6. The phytoplankton

Pierre Compère and André Iltis

6.1 Qualitative composition of the algal flora (P. Compère)

About 1300 species and intraspecific taxa of algae and plankton were collected in Lake Chad, the lower course of its main tributaries such as the Shari, the El Beïd and the Yobé, and in various ponds of the flooded zones of these rivers (Iltis and Compère 1974; Compère 1974–1977). If those collected by J. Leonard in 1964 (Compère 1967) are added to these, the total number of algal species found in the Lake Chad region is 1500. Lake Chad itself had the greatest number of taxa (1042), but the collections there were much more numerous than in the tributaries and their flood plains which had 903 taxons. The southeastern part of Lake Chad appeared to have the most varied flora with 787 taxons compared with 628 for the northern part and only 461 in the southern part, where the collections were less numerous than in the other parts (Table 1).

The green algae were by far the most numerous within this flora since they represented 52% of the total taxa, with 12% Euchlorophyceae, 8% filamentous green algae such as Ulotrichophyceae and Zygnemataceae and 32% Desmidiaceae. The Diatoms followed with 27% and the Cyanophyceae with 13% and finally, all the other classes represented a little less than 8%. Of course, these data refer to the number of taxa and not to the number of individuals. Cyanophyceae often played a much more important part in the appearance and biomass of the plankton because of the mass development of some species such

Table 1 Distribution of the different algal types in the flora of the Lake Chad region.

	Lake Chad region		Tributaries		South-eastern part		South		North	
	N	%	N	%	N	%	N	%	N	%
Cyanophyceae	168	13.1	106	11.7	106	13.5	51	11.1	105	16.5
Diatoms	349	27.2	274	30.3	248	31.5	156	33.8	213	33.9
Green algae:										
. Euchlorophyceae	170	13.2	126	13.9	105	13.3	64	13.9	101	16.1
. Ulotrichophyceae + Zygnemataceae	101	7.9	65	7.2	44	5.6	16	3.5	35	5.6
. Desmidiaceae	398	31	270	29.9	251	31.9	140	30.4	136	21.7
Others	98	7.6	62	6.9	33	4.2	34	7.4	38	6.0
Total	1284		903		787		461		628	

delta and the tributaries are considered in this northern part where conductivity exceeds 500 $\mu S\ cm^{-1}$, this tendency clearly increased with Desmidiaceae representing only 17% of the flora while Diatoms represented 36% and Cyanophyceae nearly 20% (Fig. 1). In this last region, the qualitative composition of the algal flora tended to be more similar to that of the floras of North Africa.

Table 2 enables us to draw a parallel between the composition of the algal flora of the Lake Chad region and that of some tropical or subtropical regions. It was not very different from that observed previously in the lower Shari and the southeastern part of Lake Chad (Compère 1967). It is difficult to compare with the algae found in Mali (Bourrelly 1957; Couté and Rousselin 1975), in the Ivory Coast (Bourrelly 1961) or in Guinea (Bourrelly 1975) since there are no data on Diatoms on these countries (Fig. 2). In each region, the prevalence of the Desmidiaceae (from 40 to 75%) and the rather small amount of Cyanophyceae (from 3 to 10%) is emphasized. In Morocco (Gayral 1954) and Algeria (Gauthier-Lièvre 1931; Baudrimont 1974) the algal floras contained large numbers of Diatoms (37–40%) and Cyanophyceae (17–19%), while the green algae represented only 35% of the whole, among which Desmidiaceae represented only 11 to 13%. In Ennedi and Kanem, the floral composition was very similar to that of North Africa. The percentages of the various algal groups in the flora of the Lake Chad region seem to be situated between those of the North-African or Saharian floras and those of the floras from more tropical regions in Western Africa.

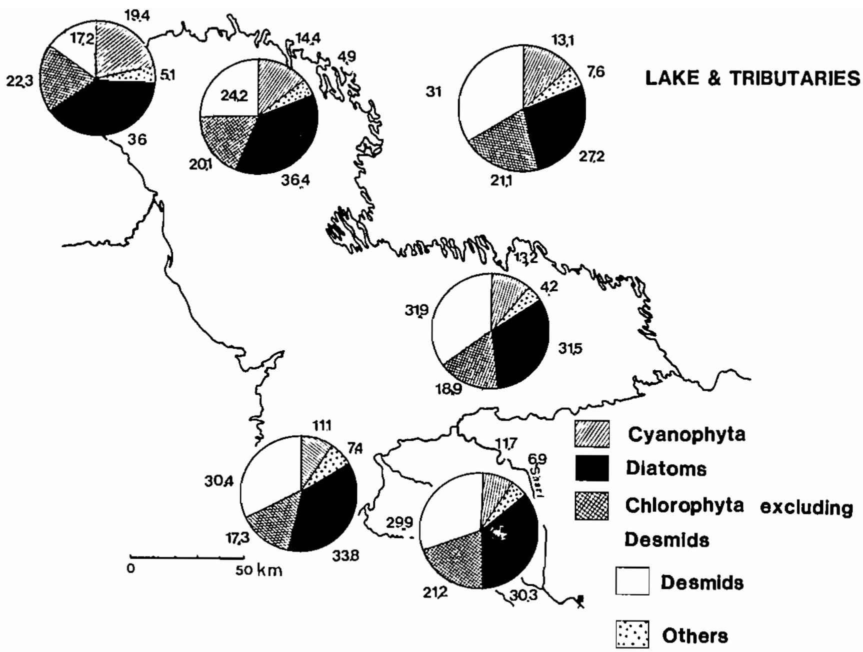

Fig. 1 Distribution of the different classes in the algal flora of Lake Chad. Upper right and outside the map for the total flora of the lake and its tributaries; inside the map, for the different local flora.

This floral composition is similar to that of the total flora of the great lakes of Eastern Africa (Van Meel 1954), although Diatoms were more abundant there than the green algae, among which the Desmidiaceae were less important. It must be pointed out that Van Meel's observations were made mainly on the plankton and in Lake Chad, we also observed that Diatoms were relatively more abundant in the plankton while Desmidiaceae were especially common in the periphyton. Finally the algal flora in Burma which was described by Skuja (1949) showed a qualitative composition similar to that of the Lake Chad region. Here Diatoms seemed to play a more discrete role, but it must be noted that the author appeared to be less interested in this class than in the others since he did not even devote even one plate out of the 37 included in his work to Diatoms.

The geographic distribution of the flora is given in Table 3 which shows that cosmopolitan or subcosmopolitan species predominated and represented more than 65% of the flora (Fig. 3). Tropical species represented more than 28% of the flora, of which the endemic or African species represented 14% and the tropical species with a wider distribution also represented 14%. The remaining 7% were algae known especially from temperate regions. The tropical compo-

Table 2 Distribution of the different algal types in a few tropical floras (in %).

	Region (Table 1) (Lake Chad)	Lake (Lake Chad) (1)	Macina (Mali) (2)	Middle Niger (Mali) (3)	Ivory Coast (4)	Guinea (5)	Kanem (6)	Ennedi (7)	Algeria (8)	Morocco (9)	Eastern Africa (10)	Burma (11)
Cyanophyceae	13.1	10.1	3	3.5	9.2	6.3	18.9	19.5	17.4	19.5	11.8	20.0
Diatomophyceae	27.2	32.0	–	30.2	–	–	40.7	36.3	40.6	37.3	45.2	17.4
Green algae												
Desmidiaceae	31	41.4	75	49.8	38.6	65.4	8.7	11.1	11.5	12.8	22.1	37.0
Others	21.1	14.8	17	9.8	16.5	10.0	20.2	19.8	23.5	21.4	18.2	16.8
Others class	7.6	1.7	5	6.7	35.7	18.2	11.5	13.4	7	9	2.6	8.6
Total number of taxa	1284	444	213	550	313	220	514	324	1025	686	1216	841

From: (1) Compère 1967; (2) Bourrelly 1957; (3) Couté and Rousselin 1975; Maillard 1977; (4) Bourrelly 1961; (5) Bourrelly 1975; (6) Iltis 1972; (7) Compère 1970; (8) Gauthier-Lièvre 1931; Baudrimont 1974; (9) Gayral 1954; (10) Van Meel 1954; (11) Skuja 1949.

Table 4 Simplified geographic distribution of a few African algal floras (in %).

	Lake Chad region	Macina (Mali) (1)	Middle Niger (Mali) (2)	Ivory Coast (3)	Guinea (4)	Ennedi (5)
Cosmopolitan + subcosmopolitan + temperate	71.4	47	61.3	61.8	63.7	82
Tropical + subtropical	14.6	25	20.0	15.9	22.7	10
African (with endemics)	14.0	28	18.7	22.3	13.6	8

From: (1) Bourrelly 1957; (2) Couté and Rousselin 1975; Maillard 1977; (3) Bourrelly 1961; (4) Bourrelly 1975; (5) Compère 1970.

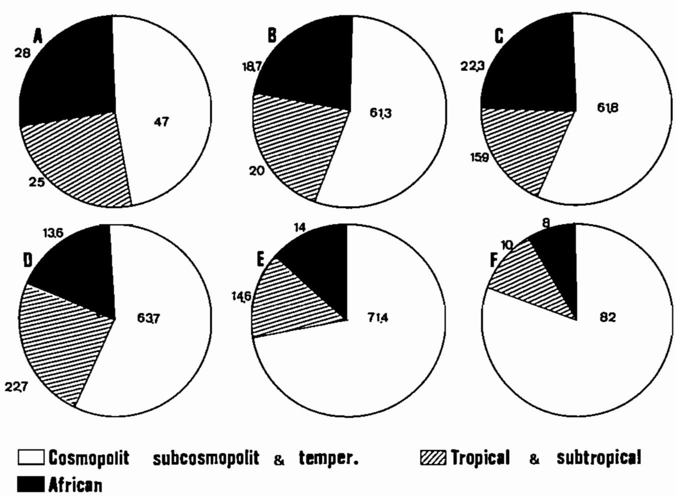

Fig. 4 Simplified geographical compositions of a few African algal florules. A, Macina, Mali, according to Bourrelly (1957); B, Middle Niger, Mali according to Couté and Rousselin (1975) and Maillard (1977); C, Ivory Coast, according to Bourrelly (1961); D, Guinea according to Bourrelly (1975); E, region of Lake Chad; F, Ennedi, according to Compère (1970).

This intermediate character was still apparent when Bourrelly's empirical indices (1957, 1961) were applied to Desmidiaceae of the flora under study. This index calculates the percentages of all the Desmidiaceae represented respectively by the total number of *Pleurotaenium* and filamentous Desmidiaceae and by the total number of *Pleurotaenium*, *Euastrum* and filamentous Desmidiaceae. Table 5 gives these indices for the Desmidiaceae belonging to our flora as well as a few tropical desmidial floras.

The resulting values are a little lower than those calculated previously for the lower Shari and the southeastern part of Lake Chad (Compère 1967). They are also lower than those calculated for various other tropical African floras and for Amazonia, but they are generally higher than those for temperate floras (Bourrelly 1957, 1961). They are very close to those calculated from Skuja's data (1949) for Burma and for Middle Niger (Couté and Rousselin 1975), and a little higher than those calculated from Van Meel's data (1954) for the plankton in the great lakes of Western Africa.

In summary, Desmids and Diatoms were qualitatively the dominant species in the algal flora of the Lake Chad region. Although they were represented by fewer taxa, Cyanophyceae played an important quantitative role. The composition of this flora clearly shows a tropical African character that was more pronounced than in the North-African floras or in those of the South Sahara massifs but certainly less pronounced than in those of the Sudano-guinean regions of Western Africa. In the region studied, this tropical African character was greater around the Shari and the southeastern part of the lake. By its floral composition and the distribution of its geographic elements the flora in the far northwest of the lake tended to approach the Sahelian and Saharian floras.

Table 5 Bourrelly's empirical indices (1957) for a few tropical desmidial floras.

	Region (Lake Chad)	Lake (Lake Chad) (1)	Macina (Mali) (2)	Middle Niger (Mali) (3)	Ivory Coast (4)	Guinea (5)	Sierra Leone (6)	Eastern Africa (7)	Amazonia (8)	Burma (9)
Pleurotaenium + fil. Desm. / total Desmids	7	8.5	13.5	5.4	15.0	11.7	11.9	6.0	13.0	8.6
Pl. + *Euastrum* + fil. Desm. / total Desmids	14	19.2	27.7	17.0	24.1	19.4	24.5	12.3	23.2	14.6

From: (1) Compère 1967; (2) Bourrelly 1957; (3) Couté and Rousselin 1975; (4) Bourrelly 1961; (5) Bourrelly 1975; (6) Grönblad et al. 1968; (7) Van Meel 1954; (8) Thomasson 1971; (9) Skuja 1949.

6.2 Phytoplanktonic communities and biomasses (A. Iltis)

The study of the Lake Chad phytoplankton was difficult for the following reasons. It is a very wide lacustrine basin with varied ecological zones and aquatic vegetation developed to varying extents depending upon the topography of the lake bottom and banks. Considerable variations in physico-chemical conditions occur in the regions, and the variety of lake zones make it necessary to sample all of them to analyze the plankton and estimate total biomass. Given the possible isolation of some regions by vegetation barriers or swampy shoals according to the variations in water level, sampling was fairly difficult in these shallow biotopes. The studies were designed to analyze the following points: seasonal variations, delimitation of the different ecological zones, species associations, plankton biomass and development during a period of drought. Studies on the primary production and its estimates were later added to these observations.

Given the shallowness of the lake, the euphotic layer included, with few exceptions, the total water column. Moreover, the samples taken below the surface could be considered as representative of the limnoplankton of the entire water surface. The analysis of samples taken in the archipelago from the surface to a depth of 5 to 6 meters showed a maximum variation in the composition and density of 14% according to the depth in the water column (Gras et al., 1967). This value is lower than the error generally occurring in plankton counts. Therefore, it can be accepted that for this study of the phytoplankton the algae were distributed homogeneously throughout the water column.

The phytoplankton biomass was estimated by counting the organisms under an inverted microscope from sub-samples taken in the lake about ten centimeters below the surface and immediately fixed in 10% formalin. The results were expressed either as the number of cells, cenobes or colonies per liter and transformed into biovolumes of living algae per liter after calculating the mean volume of each species. From 1974, titrations of chlorophyll *a* were conducted by spectrophotometry.

The studies on the phytoplankton were at first limited only to the Shari and the eastern part of the lake (Gras et al. 1967) but later extended to the whole lake. The main biotopes were then delimited for the first time (Carmouze et al. 1972), and from 1971 to 1975, general surveys provided biomass estimates and detailed analysis of the communities (Iltis 1977). Studies on primary production were also conducted in various parts of the lacustrine basin (Lemoalle 1979).

6.2.1 *Characteristics of the communities*

6.2.1.1 *Composition.* In the phytoplankton observed in the entire lake from 1964 to 1975, Cyanophyceae, Chlorophyceae and Diatomophyceae were the most important groups quantitatively, while the Pyrrhophyta, Euglenophyta, Chrysophyceae and Xanthophyceae seldom appeared in large proportions.

Cyanophyceae occurred throughout the year in the far east and the northeast where they represented 80% of the biomass and were generally the most important constituent of the phytoplankton in the archipelago zones. During the warm season, they extended into the open water and especially the Southern Open Water. *Microcystis* and *Anabaena* were the most frequent genera among which species *Microcystis aeruginosa*, *M. holsatica*, *M. elachista* and *Anabaena flos aquae* were very abundant. Moreover, *Lyngbya limnetica* and *L. contorta* occurred, forming up to 18 and 8% in the archipelago and the southern open water during certain periods. *Oscillatoria laxissima* and *Anabaenopsis tanganiikae* also appeared occasionally in considerable number.

To show the importance of Cyanophyceae in the phytoplankton biomass, it should be pointed out that out of 35 samples taken over the whole lake in February 1971, 32% of the algal biovolume was composed of Cyanophyta and in January 1972, the percentage to 49% in 40 samples. In April 1974, the mean percentage of Myxophyceae was 25% (38 samples) in the lake and decreased to 11% in November 1974 (17 samples) and to 6% in February 1975 (17 samples) after the occurrence of the drought (Table 6).

In the Diatomophyceae, *Melosira granulata* var. *angustissima*, *Nitzschia spiculum* and an unspecified *Navicula* were the three species with the highest densities in the lake during the period of 'Normal Chad'. *Melosira granulata* predominated during certain periods in both the archipelago and the open water of the southern part of the lake where considerable changes occurred during the first quarter of the year before the establishment of dense populations of Cyanophyceae in the warm season. *M. granulata* was sometimes replaced by *Nitzschia spiculum* (Iltis and Lemoalle 1976), and *Navicula* sp. formed up 25 to 30% of the biomass in the Northern Open Water in January 1972. During the period of 'Lesser Chad', *Cyclotella meneghiniana*, *Coscinodiscus rudolfii*, *Synedra berolinensis*, *Surirella linearis*, *S. muelleri* and *Nitzschia*

Table 6 Mean percentages of the different algal groups calculated from the phytoplanktonic biovolumes (analysis conducted on 147 samples collected during five surveys in Lake Chad from 1971 to 1975).

	Cya. %	Diat. %	Chlor. %	Eugl. %	Others %
February 1971 (*N*=35)	32	23	39	0	6
January 1972 (*N*=40)	49	27	22	0	2
April 1974 (*N*=33)	25	56	12	6	1
November 1974 (*N*=17)	11	47	28	10	4
February 1975 (*N*=17)	6	67	13	11	3

sp. occurred in high densities, especially in the northern part where they predominated.

In the whole lake, the average percentages of Diatomophyceae in the algal biovolume were as follows: 23% in 35 samples in February 1971, 27% in 40 samples in January 1972, 56% in April 1974, 47% in November 1974 and 67% in February 1975. Therefore, the percentage contribution of Diatoms to biomass considerably increased after the change towards the period of 'Lesser Chad'. In the northern part of the lake which was still occupied by water, 60% in April 1974, 49% in November 1974 and 89% of the phytoplankton biomass was composed of Diatoms.

Chlorophyceae represented 39% of the phytoplankton volume in the 35 samples taken in February 1971 and 22% in January 1972. In 1974 and 1975 during the period of 'Lesser Chad', this percentage decreased to 12%, 28% and 13%. The most abundant species in the phytoplankton were *Scenedesmus quadricauda*, *Oocystis* sp., *Closterium aciculare* and *C. strigosum*, *Coelastrum cambricum* and *C. microporum*, *Gonatozygon monotaenium*, *Pediastrum clathratum* and *Botryococcus braunii*. It appears that during the period of 'Normal Chad', the open water of the northern part of the lake was the richest in Chlorophyta such as *Scenedesmus quadricauda* or *Closterium aciculare*. Dense populations of *Closterium strigosum* appeared during certain periods in the archipelago of the southern part of the lake, but in most cases, the populations of Chlorophyceae were much more diverdified than those of Cyanophyceae or Diatomophyceae.

Euglenoïds only represented a considerable proportion of the biomass (up to 80%) during the period of 'Lesser Chad' in the region of the Eastern Archipelago which was divided into numerous ponds overgrown with vegetation.

Among the Pyrrhophyta, *Cryptomonas erosa* constituted more than 20% of the algal biovolume in some samples from the northern part of the lake. Moreover, it should be pointed out that an unidentified species of the genus *Peridinium* was abundant during certain periods and that *Mallomonas portae ferrae*, a Chrysophyceae, was sometimes abundant.

6.2.1.2 *Density and biomass.* The difference between the lowest and the highest phytoplankton densities was considerable. Algal biovolumes of 0.005 μ l^{-1} were found in the Southern Open Water of the lake in February 1971 and biovolumes of 305 $\mu l\, l^{-1}$ were found in the part of the northern basin still occupied by water in November 1974. Therefore, these extreme values represent respectively the poorest waters during the period of 'Normal Chad' and the richest waters during the period of 'Lesser Chad'.

The magnitude of these differences was due to the yearly variations in the lake and the change from 1973 towards a Lake Chad with pond-like characteristics. The observations in time however showed that there were profound differences between the various lake zones and that the archipelagoes were much richer than the open water (Fig. 5). The minimum, mean and maximum values observed from the analysis of samples taken during five surveys from 1971 to 1975 are given in Table 7.

During the 'Normal Chad' period, the mean algal biomass ranged from 1 to 2 mg l^{-1} and it increased considerably (up to 74 mg l^{-1}, when the lake turned into 'Lesser Chad', as a result of the drought. More specifically, the mean

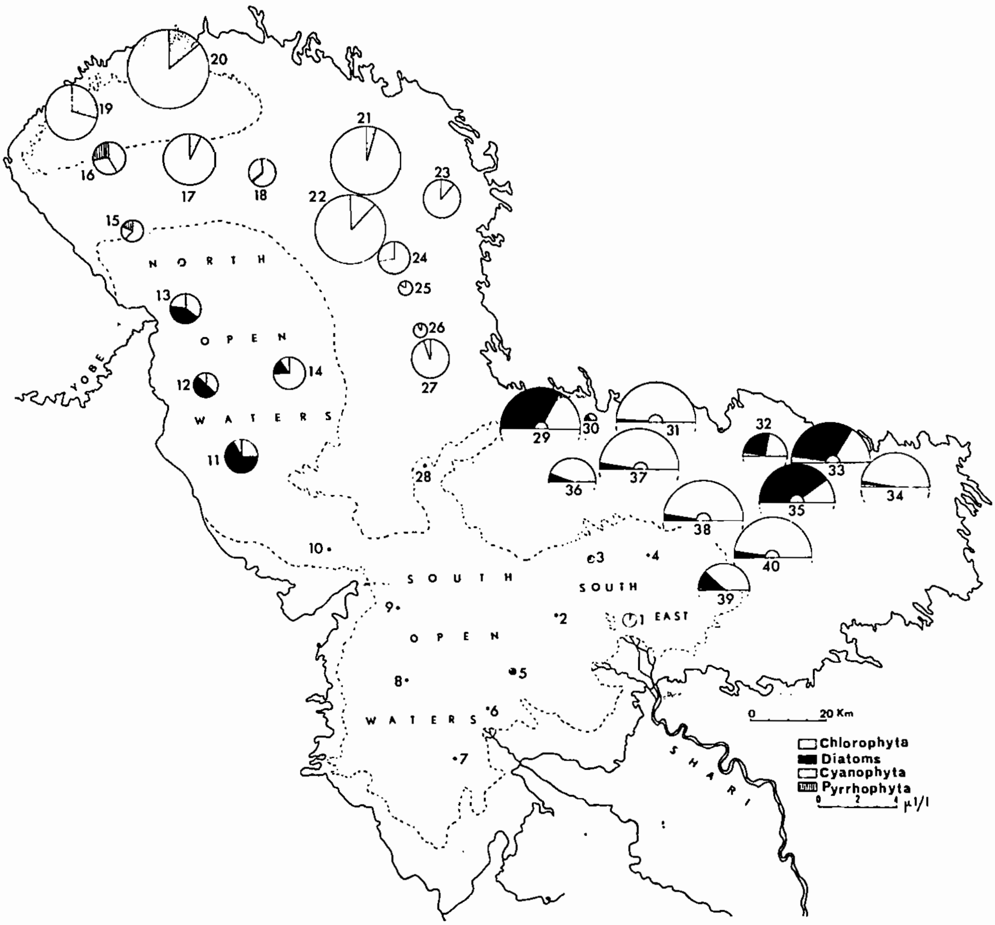

Fig. 5 Location and composition of the phytoplanktonic samples in January 1972. The diameter of the circles is proportional to the phytoplankton density except in points 29, 31, 33, 35, 37, 38 and 40 where the density is very high. The algal biovolumes which are lower than 0.2 µl l^{-1} are represented by a point. The approximate limits of the zones of open waters represented with broken lines.

Table 7 Algal biovolumes (µl l^{-1}) observed in Lake Chad during five surveys from 1971 to 1975.

	Minimum	Mean	S.D.	Maximum	
2/1971	0.005	1.1	2.11	12.1	'Normal Chad'
1/1972	0.06	2.4	2.45	10.5	
4/1974	0.74	21.8	30.79	183.1	'Lesser Chad'
11/1974	0.11	74.1	102.31	305.6	
2/1975	0.16	32.3	55.93	219.9	

biomass at this stage was obtained from the biomass of three individual waters bodies which then represented Lake Chad. The northern basin was the richest of the three and the average algal biovolume was 25.3 µl l^{-1} in April 1974, 179 µl l^{-1} in November 1974 and 74.5 µl l^{-1} in February 1975. These densities were the highest ever observed and it can be considered that from November 1974, when the maximum depth was about one meter, these biotopes were closer to the natron ponds situated in the north of Lake Chad than to lacustrine waters.

On the contrary, the open water in front of the Shari delta remained poor, with mean biovolumes of 7.8 µl l^{-1} in April 1974, 0.8 in November and 0.7 in February 1975. In the archipelago, the biovolumes observed during the same period were respectively 8.2, 0.4 and 7.6 µl l^{-1}.

Measurements of the chlorophyll *a* concentration were made by Lemoalle (1979) in different parts of the lake during various periods. During the period of 'Normal Chad', only the southern basin was sampled and two series of samples were taken in December 1970 and in June 1971 respectively. Minimum values of 5 mg m^{-3} were observed in the open water close to the delta in December 1970, while values ranging from 60 to 70 mg m^{-3} were found in the eastern part of the archipelago in June 1971. The values ranged from 15 to 70 mg m^{-3} in June 71 (period of low water) and from 5 to 36 in December (period of flood).

After 1973 during the period of 'Lesser Chad', concentrations remained very low (10 mg m^{-3}) during the flood in the southern basin in front of the delta. In that part of the open water furthest from the delta, they normally ranged from 80 to 120 mg m^{-3} in April, May and June. In the archipelago, which was divided by vegetation into a very heterogeneous group of patches water not always connected with each other, the values ranged from 2 to 325 mg m^{-3} according to the periods and stations. In the northern part of the lake which was surveyed only during the period of 'Lesser Chad', the mean chlorophyll *a* concentration, based on 7 to 11 stations around the islet of Kindjéria, was 141 mg m^{-3} in April 1974, 1658 in November 1974 and 204 in February 1975.

It seems that comparison with the other tropical environments must be made cautiously, as the available data are not very abundant or not always complete.

Moreover, they seldom represent annual averages so that values are overestimates or underestimates according to the sampling seasons. In the case of Chad, it can be assumed that the samples and the calculations from February 1971 and January 1972 underestimated the mean annual biomass. As a matter of fact, the open water in the lake was composed of the Shari flood water which was still not colonized by the plankton. Given the extent and the shallowness of this zone in relation to the whole lake, it can be estimated that the differences between the values found and those observed when the river was at its lowest ranged from 12 to 13% (Iltis 1977). Comparison of results of the analysis of algal biomass in tropical or temperate lakes is also difficult as they may be expressed in different terms: biomasses expressed per unit of area, as number of cells per liter, as dry weight, as quantity of pigments or in microliters or grams of living algae per liter or per cubic meter. The last expression (living matter per unit volume of the euphotic layer) seems to be the most practical one. Moreover, it is pointed out that in very heterogeneous environments the existing biomass in each zone or group of regions is often more interesting than a single mean value, e.g. in Lake Chad after 1974 when the three water bodies which then constituted the lake were virtually isolated from each other and developed individually. Therefore, a mean value obtained from estimates made in different environmental zones has little significant use for lake comparisons. With the exception of very shallow lakes (Lake George in Uganda, natron lakes north of Lake Chad and certain lagoons) (Lewis 1978), only the Lake Chad values obtained during the period of 'Normal Chad' can be used for comparisons as the water depth was almost always less than two meters during the period of 'Lesser Chad'.

According to the results given by Lewis (1978), Lake Chad during the normal period (values ranging from 1.2 to 2.4 mg l^{-1}) is similar to tropical lakes rich in phytoplankton (Lake Lanao, the Philippines, 1.6 mg l^{-1}; Lake Lamongan, Java, 4.2 mg l^{-1}; Lake Lagartijo, Venezuela, 2.7 mg l^{-1}) especially when considering that the calculations, made when the southeastern part was submerged by the Shari flood, were underestimated (12 to 13%). These values are only averages compared with the biomass observed between Canada and the United States in the very eutrophic Lake Erie (Munawar and Munawar 1976) where the mean values range from 1.5 to 7.1 g l^{-1} according to season and lake region.

6.2.1.3 *Species diversity and environmental constant.* The species diversity (determined by the number of species present and the distribution of the total biomass between them) was calculated according to Shannon's formula. Only the taxa representing at least 0.07% of the total biomass present in the sample were used to calculate the diversity index.

The mean diversity values for the whole lake during five surveys conducted from 1971 to 1975 seem to be very similar and ranged from 2.14 to 2.75 bits

Table 8 Diversities (in bits) observed in Lake Chad during five surveys from 1971 to 1975.

	Minimum	Mean	S.D.	Maximum	Taxa number	
					Mean	S.D.
2/1971	0.611	2.752	0.81	4.186	15.2	7.15
1/1972	0.528	2.141	0.86	3.441	12.3	3.81
4/1974	0.422	2.328	0.93	3.835	21.0	6.24
11/1974	0.378	2.553	0.76	3.938	19.9	5.19
2/1975	1.182	2.324	0.86	3.778	18.7	7.71

(Table 8). These observations were too scattered in time to provide a thorough information on the changes on the biocenoses, but they were sufficient to allow the delimitation and characterization of the different ecological zones in terms of their phytoplankton communities. Thus, for the samples taken in 1972 (Fig. 6), the mean diversity was 1.775 in the Southern Open Water and 3.078 in the Northern Open Water, while the Northern Archipelago and the Eastern Archipelago showed diversities of 2.569 and 1.705 bits respectively. The communities in the northernmost part and in the eastern part of the Eastern Archipelago which were the richest in phytoplankton had a mean diversity of about 1.942 bits.

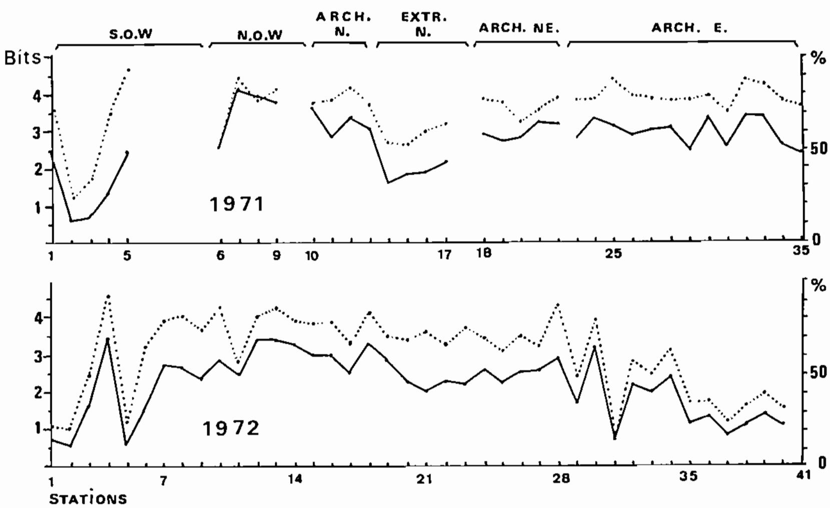

Fig. 6 Variations in the values of the specific diversity index (represented with a continuous line) and of the equitability (represented with dotted lines). (S.O.W. = southern open waters; N.O.W. = northern open waters; ARCH. N = northern archipelago; EXTR. N = far north, etc.).

The values of diversity and equitability (calculated as the percentage value of the ratio of the observed diversity to the maximum diversity) were represented on a graph in relation to the ecological zones where samples were taken. In February 1971, diversity was low in the Southern Open Water except at station 1 (perideltaic zone). Diversity increased in the Northern Open Water where it reached the maximum value (i = 4.186) and decreased abruptly in the north of the lake, especially in the northernmost stations (14 to 17) where the algal biomass was composed of only some species of Cyanophyceae. In the archipelago, the diversity index remained rather high in the north (station 18 to 21) as well as in the east (stations 23 to 35), while the easternmost stations generally had diversity indices which were slightly lower. The variations in equitability closely followed those of diversity with a high correlation between them ($r = 0.80$). In January 1972, the profile according to the ecological zones was almost identical to that of February 1971.

Diversity was low in the Southern Open Water except at the easternmost point 4 whose phytoplankton communities (with a rather high percentage of Cyanophyceae) showed similarities to that of the neighbouring stations 38 and 39. Maximum values were observed in the Northern Open Water (stations 12 and 13) and in the archipelago situated north of them (station 18), and lower values were observed in the northernmost part of the lake (stations 20 to 23). In the archipelago, diversity was rather high in the northeastern part of the lake (station 24 to 28) but very variable in the eastern zone, all the communities situated close to the open water (35 to 40) generally having diversities lower than those bordering the lake (29, 30, 32, 33, 34). As in 1971, equitability followed the variations in diversity (the correlation coefficient between these two series of values was 0.95) and provided little further information.

Several successive stages could be distinguished in the phytoplankton of the flood wave which moved from the delta towards the northwest where the open water was most extensive. Initially there was a stage with abundant Diatoms and low algal density and species diversity in the Southern Open Water. The second stage was characterized by the community of the Northern Open Water having an average phytoplankton density and a maximum diversity while Diatoms decreased in percentage contribution of total. The third stage which was related to the phytoplankton of the reed islands north of the previous zone was characterized by increasing density and decreasing diversity while the Diatom population practically disappeared to be replaced by Cryptophyceae. Finally a fourth stage could be defined in the northern part of the lake where there was a community characterized by maximum density and low diversity which was composed mainly of Cyanophyta. It is difficult to consider these stages as parts of succession cycles in phytoplankton development as shown by Margalef (1958–1967) for populations of marine algae. The changes in the phytoplankton were influenced by numerous local factors such as the presence of residual waters which were more or less mixed with flood waters when moving through the northern basin, the heterogeneity of the zones or the existing biotopes, and the increase in dissolved salt content with increasing distance from the Shari delta. These factors upset the succession of developmental cycles which would normally exist in a water body subject to relatively homogeneous environmental factors. In 1974 and 1975, when the lake consisted of only three individual water bodies, the mean species diversity varied from one to another.

For a better knowledge of the algal population structure, the distribution of species abundance was analyzed in each sample. Motomura's log-linear model (Motomura 1932; Inagaki 1967) often appeared to be the most accurate representation of the existing distributions. From an analysis of 147 samples, Motomura's law of log-linear species distribution was perfectly corroborated in 37% of the cases and fairly well in 45% of them according to the thresholds suggested by Inagaki and Lenoir (1974). The adjustment was inadequate in 18% of the samples.

As in the case of the diversity index (Table 9), the different ecological zones could be characterized by the values found during five surveys. In 1971 and 1972, the highest values were observed in the Northern Open Water and the Eastern Archipelago (Fig. 7), with the minimum values being found in the Southern Open Water, in the far north and in certain points of the Eastern Archipelago. The environmental constant was related to the number of species comprising the biomass and the correlation coefficient between these two series on values was 0.78 in February 1971 and 0.82 in January 1972. After 1973, during the period of 'Lesser Chad', the values of the environmental constant were fairly high in the open water facing the Shari delta (0.71 to 0.85) except at station 3 in April and November 1974 when Diatoms developed on a large scale. In the archipelago close to Bol, the high environmental constant was close to or above 0.8 except in November 1974 when it ranged from 0.70 to 0.80 at the different sampling points. The lowest values were found in the far northwest, north and northeast of the northern basin where the salt content was highest and at station 12 where a species of Centric Diatom predominated in the algal population. In November 1974 when variations were low, the highest

Table 9 Values of the Motomura's constant for the algal communities in Lake Chad.

	Minimum	Mean	S.D.	Maximum
2/1971	0.308	0.681	0.14	0.861
1/1972	0.256	0.628	0.13	0.794
4/1974	0.376	0.754	0.09	0.854
11/1974	0.682	0.745	0.06	0.852
2/1975	0.399	0.689	0.14	0.831

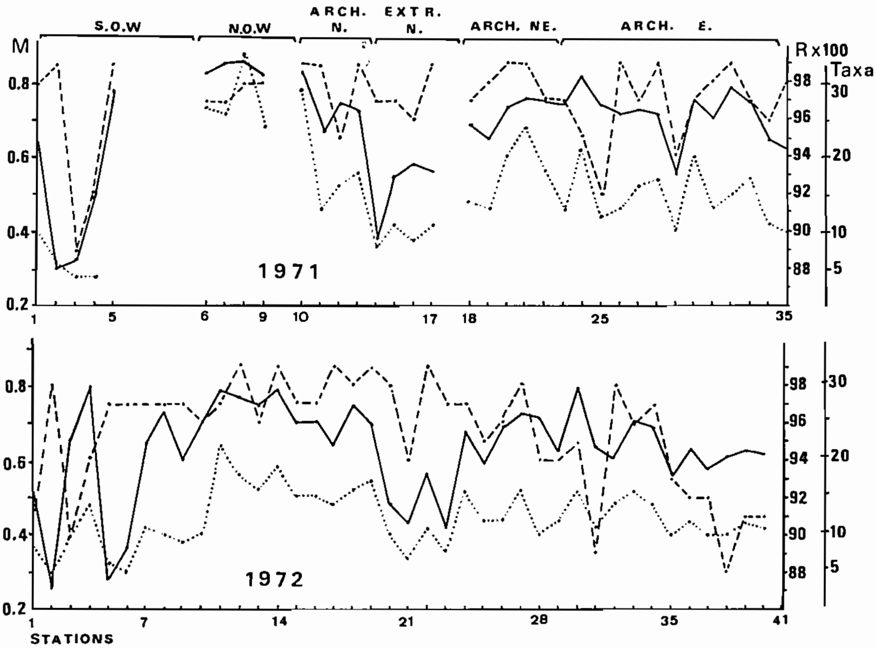

Fig. 7 Variations in the values of the 'R' coefficient between the logarithm of the biomasses of each species ranged in decreasing order of abundance and their rank (represented with broken lines); in the values of the 'constante de milieu' (represented with continuous lines); and of the number of species representing more than 0.07% of the total biovolume (represented with dotted lines). The abbreviations used are similar to those of the previous figure.

value was found at station 15 (0.776) in the far west. The lowest environmental constant values, ranging from 0.4 to 0.6, were found in February 1975.

6.2.2 *General distribution of the phytoplankton*

6.2.2.1 *Delimitation of the major ecological zones.* Despite the variety and complexity of the ecological zones present in the lacustrine system, the observations made from 1964 to 1972 during the period of 'Normal Chad' allowed the entire lake to be divided into a certain number of regions according to phytoplankton characteristics.

This zonation was determined from direct observation of the samples collected between 1964 and 1970 and after this time, and from calculation of the degrees of similarity (Spearman's correlation coefficient) existing between the quantitative surveys of the species. The correlation tables resulting from the samples collected during the two complete surveys conducted during 'Normal

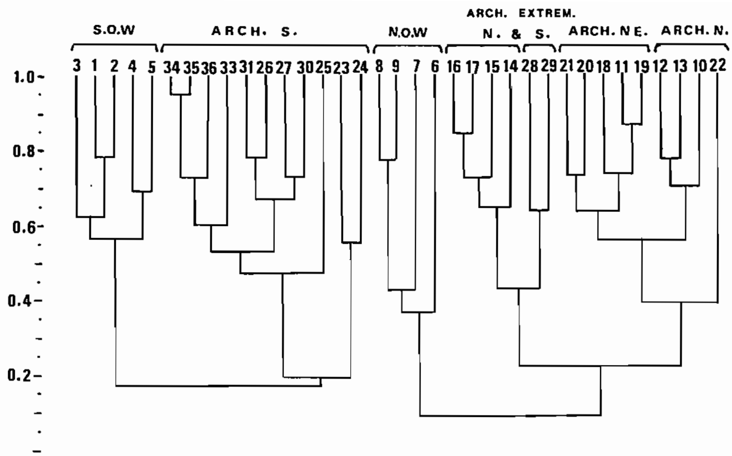

Fig. 8 Dendrogram for the interpretation of the Spearman correlation matrix between the records made in the lake in February 1971.

Chad' in 1971 and 1972 were analyzed in the form of a dendrogram. In 1971 (Fig. 8), the surveys made in the 35 stations were distributed in the following six groups: the Southern and Southeastern Open Waters, the archipelago south of the lake except the easternmost part (stations 28 and 29), the open water of the northern basin, the furthest parts of the archipelago (northeast and far east of the lake), the eastern part of the northern archipelago and the archipelago situated north of the Northern Open Water. In 1972 (Fig. 9), the resulting

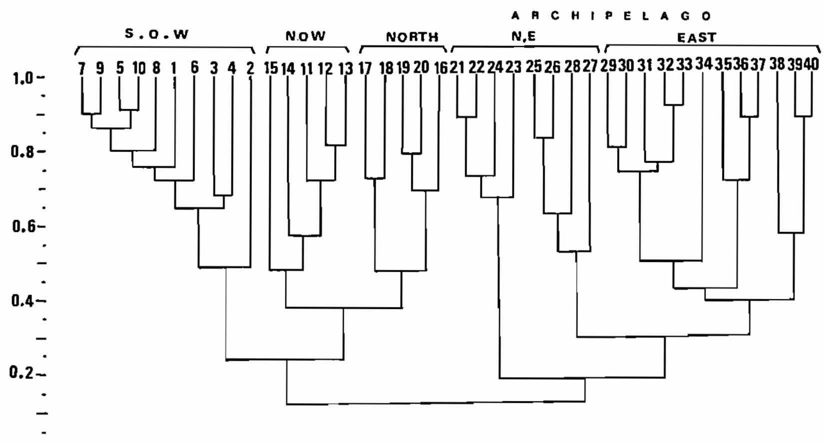

Fig. 9 Dendrogram for the interpretation of the Spearman correlation matrix between the records made in the lake in January 1972.

dendrogram was divided into five groups of surveys: those from the entire southern open water, those from the northern open waters, those from the vegetation fringe situated north of the previous group, those from the Northern Archipelago which includes a northeastern group (21 to 24) and an eastern group (25 to 28) and finally all the samples taken in the archipelago of the southern basin.

Given the phytoplankton distribution, the lake could be divided into two parts of nearly equal area by a line from Baga Kawa on the Niger coast to Baga Sola in the north of the Chad coast during the period of 'Normal Chad'. This line delimited a northern basin separated from the southern basin by a series of shallows. The northern part was characterized by high dissolved salt content (in the far north, the conductivity varied from 200 to 1300 $\mu S\ cm^{-1}$ at 25°C). The depth was comparatively greater than in the southern and eastern parts so that resuspension of the bottom sediments resulted in lower turbidity, and finally the influence of the Shari flood was less. In the southern basin, the conductivity varied from 50 to 250 $\mu S\ cm^{-1}$ at 25°C and exceeded this value only in the far northeast of the archipelago. The depth here was generally 2 to 4 meters resulting in a higher turbidity and the hydrological regime of the Shari and its tributaries caused considerable seasonal disturbances in the greater part of this zone. Each of the two basins was divided into a zone of open water and an archipelago, so that there were four major zones; two zones of open water, and two more heterogeneous archipelagoes subdivisible into two or three sub-zones

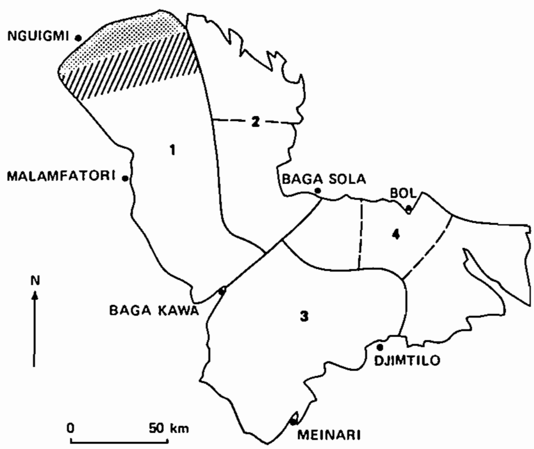

Fig. 10 Ecological zonation of Lake Chad. In 1, the northern open waters zone with, in the north, the region of the reeds islands and the vegetation fringe of the northern coast divided into two sub-zones; in 2, the northern archipelago zone divided into two zones; in 3, the southern open waters; and in 4, the southeastern archipelago divided into three sub-zones.

(Fig. 10). Particular biotopes such as the peri-deltaic zone, the immersed plant communities or the bottoms of the archipelago coves were distributed among the major zones but were so scattered and reduced in area that it was impossible to classify them into geographic regions.

The Southern Open Water included the open water situated between the Nigerian and the Cameroon banks (southern open water) and that spreading north of the Shari delta (southeastern open waters). It formed a shallow zone (3 to 4 meters) where there was frequent resuspension of the bottom sediments, especially during the rainy season (July–August) when a strong west wind blew. It was directly exposed to the disturbances caused by the outlet of the Shari waters; the flood waters which were very poor in plankton submerged the whole zone from the end of July to the beginning of January. The following species, belonging either to the Cyanophyceae, such as *Anabaena flos-aquae*, *Lyngbya limnetica* (especially in low waters) or to the Diatomophyceae, such as *Navicula* sp., *Melosira granulata*, *Gyrosigma kutzingii* and *Surirella muelleri* (especially in high waters) were the most important members of the phytoplankton. A Chlorophyceae, *Closterium aciculare* was very abundant in the northern basin and became fairly abundant in the western part of the southern basin. The diversity indices ranged from 0.53 to 3.44 bits, with an average of 1.523 in February 1971 and 1.775 in January 1972. The average environmental constant was 0.512 during the first year and 0.541 during the second year, while the mean algal biomasses were respectively 0.03 and 0.22 mg l^{-1}, the lowest values found in relation to the other regions of the lake.

The Southern Archipelago includes the whole northern zone of open water from the region of Baga Sola up to the easternmost part of the lake and the fringe of reed islands bordering the open water on the north and the east. The mean algal density was 1.4 mg l^{-1} in February 1971 and 4.5 mg l^{-1} in January 1972. The mean species diversity was 2.990 bits, in February 1971 and 1.558 in January 1972, while the average environmental constant was 0.714 and 0.639. Generally, Cyanophyceae predominated in the algae especially in the easternmost regions; Diatoms and Chlorophyceae were also abundant and formed blooms at certain periods. The whole zone was rather heterogeneous and divisible into three parts. The western region had an average plankton density (0.10 to 0.25 mg l^{-1}) and the phytoplankton was composed mainly of Chlorophyceae in January 1971 (*Oocystis* sp., *Pediastrum duplex*, *Coelastrum cambricum*). This region spread roughly from the 'Great Barrier' up to about ten kilometers east of Baga Sola. The central region around Bol was the poorest in phytoplankton and was the part of the archipelago most affected by the Shari flood during part of the year. The phytoplankton composed mainly of Diatoms (*Nitzschia spiculum*, *Melosira granulata*) and Chlorophyceae (*Oocystis* sp., *Coelastrum microporum*, *Pediastrum duplex*) in February 1971. Finally, the eastern region spread about ten kilometers west of Iseirom up to the eastern bank of the lake. It was characterized by dense phytoplankton (3 to 12 mg l^{-1})

where Cyanophyceae were predominant and the phytoplankton community was very similar to that present in the northern part of the archipelago of the northern basin.

In the northern part of the lake, the zone of open water included the Northern Open Water, the reed islands north of them and the small zone of open water spreading up to the vegetation fringe of the Niger coast. It was a rather deep zone where the highest values in the lake for species diversity were found (3.41 bits on average in February 1971 and 2.97 in January 1972). The average environmental constant reached 0.792 during the first year and 0.728 during the second year. The algal biomasses were 0.7 and 1.6 mg l^{-1} on average according to the year. While Cyanophyceae were abundant only in the northernmost part, the communities were generally very diverse and composed mainly of Chlorophyceae (*Oocystis* sp., *Closterium aciculare*, *Scenedesmus quadricauda*, *Coelastrum cambricum*, various *Pediastrum*) and Diatomophyceae (*Navicula* sp., *Synedra berolinensis*, *Fragilaria construens*). The waters in the reed islands north of the open water had a slightly different nature, characterized by abundant Pyrrhophyta belonging to the genera *Cryptomonas* and *Chroomonas*. Finally, in the northernmost part, near the plant fringe of the Niger coast, Cyanophyceae (*Microcystis delicatissima*, *Oscillatoria laxissima*, *Anabaenopsis tanganiikae*) become abundant and often predominant; the algal density was higher than further south (3 to 4 mg l^{-1}).

The archipelago of the northern basin was characterized by high phytoplankton biomass, equal to or higher than that of the Northern Open Water, especially in the northeastern part. In February 1971, the average was 1.4 mg l^{-1} and 2.0 mg l^{-1} in January 1972. The mean species diversity indices were 2.507 and 2.366 bits respectively, while the environmental constants were 0.628 and 0.588. The predominant groups of algae were the Cyanophyceae, with the following species: *Microcystis delicatissima*, *Oscillatoria laxissima*, *Lyngbya limnetica*, *L. contorta*, *Anabaenopsis tanganiikae*; and the Chlorophyceae with *Oocystis* sp., *Closterium aciculare*, *Scenedesmus quadricauda*. This zone was subdivided into two parts by a horizontal line a few kilometers north of Liwa. The region situated north of this was characterized by dense phytoplankton (1 to 4 mg l^{-1}) composed mainly of Cyanophyceae, while the southern part contained more varied and less dense populations (0.6 to 2 mg l^{-1}, where Chlorophyta were largely predominant. The characteristics of the previous zones are summarized in Table 10.

Various distinct smaller biotopes were scattered through some of these zones, e.g. the peri-deltaic regions covering an area of 5 to 8 km around the Shari delta and a lesser area near the deltas of El Beïd and the Yobé, which was a biotope having very pronounced seasonal variations in the phytoplankton and subject to the direct action of the affluents. In this latter region, a period from February to July of rich plankton alternated with a period of high water when the algae were reduced. This alternation was even more pronounced in the peri-deltaic

Table 10 Characteristics of the four ecological zones of the lake.

	Southern basin		Northern basin	
	Open waters	Archipelago	Open waters	Archipelago
Algal biovolume	0.03 & 0.22 µl l^{-1}	1.4 µl l^{-1}	0.7 & 1.6 µl l^{-1}	1.4 & 2.0 µl l^{-1}
Specific diversity	1.52 & 1.77	2.99	3.41 & 2.97	2.51 & 2.37
Motomura's constant	0.512 & 0.541	0.714	0.792 & 0.728	0.628 & 0.588
Prevailing algal groups	Diatoms Cyanophyceae	Chlorophyceae Diatoms Cyanophyceae	Chlorophyceae Diatoms	Cyanophyceae Chlorophyceae
Subdivisions	1 facies	3 sub-zones	2 facies	2 sub-zones
Seasonal variations	very pronounced	mean	low	low

zones where, in addition to river inflows during low water, dense lacustrine phytoplankton came and went with the flood. Consequently, an algal flora appeared which was more varied than that of neighbouring zones because of the different species carried over by the rivers and their flood zones.

A second distinct biotope was that of the submerged plant communities which consisted mainly of *Potamogeton*, and more rarely *Ceratophyllum*, *Vallisneria* or *Najas*. The phytoplankton was initially characterized by high diversity (the greatest number of taxa), low density, which was apparent from the high water transparency among the plants, and finally by the presence of abundant periphyton with *Gomphonema*, *Rivularia*, *Calothrix*, *Microchaete*, *Oedogonium*, etc. These biotopes existed all around the lake, in the archipelagoes and the reed island zones. They were most often found on the southeastern coast of the lake, east of the Shari delta, in the region of the 'Great Barrier' and in the northern archipelago, in the arms entering the plant fringe of the northern coast of the lake and generally in the ends of the archipelago channels.

A third distinct biotope was composed of the ends of the archipelago arms. The emergent vegetation along the banks was abundant and several meters wide. The water was transparent and often brown. The phytoplanktonic density was low and seasonal variations were insignificant. The dominant species belonged to the genera *Microcystis* and *Synechocystis*, the latter being found especially in the northern part of the lake. This biotope was often associated with the previous one, numerous cove bottoms being colonized partially or totally by submerged plant communities.

The limits of the different zones or biotopes were not always stable and water movements caused by the Shari flood or a change in the direction of the prevailing winds caused them to shift by several kilometers. For example, in 1972 (Fig. 5), the southern part of the Northern Open Water (stations 10 and 28) was similar to the Southern Open Water, so the separation between the northern plankton and the southern plankton 10 to 15 kilometers further northwest. The graphs made here, therefore, correspond to the calculation of their average position.

Moreover, this configuration of the lake was the one which existed during the period of 'Normal Chad' but it underwent profound modifications with the annual variations in water level which led to the periods of 'Greater Chad' or 'Lesser Chad'. Such was the case in 1973 when after several years of low rainfall, the lake had become separated into several different regions, thus assuming a different aspect which will be described later.

6.2.2.2 *Species associations.* In order to define the species associations related to the existing ecological zones, a factorial analysis (correspondence analysis) was applied to the surveys. This had the major advantage of illustrating the survey and the species on the same graph and it showed the reciprocal relations which existed between the surveys and their species components. Thus Fig. 11 shows the relative position of the stations and the species for the surveys made in January 1972. In this analysis, the surveys and the taxa were distributed on both sides of the axes 1, 2 and 3 which accounted for 23, 17 and 16% of the total variation respectively (a total of 56%), while 74% was represented by the first five axes. The different zones of the lake appear clearly on axes 1 and 2 (Fig. 11, top), and five groups can be distinguished:

— the group composed of the Southern and Eastern Open Water (surveys 1 to 10 and 28). The samples taken along the line separating the northern and the southern basin were related to the Southern Open Water. The following species represented the algal biocenosis: *Melosira granulata*, typical species and its variety *angustissima*, *Gyrosigma kutzingii*, *Surirella muelleri*, *Navicula* sp., *Scenedesmus acutus*, *Closterium acutum* var. *variabile*, *Lyngbya contorta* and *Anabaena flos-aquae*. *Lyngbya limnetica* was relatively abundant in the samples;

— the group composed of the Northern Open Water (stations 11 to 14) included some planktonic Diatoms, *Synedra berolinensis*, *Fragilaria construens* and

Fig. 11 Factorial analysis positions of the samples and the species occurring in the lake in relation to the axis 1 and 2 (top) and 1 and 3 (bottom) in January 1972. The long dashes delimit the groups of the southern and southeastern open waters, the dotted line delimits the groups belonging to the northern open waters; the continuous line delimits the groups of the archipelago of the southern basin; the broken and dotted line delimits the groups of the archipelago of the northern basin and the short dashes delimit the groups of the far northeastern and eastern archipelago (see Appendix I for the taxa code used).

more especially Chlorophyceae, *Scenedesmus quadricauda*, *Scenedesmus acuminatus*, *Coelastrum microporum*, *C. cambrium*, *C. proboscideum*, *Binuclearia eriensis*. The species *Navicula* sp., *Oocystis* sp., *Lyngbya contorta* and *Chroococcus limneticus* were also present;

— the group formed by the Southeastern Archipelago whose samples represented a large zone with two dominant species constituting two extremes: *Nitzschia spiculum* for stations 29, 32, 33 and 35 and *Anabaena flos-aquae* for stations 31, 36, 37, 38, 39 and 40, the latter having similarities with the populations of the Southeastern Open Water. In all the populations, there were several small species: *Nitzschia*, *Surirella muelleri*, *Anabaena spiroïdes* and *Anabaenopsis arnoldii*. Stations 30 and 34 (end coves of the archipelago) showed similarities with the following group;

— the group formed by the northernmost and northeastern parts of the lake (surveys 17 and 19 to 23) corresponded to the northern part of the archipelago in the northern basin. The related species group consisted of mainly Cyanophyceae: *Synechocystis minuscula*, *Microcystis delicatissima*, *M. aeruginosa*, *Oscillatoria laxissima*, *Anabaenopsis tanganiikae*, *A. arnoldii*, *Lyngbya limnetica*, *Raphidiopsis* sp. and a few Chlorophyceae: *Nephrochlamys subsolitaria*, *Monoraphidium contortum*, *Tetraedron minimum* and *Oocystis* sp.;

— the last group included the reed islands and the archipelago bordering the northern open water to the north (stations 15, 16 and 18) and east (stations 24 to 27). The following species, mainly Chlorophyceae, were present *Oocystis* sp., *Crucigenia triangularis*, *Botryococcus braunii*, *Tetraedron trigonum*, *T. minimum*, *Scenedesmus perforatus*, *Chodatella* sp., *Pediastrum tetras*, *P. duplex*, *Eremosphaera gigas*, *Coelastrum cambricum*, *Closterium aciculare*, *Chroomonas* sp., *Microcystis delicatissima* and *Synechocystis minuscula*.

The plot of axes 1 and 3 (Fig. 11, bottom) provided very little additional information. The five above-mentioned groups were clearly separated. The group of the Southeastern Archipelago was extended more along the horizontal line than in the previous plot and the sub-groups dominated by *Anabaena flos-aquae* and by *Nitzschia spiculum* were well separated.*

6.2.2.3 *Type communities*. From the correlations observed between the species and the calculated species biovolumes, a type community schematically showing the relative species composition of the existing populations was determined for each zone or sub-zone. In each region, the mean percentage of each well represented species was calculated from the samples from the different stations in this region. After summing these mean percentages and adjusting them to 100%, the relative composition of the existing community was determined.

* Refer to the taxa code in Appendix I for abbreviations used in the text.

At the beginning of 1971, half the biomass was composed of Cyanophyceae, with Diatoms representing more than a third of the populations, while Chlorophyta were not very abundant. In January 1972, Diatoms and Cyanophyceae were almost equal in proportion.

In the open water of the northern basin, the biomass was extremely different in composition and included the following species during the two periods under consideration:

	February 1971	January 1972
Oocystis sp.	28%	8%
Scenedesmus quadricauda	8%	17%
Coelastrum cambricum	7%	
Coelastrum microporum		5%
Pediastrum clathratum	6%	
Pediastrum tetras	4%	
Pediastrum duplex	5%	
Melosira granulata var. *angustissima*	3%	
Synedra berolinensis		11%
Fragilaria construens		9%
Navicula sp.		24%
Lyngbya contorta	6%	8%
Lyngbya limnetica		2%
Various	33%	16%

While Chlorophyta represented three quarters of the community in February 1971, they formed only a third of the biomass in 1972. The Diatoms represented more than 50% of the algae.

In the whole Northern Archipelago, the algal species were distributed as follows:

	February 1971	January 1972
Oocystis sp.	23%	37%
Eremosphaera gigas		2%
Scenedesmus quadricauda	7%	12%
Coelastrum cambricum		4%
Pediastrum tetras	5%	4%
Closterium aciculare	14%	4%

	February 1971	January 1972
Microcystis delicatissima	7%	13%
Anabaenopsis tanganiikae	8%	
Oscillatoria laxissima		4%
Cryptomonas erosa	12%	
Chroomonas sp.	7%	7%
Various	17%	13%

The communities were varied and Chlorophyta formed from half to two thirds of the biomass.

The two type communities calculated for the archipelago in the southern basin are:

	February 1971	January 1972
Oocystis sp.	22%	
Melosira granulata	10%	
Melosira granulata var. *angustissima*	21%	
Nitzschia spiculum	11%	23%
Nitzschia sp.		3%
Anabaena flos-aquae		55%
Anabaena spiroïdes		2%
Anabaenopsis tanganiikae	2%	
Lyngbya limnetica		5%
Various	34%	12%

While there was a clear prevalence of Diatoms in February 1971, at the beginning of 1972 two thirds of the biomass was composed of Cyanophyta and only about one third was of Diatoms.

Finally, in the northernmost and easternmost parts of the archipelago, particular communities developed with a prevalence of Cyanophyceae and included:

	February 1971	January 1972
Oocystis sp.	6%	9%
Microcystis delicatissima	8%	32%
Anabaenopsis tanganiikae	49%	18%
Oscillatoria laxissima	11%	28%
Lyngbya limnetica	12%	5%
Various	14%	8%

Therefore, it was observed that Cyanophyceae and Diatomophyceae were abundant in the southern basin during the period of 'Normal Chad', while the Chlorophyceae appeared to dominate in the northern basin. The furthest parts of the archipelago, whether in the northern or southern basin, were almost totally colonized by Cyanophyceae.

6.2.3 *Temporal changes in the phytoplankton*

6.2.3.1 *Seasonal variations.* A cool season was distinguishable in December and January when water temperatures could drop below 20°C and a warm season occurred in April, May and June when water temperatures exceeded 30°C. Winds blow from the northeast for about eight months, but from May to September, the strong humid monsoons blow from the southwest and are associated with rainfall (250 to 500 mm over the lake according to the latitude). Insolation was very high all the year round declining to a minimum in August–September. The different zones of the lake were not affected in the same way by the factors, as the northern part had the greatest temperature differences throughout the year. If the channels were always protected from the prevailing winds in the archipelago, the resulting turbulence led to a re-suspension of the muddy and pseudo-sandy bottom sediments in the open waters, especially in the southern basin where depth did not exceed four meters. Therefore, water transparency was about 25 cm in this zone during the rainy season.

Given the high annual rate of water renewal in the lake (55% on an average), the lacustrine plankton was most affected by the hydrological regime of the Shari. The flood begins in the deltaic region at the end of June and the flood wave with very turbid waters submerges the southeastern part in July and spreads to the whole southern part of the lake. The flood reaches its maximum in October when turbidity is high in the central part of the eastern archipelago towards Bol. Thus the southern and southeastern open waters, the central part of the eastern archipelago and the southern fringe of the northern open waters are subject to the greatest seasonal variations.

A study conducted from August 1964 to July 1965 (Gras et al. 1967) in different zones and biotopes of the eastern part of the lake provided partial knowledge of these variations (Table 11). Quantitative estimates were made each month at eleven stations distributed over the Shari delta, the Peri-deltaic Zone, the Southeastern Open Waters, the plant communities east of the delta, the central part of the archipelago towards Bol and the eastern part (Fig. 13). They were expressed as number of cells per liter with all the cells being counted whether they were isolated or arranged in cenobes or colonies. The density values in Table 11 need to be multiplied by 10^5 to obtain the number of plant cells present in each liter (Fig. 14).

Table 11 Algal biomasses expressed in number of cells per liter in the different stations of the eastern part of the lake within a year (from August 1964 to July 1965).

Biotops	Shari	Peri-deltaic	Immersed plants	Open Waters SE		Archipelago (Center)		Archipelago (East)			N.E. Arms Ends
Stations	Delta	St 1	Adjilélé	St 2	St 3	St 5	Bol St 6	St 7	St 8	St 9	St 10
August	256	650	985	1099	1099	1178	5165	10 735	11 071	10 663	4890
September	73	75	535	638	946	2154	5801	11 936	12 777	10 658	5836
October	71	74	281	659	914	1247	5345	12 569	12 770	10 374	6079
November	43	64	814	629	1156	1080	6127	10 429	10 461	11 954	5530
December	43	64	800	792	1440	981	4857	10 996	11 840	12 809	5799
January	115	722	589	1783	1291	760	5472	12 164	12 821	12 291	6406
February	114	1415	614	1316	1279	582	5532	9370	12 454	10 772	5045
March	1410	3813	811	1987	1012	955	5691	10 507	11 669	10 831	5252
April	2075	4366	1175	2807	3638	3067	10 167	12 837	10 866	11 361	4930
May	1748	5454	3606	2625	2285	3545	9516	11 513	11 759	10 667	5216
June	1955	5626	3981	3360	3117	3103	8395	10 803	10 340	11 295	6030
July	318	4677	4471	3166	1366	1218	6146	10 220	10 837	11 008	8713
Annual mean	685	2250	1555	1738	1628	1657	6518	11 173	11 638	11 224	5810

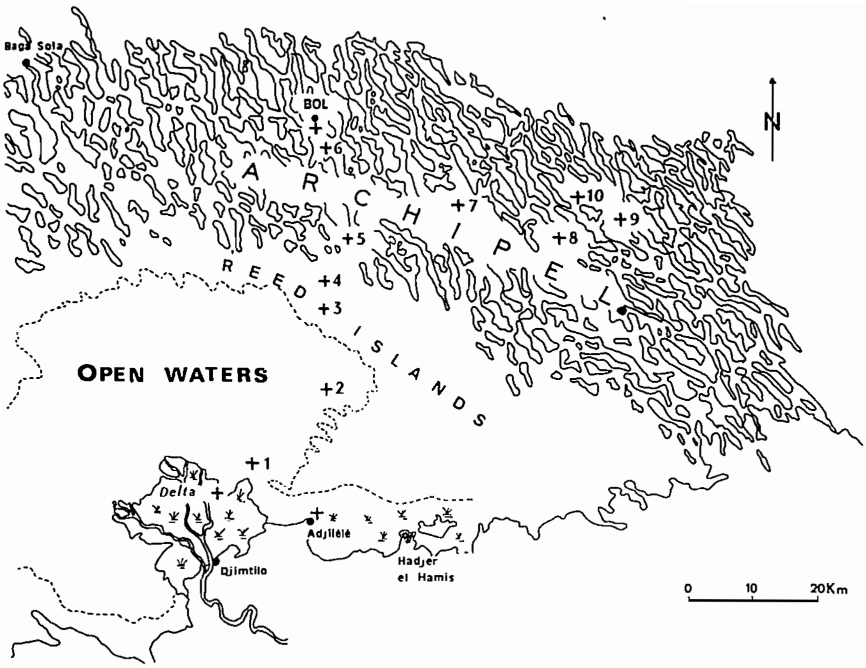

Fig. 13 Location of the sampling points which were regularly examined to analyze the seasonal variations of the plankton (1964–65).

If the seasonal development of the phytoplankton density is analyzed in each of these zones or biotopes, a fairly rich period in the Shari delta and peri-deltaic region can be observed in April, May and June when the water was low and warm. An impoverished period occurred from September to March with minimum values in November–December when the flood reached its peak. In the peri-deltaic zones, the algal density which was very low during the flood became higher than in the neighbouring open water during low water periods. However, the phytoplankton density was generally lower in the plant community zones situated east of the Shari delta towards Adjilele. In the Southeastern Open Water (stations 2 and 3), the minimum density resulting from the flood was very apparent during the last quarter of the year, while in the central part of the archipelago (stations 5 and 6), the low density was still observable from December to February especially in the southernmost part (station 5). In the eastern part of the archipelago (stations 7, 8 and 9), the algal density was very high (more than one million cells per milliliter) and remained stable throughout the year. At station 10 which was representative of the zones in the end coves of the archipelago, the biomass was only the half of that in the surrounding archipelago and there were virtually no variations throughout the year.

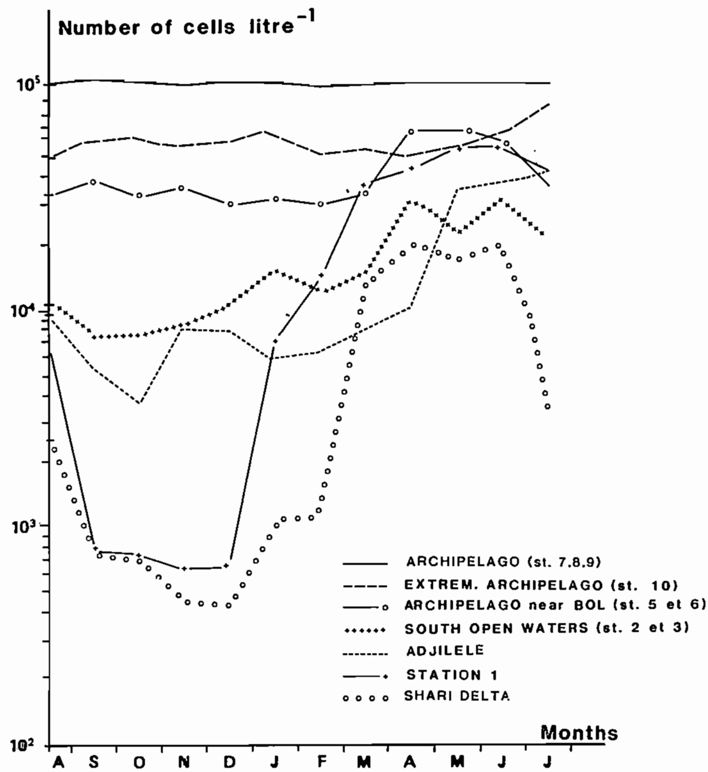

Fig. 14 Seasonal changes in the number of cells per liter in the different parts of the eastern zone of the lake. The mean related to 2 or 3 stations was represented in the Southern Open Water, in the archipelago towards Bol, and in the eastern archipelago.

The proportions of the three algal groups present in the samples from the river near the delta up to the end coves of the archipelago are presented on six graphs (Fig. 15). The Cyanophyceae expressed as the number of cells per liter, were generally composed of colonial species such as *Microcystis*, with numerous small cells and the percentages were always high. The proportion of Diatoms was equal to or slightly higher than that of the Cyanophyceae in the Shari delta and the peri-deltaic zone in September. Then Chlorophyceae became predominant in the Shari in December at the beginning of the flood when the plankton from the flood zones flowed back towards the river bed. A maximum number of Chlorophyceae also appeared in the peri-deltaic regions in November, but from January, Cyanophyceae predominated (more than 90% of the cells) until the time of the next flood. In the communities situated east of the delta, Diatoms and Chlorophyceae contributed 10 and 20% respectively in

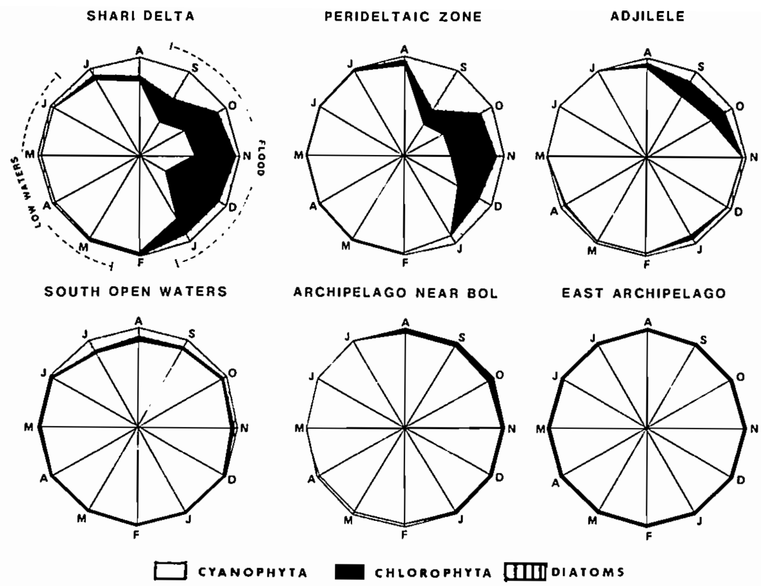

Fig. 15 Seasonal variations in the percentage of each of the three main groups of algae calculated from the number of cells per liter in the eastern part of the lake (1964–1965).

September and October but Cyanophyceae comprised more than 90% of the cells during the rest of the year. According to the average of stations 2 and 3, the percentage of Diatoms was about 10% (13% max.) in the southern open waters in July, August and September when the resuspension of the Diatom rich bottom film was related to the waves formed by the west winds. 5% of the cells were composed of Chlorophyta from August to December, but Cyanophyceae contributed 90% of the cells for nine months of the year. Finally 5% of Chlorophyceae were observed in the center of the archipelago from September to January followed by the development of *Melosira granulata* in February, while the Cyanophyceae, still forming 90% of the cells reached 98% between March and July. Diatoms were always insignificant in the eastern region and in the distinct biotopes of the end channels, while Chlorophyceae represented 2% of the cells and Cyanophyceae 98%, throughout the year.

During the period of 'Normal Chad', considerable seasonal variations in the phytoplankton occurred only in the peri-deltaic regions and the Southern and Southeastern Open Waters of the eastern part of the lake. In these regions, there was an alternation of a six-monthly period with considerable variations, with six stable months. Few observations were made in the northern part of the lake but it appeared that only the southern part of the open water and the region of the Yobé delta were affected by the flood.

6.2.3.2 *Annual variations.* Since the water level of the lake depended upon the balance between the inflows and evaporation, climatic variations which were similar for several years led to changes in the level, with rainfall excesses resulting in a period of 'Greater Chad' and rainfall deficiencies resulting in 'Lesser Chad', as happened from 1972 onwards. In this case the phytoplankton varied considerably from year to year, and in the following pages, the changes which occurred between 1971 and 1975 when the lake underwent considerable contraction are analyzed.

During 'Normal Chad', there were practically no long-term observations made on the plankton over several consecutive years, but from a few data obtained between 1964 and 1968 when the lake was slowly contracting, it would seem that the phytoplankton varied little from one year to another.

Apart from the regular changes resulting from the occurrence of the annual Shari flood in the southern basin, the southern and southwestern open waters were occupied by populations of *Anabaena flos aquae* each year during low water. Species such as *Melosira granulata, Micractinium pusillum* or *Mallomonas portae-ferrae* developed on a large scale in the archipelago of the southern basin from March to April. In the Northern basin, *Closterium aciculare* was predominant in the open water each year.

But current knowledge of the algal communities is still too limited in time to predict the composition and changes of the plankton over a long period during which the mean level of Chad remains stable.

6.2.4 *Dynamics of the phytoplankton during a dry period*

6.2.4.1 *History of the revolution of the lake towards the period of 'Lesser Chad'.* Towards the middle of 1972, the constant and regular lowering of the lake that had been occurring since 1964 led to a decrease in depth, to the exposure of a 3 to 20 kilometers wide fringe along the southern and western coasts of the lake and the occurrence of shelves in the archipelago channels whose aspect underwent changes. However, all the regions of the lake were connected with each other and the lake was still considered to be in the period of 'Normal Chad' up to the first quarter of 1973. But, since the 1972 flood was deficient (17.5 billion m^3 against 40 billion on average), a separation occurred between the southern and the northern basin during the second quarter of 1973 as a result of the exposure of the shallows situated in the place of the former 'Great Barrier' which existed at the time of Tilho's survey. In July 1973, the archipelago of the southern basin became separated from the zone of open water facing the delta; the shallow arms dried up and abundant vegetation developed. During the second half of 1973, this situation was temporarily modified by the inflows of the Shari flood, the Southeastern Archipelago was again occupied by water and very low inflows reached the northern basin. But, from March 1974, the lake was again divided into three parts: the Southeastern

Open Water connected to the river system and situated north of the delta (about 1300 km^2), the Southeastern Archipelago reduced to a few channels which were usually covered with aquatic vegetation (about 150 to 200 km^2) and the very shallow northern basin (about 6000 km^2) separated from the southern basin by a wide vegetation barrier from Baga Sola to Baga Kawa. In July 1974, in the northern basin, the northern and eastern parts dried up and numerous islands appeared in the remaining water bodies.

In November 1974, the southern basin received considerable inflows from the Shari and from September, the Southeastern Archipelago was again occupied by water and connected to the open waters. However, extensive vegetation consisting of *Cyperus papyrus* and *Aeschynomene* covered the flooded regions. The northern part of the lake remained isolated by the vegetation barrier between the northern and southern basins; the water area was reduced and the depth barely exceeded one meter. In January 1975, the whole of the southern basin reached a level which was higher than that of the lake in 1972, but the southern coastal zone of the lake and the archipelago were always covered with vegetation although again occupied by water. In the northern basin, water inflows passed through the 'Great Barrier' and in February 1975, a slight increase (from 30 to 40 cm) was observed in the water level together with a decrease in the dissolved salt content. In June 1975, there were only a few ponds left in the northern part and almost total drying up occurred in August.

The chapter on the hydrological development of the lake could be referred to for locating this contraction period in the complete hydrology of the lake from 1960 to 1976, which is considered to provide an accurate description of the Chad situation when the phytoplankton samples were taken.

6.2.4.2 *Development of the phytoplankton.* During a dry period, starting from a period of 'Normal Chad', two stages can be observed in the development of the algal populations. During the first stage, the water cover still represented an hydrological unit as in 1971 and 1972, although its level decreased along with a considerable increase in the mean algal biovolume of the lake from 1 $\mu l\, l^{-1}$ in February 1971 to 2.4 $\mu l\, l^{-1}$ a year later. This increase was felt in all the zones of the lake and mainly in the archipelago of the southern basin. It was accompanied by a decrease in the species diversity index from an average of 2.752 to 2.141 and by a decrease in equitability from 72 to 59%. The mean number of taxa contributing to the biomass (above a threshold of 0.07% of the sample biovolume) decreased from 15.2 to 12.3. The environmental constant was 0.681 in February 1971 and 0.628 in January 1972.

The phytoplankton as a whole underwent few modifications in composition during this period. Almost the same taxa were found but the major algal groups were sometimes present in different proportions in the various zones. Cyanophyceae and Diatoms represented most of the algae in the Southern and Southeastern Open Waters. In the eastern archipelago, Diatoms were dominant in February 1971 with a rather high percentage of Chlorophyta, while Cyanophyta represent two thirds of the much higher biomass the following year.

In the northern basin, Cyanophyceae predominated in the northernmost part, while further south Chlorophyceae predominate in February 1971 and Diatoms in January 1972. In the Northern Archipelago, Chlorophyta were always dominant except in the far northeast. Therefore it is possible that, from 1972 onwards, given the decrease in the mean level of the lake by 30 to 40 cm as compared with the previous year, the flood waters were checked at the level of the reed islands bordering the Southeastern Open Water in the north. The flooding of the archipelago was smaller and slower, allowing the Cyanophyceae to quickly colonize. The flood waters which were rich in Diatoms moved far beyond the Great Reef increasing their percentage in the open water of the northern basin where they become dominant. In the parts of the archipelago furthest from the Shari delta, whether in the northern basin or in the southern basin, Cyanophyceae always represent about 90% of the biomass.

Thus this first stage was particularly characterized by an increase in the mean phytoplankton biomass, with a decrease in the species diversity values and in the environmental constant. The proportions of the different algal groups changed, mainly in the archipelago of the southern basin and in the Northern Open Water.

From 1974 onwards Lake Chad was no longer an hydrological unit. Three individual water bodies remained in the entire lacustrine basin. During this second stage, changes in the algal communities could only be observed by examining developments in each individual water body (Fig. 16).

In the Southeastern Open Water, the phytoplankton density was higher than in previous stages: 0.8 μl of algae per liter in November 1974; 0.7 in February 1975 and 7.8 $\mu l\, l^{-1}$ in April 1974 when water level was low. The community diversity and the values of the diversity index, which were lower than 2 bits on average during the period of 'Normal Chad', were greater than 2.5 in 1974 and over 3 in February 1975. The mean number of taxa contributing more than 0.07% of the biomass was 6 in February 1971 and 25 in February 1975. The algal community which was composed mainly of Diatoms and Cyanophyceae during the period of 'Normal Chad' increased with large numbers of Euglenoids occurring during the warm season, and with Chlorophyceae and Chrysophyceae present from November 1974 onwards.

The plankton of this region thus evolved towards a more pronounced river type which was characterized by greater variety and by the existence of considerable differences between the poorer flood waters and the much richer low waters. If the water inflows from the Shari were sufficient to keep the southern and southeastern open water zones submerged, the communities in the southern and western parts were different from those in the eastern part but these subdivisions disappear with the flood. If the water inflows from the Shari

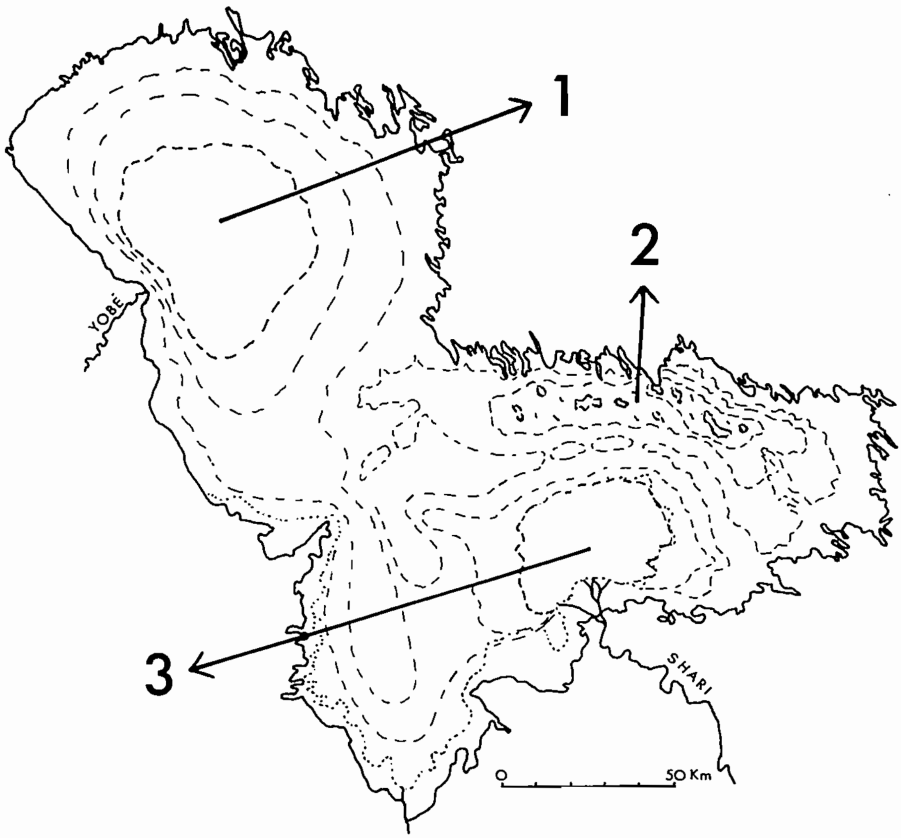

Fig. 16 Representation of the drying up of Lake Chad from 1972 to 1975 and development of the different parts of the lake; 1, towards a facies of natron pond; 2, towards a facies of swamp; 3, towards a facies of river.

remained very low, the pond-like character of this region was more marked. Cyanophyceae and Euglenoids increased during time of low water, while large numbers of Diatoms were always present during other seasons.

On the whole, apart from the development of the Euglenoids and the abundance of a Diatom *Synedra berolinensis* which was previously non-existent or rare in the samples, the phytoplankton has varied little in its components and this zone of the lake could be considered part of the lake which changed least during a dry period.

In the archipelago of the lake, after an increase in biomass in the period before the change towards 'Lesser Chad' (average 1.4 mg l^{-1} in April 1974 and 7.6 in February 1975) biomasses as a whole were still higher during this period (average 8.2 mg l^{-1} in April 1974 and 7.6 mg l^{-1} in February 1975). However, the flooding of this zone by water from the south which filtered through the reed islands surrounding the open water considerably impoverished the environment (0.4 mg l^{-1} in November 1974) during certain periods (for instance October–November 1974). In this group of fairly large biotopes which were either isolated or connected with one other, and has a varied water supply during high water, the rather diversified algal populations (2.3 to 3.2 bits on average depending on period) were generally composed mainly of Euglenoïds with Chlorophyta and Diatoms reaching considerable proportions locally; Cyanophyceae were always low in proportion.

This group of ponds became established during the period of 'Lesser Chad' and evolved towards a swamp dominated by Euglenophyta, and occupied by aquatic macrophytes, whose importance varied with the water inflow from the south which affected the depth of these habitats. The chlorophyll measurements made by Lemoalle (1979) corroborated the differences which existed between the remaining ponds. After a concentration stage in 1972 and 1973 when values were high (more than 250 mg m^{-3}), water circulation resulting from infiltrations through the vegetation caused a decrease in chlorophyll content which rarely exceeded 100 mg m^{-3}. At the end of 1975, the chlorophyll content did not exceed 2 mg m^{-3} in most places.

As in the rest of the lake, the last stages of the 'Normal Chad' period in the northern basin were characterized by an increase in algal biomass from an average of 1.09 to 1.73 mg l^{-1} between 1971 and 1972. The evolution of the water body towards the period of 'Lesser Chad' then became rapid as a result of the low water inflows from the Yobé river during the flood period and from the southern basin through the restored 'Great Barrier'. As soon as this part became isolated, the average algal biovolume increased considerably to 179 μl l^{-1} in November 1974. This change was well reflected in the chlorophyll

Table 12 Chlorophyll *a* contents observed in the central part of the northern basin from March 1973 to April 1976.

Time	Station number	Chl (mg m^{-3})	S.D.
21/24 March 1973	9	39	5.1
24/29 April 1973	11	40.7	13.5
18 September 1973	8	82.5	20
11/22 November 1973	14	102.9	16
19/27 April 1974	11	141.2	37
26/31 July 1974	21	343	214
25/30 November 1974	7	1658	360
16/18 February 1975	9	204	107
10/13 April 1975	16	464	257
16/21 April 1976	6	208	41

temporary hydrological connections between the archipelago and the southeastern waters during certain periods, the phytoplankton in each zone maintained particular characteristics different to these of the other two zones.

Therefore the composition of the plankton in the three water bodies will be examined individually.

6.2.4.3.1 *Southeastern Open Water.* In the Southern Open Waters, the community was composed mainly of Diatoms during the Shari flood and of Diatoms and Cyanophyceae during the period of low water. Euglenoïds could amount to 20% of the biomass in certain zones during the warm season. The most abundant species were: *Melosira granulata*, *M. granulata* var. *angustissima*, *Synedra ulna*, *S. berolinensis*, *Surirella linearis*, *S. muelleri*, *Nitzschia spiculum*, *Gonatozygon monotaenium*, *Eudorina elegans*, *Anabaena flos-aquae*, *A. spiroides*, *Lyngbya limnetica*, *L. contorta*, *Microcystis elachista*, *Euglena* sp. and *Mallomonas portae-ferrae*. The phytoplankton densities remained low during the flood of the Shari (0.8 $\mu l\, l^{-1}$ of algae on an average in November 1974 and 0.7 in February 1975) and were much higher in low water during the warm season (7.8 $\mu l\, l^{-1}$ on average in April 1974) with higher biovolumes than in 'Normal Chad' in the same zone.

The average species diversity was 2.51 bits in April 1974 and it increased to 2.70 in November and 3.10 in February 1975, while the values of the environmental constant were respectively 0.717, 0.786 and 0.801.

The type-communities which were defined included the following species in April 1974 when the waters was low (Fig. 17).

30%	*Nitzschia spiculum*
17%	*Anabaena flos-aquae*
9%	*Euglena* sp. which are red on the surface
8%	*Melosira granulata*
7%	*Melosira granulata* var. *angustissima*
5%	*Lyngbya contorta*
5%	*Fragilaria contruens*
3%	*Anabaenopsis tanganiikae*
13%	various species

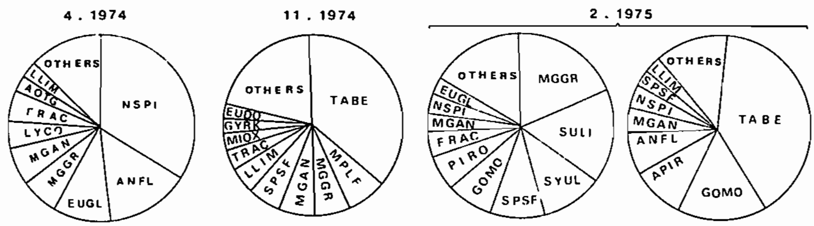

Fig. 17 Type-communities occurring in the southern open waters from April 1974 to February 1975 (cf. Appendix I for taxa code).

The community was composed of about a third Cyanophyceae, more than 50% Diatomophyceae and 10% Euglenophyta.

During the flood in November 1974, the algal biomass was composed roughly of:

35%	*Synedra berolinensis*
8%	*Melosira granulata*
8%	*Mallomonas portae-ferrae*
6%	*Melosira granulata* var. *angustissima*
6%	*Surirella muelleri*
5%	*Lyngbya limnetica*
4%	*Trachelomonas* plur. sp.
3%	*Microcystis elachista*
2%	*Gyrosigma kutzingii*
2%	*Eudorina elegans*
21%	various species

There were about two thirds Diatomophyceae, 10% of Cyanophyceae and 10% Chrysophyceae.

In February 1975 when the decrease of water ended, two type-communities could be distinguished in the zone of open water which then occupied the southern and southeastern regions of the lake.

	Western part	Eastern part
Gonatozygon monotaenium	8%	15%
Spirogyra sp.	6%	
Melosira granulata	19%	
Melosira granulata var. *angustissima*	4%	4%
Synedra ulna	10%	
Synedra berolinensis		41%
Fragilaria construens	5%	
Surirella muelleri	9%	3%
Surirella linearis	17%	
Nitzschia spiculum	4%	4%
Anabaena spiroïdes		9%
Anabaena flos-aquae		8%
Lyngbya limnetica		3%
Euglena sp.	2%	
Various sp.	16%	13%

1974 and 2.365 in February 1975. The values of the environmental constant was respectively 0.848, 0.726 and 0.796.

Despite the heterogeneity of the algae present in these environments with infrequent connections, type communities were defined for the three periods under study (Fig. 18).

	April 1974	November 1974	February 1975
Dictyosphaerium pulchellum		4%	4%
Closterium strigosum		27%	
Melosira granulata			
var. *angustissima*	16%		24%
Synedra ulna	7%		
Nitzschia sp.		2%	
Oscillatoria sp.		9%	
Cryptomonas erosa	7%		13%
Euglena plur. sp.	26%	6%	31%
Trachelomonas plur. sp.	7%	41%	18%
Strombomonas fluviatilis	16%		
Lepocinclis sp.	4%		2%
Various	17%	11%	8%

In this case, Euglenophyta represented 50 to 60%, Diatoms about 25% in April 1974 and February 1975 and Pyrrhophyta 7 to 13% during the same periods.

Generally, Euglenoids represented at least half the biomass in the ponds remaining in the archipelago during the period of 'Lesser Chad'. Although Chlorophyta and Diatoms reached considerable numbers locally, Cyanophyta were always low in proportion. The populations were very variable in density according to water movements through this region. The biomass enrichment in relation to the period of the larger lake resulted from the development of Euglenoïds and was interrupted by total reflooding of the whole zone in November 1974. This led to an increase of 2.50 m in the water level, and this flood wave was quickly colonized by very dense phytoplankton in February 1975.

6.2.4.3.3 *Northern basin.* During the period of 'Lesser Chad', Diatomophyceae generally dominated in the phytoplankton with the two abundant species being *Coscinodiscus rudolfii* and *Cyclotella meneghiniana*. Chlorophyceae were most usually abundant and the main species were *Scenedesmus quadricauda*, *S. opoliensis*, *S. intermedius*, *Pediastrum tetras*, and *Oocystis*. Finally, in April 1974, Cyanophyceae were abundant in the northern and northeastern parts of the basin and in the part of the archipelago occupied by water; the most abundant species were *Anabaenopsis tanganiikae, Lyngbya contorta, L. limnetica, Oscillatoria laxissima* and *Chroococcus limneticus.*

The algal biomass was high with an average of 25.3 mg l^{-1} in the samples from April 1974 and 179 mg l^{-1} in the seven samples from November 1974 when the water level did not exceed one meter in the deepest zones. In February 1975 when the northern basin was again fed by low water infiltrations (30 to 40 cm) through the 'Great Barrier', the average biomass was 74 mg l^{-1}. The chlorophyll *a* estimates around the island of Kindjéria in the center of the northern basin had means of 141 mg m^{-3} in April 1974, 1659 mg m^{-3} in November and 204 mg m^{-3} in February 1975.

The species diversity values were very variable in April 1974 and ranged from 0.4 to 3.8 bits (mean: 2.217). The lowest values were either from the populations in the northernmost and northeasternmost parts of the lake where *Anabaenopsis tanganiikae* was dominant, or from the populations in the center of the basin where *Coscinodiscus rudolfii* was largely dominant. In November 1974 and February 1975, the communities had homogeneous diversities of 2.422 and 1.536 bits on average. The mean values of the environmental constant were 0.741 in April 1974, 0.704 in November and 0.531 in February 1975.

The composition and proportions of the different species can be defined by two types of community in April 1974 (Fig. 19). The first corresponded to the plankton in the center, the south and west of the lake, while the second was representative of the surveys in the north, the northeast and east of the lake, i.e. the archipelago. In November 1974 and February 1975, the plankton of this region could be considered as homogeneous (Table 13).

If, in April 1974, two thirds of the population were still represented by Cyanophyceae, 25% by Diatoms and 10% by Chlorophyta in the north and the east of the northern basin, Diatoms (three quarters of the population and 10% of Chlorophyta) predominated in the southern and western parts. In November, the type community included about 50% Diatoms, 40% Chlorophycea and 10% Cyanophyceae and in February 1975, Diatomophyceae were almost 90%.

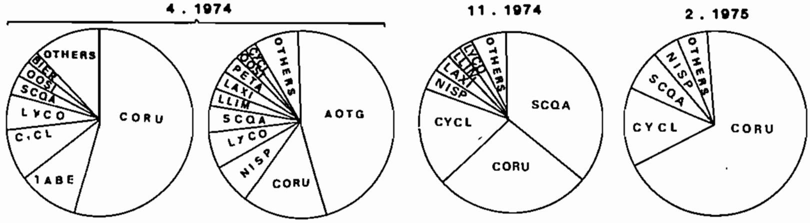

Fig. 19 Type-communities occurring in the northern basin from April 1974 to February 1975 (cf. Appendix I for taxa code).

Table 13 Changes in the relative composition of the algal communities in the northern basin of the lake from April 1974 to February 1975.

North basin	April 1974		November 1974	February 1975
	S and W parts	N and E parts		
	(%)	(%)	(%)	(%)
Oocystis sp.	3	2		
Scenedesmus quadricauda	3	5	36	7
Pediastrum tetras		3		
Binuclearia eriensis	2			
Cyclotella meneghiniana	9	2	18	14
Coscinodiscus rudolfii	54	15	27	69
Synedra berolinensis	11			
Nitzschia sp.		7	4	5
Anabaenopsis tanganiikae		46		
Oscillatoria laxissima		3	4	
Lyngbya limnetica		3	2	
Lyngbya contorta	6	6	2	
Others	12	8	7	5

Thus a very high algal density developed in the northern basin during the period of 'Lesser Chad' and Diatoms were particularly abundant. The partitioning of the northern basin into two different ecological zones such as the archipelago and the open water which existed during the period of 'Normal Chad', was still present in April 1974, so that with the permanent decrease in the water level, the algal populations become uniform in the reduced water cover existing at the end of 1974 and in early 1975.

In conclusion, after contraction of the lake, the composition of the algal communities seems to have changed little in the open water in the southern basin. In the archipelago the major change was caused by the Euglenoïds. Species composition in the Northern basin was very different because of the abundance of Centric diatoms and the occurrence prior to the drying up of the lake, of Cyanophyceae which were typical of the sodium ponds.

6.2.5 *General conclusions*

From the surveys made between 1971 and 1973, 'Normal Chad' can be classified as a tropical lake rich in phytoplankton compared with data from some lakes in the Philippines, Indonesia or Venezuela (Lewis 1978). Moreover, the surveys showed an increase in the algal biomass when the lake moved towards the stage of 'Lesser Chad' during the drought period. This increase

several groups, ranging from the ultra-oligotrophic lakes with maximum biomasses lower than one gram per cubic meter to the highly eutrophic lakes with maximum biomasses higher than ten grams per cubic meter. It seems difficult to apply this classification here since the observations were limited in time. Nevertheless, it can be assumed that starting with the analysis of the seasonal variations during the period of 'Normal Chad' (Gras et al. 1967), the open waters zones can be classified as mesotrophic environments, while the northern and southeastern archipelagoes were meso-eutrophic. On the contrary, the furthest parts from the deltas of the Shari, El Beïd and the Yobé (far east and far northeast where Cyanophyceae represented at least 90% of the algal biovolume throughout the year) ranged from eutrophic to highly eutrophic environments. During the period of 'Lesser Chad', the archipelago of the southern basin could be considered as eutrophic, while the waters of the northern basin and the zone of open water near the Shari delta were highly eutrophic.

Since the eutrophic zone extended to the bottom and the plankton was considered to be fairly well distributed in the water column, the total biomass was calculated from the data on surface algal density. The area and bathymetrical data used were those defined by Roche (1971) for the different regions. The results expressed in weight of living matter were in some way imprecise because of the numerous sources of errors likely to occur (methods of sampling and sub-sampling the phytoplankton, countings under the inverted microscope and conversion into biovolume calculation of areas, mean depths and dried up areas in relation to the level). However these estimates will be useful for calculating the general energy balance of the lake.

The algal biomass (Table 14) was estimated as 40 800 tons for a water area of 18 000 km^2 in February 1971. In February 1975, it reached 244 100 tons in a flooded area of about 11 000 km^2. It appears that phytoplankton increase varied greatly with seasons in the open waters of the southern basin, was greater in the archipelago and considerable in the remaining water of the northern basin.

However, these estimates only concerned the limnoplankton. In this type of shallow lake, the floating vegetation, whether submerged or not, covered considerable areas. In addition to floating 'Kirtas' and reed islands, there was submerged vegetation in all the sheltered zones of the archipelago and in the shallow border of the open water allowing abundant periphyton to develop. Wetzel (1964) showed in a Californian lake that the periphyton represented most of the primary production, limnoplankton contributing only 25%.

In Lake Chad, because of the hydrological instability leading to frequent modifications in water level and structure, the primary production was observed in three forms (limnoplankton, macrophytes, periphyton) which differed in proportions according to hydrological developments in the lake. Therefore, in the northern basin, the evolution towards 'Lesser Chad' under a

Table 14 Total algal biomasses (in tons, f.w.) for the different regions of the lake, from 1971 to 1975.

	2. 1971		1. 1972		4. 1974		11. 1974		2. 1975	
	Area (Km^2)	Biomass (t)	Area (Km^2)	Biomass (t)	Area (Km^2)	Biomass (t)	Area (Km^2)	Biomass (t)	Area (Km^2)	Biomass (t)
Southern basin										
Open waters	5410	305	4910	1535	1300	14 195	4910	6140	4910	5030
Archipelago	3405	9375	3405	26 135	200	2295	3405	2135	3405	37 955
Northern basin										
Open waters	6160	15 780	5660	29 730	6000	166 980	2000	179 000	300	201 150
Archipelago	3160	15 340	3160	19 425						
Total	18 135	40 800	17 135	76 825	7500	183 470	10 315	187 275	11 315	244 135

dry climate leads to a reduction in the macrophyte belts covered by periphyton. The primary production was mainly due to a very dense limnoplankton or heleoplankton. In the southern basin, during the period of 'Lesser Chad' large developments of macrophytes and, to a lesser extent, of periphyton were observed in the archipelago while the limnoplankton remained at an average level. In the south and the west, the swampy zones towards the delta of El Beïd and the 'Great Barrier' were occupied by macrophytes.

So, limnoplankton studies do not give representative results for estimating quantitative richness of the whole plant level and establishing trophic classification of this lake. It is necessary to evaluate the importance of each class of primary producer (plankton, aquatic phanerogams, periphyton) in order to assess total primary production. The studies on the diets of fish populations in Chad (Lauzanne 1976) showed that the three forms of vegetation were used directly or indirectly by one group of fishes or another. The range of biomass values observed in the limnoplankton alone suggest that total plant production was particularly high.

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Appendix I

Taxa code

Melosira granulata	MGGR	*Monoraphidium contortum*	MOCO
Melosira granulata var. *angustissima*	MGAN	*Binuclearia eriensis*	BIER
Coscinodiscus rudolfii	CORU	*Coelastrum cambricum*	CCAM
Cyclotella meneghiniana	CYCL	*Coelastrum microporum*	CMIC
Synedra ulna	SYUL	*Coelastrum proboscideum*	COPR
Fragilaria construens	FRAC	*Ankistrodesmus* sp.	ANKG
Synedra berolinensis	TABE	*Quadrigula quaternata*	QQUA
Gyrosigma kutzingii	GYRK	*Chodatella* sp.	CHOD
Navicula sp.	NASA	*Diclyosphaerium pulchellum*	DIPU
Nitzschia sp. (petite forme)	NISP	*Botryococcus braunii*	BOBR
Nitzschia spiculum	NSPI	*Micraclinium pusillum*	MAPU
Surirella linearis	SULI	*Eudorina elegans*	EUDO
Surirella muelleri	SPSF	*Gonatozygon monotaenium*	GOMO
Tetraedron minimum	TTMI	*Closterium aciculare*	CACI
Tetraedron trigonum	TTRI	*Closterium acutum* var. *variabile*	CAVA
Nephrochlamys subsolitaria	NESU	*Closterium strigosum*	STRI
Crucigenia triangularis	CRTR	*Spirogyra* sp.	PIRO
Crucigeniella crucifera	CRUC	*Euglena* sp.	EUGL
Crucigenia tetrapedia	TETR	*Euglena oxyuris* f. *charkowiensis*	EOFC
Oocystis sp.	OOSI	*Trachelomonas* sp.	TRAC
Eremosphaera gigas	ERGA	*Strombomonas* sp.	STRO
Scenedesmus acuminatus	SCAC	*Phacus* sp.	PHAC
Scenedesmus acutus	SCCU	*Lepocinclis* sp.	LEPO
Scenedesmus intermedius	SINT	*Synechocystis minuscula*	SYAQ
Scenedesmus quadricauda	SCQA	*Synechococcus leopoliensis*	ROME
Scenedesmus ecornis	SCEC	*Chroococcus limneticus*	CHRO
Scenedesmus opoliensis	SCOP	*Microcystis aeruginosa*	MIAE
Scenedesmus perforatus	SCPE	*Microcystis delicatissima*	MIDE
Pediastrum clathratum	PSDU	*Microcystis elachista*	MIOX
Pediastrum duplex	PEDU	*Microcystis* sp.	MISI
Pediastrum tetras	PETA	*Anabaena flos-aquae*	ANFL
		Anabaena spiroïdes	APIR

Anabaena sp.	ANSA	*Oscillatoria laxissima*	LAXI
Anabaenopsis arnoldii	AOAR	*Oscillatoria platensis* f. *minor*	SPMI
Anabaenopsis tanganiikae	AOTG	*Cryptomonas erosa*	CRYP
Lyngbya contorta	LYCO	*Chroomonas* sp.	CROM
Lyngbya limnetica	LLIM	*Mallomonas portae-ferrae*	MLPF
Raphidiopsis sp.	RAFS	*Peridinium* sp.	PERD
Oscillatoria sp.	OSCI		

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