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A COMPOSITIONAL, PHYTOGEOGRAPHICAL AND ELEMENTARY STRUCTURAL ANALYSIS OF THE PHYTOPLANKTON IN A TROPICAL LAKE: LAKE LANAO, PHILIPPINES

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SUMMARY

(1) A 15-month study of the phytoplankton of Lake Lanao, Philippines, shows that the community is composed of seventy euplanktonic autotroph species, including Cyanophyta (12), Euglenophyta (4), Chlorophyta (44), Chrysophyceae (1), Bacillariophyceae (4), Dinophyceae (3), and Cryptophyceae (2).

(2) A comparison of the year-round composition of Lake Lanao phytoplankton with survey data taken in other studies indicates that in South-east Asia a lacustrine plankton community will most often contain 50–100 euplanktonic autotroph species that reach detectable abundances (>1 per ml) at least once per year.

(3) Species-richness appears to be considerably lower in tropical than in temperate phytoplankton communities. In lakes of South-east Asia, including Lanao, about half of the species are chlorophytes, and over half of all species are found in a single integrated aliquot of 1 ml taken at any time of year.

(4) South-east Asian phytoplankton communities have a higher β-diversity than communities of east alpine lakes, but there is nevertheless a generic overlap of at least 80% between tropical Asian lakes chosen at random. The generic overlap between tropical and temperate lakes is much lower (45%).

(5) The taxonomic overlap between tropical phytoplankton communities does not differ detectably between continents, and this is given as evidence for existence of a pantropical phytoplankton assemblage, of which that found in Lake Lanao is representative.

(6) A survey of the literature shows that phytoplankton biomass is considerably higher in Lake Lanao and other tropical lakes on average than in temperate lakes, either on an annual basis or during the ice-free season.

(7) In Lake Lanao, thirteen species account for 90% of annual biomass, and ten species account for 90% of the annual number of individuals. A statistical test shows no evidence that dominants are more likely to come from one taxonomic division than another.

INTRODUCTION

In plankton ecology, functional analysis of communities has generally preceded quantitative, structural analysis of communities. This is especially true of tropical communities, for which the fund of knowledge is very small. In a few cases good documentation of some aspect of community structure is available for tropical plankton communities (e.g.

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Gonzales 1961; Talling 1966; Reyes 1972; Iltis 1974), but as yet we know little about the numbers of species, dominance and relative abundance of species generally, compositional overlap between environments, and distribution. These topics are of particular interest if they extend to comparisons of lake communities across broad ranges of latitude, as such comparisons may lead us to an understanding of the factors that govern community structure in lake phytoplankton.

The present study includes structural and compositional analysis of the phytoplankton in Lake Lanao, Philippines, based on an intensive 15-month study. The plankton community-structure and species-composition of Lake Lanao are compared first with other tropical lakes, and then with lakes of the temperate zone, to yield phytogeographical generalizations as well as comparative structural data.

THE STUDY SITE

Lake Lanao is located in the Southern Philippines (latitude 8°N, longitude 124°E) on the island of Mindanao, at an altitude of 720 m (Fig. 1). The main physical features of the lake, as given by Frey (1969), are: area 357 km^2; maximum depth 112 m; mean depth 60·3 m; replacement time 6·5 yr. At the time the data were collected (1970–1) more than half of the watershed remained forested, and the overall human impact on the nutrient budget of the lake was trivial, except in certain local littoral areas.

Lake Lanao was formed by a lava dam and appears to be quite old, as it contains a swarm of endemic cyprinids (Myers 1960; Frey 1969). Rocks from the lava dam near the south end of the lake have been dated by K–Ar methods at 3·6 and 5·5 × 10^6 yr (D. G. Frey, personal communication). The plankton community is therefore probably in equilibrium with the species-pool of South-east Asia.

Weather patterns and the corresponding features of the thermal regime in Lake Lanao have already been analysed (Lewis 1973a). The main seasonal feature is a period of cool, relatively dry weather lasting from December to March (mean temperature 21·5–22·5 °C; rainfall 150–200 mm per month). November and April are transitional months with variable weather. The remaining 6 months are typically warmer and wetter (23·0–24·0 °C; rainfall 250–340 mm per month).

Lake Lanao has only a moderate content of solids (conductivity 105 μmho cm^{-1} at 25 °C), but is sufficiently well-buffered to support rapid photosynthesis (alkalinity 1·02 m-equiv. l^{-1}). Nitrate-nitrogen averages only 9 μg l^{-1} in the euphotic zone and is frequently undetectable ($<$1 μg l^{-1}). Molybdate-reactive phosphorus is somewhat more concentrated (29 μg l^{-1} PO_4–P, average), and appears to be less important than nitrogen as a limiting nutrient for autotrophs. Silicate averages 2·2 mg l^{-1} Si in the euphotic zone, and is probably never sufficiently depleted to limit diatom growth completely.

Extensive studies of primary production have shown that Lake Lanao is highly productive (Lewis 1974). The net primary production is 1·7 g m^{-2} day^{-1} C (annual mean), and gross primary production averages 2·6 g m^{-2} day^{-1} C. The lake is nevertheless quite transparent: the average depth to which 1% incident light penetrates is 12 m. High transparency despite high productivity is due to the exceptionally low amounts of non-living suspended matter in the euphotic zone, the high production per unit of autotroph biomass, and the great amount of mixing and nutrient-renewal in the upper water column.

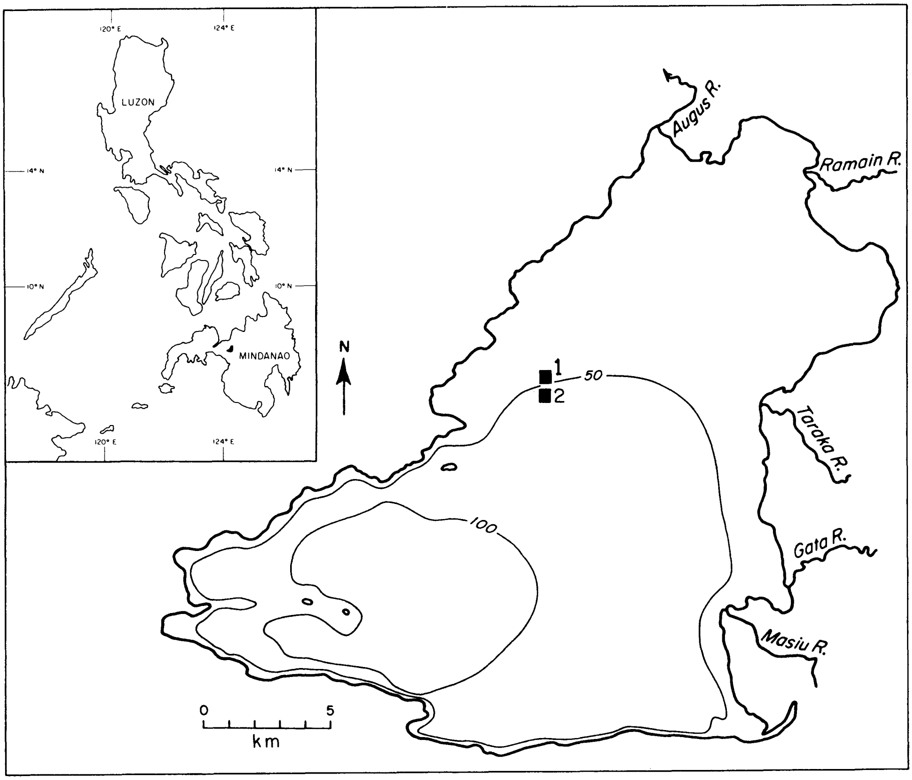

FIG. 1. Map of Lake Lanao (depth contours in m) showing the main sampling stations; the inset shows the position of Lake Lanao on the island of Mindanao.

METHODS

Phytoplankton were collected at weekly intervals over a 15-month study period (July 1970 to October 1971). In all cases the upper 15 m of the water column was sampled with a clean, weighted plastic tube (Lund & Talling 1957). This method provides an integrated sample of phytoplankton that is preferable for many purposes to a depth series. The 0–15 m stratum is very nearly identical with the euphotic zone where active cell growth occurs.

The analysis is based on four replicate samples from slightly different positions (1–5 m apart) at Station 1 (Fig. 1), and four replicates taken in the same way at Station 2, 1 km to the south of Station 1. All samples were preserved with Lugol's solution.

Phytoplankton were counted with an inverted microscope after sedimentation in a closed chamber. Ordinarily only two of the replicates at a given station were counted. The species were divided into two groups for counting: the three or four most common species were counted in a 2-ml chamber, and the rest in a 5-ml chamber. Special methods were however used to provide reliable counts for rare species. Although low abundance can to some extent be compensated for by an increase in the sedimentation volume, counting then becomes difficult and unreliable, since individuals of the less common species are obscured by those of the dominant species. For this reason the sedimentation volume was never increased beyond 5 ml. Reliable counts of less common species were obtained instead by adjustment of the number of transects in accordance with the abundance of the species. A count limit was set at 100 counting units (e.g. cells, colonies) per chamber per species. After each complete traverse of the chamber, tabulation was discontinued for species whose counts exceeded 100 units, and the water volume corresponding to the cumulative number of transects was noted for each of these species. Counting was thus focused on increasingly rare species as the count proceeded. Since the procedure could be extended indefinitely, a limit on the number of traverses counted was also set for each chamber, all counts being terminated after fifteen parallel traverses (0·72 ml). As at least one 5-ml chamber was counted for each station each week, the total weekly volume of water examined was at least 1·44 ml for the rarer species.

One potential difficulty of the multiple traverse method is uneven settling (Nauwerck 1963), which might make parallel traverses less reliable than intersecting ones. The chamber was rotated at the end of certain traverses to minimize this source of error.

Counting units were defined to maximize convenience and accuracy of tabulation. Some colonial species were counted as colonies (*Aphanocapsa*) or subcolonies (*Coelastrum*), but total cell number was recorded for the most irregular colonial species (*Dictyosphaerium, Dimorphococcus*). Solitary species (*Ankistrodesmus, Nitzschia*) were tabulated as individual cells, while filaments (*Anabaena, Lyngbya*) were tabulated as lengths. Counting units for all dates were converted to cell number from records of the mean number of cells per counting unit.

A mean volume was determined for counting units of each species, so that abundance of each species could be computed as biomass. A geometric model was used in converting mean dimensions to mean volume for a species. Skeletal material was not included in the volume estimates, and dead cells were of course excluded from the counts. The cell volume was assumed to be occupied by protoplasm having a specific gravity near 1·0, and was converted on this basis to wet biomass.

A record was kept of the mean number of cells per independent unit in each species. These units are referred to in the analysis as 'plankton units'. For example, *Melosira granulata* filaments on average consisted of four attached cells, and hence the volume of a plankton unit for this species was four times the volume of an individual cell. Certain aspects of the ecology of the species can be analysed realistically only if it is specified that *Melosira* biomass is packaged in units of this size. The concept of the plankton unit was used by early plankton biologists (e.g. Chandler 1940, 1942) to quantify the abundance of phytoplankton. Although this is obviously the method of choice whenever numbers of particles are of greater interest than biomass, the concept is not currently much used; instead, counts are frequently given in terms of cell number or other arbitrary units which bear an unknown relation both to biomass and to particle number.

Thus to summarize, abundance data were collected for each station and each date for all species, expressed as (1) counting units, (2) total cell number, (3) total volume (live weight biomass), and (4) number of plankton units. The most useful of these quantities are biomass and number of plankton units, either of which can be expressed per unit volume or per unit surface area of lake.

RESULTS AND DISCUSSION

The species list in Table 1 is a complete compilation of the seventy living autotrophic forms that were observed in samples from Stations 1 and 2 over the study period. The seven species listed only by code number were of such little quantitative importance that classification did not seem worthwhile. A special effort was made to separate species correctly, so that the counts could be used in the evaluation of succession and community structure.

Number of species in a sample

Table 2 compares the composite number of species found over the 15-month study period in Lake Lanao with the mean number found each week. The table shows that a majority of the total plankton species can be found in a single integrated sample of 1·5 ml taken at any time of year. The very rarest species may not have received fair treatment, as there is a tendency for a single specimen of a rare species to be overlooked. Nevertheless, Table 2 provides evidence for a strong element of temporal continuity in the species-composition over the year. All of the major taxa seem to be similar in this respect, as half or more of the total species in any of the major groups will generally occur in an integrated sample of size 1·5 ml taken at a random time of year.

Ruttner's (1952) data from fifteen lakes on Java, Sumatra and Bali (the 'Sunda' lakes) are also summarized in Table 2, to facilitate comparison of temporal variation with variation between lakes in South-east Asia. Ruttner counted the contents of 0·052 ml of lakewater at each of several depths in the water column. His samples represent a single day or a very short time span.

Because Ruttner did not sample with a net and because he counted all autotrophs, his data are easily compared with the Lanao data. Ruttner's samples within the trophogenic zone of individual lakes numbered about eight on average. The total volume counted by sedimentation was thus about 0·4 ml. Some larger species, especially desmids, were added to the counts on the basis of net samples.

Since the volume of water examined can be roughly equated with the number of individuals counted, the numbers of species tabulated per week in Lanao should be slightly greater than for the fifteen Sunda lakes, if Lake Lanao had similar complexity of species-composition to the Sunda lakes in general. As Table 2 shows, the mean number of species per week in Lanao is forty-three, which is in fact slightly higher than the average number in the Sunda lakes (thirty-one). Complexity of the Lanao community thus appears to be much the same as in other South-east Asian lakes.

Table 2 suggests that the total number of planktonic autotroph species in the tropical lakes of insular South-east Asia is ordinarily between 50 and 100 on an annual basis, and that half or slightly more of these species can be found in a sample of about 1 ml taken at any time of year. This estimate probably cannot be made much more precise even with more extensive data, as the exact species count is determined by the taxonomic zeal of the tabulator, by the line of exclusion drawn between tychoplankton and euplankton, and by the measures taken to discover very rare species.

Complete tabulations of species over year-long periods in the tropics are generally not available for comparison with the Lanao data of Table 2. Schmidt & Uherkovich (1973) found an average of thirty-seven species in fourteen monthly samples from Lago Castanho, a flood-plain lake of the Amazon, but Schmidt and Uherkovich used a net, hence direct comparison with the data of Table 2 is difficult. Taxonomic work on tropical African lakes that are highly saline (Iltis 1974) or very shallow (Ganf 1974a) has shown that the phytoplankton composition of such lakes is much simpler than for the lakes listed in Table 2, as would be expected.

Table 2 also shows that about half of the plankton species in lakes of insular South-east

TABLE 1. Details of phytoplankton analyses from Lake Lanao, July 1970 to October 1971

	Cells per plankton unit	Volume per plankton unit (μm^3)	Biomass (μm^3 ml^{-1})	Rank	Numbers Plankton units (ml^{-1})	Rank
Cyanophyta						
Chroococcus minutus (Kutz.) Naeg.	4	280	44 389	11	158·5	15
Aphanothece nidulans P. Richt	15	13	63 062	7	4851	1
Aphanocapsa elachista W. et G. S. West	200	100	328·5	49	3·3	43
Gloeothece linearis Naeg.	15	14	429·6	47	30·7	29
Dactylococcopsis fascicularis Lemm. fa. *solitaris*	1	10	1794	32	179·4	14
*D. woltereck*i Behre	1	15	3433	27	228·9	12
Anabaena sphaerica Born. et Flah. var. *tenuis* G. S. West	12	246	63 867	6	259·2	11
A. spiroides Kleb.	30	1000	19 496	16	19·5	33
Lyngbya limnetica Lemm.	15	24	95 673	4	3986	2
Rhabdoderma sp. 1	3	3	111·2	52	37·1	25
Spirulina laxissima G. S. West	4	100	0·3	70	0	66
Synechococcus sp. 1	1	5	2058	31	411·6	8
Euglenophyta						
Trachelomonas perforata Awerniz.	1	35	69·0	55	2·0	49
T. bacillifera var. *minima* Playf.	1	50	1389	35	27·8	30
Trachelomonas sp. 1	1	150	67·6	56	0·5	54
Trachelomonas sp. 2	1	20	1528	34	76·4	21
Chlorophyta						
Chlamydomonas sp. 1	1	275	716·7	41	2·6	46
Tetraedron minimum (A. Braun) Hansgirg	1	25	3519	26	140·8	16
Treubaria triappendiculata Bern.	1	20	1·0	69	0	66
Sphaerocystis schroeteri Chod.	6	480	60 152	8	125·3	17
Chlorella sp. 1	1	10	10 696	19	1070	5
Oocystis submarina Lagerheim	2	140	100 667	3	719·1	6
O. lacustris Chodat	2	500	13 865	17	27·7	31
O. gigas A. Braun var. *incrassata* Lemm.	1	10 500	2762	29	0·3	58
Franceia droescheri (Lemm.) G. M. Smith	1	30	1015	38	33·8	27
Chodatella subsalsa Lemm.	2	250	50 486	9	201·9	13
Chodatella sp. 1	1	40	2934	28	73·3	23
Ankistrodesmus setigerus (Schroeder) G. S. West	1	35	4157	25	118·8	18
Ankistrodesmus sp. 1	1	25	1·4	68	0·1	60
Ankistrodesmus sp. 2	1	4	13·6	64	3·4	42
A. gelifactum (Chod.) Bourr.	4	100	378·1	48	3·8	41
Kirchneriella elongata G. M. Smith	10	250	805·0	40	3·2	44
K. obesa (W. West) Schmidle	10	400	604·7	44	1·5	52
Selenastrum minutum (Naeg.) Collins	1	5	46·7	58	9·3	37
Selenastrum sp. 1	1	2	1283	36	641·3	7
Eutetramorus planctonica (Korch.) Bourr.	18	600	5·5	66	0	66
Botryococcus braunii Kutz.	500	25 000	230·8	51	0	66
Dictyosphaerium pulchellum Wood	10	500	160 214	2	320·4	10
Dimorphococcus lunatus A. Braun	10	700	39 383	12	56·3	24
Coelastrum cambricum Arch.	35	2500	46 627	10	18·7	35
Scenedesmus quadricauda (Turp.) De Brebisson	4	1000	521·9	45	0·5	54
S. ecornis (Ralfs) Chod. var. *polymorphus* Chod.	4	480	4277	24	8·9	38
Scenedesmus sp. 1	4	100	1660	33	16·6	36
Crucigenia rectangularis (A. Braun) Gay	8	200	635·5	43	3·2	44
Pediastrum clathratum (Schroeter) Lemm.	36	9000	69·2	54	0	66
P. duplex Meyen	8	5000	23·1	61	0	66

Pediastrum tetras (Ehrenb.) Ralfs	7	300	19·4	62	0·1	60
Coccomyxa sp. 1	1	4	13 656	18	3414	3
Closterium setaceum Ehrenb.	1	1500	13·8	63	0	66
Closterium sp. 1	1	80	2538	30	31·7	28
Closterium sp. 2	1	35	1238	37	35·4	26
Micrasterias foliacea Bail.	4	2000	4·6	67	0	66
Staurastrum paradoxum Meyen	2	350	658·0	42	1·9	51
Unknown chlorophyte 28	8	80	5940	21	74·4	22
Unknown chlorophyte 29	1	400	1008	39	2·5	48
Unknown chlorophyte 35	1	20	40·6	59	2·0	49
Unknown chlorophyte 36	2	40	262·8	50	6·6	39
Unknown chlorophyte 37	25	250	24·0	60	0·1	60
Unknown chlorophyte 38	1	25	9·1	65	0·4	56
Unknown chlorophyte 39	1	30	78·3	53	2·6	46
Chromulina sp. 1	1	100	9457	20	94·6	19
Bacillariophyceae						
Nitzschia baccata Hust.	1	190	555 371	1	2923	4
N. acicularis W. Sm.	1	150	61·2	57	0·4	56
Melosira granulata (Ehrbg) Ralfs	4	1200	29 486	13	24·6	32
M. agassizii Ostenf.	4	6000	5631	22	0·9	53
Dinophyceae						
Gymnodinium sp. 1	1	1200	22 767	15	19·0	34
Peridinium sp. 1	1	1150	5424	23	4·7	40
Ceratium hirundinella (O. F. Müller) Schrank	1	50 000	461·5	46	0	66
Cryptophyceae						
Rhodomonas minuta Skuja var. *nannoplanctonica* Skuja	1	70	28 273	14	403·9	9
Cryptomonas marssonii Skuja	1	1200	94 977	5	79·1	20

Asia are chlorophytes. In Lake Lanao, and prŏbably in other lakes as well, this is true at any specific time of year. The apparent disappearance of a species at certain times of the year is of course more properly viewed as a drop in its abundance that carries it below the detection limit of standard counting techniques; for small species, this limit is approached at a density of *c.* 1 individual ml^{-1}.

Hutchinson (1967) has emphasized the distinction between absolute and relative abundance with respect to habitat space, and his line of reasoning is relevant to the interpretation of Table 2. To use Lanao as an example, a small species (<50 μm in size) present at a steady concentration of one individual per litre might easily have escaped

TABLE 2. Variation in the number of phytoplankton species over time and space in Lake Lanao and in fifteen other tropical lakes of South-east Asia (data of Ruttner 1952)

	Lanao—species per week (1·5 ml sample)				Sunda lakes—species per lake (0·4 ml sample)			
	Max.	Min.	Mean	All weeks (65)	Max.	Min.	Mean	All lakes (15)
Cyanophyta	10	5	8·1	12	6	0	3	16
Euglenophyta	3	0	0·8	4	6	0	1	20*
Chlorophyta	30	24	26·9	44	35	4	17	130
Chrysophyceae	1	1	1·0	1	4	0	1	3
Bacillariophyceae	3	1	2·4	4	10	1	4	25
Dinophyceae	3	0	1·7	3	6	1	3	13
Cryptophyceae	2	2	2·0	2	2	0	1	2
All species	51	36	42·9	70	56	8	31	199

* Includes miscellaneous species of other taxa.

detection over the 15 months of continuous counting effort, during which about two million biomass units were examined for identity. Even at the low relative abundance of one per litre, a hypothetical species would still comprise a total population of about 10^{10} in a lake the size of Lanao. The disappearance of a species from a list such as those which made up Table 2 is thus hardly indicative of the extinction of the species within the habitat.

Another significant feature of Table 2 is the column showing total numbers of species recorded by Ruttner for the fifteen Sunda lakes. The total volume of lakewater examined by Ruttner for all lakes combined would amount to about 5% of the total volume (or number of individuals) examined in the intensive study of Lake Lanao. Thus if all of Ruttner's lakes had been identical in plankton composition, the total number of species would be expected to be less than the total number for Lanao, since Table 2 shows that Ruttner's lakes are individually about equal to Lanao in species-richness. Table 2 shows instead that almost three times as many species were recorded in the samples from the Sunda lakes than from Lake Lanao. This difference is tangible evidence of β-diversity (*sensu* Whittaker 1972: diversity between habitats). The β-diversity for these tropical lakes can be quantified to provide a basis for comparison with temperate lakes. The simple index discussed by Whittaker (1972) is satisfactory for an approximation:

$$\mathrm{BD} = \frac{S_c}{\bar{S}}$$

where BD is an estimate of β-diversity, S_c is the composite number of species (for fifteen lakes in this case), and $\bar{S}$ is the mean number of species per lake. The value of BD for Ruttner's fifteen Sunda lakes is 6·4. The best comparison is with data taken by the same author (Ruttner 1937) for twelve east alpine lakes in Austria and south Germany: total species number for the twelve lakes was 75, and the mean number of species per lake was 25·4, so the value of BD is 3·0. This suggests that the β-diversity between lakes in South-east Asia is greater than between east alpine lakes. The alpine group is probably more uniform physically and chemically, however, than the Sunda lakes, and this may account for part of the difference in β values. More extensive analysis of data from other regions is obviously needed before general conclusions can be formulated, but Table 2 provides foundation for the hypothesis that tropical lake communities show higher β-diversity than temperate ones.

Compositional overlap between lakes

The Lake Lanao phytoplankton assemblage is compared with those of other tropical and temperate lakes in Table 3. The table gives generic rather than specific overlap, to avoid the uncertainties of species-assignments in the phytoplankton when data from a large number of investigators are compared. All of the studies represented in Table 3 are principally ecological in orientation. This is significant in that no attempt was made in any of these studies to search specifically for rare species, as might be the case in studies of greater systematic orientation.

In general, there is less overlap between lakes if more rare species or genera are used in a comparison. For example, Reyes (1972) did a much more complete taxonomic study of Lake Lagartijo, Venezuela, than the one by Lewis & Weibezahn (1976) used in Table 3. The work by Reyes includes some very rare species and some tychoplankton species, as one purpose of the work was taxonomic rigour. Significantly, the generic list of Reyes overlaps less completely with that of Lanao than does the abbreviated list from Lewis and Weibezahn, which excludes the rarest species and the tychoplankton. Similarly, Ruttner's (1952) list for Lake Toba, Sumatra, overlaps less completely with that for Lanao than do his lists for the other Sunda lakes (Table 3). This is explained by the greater effort put into the Toba study, and the consequent inclusion of rarer taxa in the list for that lake. It would thus appear that the twenty most abundant genera of a tropical lake are much more likely to be shared with another tropical lake than the genera ranking 21–40 in abundance.

Despite some variation in the rigour with which the lists were established, the data of Table 3 provide an approximation of overlap in the top twenty phytoplankton genera of

TABLE 3. Comparison of phytoplankton genera recorded from Lake Lanao with those from other tropical and temperate lakes

	All phytoplankton			Chlorophyta only		
	Genera	Shared with Lanao	Shared (%)	Genera	Shared with Lanao	Shared (%)
Tropical lakes						
Mainit (Phillipines)[1]	24	22	92	13	12	92
Lamongan (Java)[2]	23	16	70	13	10	77
Ranau (Sumatra)[2]	14	10	71	8	5	63
Singkarak (Sumatra)[2]	22	17	77	14	11	79
Maninjau (Sumatra)[2]	15	12	80	11	9	82
Toba (Sumatra)[2]	32	21	66	13	10	77
Valencia (Venezuela)[3]	24	21	88	10	9	90
Lagartijo (Venezuela)[3]	16	16	100	6	6	100
Guanapito (Venezuela)[3]	18	13	72	6	5	83
Guri (Venezuela)[3]	22	16	73	9	7	78
Mean	**21**	**16·4**	**79**	**10·3**	**8·4**	**82**
Temperate lakes						
Erken (Sweden)[4]	71	25	35	25	12	48
Banyoles (Spain)[5]	47	20	43	12	8	67
Vila (Spain)[6]	32	16	50	11	9	82
Gull (Michigan)[7]	35	15	43	12	8	67
Lunzer Untersee (Austria)[8]	22	10	45	7	4	57
Traunsee (Austria)[8]	29	12	41	12	6	50
Wolfgangsee (Austria)[8]	29	13	45	12	8	66
Altaussersee (Austria)[8]	18	9	50	5	3	60
Esrom (Denmark)[9]	53	26	49	20	14	70
Hogan's (Newfoundland)[10]	27	14	52	12	7	58
Mean	**36·3**	**16·0**	**45·3**	**12·8**	**7·9**	**62·5**

[1] Lewis 1973b; [2] Ruttner 1952; [3] Lewis & Weibezahn 1976; [4] Nauwerck 1963; [5] Planas 1973; [6] Emiliani 1973; [7] Moss 1972; [8] Ruttner 1937; [9] Jonassen & Kristiansen 1967; [10] Davis 1972.

tropical lakes both within and outside a region. There is no indication that overlap is any more extensive between lakes in South-east Asia than between a lake in South-east Asia and one in tropical America. Overlap is extensive, even though the lakes vary greatly in chemistry and morphometry. For example, Guri is a dystrophic reservoir, Valencia is heavily loaded with allochthonous nutrients, and Lamongan is small by comparison with the other lakes. Despite these basic differences and the geographic separation of the lakes, the phytoplankton lists overlap almost 80% at the generic level with Lanao. The Lanao phytoplankton genera thus belong in large part to a pantropical phytoplankton assemblage typified by many of the genera common in Lanao. Lakes with extreme morphometry (e.g. Lake George, Uganda, Ganf 1974a, b) or chemistry (e.g. Nakuru, Melack &

Kilham 1974; lakes of Chad, Iltis 1974) are in a special category with regard to species-composition, as they are dominated by certain specialized species.

The Chlorophyta account for almost half of the genera in the list of tropical phytoplankton assemblages in Table 3. Variation among lakes is surprisingly slight in this respect; hence this aspect of composition is evidently a general feature of the pantropical assemblage. Some data for Lago do Castanho, Brazil, collected by Uherkovich & Schmidt (1974) appear discordant, due to the large number of euglenophyte taxa on their lists derived from net samples (fifty-four species). Many of these species are almost certainly not euplanktonic, however, and would thus not be included in lists compiled from sedimentation counts.

The percentage overlap of Chlorophyta between lakes is almost identical to the overlap of all other taxa combined. Overlap is thus not primarily a feature of only one division, but is shared by all major divisions contributing to the phytoplankton.

Table 3 also indicates that overlap of the Lanao phytoplankton with phytoplankton of other tropical lakes, no matter what their distance, is greater than with temperate lakes. As in the previous comparisons, there is a degree of subjectivity in the evaluation of data. Lake Erken, for example, probably supports the most thoroughly-studied phytoplankton assemblage in the world, hence the length of Nauwerck's species-list may be as much a testimony to Swedish limnology as it is a reflection of nature. There is, nevertheless, a marked tendency for the number of genera to be higher in the temperate lakes and for the percentage overlap with Lanao to be less. The higher number of genera is in part explained by the importance of the Chrysophyceae in the temperate lakes; this group is virtually absent in the plankton of the lowland tropics. The presence of Chrysophyceae in temperate lakes thus contributes to the reduced overlap between temperate and tropical lakes. Other factors may be involved as well, however, since the overlap within the Chlorophyta alone seems poorer between temperate and tropical lakes (Table 3).

Total biomass and distribution of biomass among major taxa

In Lake Lanao, the average annual autotroph biomass is divided quite unequally among the major taxa (Table 4). The inequalities in biomass only partly parallel the inequalities in numbers of species among these groups. Diatoms are as important as chlorophytes in terms of biomass, despite the vast difference in species-richness of these two groups. The Cryptophyceae also account for a rather large biomass considering that only two species are represented in Lake Lanao. Three other groups (Euglenophyta, Chrysophyceae, Dinophyceae) are also poor in species but these make only small contributions to the total biomass.

The average biomass composition of the plankton in Ruttner's fourteen Sunda lakes is remarkably similar to that of Lake Lanao (Table 4). The only exception is the greater biomass of dinoflagellates in Ruttner's series. Ruttner's data in fact show a dichotomy with respect to the dinoflagellates: among the fourteen plankton communities, three (Klindungan, Tjigombong, Sindanglaja) contained more than 60% dinoflagellate biomass, whilst the rest contained less than 10%. All of the lakes with high dinoflagellate biomass are very small, but not all of the small lakes in Ruttner's series contained a high proportion of dinoflagellates. Ruttner's samples spanned only a few days at each lake, so it is not clear whether the dinoflagellate blooms were transient or typical in the lakes where they occurred. No such blooms ever occurred in Lanao.

The average number of plankton units in Lake Lanao is greatest for the three groups

TABLE 4. Distribution of plankton units (=individuals) and biomass (=cell volume) among taxa in Lake Lanao (annual average, $n=65$) and in fourteen lakes on Java, Sumatra and Bali (computed from Ruttner 1952)

	Lake Lanao—annual mean*				14 Sunda lakes†	
	Plankton units (individuals ml^{-1})	Proportion (%)	Cell volume (μm^3 ml^{-1})	Proportion (%)	Cell volume (μm^3 ml^{-1})	Proportion (%)
Cyanophyta	10 165	48	294 600	19	988 200	18
Euglenophyta	107	1	3100	0	~ 54 900	<1
Chlorophyta	7172	34	533 200	34	1 152 900	21
Chrysophyceae	95	1	9500	1	~ 54 900	<1
Bacillariophyceae	2949	14	590 600	37	1 866 000	34
Dinophyceae	24	0	28 700	2	1 262 720	23
Cryptophyceae	483	2	123 300	8	109 800	<2
Total	**20 994**	**100**	**1 582 800**	**100**	**5 489 400**	**100**

* Integrated between 0 and 15 m (=euphotic zone).
† Integrated to the depth of half cumulative biomass (≃euphotic zone).

ranking highest in biomass (Table 4). The order of dominance is significantly altered, however, if abundance is measured as plankton units rather than as biomass, since the blue-greens are packaged on the average in much smaller units. About 50% of random encounters with autotroph particles would be with blue-greens, even though this group comprises only 20% of the biomass (Table 4). The annual average size per plankton unit for all groups, which can be computed from the totals of columns 1 and 3 of Table 4, is only 75 μm^3.

Table 5 compares the average phytoplankton biomass of Lake Lanao with that of other tropical lakes. Since only the Lanao data are drawn from an annual series of samples, the data must be interpreted with caution. The average for tropical lakes may be biased toward low values, as almost all of Ruttner's samples were taken during the cool season when biomass is likely to be lowest.

For purposes of Table 5, biomass per unit volume or area has been computed over the

TABLE 5. Autotroph biomass in the euphotic zones of selected tropical and temperate lakes.

	Euphotic zone (m)	Wet biomass (mg m^{-2})		Euphotic zone (m)	Wet biomass (mg m^{-2})
Tropical lakes			Temperate lakes		
Lanao (Philippines)*	15	23 745	Erken (Sweden)†,[4]	10	14 800
Mainit (Philippines)[1]	15	22 530	Lucerne (Switzerland)†,[5]	15	10 500
Lamongan (Java)[2]	10	42 000	Castle (California)†,[6]	15	9000
Ranau (Sumatra)[2]	12	2500	Beasley (Colorado)*,[7]	5	9000
Singkarak (Sumatra)[2]	12	2800	Estes (Colorado)*,[7]	5	6900
Maninjau (Sumatra)[2]	15	2700	Grand (Colorado)*,[8]	15	6600
Toba (Sumatra)[2]	18	240	Lunzer Untersee (Austria)[9]	10	3250
Valencia (Venezuela)[3]	10	7413	Traunsee (Austria)[9]	10	4710
Lagartijo (Venezuela)[3]	10	26 975	Wolfgangsee (Austria)[9]	10	6530
Guanapito (Venezuela)[3]	10	16 499	Altaussersee (Austria)[9]	10	750
Guri (Venezuela)[3]	10	4516	Lahngangsee (Austria)[9]	10	9760
Mean		**13 811**	**Mean**		**7518**

* Annual average; † Average for the ice-free season.
[1] Lewis 1973b; [2] Ruttner 1952; [3] Lewis & Weibezahn 1975; [4] Nauwerck 1963; [5] Bloesch 1974; [6] de Amezaga, Goldman & Stull 1973; [7] Pennak 1949; [8] Pennak 1955; [9] Ruttner 1937.

euphotic zone only, which is equated with the top 15 m in Lake Lanao. For other lakes used in the comparisons, the 1% light level, if known, is assumed to be the boundary of the euphotic zone; if the 1% light level is found at less than 10 m in a lake of moderate size (10–100 km^2), the euphotic zone is equated with the upper 10 m, as mixing usually brings the phytoplankton routinely to the surface from 10 m depth in such lakes. For small lakes (<10 km^2), the minimum thickness of the euphotic zone is assumed to be 5 m.

The biomass values of Table 5 range over two orders of magnitude, partly because they are generally not annual averages, and thus reflect temporal variability as well as variability between lakes. The values indicate that Lake Lanao is in the upper or upper middle range of tropical lakes with respect to autotroph biomass. Very shallow lakes, which constitute a special case, have been omitted from the list (e.g. Lake George, Uganda, biomass 46·8 g m^{-2} (Burgis *et al.* 1973); Lago do Castanho, Brazil, biomass 19·0 g m^{-2} (Schmidt 1973); saline lakes of Chad, biomass >100 g m^{-2} (Iltis 1974)).

The temperate lakes listed in Table 5 average about half the phytoplankton biomass of the tropical lakes. The temperate lakes of Table 5 have been selected to rule out special cases, especially lakes subject to heavy artificial nutrient loading that might result in a spuriously high mean biomass (e.g. Rotsee, Switzerland, biomass 65 g m^{-2} for the ice-free season (Bloesch 1974)).

The mean phytoplankton biomass of Lanao is considerably above the biomass of the naturally eutrophic temperate lakes listed in Table 5, even when the low winter biomasses of the temperate lakes have been omitted from consideration.

Distribution of dominant species among major taxa

In Lake Lanao, as in all other lakes for which the seasonal cycle is known, a few species account for a large proportion of the annual mean biomass (Fig. 2). The species comprising 90% of the stock will be considered dominants for present purposes. If abundance is measured as biomass, there are thirteen dominants, whereas if abundance is measured as

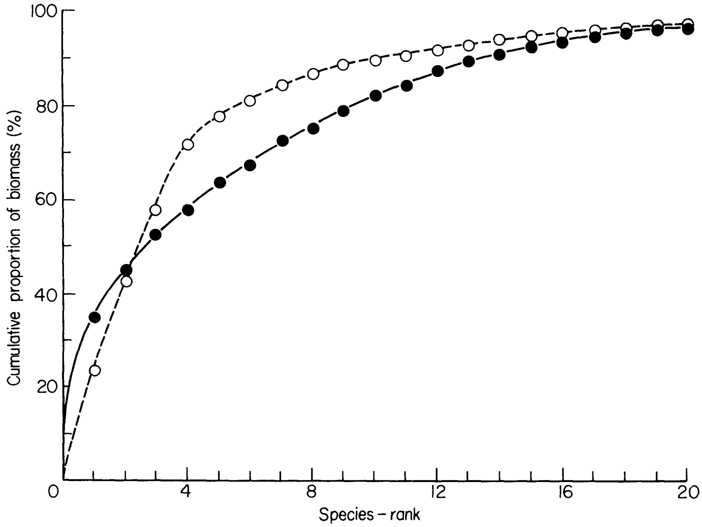

FIG. 2. Cumulative proportions of biomass (—●—) and numbers of individuals (plankton units) (– –○– –) in Lake Lanao accounted for by successive species ranked in order from most abundant to least abundant; the data are drawn from annual averages.

bioplankton units, there are ten dominants. The individual identities of these dominants can be determined by reference to the ranks listed in Table 1.

Casual examination of Table 1 might suggest that the species of some major taxa account for a disproportionate share of dominants. This impression can be tested statistically with the data at hand. Of the seventy species in Lanao, forty-four belong to the Chlorophyta. Among the thirteen dominants as determined by biomass, six are chlorophytes. The expected number of dominants among the chlorophytes is $(44 \div 70) \times 13$, or 8·2. Chi-square with correction for continuity (Sokal & Rohlf 1969) yields the value 0·43 for a test of the ratio of dominants to non-dominants among the Chlorophyta; this value is not statistically significant, and hence there is no evidence for any real departure from a random distribution of dominants between chlorophytes and non-chlorophytes. Thus it would appear that the chance of a given species being a dominant is independent of the major taxon to which the species belongs.

The statistical test on the Chlorophyta can be repeated using numbers of plankton units rather than biomass as an index of abundance. In this case there are ten dominants, of which five are chlorophytes. The observed value of 5 does not differ significantly from the expected number of dominants among the Chlorophyta (6·2), based on an even distribution of dominants among the major taxa.

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