ECOLOGY OF LAKE CHAD

A TROPICAL SHALLOW LAKE

(AFRICA)

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1. THE LACUSTRINE ENVIRONMENT

Lake Chad is situated between 12° and 14°20 latitude north and 13° and 15°20 longitude east. The lacustrine basin occupies a large region of 25 000 km^2 with few depressions, which is no more than 1/16 th of the surface it occupied between 5,000 and 6,000 years B.P. (Servant, 1970). It is subject to the influence of a tropical climate, comprising a hot, dry season from March to June, a rainy season from June to October, and a dry, cool, season from November to February. The mean annual rainfall on the lake is 320 mm. Insolation is high with a monthly average of 275 to 310 hours and the mean daily radiation is 550 $cal/m^2/day$. The lake is fed for the most part by waters from the Chari and Logone Rivers, which represent 95% of the river inflows. The rains represent only 10% of the total input which averages 47 x 10^9 $m^3/year$. The lake being of an endorheic type has no exit therefore and 90 to 95% of the losses are due to the important evaporation (2.20 m per year), the rest being lost by infiltration (Carmouze, 1971).

Because of the shallow depth, estimated at an average 3 m for a water level altitude of 281 m, the volume of the lake is small and the level presents important annual and interannual variations, for the balance between inflow and loss is rarely attained. The waters remain in the lake on an average one and a half years (Carmouze, 1976). The inflows vary in relation to the characteristics of the pluviometry and, since 1963, pluviometric conditions having been unfavourable, the level fell continuously until 1975, leading to profound modifications in the environment and populations. Three states of the lake may be distinguished according to the level of the water, the surface and the aspect of the lake (Tilho, 1928) :

- Great Chad : water level altitude 283 m, surface estimated at 25,000 km^2. This was the state of the lake between 1963 and 1965.
- Normal Chad : water level altitude 281-282 m, surface around 20,000 km^2. This was the state of the lake between 1965 and 1971, the period during which most of the hydrobiological observations were made.
- Little Chad : water level altitude 280 m, with separation of the north and south basins and exundation of the Great Barrier. The north basin, no longer being fed, dries up and the lake is reduced to part of the south basin. These extreme conditions occurred in 1975 and have continued until 1979.

During the Chad Normal period, three types of landscapes are to be seen : the open waters devoid of aquatic vegetation, the reed-islands which are islands of vegetation (*Papyrus, Phragmites*) and the archipelagoes consisting of about a thousand sandy islands corresponding to the dune crests of a settled, partly immerged erg. These various environmental types make it possible to ditinguish several large natural regions (fig. 1). There is no rocky or stony substrate anywhere in the lake and the bottom consists exclusively of loose sediments : mud, clay, sand and pseudo-sand (Dupont, 1970).

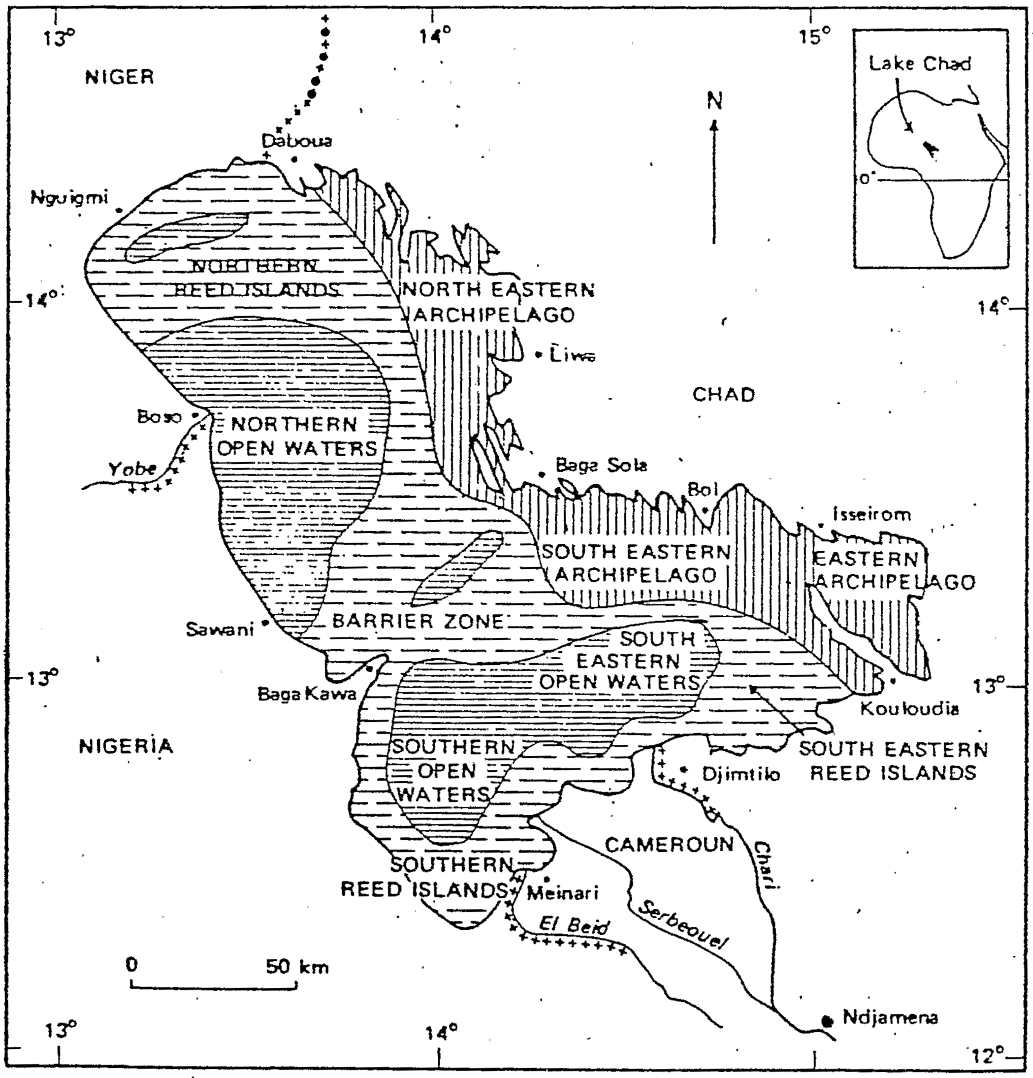

Figure 1 - Lake Chad : main types of landscapes (water level altitude : 282 m)

The temperature of the waters follows a seasonal cycle in accordance with the climatic cycle, with a minimum in January (19° C) and a maximum in May-June (31° C). Transparency is not very great because of the shallow depth favouring suspension of sediment due to the action of the wind, the abundance of phytoplankton in certain regions and river inflows loaded with solid material. The pH, slightly more than 7 in the south basin, reaches 8.5 in the east archipelago and rises to 9 in certain arms of the north-east archipelago.

Salinity ranges from 70 to 1 000 mg/l of dissolved salts which corresponds to a conductivity of 50 to 1 100 µmhos/cm.

From the predominantly calcic free waters of the south, there is a change to a salt predominance in the north. Although the lake is an accumulation basin where the salts should concentrate, due to intense evaporation, yet the average salinity of the waters is seen to vary little from one year to the next. Some balance seems then to exist between the ion input and loss and this salt regulation is ensured by two main types of mechanisms : non-selective evacuation of salts by infiltration of the waters along the north bank of the lake (63% of the ions deposited annually in the lake) and selective sedimentation of the rest of the inputs, principally in the form of neoformations of smectites and precipitation of calcite (Carmouze, 1976).

2. POPULATIONS, BIOMASSES AND PRODUCTIVITY

2.1 PHYTOPLANKTON AND PRIMARY PRODUCTION

Over a thousand species and taxons have been enumerated in Lake Chad (Compère, 1967, 1974-1978; Iltis & Compère, 1974). The algal florule is dominated qualitatively by the Desmidiaceae and Diatoms, but the Cyanophyta play an important role from the quantitative point of view.

During the Normal Chad period, there is a difference in the populations and phytoplanktonic densities between the south basin (conductivity of 50 to 250 µmhos, strong turbidity, influence of the Chari flood waters) and the north basin which is richer in plankton (conductivity of 200 to 1 300 µmhos, slight turbidity). Moreover, for each of these basins, the algal populations of the open waters are distinct from those of the archipelagoes. These four large zones can be characterised by the predominance of species and groups of species (Carmouze *et al*, 1972; Iltis, 1976-1977- (fig. 2) :

- The open waters of the north where the Desmidiaceae, *Closterium aciculare* predominate for long periods of the year. *Pediastrum*, *Botryococcus* and *Mycrocystis* are abundant and the Diatom, *Melosira granulata* is absent.
- The north-eastern archipelago where the Cyanophyta, *Anabaena* and *Mycrocystis* are predominant. *Closterium*, *Pediastrum* and *Botryococcus* are still abundant.
- The open waters of the south and south-east, directly influenced by the floods of the Chari, where the Diatoms, *Melosira granulata* and *Surirella muelleri* constitute the bulk of the population.

- The eastern and south-eastern archipelagos where the Cyanophyta, *Microcystis* and *Anabaena* are abundant, and occasionally *Surirella*, *Pediastrum* and *Melosira*.

The mean biomass is low in the open waters of the south, the highest values having been found in the north basin (table 1). The total phytoplanktonic biomass for an elevation of 281 m of the water level, has been estimated at 40 800 tons (fresh weight in biovolume) in February 1971 (Iltis, 1977).

A drop in the water level, particularly noticeable after 1971, is accompanied by a rise in the density of phytoplankton. The total biomass (expressed in tons of fresh weight) thus passed from 76,800 in January 1972 to 183,000 in April 1974 and 244,000 in February 1975 (Iltis, 1976). At the same time, changes were seen in the populations : in the open waters, where Diatoms and Cyanophyta were predominan in 1971-1972, Euglenophyta were seen to appear in large proportions in April 1974, and then Chlorophyta and Chrysophyta (November 1974). In the north basin the phytoplanktonic population changes to resemble that of a natron pond with a preponderance of centric diatoms accompanied or followed by the apparition and development of *Oscillatoria platensis*, a blue-green alga characteristic of the natron waters from the northern border of Lake Chad.

	South basin		North basin	
	open waters	archipelagoes	open waters	archipelagoes
algal density	0.03 - 0.22 µl/l	1.4 µl/l	0.7 - 1.6 µl/l	1.4 - 2 µl/l
dominant groups	Diatoms Cyanophyta	Chlorophyta Cyanophyta	Chlorophyta Diatoms	Cyanophyta Chlorophyta
seasonal variations	very marked	average	slight	slight

Table 1 - Characteristics of ecological zones established for phytoplankton. The algal density is expressed in biovolume (from ILTIS, 1977)

Primary production has been measured over a period of several years in the south-east archipelago at Bol and in the south basin during the Normal Chad period. The daily total radiation (I_o) averages 5,410 $Kcal/m^2$ and the part of the radiation likely to be used by the algae is given in the relation : $I'o = 0.437\ Io$. I'o equals an annual average of 325 $Kcal/m^2/h$ between 11 h and 14 h.

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The transparency of the waters had been measured with a Secchi disc and the values obtained have been converted into coefficient values of vertical extinction by water (ε min) by the experimental equation : $\frac{I}{\varepsilon \ min} = 0.7$ (D.S.) where D.S. is expressed in meters.

A model has been evolved allowing the estimation of hourly production around midday (Σ A) from numerous series of observations (Lemoalle, 1973) :
Σ A = Aopt x Zi, where Zi = 2.07 D.S. in water of clay turbidity
or Zi = 1.20 D.S. in water of organic turbidity, with
Σ A in $gO_2/m^2/h$, Aopt being the optimal hourly production measured in situ or in an incubator, expressed in $gO_2/m^3/h$. The daily production $\Sigma\Sigma$ A is obtained by the equation $\Sigma\Sigma$ A = 9.1 Σ A with $\Sigma\Sigma$ A in gO_2/m^2/day. In the eastern archipelago, the mean daily primary production is 4.2 gO_2/m^2/day i.e. 550 g/m^2/year of organic carbon, in the Normal Chad period. During the dry period the decreasing depth brought about an increase in turbidity and consequently a reduced transparency, partly compensated for by an increase in algal concentration and the optimal productivity per volume unit. Thus in 1973 and 1974, the mean annual daily activity was 7.4 gO_2/m^2/day in the eastern archipelago. On the other hand, it was no more than 2.7 gO_2/m^2/day in 1975 (Lemoalle, 1979).

Primary production is slightly lower in the other regions of the south basin than in the east archipelago. On the other hand, it is higher in the northern of the lake.

2.2 MACROPHYTES

The reeds cover about 2 400 km^2 during the Normal Chad period (Carmouze *et al*, 1978) and a dozen plant associations are really important on the lake (Leonard, 1969 ; Carmouze *et al*, 1972). In particular there is a notable abundance of *Vossia cuspidata* in the whole delta region of the Chari and of *Cyperus Papyrus* in the south basin. These species disappear progressively in the north basin, giving way to *Typha australis*. The *Phragmites australis* are well represented everywhere.

The biomasses of the aerial parts of the reed beds has been estimated, in dry weight, at 31 t/ha for *Phragmites*, 28 t/ha for *Cyperus papyrus*, 17.5 t/ha for *Vossia* and 15.5 t/ha for *Thypha*, i.e. a total 7.2 x 10^6 t for the whole lake. The total biomass of roots is assayed at 13 x 10^6 t approximately (dry weight). An analysis of the chemical composition of the different species has enabled the determination of the quantities of salts stocked in the macrophytes : 200 x 10^3 t for K, 60 x 10^3 t for Ca, 38 x 10^3 t for Mg, 10 x 10^3 t for Na and 2 340 x 10^3 t for SiO_2, representing respectively 16.5%, 3.4%, 4.5%, 0.4% and 68.8% of the dissolved lacustrine stocks (Carmouze *et al*, 1978). 8388

During the dry period, a very notable impoverishment of the aquatic vegetation in the north basin was first seen, whereas on the contrary, the south basin was overrun with *Aeschynomene elaphroxylon*, as well as *Vocsia cuspidata* and *Ipomoea aquatica* (Fotius, 1974). Later *Aeschynomene* and *Typha australis* developed north of the lake, whereas in the south, great extents of *Aeschynomene* were partly destroyed, giving way to *Vossia* and *Cyperus papyrus*. *Pistia stratiotes*, *Nymphea* and *Cyperus nudicaulis* were also seen to develop in the south (Fotius & Lemoalle, 1976).

2.3 ZOOPLANKTON

Rotifers are represented in Lake Chad by some twenty species (Pourriot *et al*, 1968). The planktonic crustacean populations consist for the most part of eight species of Cladocera (among which *Moina micrura*, *Diaphanosoma excisum*, *Bosmina longirostris*, *Daphnia barbata*, *Cerodaphnia cornuta*) and four species of Copedods (*Tropodiaptomus incognitus*, *Thermodiaptomus galebi*, *Thermocyclops neglectus* and *Mesocyclops leuckarti*) representing 99% of the biomass (Dussart et Gras, 1966; Gras *et al*, 1967; Rey & Saint-Jean, 1968, 1969).

Three large ecological zones may be distinguished in the Normal Chad period, according to the zooplankton density and the seasonal cycle of abundance (Carmouze *et al.*, 1972), for no important variations have been observed in the specific composition at the scale of the lake (fig. 3) :

- the open waters of the south-east are the poorest (93 mg/m^3 in dry weight and in mean annual density). The seasonal variations subject to the influence of the flood waters of the Chari are important, with a minimum from July to February and a maximum during the hot season (Gras *et al.*, 1967);
- the archipelagoes and reed-islands of the south basin, where the seasonal variations are small, have a high mean density (315 mg/m^3 in dry weight);
- the north basin has a smaller density (216 mg/m^3) than the south basin, but is very much deeper. The seasonal variations are small (Robinson, 1971).

The total zooplanktonic biomass was estimated at 12,200 tons (dry weight) in February 1971. Its dry weight averages 8.9 kg/ha in the north basin which contains 60% of the zooplanktonic stock, 6.9 kg/ha in the eastern archipelagos and 2.5 kg/ha in the southern and south-eastern open waters.

Embryonic development lasts about as long with the Cladocera as with the Copepoda studied : between 1 and 1.5 days at 30° C, 1.4 and 2 days at 25°, 1.9 and 2.3 days at 22° (Gras et Saint-Jean, 1969, 1976, 1978, 1979).

Regarding the Cladocera, one group has a rapid post-embryonic development, the egg to egg cycle lasting 1.2 and 2.3 days at 30° C (*Moina micrura*, *Diaphanosoma excisum*, *Cerodaphnia cornuta*), and another group comprising three species of *Daphnia* with a much longer cycle : over 4.3 days at 30° C.

With the Copepoda, the post-embryonic development of the Diaptomids is much longer than with the Cladocera : at a temperature of 30° C, it lasts respectively 26 days for *T. incognitus* and 11 days for *T. galebi*. With the Cyclopids, *M. leuckarti* and *T. neglectus*, it is no more than 6 days at 30° C. The increase in weight of these different species of Copepoda has been determined by evaluating the individual weights and the length of the stages at 30° G (Gras & Saint-Jean, 1978).

	$\bar{B}$ annual (mg/m^3)	P annual (mg/m^3)	P/$\bar{B}$
Cladocera			
Moina micrura	16.5	3,148	190.8
Diaphanosoma excisum	27.5	3,242	117.9
Bosmina longirostris	29.6	2,123	71.7
Daphnia	27.8	2,102	75.6
Cerodaphnia cornuta	23.1	3,495	151.3
Total Cladocera	124.5	14,110	113.3
Total Diaptomids	151.9	3,504	23.2
Total Cyclopids	56.4	3,580	63.5
Total zooplankton	332.8	21,194	63.7

Table 2 - Mean biomass (B), annual production and P/B ratio for the different groups of zooplanktonic crustacea in 1964 and 1965 in the eastern archipelago. The mean temperature during the year was 26.2° C (from GRAS and SAINT-JEAN).

It has been possible to calculate zooplankton production in the sourse of an annual cycle in the eastern archipelago (table 3) : it averages 21.2 g/m^3 in dry weight, two thirds of this production being due to Cladocera. The annual P/$\bar{B}$ is 113 for Cladocera, 23 for Diaptomids and 63 for Cyclopids, i.e. a mean 65 for the whole of the population (Gras & Saint-Jean, in preparation).

In 1971, the annual production was estimated at about 860.000 tons (dry weight) for the whole of the lake, i.e. a mean 474 kg/ha or 2.50 x 10^6 Kcal/ha.

2.4 BENTHIC FAUNA

Some systematic inventories have been made : oligochets (Lauzanne, 1968); molluscs (Lévêque, 1968, 1972); insects (Dejoux, 1968, 1969, 1970, 1971, 1973). If the insects are represented by numerous species (approximately 200), only a dozen species of molluscs and six species of oligochets are found.

The type of bottom sediment is one of the main factors intervening in the distribution and abundance of species of worms and molluscs. Shallow depths do not appear to play any role in the Normal Chad period, oxygenation at the bottom always being adequate. The chemical composition of the waters do however exert some influence (Dupont & Lévêque, 1968; Dejoux, Lauzanne & Lévêque, 1971 ; Carmouze *et al.*, 1972; Lévêque, 1972). A study of the variations of abundance in several stations of the south basin has revealed a seasonal cycle in the worms and insects with a maximum density in the cool season (December to March), corresponding also to the high water period of the lake, and a minimum at the end of the cool season (May-August) (Dejoux, Lauzanne, Lévêque, 1969). These results proved valid in 1970 for other regions of the lake (Carmouze *et al.*,1972).

Benthic communities were studied in 1970 over the whole lake (Carmouze *et al.*, 1972). For each principal group extensive distribution zones were established according to the dominant species and the biomasses, and a general benthos zonation pattern was drawn. (fig. 4 and table 3).

As regards the oligochets, the north basin is populated essentially with Tubificidae (*Aulodrilus remex* and *Euilodrilus, sp.)* which abound particularly in the open waters, whereas the Alluroididae (*Alluroides tanganyikae)* are widely predominant in the southern and south-eastern open waters. In the archipelagoes of the Great Barrier and the eastern zone, two families are equally represented (Carmouze *et al.*, 1972). The mean biomass is 2.9 kg/ha for the whole of the lake, but is usually within 1 to 2 kg/ha, with the exception of the northern open waters where it reaches 8 kg/ha.

Among the molluscs, the *Melania tuberculata* are numerically predominant in the north basin and the *Cleopatra bulimoides* in the eastern archipelago (zone 7). Both these species are also represented in the south-eastern open waters (zone 5) and the Great Barrier (zone 4). *Bellamya unicolor* is abundant in the northern open waters, the northern archipelago and the Great Barrier, were it constitutes between 48 and 72 kg/ha (dry body weight, not including the shell). The molluscs disappear towards the north of the lake (biomass of 0.2 kg/ha) and are also less abundant to the east (10.6 kg/ha).

Finally, concerning the Chironomids, several ecological zones have been found, but their boundaries vary with the seasons (Carmouze *et al.*, 1972; Dejoux, 1976). This instability may be due to the rapid development cycles and to the active dispersion capacity of these organisms. On the whole, the biomass of insects is always small in benthos, particularly in the south basin (table 6).

The benthic biomass was estimated at 71,000 tons in 1970 (dry weight, not including the shell for the molluscs). Molluscs represent nearly 90% with an average 32.9 kg/ha for organic matter and 210 kg/ha for shells. This great biomass of molluscs is an original characteristics of Lake Chad and is due to the fact that the whole sur-

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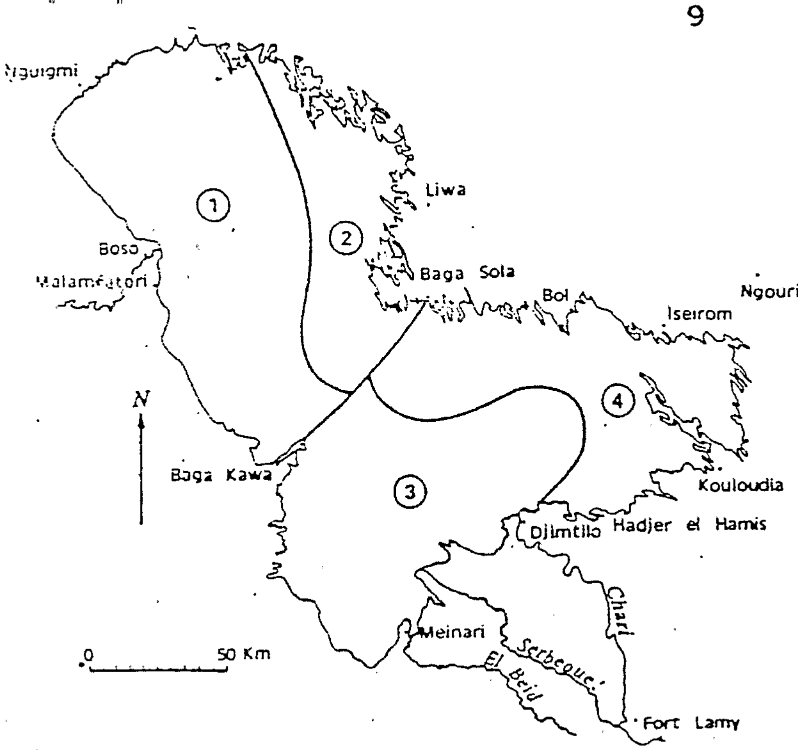

Figure 2 - Main ecological zones of phytoplankton (from Carmouze et al,1972).

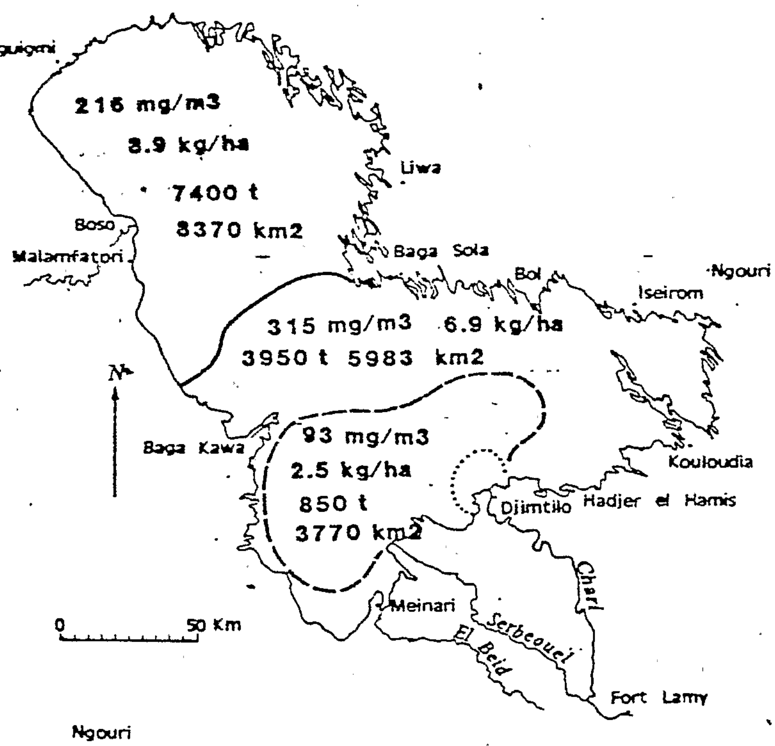

Figure 3 - Main ecological zones of zooplankton in 1971: density and biomasses (from Carmouze et al,1972).

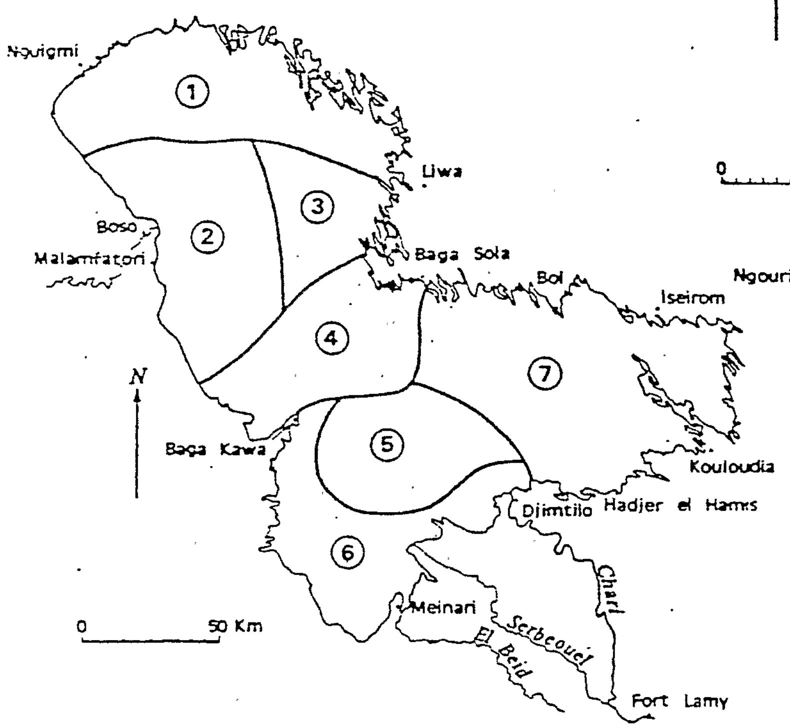

Figure 4 - Main ecological zones of the benthic fauna in 1970 (see table 6) (from Carmouze et al,1972).

face can be assimilated to a vast littoral zone, because of the shallow depths.

The evolution of malacological communities was followed from 1967 to 1972 in the eastern archipelago (region of Bol) and from 1968 to 1972 in the other parts of the lake. In general the density of the species was seen to diminish considerably, partly as a consequence of the falling level of the lake. In fact this has caused an increased agitation of the bottom waters which are effected by rather strong winds throughout the year and disturbed sediment is unfavourable to molluscs (Carmouze *et al.*, 1972).

	Worms	Insects	Molluscs		
Zones	$\bar{B}$ Kg/ha	$\bar{B}$ Kg/ha	$\bar{B}$ Kg/ha	P kg/ha/an	P 10^3 Kcal/ha/an
1	2.1	1.4	0.2	1	4
2	8.0	2.1	64.2	353	1,410
3	1.1	2.9	47.8	241	960
4	1.9	1.6	72.0	256	1,020
5	1.5	0.1	38.6	114	460
6	2.6	0.1	11.8	38	150
7	0.8	0.6	10.6	30	120
Total biomass (dry weight tons)	5,540	2,300	63 280		
Mean biomass (Kg/ha)	2.9	1.2	32.9		
Total production				279.090 dry weight tons	$1,116 \times 10^9$ Kcal
Mean production				145 kg/ha/an	580×10^3 Kcal/ha/an

Table 3 - Benthic fauna : mean biomass (B, in kg/ha,dry weight) in worms, insects and molluscs in seven zones of Lake Chad (fig. 4), and production of molluscs.

Only the production of molluscs, which constitute the bulk of the benthic biomass, has been studied. The growth rate of the main species was determined by in situ breeding and theoretical growth curves have been calculated using the von Bertalanfly model (Lévêque, 1971). Reproduction occurs throughout the year with the Prosobranchs (*Melania, Bellamya* and *Cleopatra*) and during the cool season with *Corbicula*. Production was calculated during an annual cycle in different biotopes and different regions of the lake (Lévêque, 1973) and the mean annual P/B ratio was estimated at 4.4 for *Melania tuberculata*, 5.8 for *Bellamya unicolor*, 2.6 for *Cleopatra bulimoides* and *Corbicula africana* and 2 for *Caelatura aegyptiaca*.

The annual production of benthic molluscs for Lake Chad was 279,000 tons (dry weight) of organic matter in 1969-1970 and 1,883,000 tons of shells, i.e. an average respectively of 14.5 g/m^2/year and 98 g/m^2/year. Expressed in calories

(Lévêque, 1973), this production is 1116 x 10^9 Kcal, i.e. an average 58 Kcal/m^2/year. The greater part of this production is made up of Prosobranchs and above all *Bellamya*. These production studies were completed by breathing measurements, in order to estimate assimilation. Energy budgets have been established for natural populations whose production had been studied in the course of an annual cycle. The yield of assimilated energy uptake for growth (P/A) is fairly high in the Prosobranchs (between 20 and 30 for *Melania*, 13 and 20 for *Cleopatra*, 32 for *Bellamya)* and low for the Lamellibranch C. *africana* (between 9 and 11%).(Lévêque, 1973).

For insects, the length of the larval cycle is 17 days et 26° C and 13 days at 30° C in the laboratory for *Chironomus pulcher* (Dejoux, 1971) and 18 days between 18° and 23° C for *Tanytarsus nigrocinctus* in conditions close to natural ones (Dejous, 1976). For this last species, the daily P/B has been estimated at 0.24 in the cool season in the north basin (Dejoux, 1976).

2.5 FISH

The ichthyological fauna of the lake and its basin listed by Blache (1964) consists of about 140 species.

In the south-eastern open waters, the *Schilbe* are abundant and several large-sized species are found (*Citharinus citharus, C.distichodoides, Labeo coubie)*, but the number of species caught is much lower than in the rest of the south basin. In the south-eastern archipelago, *Alestes baremoze, Alestes dentex, Synodontis frontosus* and *Brachysynodontis batensoda* are to be found in particular, as well as *Heterotis niloticus,Tilapia spp*. The fauna of the southern shore of the lake, in the neighbourhood of the Chari delta, is more varied, because of the proximity of the river system. It is the compulsory passageway of all fluvio-lacustrine species on migration.

The ichthyological communities in the north basin differ from those of the south basin by the fact that certain species disappear beyond the Malamfatori-Baga Sola line : this is the case with *S. mystus* and most of the *Synodontis* species. There are less and less species in the communities towards the north-east (Carmouze *et al.*, 1972; Durand, 1972).

The biology and growth of a certain number of species has been studied : *Alestes baremoze* (Durand, 1978; Durand et Loubens, 1969, 1970, 1971; Hopson, 1968, 1972), *Lates niloticus* (Hopson, 1968, 1972; Loubens, 1974), *Schilbe mystus* and *Schilbe uranoscopus* (Mok, 1974, 1975), *Citharinus citharus* (Benech, 1974), *Brachysynodontis batensoda* (Benech, 1975), *Sarotherodon galilaeus* (Lauzanne, 1978); *Micralestes acutidens* (Lek & Lek, 1977), *Ichthyoborus* (Lek & Lek, 1978). Most of these species reproduce at the time of the river floods and carry out their anadromous migrations in order to spawn near the flood plains. The population dynamics of *Alestes baremoze* has been the subject of detailed studies, due to the importance of this species in fisheries (Durand, 1978).

It has not been possible to make any estimation of the ichthyological biomass in Lake Chad, with the exception of some ichthyotoxic species in particular environments (Loubens, 1969, 1970).

At the beginning of 1973, the level being considerably lower, the lake broke up into three collections of water separated by shoals. This led, in certain regions, to massive fish mortalities, due to the temporary deoxygenation of the waters, following periods of wind disturbance bringing about a resuspension of the sediment (Benech *& al.*, 1976). The predator species were those most affected (*Lates niloticus, Hydrocynus brevis, Hydrocynus forskalii*), but some species reputed to be resistant to anoxia, such as the *Tilapia*, also fell victim to this situation.

By 1977 the north basin, which had dried up in 1975, was no more than a sort of temporaty marsh. The lake was thus reduced to the south basin and in the open waters connected with the river network the population diversified and the stock of *Alestes* was renewed.

With the drop in the level of the lake, fishing intensified. In 1974 the north basin was so well exploited that stocks were pratically exhausted before this region dried up in 1975. The fishermen moved consequently towards the south basin which has since provided the bulk of the catches.

3. TROPHIC RELATIONSHIPS

3.1 FEEDING OF PLANKTONIC CRUSTACEA

A study of the food diet of planktonic crustacea (Gras, Iltis & Saint-Jean, 1971) shows that the main species of Cladocera ingest all planktonic algae, monocellular or colonial, whose size ranges from about 4 µ to 30 µ. The Cyanophyta, *Anabaena flos aquae* however, which represents an important part of the algal biomass, is not normally consumed by the Cladocera. On the other hand it constitutes an appreciable part of the food of the Diaptomid, *Tropodiaptomus incognitus* (a predominant species in the zooplankton biomass) and of the Cyclopid, *Thermocyclops neglectus*. The consumption of *Anabaena* by both these species does not appear to be regular however and could depend on the abundance of the algae and of the state in which the cells chains are found.

If Cladocera and Diaptomids are essentially phytophagous, bacteriophagous and detrivorous, on the contrary the Cyclopids have a more carnivorous diet. *Thermocyclops neglectus* has a mixed diet, just as the copepodit stages of *Mesocyclops leuckarti* and *Thermocyclops incisus*, whose diet is predominantly phytophagous during the first stages and carnivorous at stage 5. The adults of both these latter species are essentially carnivorous.

3.2 FEEDING OF FISH

A study of food diets (Lauzanne, 1976) has enabled the classification of the main species into large groups of consumers, according to trophic levels. The first level consisting of "primitive" food sources (algae and detritus), three other levels have been revealed :

- The second level is formed of primary consumers. Among these we distinguish the phytoplankton-feeders (*Sarotherodon galilae)* and detritivores (*Labeo senegalensis, Citharinus citharus...)*. The essential difference between these diets is due to the different feeding behaviours. *Sarotherodon galilae* is a typical filter-feeder selecting above all algae, and even certain types of algae (Lauzanne & Iltis, 1975), whereas *Labeo* and *Citharinus* eat the bottom organic film, consisting mainly of sedimented algae. The primary consumers also comprise the dominant macrophytes-feeders, such as *Alestes macrolepidotus*.

- The third level consistes of secondary consumers. These include the strict zooplankton-feeders, such as *Alestes baremoze* or *Hemisynodontis membranaceus* or dominant ones such as *Brachysynodontis batensoda* and *Alestes dentex*. The benthos-feeders, such as *Synodontis schall, Hyperopisus bebe, Heterotis niloticus*... feed on benthic invertebrates consuming the organic film at the bottom (insect larvae, ostracods, molluscs). The insect larvae consumed are essentially the Chironomids (*Chironominae* and *Tanipodinae)*, Ephemera and Trichoptera.

- The fourth and last level is formed by the terminal consumers. Certain are strict fish-feeders : *Latès niloticus, Hydrocynus brevis*. Diets of other species are more varied : *Hydrocynus forskalii, Bagrus bayad, Eutropius niloticus, Schilbe uranoscopus*... Besides fish, these species eat shrimps and aquatic insects. It should be noted that *B. bayad, S. uranoscopus* and *E. niloticus* consume not only whole fish but also large quantities of fish debris. In the group of the non-strict fish-feeders, these three species are quite apart from the carnivores feeding essentially on living prey such as *Hydrocynus forskalii*.

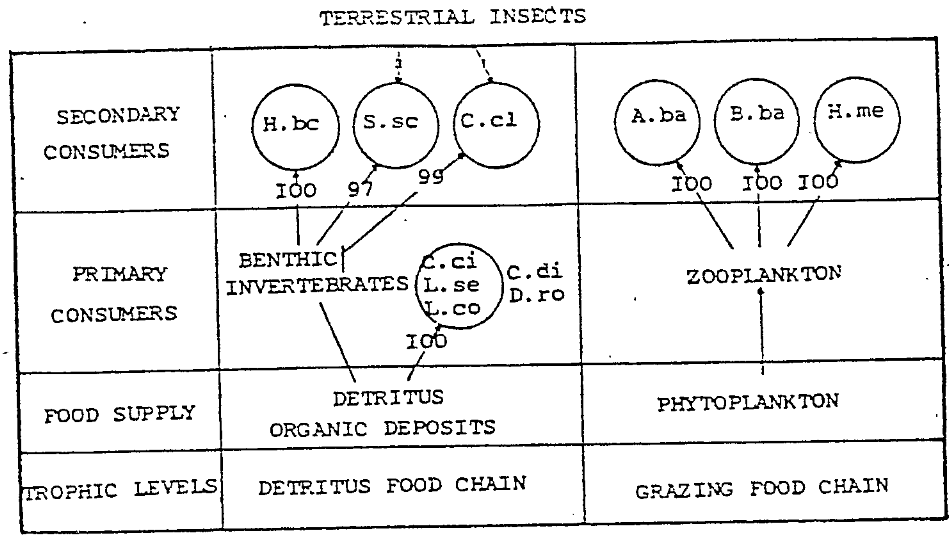

Fig. 5 - Food chains of primary and secondary consumers in Lake Chad open waters. The arrows indicate the direction of inputs and the numbers and volumetric percentages of these contributions to the food dicts. Numbers in cercles correspond to preys whose trophic position is unknown. S. sc : *Synodontis schall*, H. be : *Hyperopisus bebe*, H. ni : *Heterotis niloticus*, A. ba : *Alestes baremoze*, H. me : *Hemisynodontis membranaceus*, B. ba : *Brachysynodontis batensoda*, A. de : *Alestes dentex*, A. ma : *Alestes macrolepidotus*, T. ga : *Tilapia galilaea*, C. ci : *Citharinus citharus*, C. di : *Citharinus distichodoides*, L. se : *Labeo senegalensis*, L. co : *Labeo coubie*, D. ro : *Distichodus rostratus*, S. cl : *Synodontis clarias* (from Lauzanne, 1976).

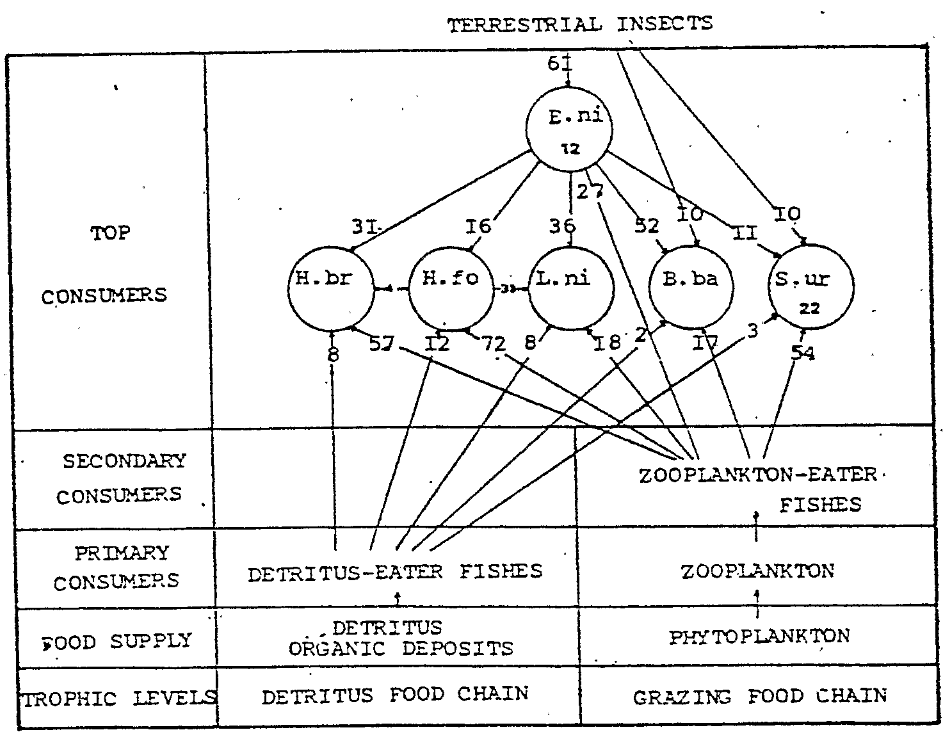

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Fig. 6 - Food webs of terminal consumels in Lake Chad open waters. L. ni : *Lates niloticus*, H. fo : *Hydrocynus forskalii*, H. br : *Hydroxynus brevis*, E. ni : *Eutropius niloticus*, B. ba : *Bagrus bayad*, S. ur : *Schilbe uranoscopus* (from Lauzanne, 1976).

The importance of the different groups of consumers differs between the archipelago and the eastern open waters.

The archipelago is often distinguishable by the abundance of plankton-feeders and above all zooplankton-feeders which represent 44% of the ichthyomass, and the presence of a strong and stable planktonic biomass throughout the year.

The open waters are strongly dominated by the group of terminal consumers forming 64% of the fish biomass. The maintenance of this great biomass seems to depend indirectly on the fall of land insects and the abundance of small zooplankton-feeding prey fish, *Micralestes acutidens* and *Pollimyrus isidori* whose production is high. (fig. 5 and 6).

To conclude, the food resources available in lacustrine environments during the Normal Chad phase seem to have been relatively well consumed. The macrophytes of the archipelago however could probably feed a denser population of herbivores.

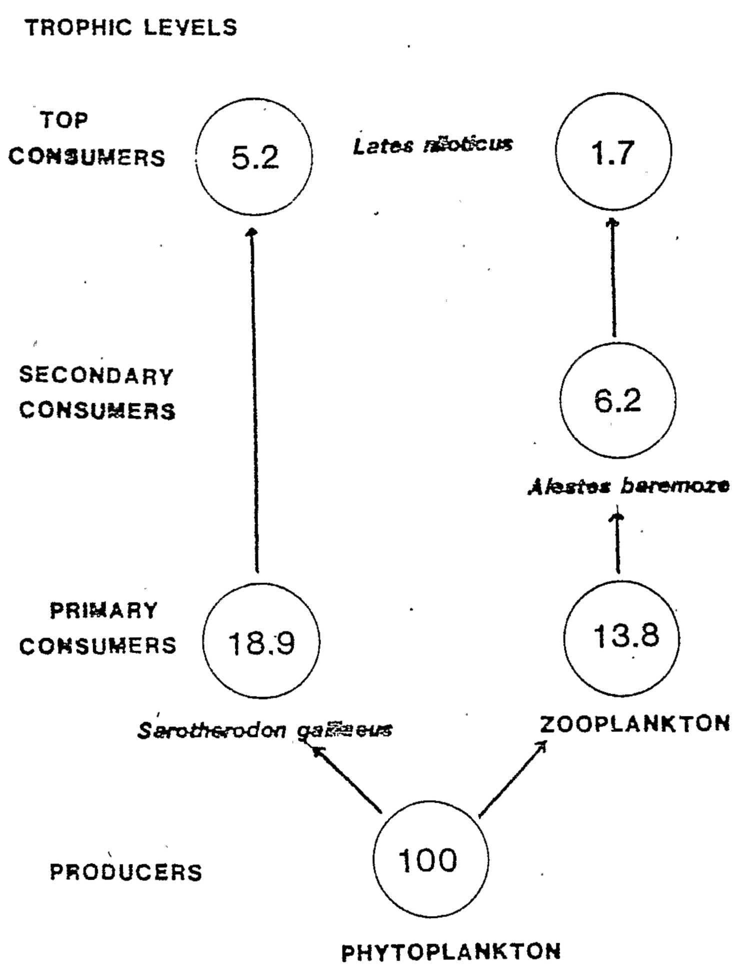

Figure 7 - Energy accumulated (in calories) by Lates niloticus according to the food chain used, starting from 100 calories for phytoplankton (from LAUZANNE,1976). 8388

From the quantitative point of view the food conversion rates have been determined for three species, each corresponding to a consumer level (Lauzanne, 1972, 1978). This rate (Kg) is the percentage between the increase in weight of the fish and the quantity of food ingested, expressed in fresh weight. If energetic equivalents are used, this ratio then represents the energic coefficient of first order growth (K_1). Kg and K_1 are respectively equal to 3.1 and 18.9 in *Sarotherodon galilaeus* (phytophagous), 8.8 and 44.8 in *Alestes baremoze* (zooplankton-feeder) and 26.4 and 27. 3 in *Lates niloticus* (piscivore).

Values found for *S. galilaeus* are fairly low. There is in fact a poor use of the food ingested in *A. baremoze*, as is generally the case with phytoplankton-feeders. The conversion rate is also low (8. 8%), but the energy coefficient is definitely higher. For *L. niloticus*, a predator, the energetic coefficient is half way between those of the preceding species.

All these results form a pattern of the transfers of energy according to two possible chains ending with *Lates niloticus* (fig. 7). Starting with 100 calories provided by the algae, *L. niloticus* accumulates 1. 7 in the case of two intermediary links and 5.2 in the case of a single link (S. galilaeus). This pattern also shows that the global energy output of the fish population of the archipelago, formed mainly of zooplankton-feeders, must be considerably higher than that of the populations of the open waters where terminal consumers dominate (Lauzanne, 1976).

4. CONCLUSIONS

Due to the variety of its biotopes and to the important number of species present, Lake Chad is a complex and heterogenous environment. The south basin, submitted to the action of the flood waters of the Chari is richer in fluviatile species and may be considered to be an extension of the river system, in comparison with the north basin, more stable but poorer in the number of species, yet which constitutes the real lacustrine environment, strictly speaking (Carmouze *et al.*, 1972).

Moreover, because of the average shallow depths, Lake Chad is an unstable ecosystem, the surface of wich may vary from one to four times within a few years, according to the amount of rainfall over the whole basin. These oscillations in the level do not appear to have any well-defined periodicity and they result in considerable changes in the environment and the communities. Thus, following a rapid drop in the level occurring after 1972, the north basin driep up and the macrophytes overran a greater part of the south basin, the lake being reduced to the eastern open waters. Obviously the biomasses of organisms and the productivity of the different groups were greatly affected by these modifications. The results obtained however during the so-called "Normal Chad Period", i.e. for a water level between 281 and 282 m, may be considered representative of the average state of the lake.

Lake Chad as a whole, because of its low average depth and its well-oxygenated water, may be assimilated to a vast littoral zone. Consequently the macrophytes develop considerably, producing a very large biomass, and the benthic fauna is well-developped. With its average 37 kg/ha (dry weight) Lake Chad is indeed one of the richest lakes from the benthic fauna point of view. For comparison's sake, the mean benthic biomass is only 7.4 kg/ha (dry weight) in Lake George, another shallow African lake (Burgis *et al.*,1973). It must be emphasized that molluscs largely dominate in the benthos of Lake Chad and this phenomenon was already observed in Lake Léré (Dejoux, Lauzanne et Lévêque, 1971), as in other lakes of the Sudan.

The mean zooplankton biomass of 6.8 kg/ha is very close to that observed in Lake George (8.3 kg/ha dry weight) by Burgis *et al.*, (1973). It should be noted that variations in this biomass are relatively unimportant during the year, whereas in lakes of temperate regions, the zooplankton biomass can reach much higher values during the summer period, but decreases to a lower level during a large part of the year.

It has not been possible to determine the biomasse of fish in Lake Chad. Fisheries production however has been estimated at about 100 kg/ha (fresh weight) which should correspond to a biomass 2 to 3 times higher at least.

		Mean annual biomasses and productions (kg/ha dry weight)	energy equivalents Kcal / m^2	Total biomasses and productions (tons dry weight)
Incident energy			201.5×10^4	
Phytoplankton	B	3.4	1	6,200
	P	(1800) (1)	(540) (1)	3.2×10^6
Macrophytes	B or P	(11000)	(4730) (2)	(20×10^6)
Zooplankton	B	6.8	3.8 (3)	12,200
	P	474	265	860,000
Benthos	B	37	15.3	71,000
	P	(180)	(90)	(350,000)
Fish	B or P	(250 F.W.)	(37.5) (4)	(450,000) F.W.

Table 4 - Lake Chad : biomasses, productions, and energy budget. (1): gross primary production= 550 gC/m^2/year; net primary production is assumed to be 10 % of gross production, and 1 gC= 3.3 g dry weight (2): 4300 cal / g dry weight (3) : 5600 cal / g dry weight (4) : 1500 cal / g fresh weight. N.B. fresh weight is used for fish.

Incident energy at the level of the lake is 2 308 joules/cm^2/day, or 210.5 x 10^4 Kcal/m^2/year. Measurements of phytoplanktonic primary production have allowed an estimation of the photosynthetic yield to be made at about 0.25% of the incident energy (annual mean). Gross production is thus around 5,400 Kcal/m^2/year, and net production is roughly 10% of gross phytoplankton production. Production of macrophytes is in the same order of magnitude than gross phytoplankton production, but net production is much higher for macrophytes.

The zooplankton production of 265 Kcal/m^2/year corresponds to 5% of the gross production of phytoplankton or 0.013% of the incident energy. As for the benthic production, it as been determined at 90 Kcal/m^2/year, i.e. 0,0045% of the incident energy. Lastly, fish production is roughly 0,002% of the incident energy.

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Proceedings of the international scientific workshop on

Ecosystem Dynamics in Freshwater Wetlands and Shallow Water Bodies

Volume 1

USSR,
Minsk-Pinsk-Tskhaltoubo,
July 12–26 1981

Centre of International Projects GKNT

Moscow 1982