. Certainly the basic mechanisms of mixed-layer thickening, i.e. stirring from above and shear generated at the base of the epilimnion, occur at all latitudes. It is the relative importance of these processes that we know little about. Regardless of the

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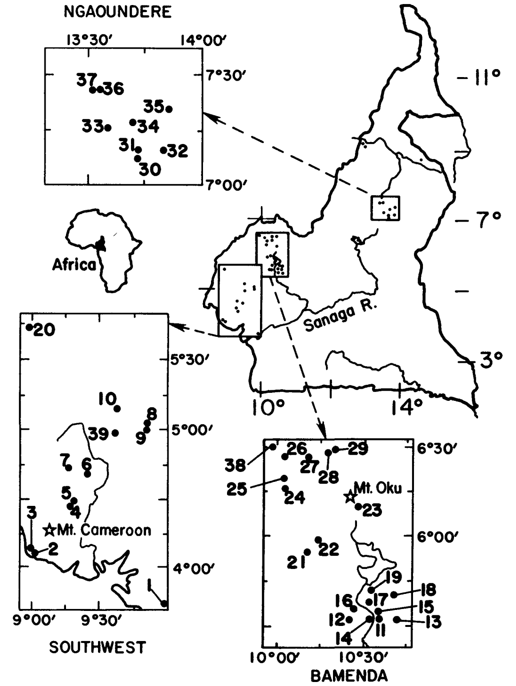

Fig. 1. Location map. Numbers correspond to names of lakes in Table 1.

dominant process of mixed-layer thickening, however, a given energy input applied to a smaller density gradient will produce a deeper mixed layer.

The present study of 39 natural lakes in Cameroon, West Africa, was designed to test the hypothesis that persistent thermocline depths are deeper in tropical lakes than would be expected in similar temperate lakes, to examine the morphometric features of these lakes as they relate to overall stability of the water column, and to identify patterns of light attenuation within and between lakes and test their relationship to mixing and stratification. The Cameroon lakes, which were studied during February–October 1985, September 1986, and May 1987, offer great diversity and are thus ideal for comparative research (Kling 1987*a*). Previous studies of physical limnology in these lakes have been restricted to the bathymetric survey of eight lakes (Hassert 1912) and to observations of temperature in three lakes (Green et al. 1973, 1974; Corbet et al. 1973).

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Description of the study area

Cameroon lies on the coast of West Africa between 8° and 16°E long (Fig. 1). Nearly all of its lakes lie on or close to the central highland backbone of the country. Exceptions include deltaic lakes at the mouth of the Sanaga River and lakes beside the Benue River in the north. There are three lake districts, each of which was included in the sampling program: the Southwest, the Bamenda, and the Ngaoundere (Fig. 1; Table 1). The lakes are distributed from 3°47′ to 7°26′N lat, and range in elevation from Ossa at sea level to Bambili at 2,264 m asl (Table 1).

At least 34 of the 39 study lakes have formed in volcanic basins. These lakes occur mainly in the trachytic and Recent basaltic series, although their precise ages are unknown. Many of the lakes are maars, surrounded by cliffs and tuff rings of pyroclastic material from 5 to 200 m high (Table 1). Monoun and Nyos are two volcanic lakes of special interest, as they are the sites of lethal gas releases in 1984 and 1986 (Kling et al. 1987).

Methods

Depths were measured along transects with a sounding line or a seismic recorder and transceiver or were taken from Hassert (1912). The geographic features presented in Table 1 were obtained from maps. A YSI model 46 telethermometer, readable to 0.05°C, and thermistor probe were used to measure the vertical distribution of temperature. The meter and probe were calibrated frequently against a certified ther-

Table 1. Geographic and morphometric features of Cameroon lakes: median crater rim height above the lake surface—rim; maximum depth—z_{max}; mean depth—$\bar{z}$; volume development—$3\bar{z}/z_{max}$; relative depth—z_r.

	Lake	Elev (m asl)	Area (ha)	Rim	z_{max}	$\bar{z}$	$3\bar{z}/z_{max}$	z_r (%)
				(m)				
1	Ossa	1	1,300	10	—	—	—	—
2	Debundsha	54	6	40	13.5	—	—	4.88
3	S. Debundsha	54	1	10	—	—	—	—
4	Mboandong	143	20	5	—	—	—	—
5	B. Kotto	106	140	30	5.5	4.5	2.45	0.34
6	Barombi Mbo	301	415	100	110	68.7	1.87	4.78
7	Disoni	455	165	100	80	41.2	1.54	5.52
8	Manengouba-F	1,920	22	100	168	61.8	1.10	31.7
9	Manengouba-M	1,900	2	70	92	55.0	1.79	57.6
10	Beme	500	60	60	14.5	—	—	1.66
11	Mfouet	1,120	7	70	14	—	—	4.69
12	Baleng	1,374	8	70	52	—	—	16.3
13	Mfou	1,350	8	200	58	—	—	18.2
14	Negop Ghang	1,120	8	70	23	—	—	7.21
15	Monoun	1,080	53	20	96	25.8	0.81	11.7
16	Banefo	1,100	6	20	64	—	—	23.2
17	L. Monoun	1,100	25	30	49	—	—	8.69
18	Petponoun	1,120	30	3	12	—	—	1.94
19	Nchout	1,140	13	40	16	—	—	3.93
20	Ejagham	100	70	10	17	11.4	2.01	1.80
21	Bambuluwe	2,053	28	50	58	39.3	2.03	9.71
22	Bambili	2,264	28	100	4	—	—	1.49
23	Oku	2,227	243	80	52	32.0	1.85	2.96
24	Enep	697	50	200	78	—	—	9.78
25	Elum	960	50	120	35	—	—	4.39
26	Wum	1,177	45	20	124	48.4	1.17	15.5
27	Nyi	1,316	50	50	47	—	—	5.89
28	Nyos	1,091	158	70	208	111.7	1.61	14.7
29	Njupi	1,020	30	10	—	—	—	—
30	Gegouba	1,180	20	30	104	—	—	20.6
31	Ngaoundaba	1,160	10	30	62	—	—	17.4
32	Baledjam	1,249	25	15	13	—	—	2.3
33	Tizong	1,160	8	70	48	26.2	1.64	15.0
34	Massot	1,054	5	5	—	—	—	—
35	Mbalang	1,130	50	40	52	30.0	1.73	6.52
36	Dang	1,079	80	5	—	—	—	—
37	Bini	1,079	20	5	—	—	—	—
38	Benakuma	576	154	200	138	—	—	9.86
39	Edib	1,280	2	60	12.5	—	—	7.83

mometer traceable to the National Bureau of Standards. Water for oxygen analysis was collected with a 4-liter Van Dorn sampler, fixed immediately with Winkler reagents when brought to the surface, and titrated within 6 h with phenylarsine oxide. Electrical conductivity was measured in the field with a 0.1 scale cell, and the values were later corrected to 25°C (K_{25}).

Light attenuation was measured on clear days between 1100 and 1200 hours with a recently calibrated LiCor 185 quantum meter and 2-pi cosine sensor. The photon flux density of PAR (400–700 nm) was recorded in μEinst m^{-2} s^{-1}. Diffuse attenuation coefficients (k, m^{-1}) were taken as the slope estimate of the regression z on $\ln(H_z)$, where H_z is the downwelling PAR irradiance at depth z. Underwater light penetration was also estimated with a 20-cm Secchi disk.

Lake stability (S) was calculated following Idso (1973) and expressed in J m^{-2}. Water density increases due to chemical stratification were determined with the chemistry values in Kling (1987*a*) and Kling et al. (1987) and following the method presented in MacIntyre and Melack (1982) and Chen and Millero (1977). The waters of lakes

Table 2. Secchi depth and diffuse attenuation coefficients (k). N is the number of points used in regressions to calculate k. Values in parentheses are the standard errors of the estimates of k.

Lake	Secchi (m)	N	k (m^{-1})
Barombi Mbo 14 Feb 85	11.0	41	0.148(0.004)
Barombi Mbo 26 Feb 85	—	29	0.163(0.004)
Barombi Mbo 27 Feb 85	—	31	0.169(0.004)
Oku	10.9	26	0.178(0.002)
Disoni	10.0	31	0.158(0.006)
Benakuma	7.80	—	—
Mfou	5.60	—	—
Gegouba	5.55	35	0.300(0.007)
Negop Ghang	5.30	—	—
Wum	5.15	53	0.305(0.006)
Baleng	5.00	—	—
Manengouba-F	5.00	45	0.262(0.003)
Banefo	4.50	—	—
Beme	4.50	23	0.353(0.004)
Ejagham	3.95	69	0.425(0.004)
Tizong	3.95	77	0.343(0.002)
Petponoun	3.55	61	0.717(0.010)
Nchout	3.50	—	—
Mbalang	3.45	24	0.267(0.006)
Ngaoundaba	3.45	53	0.427(0.008)
L. Monoun	3.10	—	—
Baledjam	2.96	63	0.675(0.007)
Bambuluwe	2.45	51	0.517(0.010)
Debundsha	2.15	45	0.534(0.006)
Monoun	1.25	43	1.88 (0.024)
Mfouet 20 May 87	1.20	—	—
Mfouet 16 May 85	0.05	—	—
Edib	0.80	—	—
B. Kotto	0.75	36	1.70 (0.025)

Monoun and Nyos can be considered metastable and were highly charged with CO_2. Chemical stability in these two lakes was calculated ignoring the density contribution of this gas. This is necessary because measurements of CO_2 in situ are not available and because the fundamental fluid dynamics equations are inadequate to describe water movement in a gas-charged fluid. For example, the effervescence of CO_2 as water is brought from depth to the surface will produce not only a large increase in bulk buoyancy but also an increase in turbulence. Water column stability will thus be reduced independent of external energy inputs. Birge's (1916) work of the wind was calculated after Hutchinson (1957).

Results

Morphometric features—The morphometric features for 32 of the 39 lakes are listed in Table 1 (lake numbers correspond to numbers in Fig. 1). The smallest lake surveyed by boat was Edib (2 ha), and the largest was Barombi Mbo (415 ha). Lake Ossa has the greatest surface area (1,300 ha) of any lake in the country except Lake Chad and the reservoirs Bamendjing and Mbakaou; the median area of the 39 study lakes is only 28 ha. The deepest is Nyos (208 m), although it was not surveyed by boat before the 21 August 1986 gas release. Visual evidence for annual lake level fluctuations of 1–2 m was common. Most lakes were closed in the dry season and appeared to have surface outflow in the wet season.

The volume development of a lake is the ratio of lake volume to that of a cone of equal area and height and is given by three times the ratio of mean depth ($\bar{z}$) to maximum depth (z_m) (Hutchinson 1957). Values approaching 1.8 exceed those of most lakes but are typical for small, deep crater lakes. The value of 2.45 for Lake Kotto is extraordinary and results from a shoreline dropping steeply to a flat, expansive bottom. Relative depth (z_r) is the maximum depth as a percentage of the mean lake diameter (Hutchinson 1957). The center of a lake is usually closer to the bottom than to any shore. Apparently the Manengouba lakes have the fourth and fifth largest z_r values known (58 and 32%), after Lake Kauhako in the Hawaiian islands (z_r = 375%: Maciolek 1975), Lake Tritriva in Madagascar (z_r = 89%: Kling 1987*a*), and Lake Kanyangeye in Uganda (z_r = 71.5%: Melack 1978).

Transparency—Secchi depths ranged from 5 cm in Lake Mfouet to 11 m in Barombi Mbo (Table 2). The depth at which 1% of the surface irradiance of PAR remains ($z_{0.01}$) defines the euphotic zone (Talling 1971). The $z_{0.01}$ corresponding to the unusually low Secchi depth of the algal-rich Lake Mfouet is unknown; the lowest measured $z_{0.01}$ (2.61 m) was in Lake Monoun and the highest (29.67 m) was in Barombi Mbo.

Attenuation coefficients ranged from

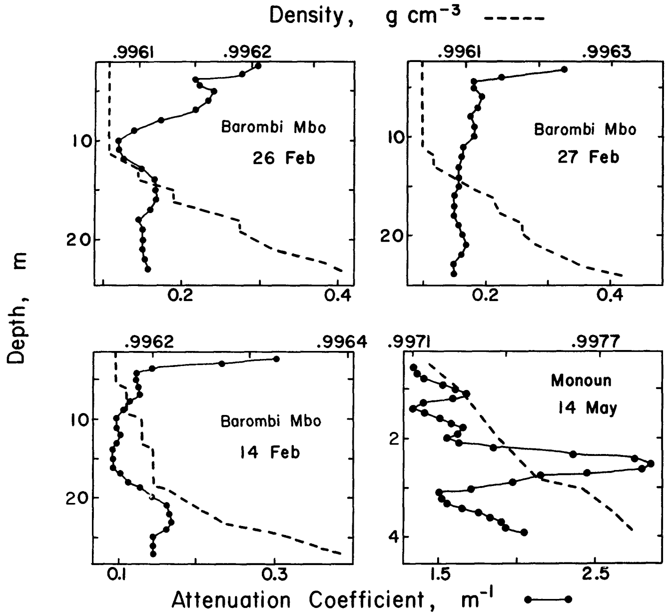

Fig. 2. Lagged attenuation coefficient (k_z) for thin water layers and total density of water plotted against lake depth (*see text*).

0.158 in Lake Disoni to 1.88 in Lake Monoun (Table 2). Coefficients for specific water layers were calculated by comparing each H_z to the irradiance in a layer of water just above it instead of to the irradiance at the surface. For example, the irradiance value H_8 in any lake was compared to H_7 instead of to H_0 in determining k (Fig. 2). These values best illustrate variation related to particulate material and mixing. In several lakes there was a sharp discontinuity and sudden increase in k between the epilimnion and the metalimnion that may be related to plankton or to an accumulation of particles in strong density gradients (Fig. 2). In Lake Monoun, for example, water samples indicated a large concentration of *Chaoborus* suspended at 2.5 m, but not at 1.5 or 3.5 m. The attenuation profiles for specific layers also reveal a slight increase in k for Barombi Mbo near the top of the metalimnion (Fig. 2). The effect moved from about 22.5 m on 14 February up to 15 m on 26 February, in concert with a rising metalimnion, but by 27 February the disturbance was positioned just above the metalimnion and was smaller. There was also a second disturbance at 21 m on this last date. Similar variations in the underwater light field have been observed in other strongly stratified lakes (Bowling and Tyler 1986).

Temperature—The temperatures of surface waters ranged from 18.6°C in Oku, at 2,227 m to 32.5°C in Debundsha at 54 m. Diurnal changes as high as 1.8°C at the surface were recorded in Barombi Mbo, and changes of 1°C were common in other lakes. In addition, there are seasonal and annual changes in surface temperatures. A 9-month thermal record for Barombi Mbo (Kling 1987*b*) showed that the early-morning surface temperature dropped steadily from 28.65°C in February to 26.65°C in September, closely following the annual cycle of air temperature and insolation. The surface temperature was 29.5°C in April 1972 (Green et al. 1973).

Thermal stratification—Of the 31 lakes whose thermal profiles were taken, 26 showed some degree of stratification. Seventeen of these lakes had distinct thermoclines and well-developed hypolimnia (Figs. 3–6). All lakes >18 m deep showed pronounced stratification. No lakes <18 m deep formed hypolimnia, although six had well-defined epilimnia and thermoclines (Figs.

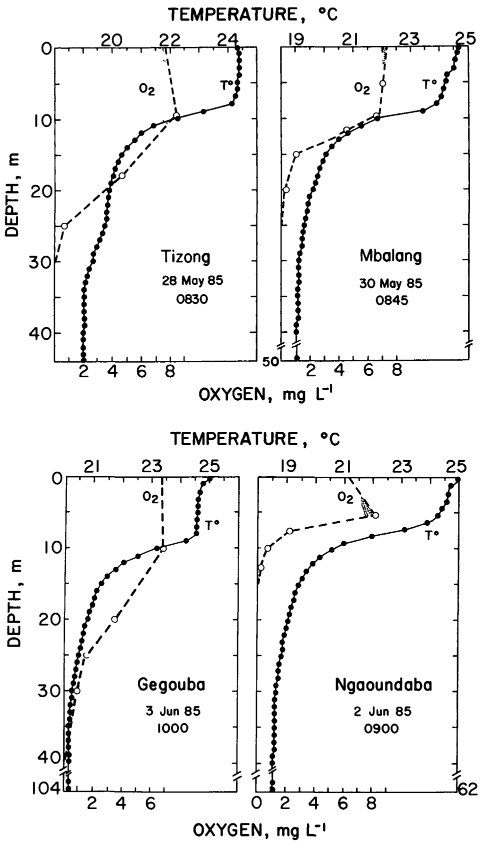

Fig. 3. Temperature and dissolved oxygen plotted against depth for the dates and times shown in representative lakes. Stippled area represents O_2 saturation >100% with respect to the surface. Thermal and oxygen data for lakes 11, 12, 13, 14, 16, 17, 19, 24, 38, and 39 (*see Table 1*) are given elsewhere (Kling 1987*a*).

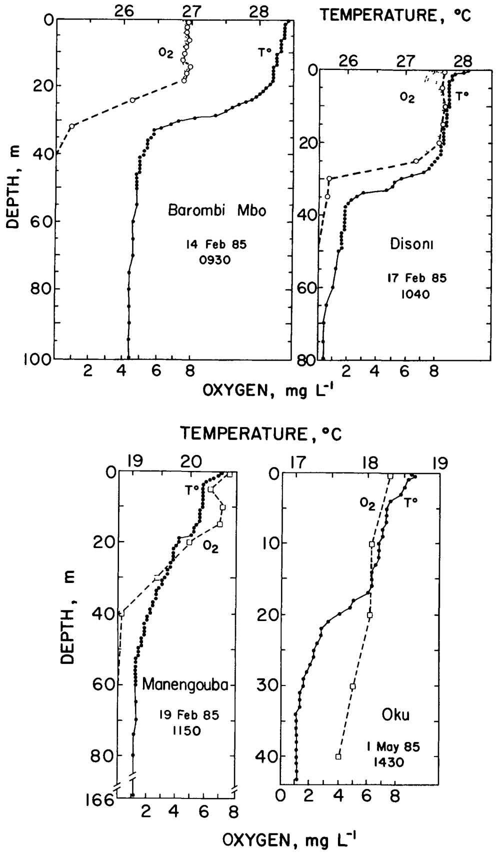

Fig. 4. As Fig. 3.

5, 6). Lake Kotto also was not stably stratified in March or April 1972 (Green et al. 1973, 1974). Five lakes had very striking metalimnia at depths between 8 and 12 m (temperature gradients of 2.0–3.5°C: Figs. 3, 5, and 6). Much deeper metalimnia (28–36 m) were found in Barombi Mbo and Disoni (Fig. 4). Green et al. (1973) reported that Barombi Mbo had a metalimnion around 18 m and was strongly stratified in April 1972. The greatest temperature range was in Lake Monoun, where the temperature decreased from 26.70°C at the surface to 20.40°C at 8 m, which included a single drop of 2.5°C between 3.5 and 4 m.

Inverse stratification at the surface was observed in several lakes. Evaporative cooling or sensible heat loss could explain the slight surface instability of Beme, Ejagham, Oku, and Tizong (Figs. 3–5), while very heavy rains the evening before the second profile was taken in Ejagham may have contributed to its inverse stratification. The diel variation in Ejagham is apparent from the profile taken in late afternoon compared to that of the following morning. Superficial diurnal stratification was clearly illustrated in Manengouba, Ejagham, and Oku (Figs. 4, 5), and is common in lakes exposed to intense solar heating (*see* Wetzel 1983; Vincent et al. 1984). The unusual profile for Monoun was distinguished by a maximum temperature at the surface, a minimum of 20.20°C at 10 m, and an increase to 21.80°C at 74 m (Fig. 5). Such dichothermic profiles have been observed in other tropical (Beadle 1981) and temperate (Hutchinson 1957) lakes.

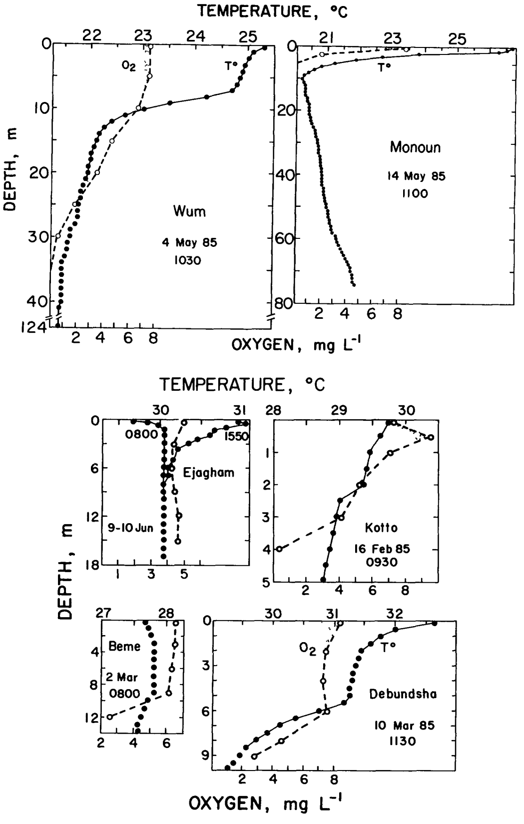

Fig. 5. As Fig. 3.

Multiple thermoclines found in some lakes were the most common deviation from the classical thermal profiles found in Gegouba, Ngaoundaba, and Mbalang. The formation of multiple thermoclines occurs when a relatively cool epilimnion is subjected to a period of surface warming in a time of low wind stress during which a second thermocline develops above the first. The clearest example is in Disoni, where a thermocline at 29 m formed over a deeper and sharper thermocline at 33.5 m (Fig. 4). Petponoun, Bambuluwe, and Tizong also showed evidence of a second thermocline, and two of the lakes of highest elevation, Oku (2,227 m) and Manengouba (1,920 m), exhibited intense vertical microstructure with many narrow, homogeneous temperature layers superimposed on the typical stratification curve (Fig. 4). These layering phenomena commonly occur in oceans and temperate lakes (Simpson and Woods 1970; Dillon et al. 1975), although strong secondary thermoclines may be more persistent in tropical lakes (Lewis 1983).

Oxygen—Maximal oxygen concentrations were measured in the metalimnia of Ngaoundaba, Baledjam, and Tizong, and in the upper mixed layer of all other lakes. Oxygen saturation of surface water varied from 66% in Ejagham to 121% in Disoni, and oxygen saturation in excess of 100% occurred throughout the epilimnion in several lakes (Figs. 3–6). Metalimnetic oxyclines were well defined, and anoxic or nearly anoxic conditions were found in the hypolimnia of all stratified lakes. In the shallow Petponoun and Baledjam, water became anoxic below the bottom of the metalimnion at 10 m, while in lakes >50 m deep the anoxic boundary ranged from 15 to 50 m (Figs. 3–6). The anoxia beginning

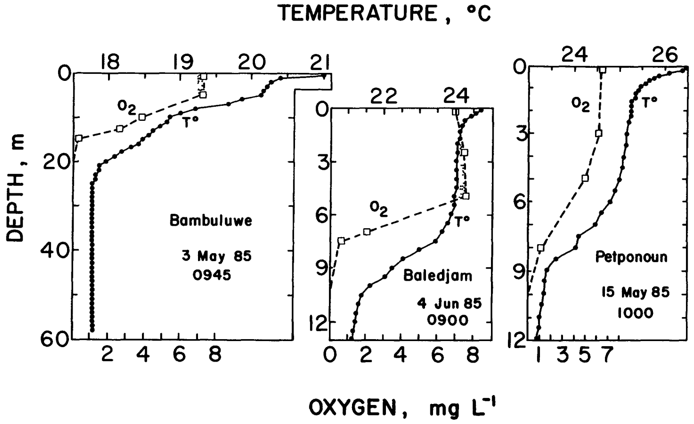

Fig. 6. As Fig. 3.

Table 3. Stability (S), work of the wind (B), and total work (G) in J m^{-2} calculated for Cameroon lakes on the dates shown in Figs. 3–6 (except Nyos). Area is in km^2 and z_{max} is in m. Values for comparison were calculated from the raw data of Ruttner (1931), or taken from Hutchinson (1957), Johnson et al. (1978), or Lewis (1983).

Lake	S	B	G	Area	z_{max}
		Cameroon lakes			
Barombi Mbo	5,784	9,294	15,078	4.15	110
Wum	3,068	662	3,730	0.45	124
Manengouba-F	2,115	910	3,025	0.22	168
Disoni	1,925	2,223	4,148	1.65	80
Mbalang	1,627	949	2,576	0.50	52
Tizong	1,291	999	2,290	0.08	48
Bambuluwe	847	355	1,202	0.28	58
Oku	320	434	754	2.43	52
Monoun	1,550	—	—	0.53	96
Nyos	6,870	—	—	1.58	208
		Other tropical and temperate lakes			
Atitlan	21,084	3,669	24,753	137	341
Ranau	6,599	4,728	11,327	126	229
Pakis	4,846	1,489	6,335	0.40	156
Minindau	4,816	5,991	10,807	97.9	169
Lamongan	442	253	695	0.30	28.5
Amatilan	407	737	1,144	8.20	34
Valencia (1978)	345	3,095	3,440	350	39
Güija	172	939	1,111	44.3	26
Pyramid (1914)	10,057	3,977	14,034	532	104
Mendota	504	1,186	1,690	39.2	26
Lunzer Untersee	382	525	907	0.68	34
Lawrence	204	295	499	0.05	13
Mirror	132	276	408	0.15	11
Findley	130	172	302	0.114	24

at 5 m in Lake Monoun was unusual among the Cameroon lakes. Green et al. (1973) reported anoxia below 19 m in a study of Barombi Mbo (April 1972), which contrasts with the presence of oxygen to about 40 m in 1985. Although thermally stratified, Debundsha and Oku had oxygenated hypolimnia (Figs. 4, 5). Oxygen was also present throughout the water column in Ejagham, Beme, Debundsha, and Kotto, but concentrations were reduced at greater depths in the latter three lakes (Fig. 5).

Stability and work of the wind—Stability (S) ranged from 0 in the unstratified lakes to 5,784 J m^{-2} in Barombi Mbo (Table 3). The value of S for Barombi Mbo probably represents its maximum annual value, while the stabilities shown in Table 3 for the other Cameroon lakes may not, because they are computed from single profiles. Slight to moderate stratification of inorganic ions was found in all lakes with anoxic hypolimnia (Table 4). Even though the proportional increase in hypolimnetic conductivity relative to the surface was great in many lakes, chemical stratification contributed insignificantly to overall stability. For example, in Barombi Mbo the density changes due to dissolved ions increased S by $<1\%$. The only exceptions to this generality are Monoun and Nyos, although, as explained earlier, their S values must be considered approximate. Chemical stability in Monoun (460 J m^{-2}) was roughly half that of thermal stability (1,090 J m^{-2}). There is evidence that the 21 August gas release from Nyos was associated with substantial mixing in the water column (Kling et al. 1987), and just after the event the lake was nearly isothermal and estimated stability was due entirely to chemical stratification. The Cameroon lakes can be grouped as minimally stable (Kotto and Ejagham), slightly stable (Bambuluwe and Oku), moderately stable (Manengouba-F, Disoni, Mbalang, and Tizong), strongly stable (Barombi Mbo and Wum), and metastable due to high CO_2 concentrations (Monoun and Nyos). The scar-

Table 4. Conductivity (K_{25}) for lakes with anoxic or nearly anoxic hypolimnia.

Lake	K_{25} (μS cm^{-1}) Surface	Bottom
Edib	13.2	39.4
Debundsha	14.5	14.2
Bambuluwe	15.0	50.8
Petponoun	29.0	36.8
Disoni	33.0	71.2
Manengouba-F	35.0	43.8
Wum	44.8	64.8
Barombi Mbo	49.1	80.2
Benakuma	73.0	306
Manengouba-M	96.0	327
Baledjam	112	136
Monoun	112	2,190
Nchout	113	120
Enep	114	179
Ngaoundaba	142	206
Mbalang	167	194
Gegouba	168	185
Baleng	213	255
Banefo	221	297
L. Monoun	226	406
Tizong	235	258
Mfou	243	272
Negop Ghang	273	287
Mfouet	357	446

city of similar data makes comparisons difficult, but these stabilities are similar to or higher than those calculated for other tropical and temperate lakes.

Birge's (1916) work of the wind (a misnomer, because heat transport is effected by turbulence from convective mixing as well as from wind stress) is computed over the time between minimum and maximum heat content, which is known only for Barombi Mbo. Minimum heat contents were estimated assuming homiothermy at the lowest hypolimnetic temperature of each lake, and the heat content at the time the profiles were taken was used instead of the maximum heat content. Thus the values of B are underestimates, but they do provide a lower bound. As might be expected, B is significantly related to thermocline depth (Table 5). The sum of S and B is the total work (G) required to heat the lake from its minimal temperature to the observed mean temperature without stratification (Hutchinson 1957). The grouping of lakes according to values of B or G was similar to grouping by S (Table 3).

Table 5. Regression equations for stability (S), work of the wind (B), thermocline depth (z_t), maximum depth (z_{max}), and associated morphometric features including area (A) and fetch (F). Values in parentheses below each parameter are the standard errors of those estimates.

	N	r^2
$[\log S] = 0.416 + 1.48[\log z_{max}]$ (0.250) (0.138)	22	0.852
$[\log B] = -0.17 + 0.45[\log z_t]$ (0.26) (0.09)	9	0.77
$[z_t] = 9.94\ [F]^{0.300}$ (0.959) (0.019)	52	0.83
$[\log z_t] = 0.996 + 0.168[\log A]$ (0.026) (0.015)	52	0.715

Hutchinson (1957) and Wetzel (1983) stressed the apparent strong dependence of S and G on lake area. This dependence may not apply to tropical lakes. Most Cameroon lakes, for example, have higher stabilities than Lake Valencia (Table 3), which is almost two orders of magnitude larger than Barombi Mbo. In addition, the relationship is not found in the range of areas spanned by the Cameroon lakes, as Kotto and Oku are two of the largest lakes and yet are least stable. Given similar heat incomes, the more sheltered crater lakes would be expected to have lower rather than higher values of S compared to lakes similar or larger in size that are more exposed to the wind. It is obvious from the data in Table 3 that maximum lake depth is related more strongly to S than is lake area (Fig. 7; Table 5).

Mixing depth—Morphometric controls on the extent of mixing, as measured by epilimnion depth, thermocline depth, or depth to anoxia, have been noted in temperate (Patalas 1984; Gorham and Boyce pers. comm.) and tropical (Ruttner 1931; Melack 1978) lakes. A persistent thermocline is the most common measure of mixing depth, although a thermocline can be buried in a metalimnion of any thickness, and thus bears an uncertain relationship to the depth of the mixed layer. Modeling of temperate lakes has established that summer thermocline depth is predictable and that it increases as a function of lake fetch or area (Patalas 1984; Gorham and Boyce pers. comm.). This relationship is strong for temperate lakes up to about 30 km in fetch, but in the Laurentian Great Lakes observed

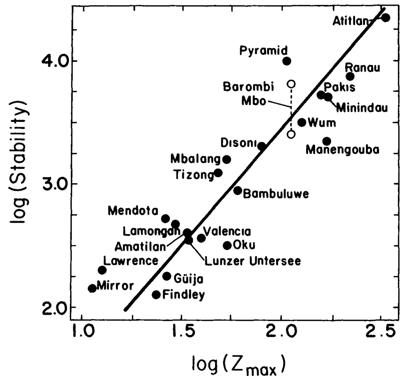

Fig. 7. Relationship between log of calculated stability (log *S*) and log of maximum lake depth (log z_{max}) for temperate and tropical lakes. Data references in Table 3; regression equation in Table 5.

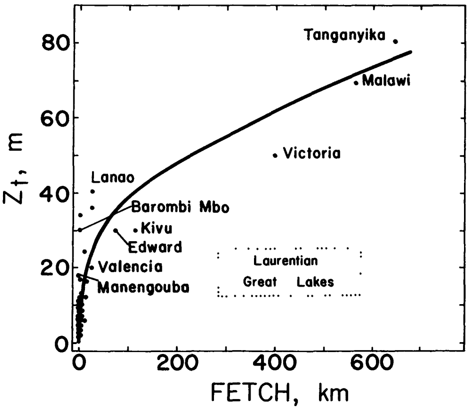

Fig. 8. Relationship of thermocline depth (Z_t, m) and maximum lake fetch for tropical lakes. Data from references given in Table 3, Hutchinson (1957), and G. Coulter (pers. comm.).

thermocline depths of 15–20 m are much less than predicted (40–60 m: Patalas 1984; Gorham and Boyce pers. comm.).

For a combination of tropical lakes in Cameroon, East Africa, Indonesia, and South America, there is a well-defined relationship between thermocline depth and lake fetch (Fig. 8; Table 5). Figure 8 also shows that the large East African Rift lakes have much deeper thermoclines than the Laurentian Great Lakes. The curvilinear nature of this relationship disappears when the largest lakes are removed, and a power function fits the remaining data poorly. In addition, the residuals around the regression line for all lakes show that the parameter estimates used for prediction are inefficient. Linearizing the relationship by log-transforming the data corrects the problem. On this basis, lake area is a better predictor of z_t than is fetch or the minimum height of the crater rim around the lake (Table 5).

To facilitate comparison, I have superimposed relationships for temperate lakes on a plot of thermocline depth in tropical lakes of fetch <10 km (Fig. 9). It is apparent from Fig. 9 that most thermocline depths are greater in the Cameroon and other tropical lakes. Gorham and Boyce (pers. comm.) proposed that the high relative mixing depths in English lakes are caused by lower water temperatures (smaller density gradients) and greater wind force, which is consistent with observations from northern Canada (Patalas 1984).

Discussion

Plankton maxima or particle accumulation at mixing interfaces can abruptly change light attenuation, and although the epilimnion is often considered well mixed and homogeneous, it may not always be so. For example, peak epilimnetic oxygen concentrations were found at the same depths as increases of *k* in Barombi Mbo, Ngaoundaba, and Tizong and were probably caused by phytoplankton. Such variation may have diurnal and seasonal structure; measurement of this structure is uncommon, perhaps because of the equipment necessary (*see* Talling 1981). Examining the spectral effect of narrow water layers requires only irradiance-depth profiles, however, and these are widely available. Algal growth models requiring irradiance data as input (Denman and Marra 1986; Powell and Richerson 1985) thus might be refined by studying light intensity microstructure in relation to epilimnetic mixing.

Direct solar heating of lower water levels may be of special importance in transparent lakes where shelter and small size reduce the potential contribution of the wind to heat distribution (Jassby and Powell 1975). For a given solar input under similar wind conditions, a decrease in optical density of the water will increase the depth of diurnal stratification (the "trapping depth" of Price et al. 1986) and will thus reduce the net buoyant resistance of the epilimnion to vertical transport of heat and momentum. On

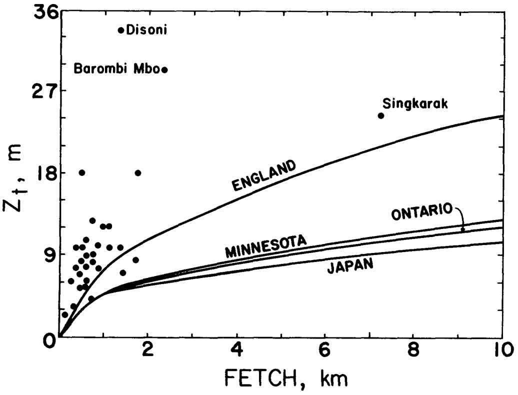

Fig. 9. Plot of thermocline depth (Z_t, m) and maximum fetch for tropical and temperate (Gorham and Boyce pers. comm.) lakes. Points are shown only for tropical lakes; actual data points for the temperate lakes fall very close to the regression lines presented (Patalas 1984).

the basis of a stratification criterion incorporating the effects of solar radiation penetrating the water column, Holloway (1980) showed that the critical wind speed for mixing decreases in clearer waters. If this mechanism operates in lakes and is important enough to be reflected in seasonal thermocline depth, then a necessary consequence is a pronounced relationship between mixing depth and water transparency. Data from sheltered lakes in Cameroon, Uganda, and Japan show that a significant proportion of the variance in mixing depth is explained by light penetration (Fig. 10). For the tropical lakes, partial r^2 values from stepwise regression indicate that Secchi depth explains 71% of the variation in thermocline depth, and lake area only explains an additional 2%. Collinearity between the predictor variables, Secchi depth and area, is negligible. This analysis suggests that reduction in buoyant resistance to vertical mixing, caused by deeper penetration of solar energy into the water column, is partly responsible for establishing deeper mixing depths in clearer lakes. This mechanism may be important in other lakes more exposed to the wind or of larger size, because the effects of greater solar penetration are independent of whether turbulence from wind mixing or from convection is actually deepening the mixed layer. For example, Salonen et al. (1984) reported that in southern Finland clear-water lakes circulate more deeply than brown-water lakes—independent of lake fetch. If conditions are such that boundary-layer shear dominates turbulent mixing in the metalimnion (e.g. from an internal seiche, *see* Spigel et al. 1986), transparency will be less important because the solar penetration mechanism only affects stirring within the epilimnion.

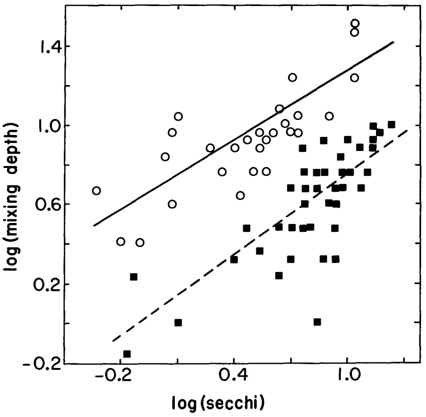

Fig. 10. Log-log plot of mixing depth vs. Secchi depth (z_{Secchi}) for Cameroon and Uganda crater lakes (○ and solid line; data from this study and Melack 1978) and Japanese lakes (■ and dashed line; data from Yoshimura, *cited by* Hutchinson 1957). Mixing depths are represented by the top of the metalimnion (z_{meta}) in Japanese lakes and by the thermocline (z_t) in tropical lakes; this may account for the different intercepts. The best-fit simple regression equations are: tropical lakes (z_t) = 2.11 + 1.95 (z_{secchi}), $N = 31$, $r^2 = 0.70$, SE intercept = 1.18, SE slope coefficient = 0.240; temperate lakes (z_{meta}) = 0.77 + 0.53 (z_{Secchi}), $N = 45$, $r^2 = 0.61$, SE intercept = 0.53, SE slope coefficient = 0.06.

The effects of lake morphometry on water column stability, and thus on the potential for mixing, are not entirely understood. Lake stability is time-integrated, but its measure at a single time offers no information on time-dependent processes. Its magnitude increases with the depth of the lake, the density gradient across the thermocline, and the depth of the thermocline to a point defined by basin morphometry. In a deep lake, the increased mass of dense water below the pycnocline contributes to the observed relationship between S and lake depth. The complex interaction of thermocline lowering and density gradient production is not well studied, and stability as a single measure may be viewed as a poor indicator of physical process and heat distribution. It remains a useful three-dimensional index of comparison, however, and serves to evaluate both the potential for hypolimnetic gas accumulation and the energy required for the upward mixing and release of gas.

Reduced stability and water column mixing are dependent on appropriate conditions for heat loss. In the tropics, shallow lakes may mix thoroughly each day (MacIntyre and Melack in press), but the deeper lakes typically experience a period of minimum stability and deep if not complete mixing during the hemispheric winter (Talling 1969; Lewis 1983). This pattern may not hold in parts of West Africa, where the period of mixing is coincident with minimum air temperatures and insolation during summer (Kling 1987*b*). There is no reason to believe that the stratified Cameroon lakes do not experience a period of deep mixing, but the moderate and large stability values found in some lakes suggest that yearly mixing may not affect the entire water column.

Several physical factors may be involved in formation of deeper mixing depths in tropical lakes. They include the decreased water viscosity at higher temperatures, the intensity of storms or maximum wind speeds, the smaller density gradients encountered in warmer waters, and the reduced Coriolis effects at low latitudes. Kato and Phillips (1969) showed that viscosity can eventually become important to entrainment rates at low Reynolds numbers, although viscosity effects can generally be ignored under most conditions (Turner 1973; Moum and Caldwell 1985). There may be consistent differences in wind power between specific latitudinal belts, but generalities of storm intensity are difficult to make, and any effects would be smoothed by the cross-sectional nature of the tropical lake data set. The differences in density gradients found in tropical and temperate lakes, however, are striking. For example, the mean of the maximum density difference within the water columns of the tropical lakes examined here was 0.00065 g cm^{-3} ($N = 52$; SE = 0.00005), whereas the density difference between 4° and 20°C in a temperate lake during summer stratification is about three times greater (0.00176 g cm^{-3}). In addition, the maximum change in water density ($d\rho/dz$) over 1 m in the strongly stratified Cameroon lakes averaged 0.00023 g cm^{-3} ($N = 24$; SE = 0.00003), which is much less than that found in several ELA lakes (~0.00090 g cm^{-3}: Schindler 1971). A final factor to consider is the smaller Coriolis effect at lower latitudes. The magnitude of this effect would be unnoticeable in all but the largest lakes (Phillips 1977; cf. Garwood et al. 1985). In the Laurentian Great Lakes, Coriolis effects produce nearshore downwelling and reduce turbulent mixing from internal seiches, which together limit the comparatively shallow mixing depths (Mortimer 1974; Gorham and Boyce pers. comm.). The absence of a strong rotational component at equatorial latitudes may in turn help explain why the great lakes of East Africa have such deep mixed layers. Detailed measurements on the dynamics of density structure in tropical lakes are needed, but it appears that regardless of the dominant process of mixed-layer deepening the smaller absolute density gradients at tropical latitudes play a substantial role in formation of the deeper thermoclines found in many tropical lakes.

References

BEADLE, L. C. 1981. The inland waters of tropical Africa, 2nd ed. Longman.

BIRGE, E. A. 1916. The work of the wind in warming a lake. Trans. Wis. Acad. Sci. **18:** 341–391.

BOWLING, L. C., AND P. A. TYLER. 1986. The underwater light-field of lakes with marked physicochemical and biotic diversity in the water column. J. Plankton Res. **8:** 69–77.

CHEN, C-T., AND F. J. MILLERO. 1977. The use and misuse of pure water PVT properties for lake waters. Nature **266:** 707–708.

CORBET, S. A., J. GREEN, J. GRIFFITH, AND E. BETNEY. 1973. Ecological studies on crater lakes in West Cameroon. Lakes Kotto and Mboandong. J. Zool. Lond. **170:** 309–324.

DENMAN, K. L., AND J. MARRA. 1986. Modelling of the time dependent photoadaptation of phytoplankton to fluctuating light, p. 341–359. *In* J. C. J. Nihoul [ed.], Marine interfaces and ecohydrodynamics. Elsevier.

DILLON, T. M., AND T. M. POWELL. 1979. Observations of a surface mixed layer. Deep-Sea Res. **261:** 915–932.

———, ———, AND L. O. MYRUP. 1975. Low frequency turbulence and vertical temperature microstructure in Lake Tahoe, California-Nevada. Int. Ver. Theor. Angew. Limnol. Verh. **19:** 110–115.

FOSTER, T. D. 1971. A convective model for the diurnal cycle in the upper ocean. J. Geophys. Res. **76**: 666–675.

GARWOOD, R. W., JR., P. MULLER, AND P. C. GALLAGHER. 1985. Wind direction and equilibrium mixed layer depth in the tropical Pacific ocean. J. Phys. Oceanogr. **15**: 1332–1338.

GREEN, J., S. A. CORBET, AND E. BETNEY. 1973. Ecological studies on crater lakes in West Cameroon: The blood of endemic cichlids in Barombi Mbo in relation to stratification and their feeding habits. J. Zool. Lond. **170**: 299–308.

———, ———, AND ———. 1974. Ecological studies on crater lakes in West Cameroon. Debundsha Lake. J. Zool. Lond. **173**: 199–223.

HASSERT, K. 1912. Seenstudien in Nord-Kamerun. Z. Ges. Erdk. Berl. **1912**: 7–41, 135–144, 203–216.

HENDERSON-SELLERS, B. 1984. Development and application of "U.S.E.D.": A hydroclimate lake stratification model. Ecol. Model. **21**: 233–246.

HOLLOWAY, P. E. 1980. A criterion for thermal stratification in a wind-mixed system. J. Phys. Oceanogr. **10**: 861–869.

HUTCHINSON, G. E. 1957. A treatise on limnology. V. 1. Wiley.

IDSO, S. B. 1973. On the concept of lake stability. Limnol. Oceanogr. **18**: 681–683.

IMBERGER, J. 1985. The diurnal mixed layer. Limnol. Oceanogr. **30**: 737–770.

JASSBY, A., AND T. POWELL. 1975. Vertical patterns of eddy diffusion during stratification in Castle Lake, California. Limnol. Oceanogr. **20**: 530–543.

JOHNSON, N. M., J. S. EATON, AND J. E. RICHEY. 1978. Analysis of five North American lake ecosystems. 2. Thermal energy and mechanical stability. Int. Ver. Theor. Angew. Limnol. Verh. **20**: 562–567.

KATO, H., AND O. M. PHILLIPS. 1969. On the penetration of a turbulent layer into a stratified fluid. J. Fluid Mech. **79**: 753–768.

KLING, G. W. 1987*a*. The comparative limnology of lakes in Cameroon, West Africa. Ph.D. thesis, Duke Univ.

———. 1987*b*. Seasonal mixing and catastrophic degassing of tropical lakes, Cameroon, West Africa. Science **237**: 1022–1024.

———, AND OTHERS. 1987. The August 1986 gas disaster at Lake Nyos, Cameroon, West Africa. Science **236**: 169–175.

KRAUS, E. B., AND J. S. TURNER. 1967. A one-dimensional model of the seasonal thermocline, part 2. Tellus **19**: 98–105.

LEWIS, W. M., JR. 1973. The thermal regime of Lake Lanao (Phillipines) and its theoretical implications for tropical lakes. Limnol. Oceanogr. **18**: 200–217.

———. 1983. Temperature, heat, and mixing in Lake Valencia, Venezuela. Limnol. Oceanogr. **28**: 273–286.

———. 1984. A five-year record of temperature, mixing, and stability for a tropical lake (Lake Valencia, Venezuela). Arch. Hydrobiol. **99**: 340–346.

MACINTYRE, S., AND J. M. MELACK. 1982. Meromixis in an equatorial African soda lake. Limnol. Oceanogr. **27**: 595–509.

———, AND ———. In press. Frequency and depth of vertical mixing in an Amazon floodplain lake (L. Calado, Brazil). Int. Ver. Theor. Angew. Limnol. Verh. **23**.

MACIOLEK, J. A. 1975. Limnological ecosystems and Hawaii's preservational planning. Int. Ver. Theor. Angew. Limnol. Verh. **19**: 1461–1467.

MELACK, J. M. 1978. Morphometric, physical and chemical features of the volcanic crater lakes of western Uganda. Arch. Hydrobiol. **84**: 430–453.

MORTIMER, C. H. 1974. Lake hydrodynamics. Mitt. Int. Ver. Theor. Angew. Limnol. 20, p. 124–197.

MOUM, J. N., AND D. R. CALDWELL. 1985. Local influences on shear-flow turbulence in the equatorial ocean. Science **230**: 315–316.

PATALAS, K. 1984. Mid-summer mixing depths of lakes of different latitudes. Int. Ver. Theor. Angew. Limnol. Verh. **22**: 97–102.

PHILLIPS, O. M. 1977. The dynamics of the upper ocean. Cambridge.

POLLARD, R. T., R. B. RHINES, AND R. O. R. Y. THOMPSON. 1973. The deepening of the wind mixed layer. Geophys. Fluid Dyn. **4**: 381–404.

POWELL, T., AND P. J. RICHERSON. 1985. Temporal variation, spatial heterogeneity and competition for resources in plankton systems: A theoretical model. Am. Nat. **125**: 431–464.

PRICE, J. F., R. A. WELLER, AND R. PINKEL. 1986. Diurnal cycling: Observations and models of the upper ocean response to diurnal heating, cooling, and wind mixing. J. Geophys. Res. **91**: 8411–8427.

RUTTNER, F. 1931. Hydrographische und hydrochemische Beobachtungen auf Java, Sumatra und Bali. Arch. Hydrobiol. Suppl. 8, p. 197–454.

SALONEN, K., L. ARVOLA, AND M. RASK. 1984. Autumnal and vernal circulation of small forest lakes in southern Finland. Int. Ver. Theor. Angew. Limnol. Verh. **22**: 103–107.

SCHINDLER, D. W. 1971. Light, temperature, and oxygen regimes of selected lakes in the Experimental Lakes Area, northwestern Ontario. J. Fish. Res. Bd. Can. **28**:157–169.

SIMPSON, J. H., AND J. D. WOODS. 1970. Temperature microstructure in a fresh water thermocline. Nature **226**: 832–835.

SPIGEL, R. H., J. IMBERGER, AND K. N. RAYNER. 1986. Modeling the diurnal mixed layer. Limnol. Oceanogr. **31**: 533–556.

TALLING, J. F. 1969. The incidence of vertical mixing, and some biological and chemical consequences, in tropical African lakes. Int. Ver. Theor. Angew. Limnol. Verh. **17**: 998–1012.

———. 1971. The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. Mitt. Int. Ver. Angew. Limnol. 19, p. 214–243.

———. 1981. The development of attenuance depth-profiling to follow the changing distribution of phytoplankton and other particulate material in a productive English lake. Arch. Hydrobiol. **93**: 1–20.

TURNER, J. S. 1973. Buoyancy effects in fluids. Cambridge.

VINCENT, W. F., P. J. NEALE, AND P. J. RICHERSON. 1984. Photoinhibition: Algal responses to bright light during diel stratification and mixing in a tropical alpine lake. J. Phycol. **20:** 201–211.

WETZEL, R. G. 1983. Limnology, 2nd ed. Saunders.

WOOD, R. B., M. V. PROSSER, AND R. M. BAXTER. 1976. The seasonal pattern of thermal characteristics of four of the Bishoftu crater lakes, Ethiopia. Freshwater Biol. **6:** 519–530.

WOODS, J. D. 1980. Diurnal and seasonal variation of convection in the wind-mixed layer of the ocean. Q. J. R. Meteorol. Soc. **106:** 379–394.

———, AND W. BARKMANN. 1986. The responses of the upper ocean to solar heating. 1: The mixed layer. Q. J. R. Meteorol. Soc. **112:** 1–27.

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