V

17. The lacustrine ecosystem during the 'Normal Chad' period and the drying phase

Jean-Pierre Carmouze, Jean-René Durand and Christian Lévêque

Between 1964 and 1978, multidisciplinary research was carried out on Lake Chad, a shallow endhorheic lake which is particularly sensitive to variations in water supply. From 1964 to 1971, its area did not change much, in spite of a significant lowering of water level. It was during this period called 'Normal Chad' that most of the quantitative studies were carried out. Here we will draw up a general balance of physical, chemical and biological characteristics of the environment in an attempt to understand its functioning, especially the hydrochemistry and the balance of energy and matter.

Due to decreased floods, the area of the lake was considerably reduced after 1972, involving at first the separation of the two basins, then the partition of the south basin and the drying up of the north basin in 1975. Over the course of this period, there was considerable transformation of the lacustrine environment and communities and we will try to draw up a general scheme of these changes.

It is obvious that considerable gaps exist in our knowledge of the functioning of the ecosystem. This is especially true for all bacterial activity (decomposition, mineralization, production, and role in the trophic systems) which almost certainly play a major role but cannot be quantified. However, the diversity of data collected and especially the length of the period of observations make the studies on Lake Chad almost unique for tropical Africa. The only ecosystem investigated in a similar way was Lake George, Uganda, studied between 1966 and 1972, as part of the International Biological Programme thus allowing a comparison of two shallow lakes, one equatorial and one tropical. It would also have been interesting to make an analogous comparison for the drought period but the study on Lake Chilwa, which had a similar dry phase did not give sufficient quantitative results for that period.

17.1 'Normal Chad': aspects of its functioning

17.1.1 *The environment*

17.1.1.1 *The recent quaternary lakes and the present topography.* The Chad basin extends over 250 000 km^2 between 5° and 25° N and 7° and 25° E. The

J.-P. Carmouze et al. (eds.) Lake Chad

ISBN 90 6193 106 1. Printed in the Netherlands

lacustrine environments of this area have been considerably modified over the recent quaternary, during which three main periods can be distinguished within the sensitivity of C_{14} measurements:

— between about 40 000 and 18 000 years BP the lake basin was occupied by much more numerous lakes than now, in which Ostracod shells and diatoms were deposited. Some eolian layers in these deposits indicate that the lakes were subjected to temporary drying periods;
— between 18 000 and 13 000 years BP the lakes disappeared and the region was altered considerably by wind. The southern limit of the desert zone moved 500 km towards the equator;
— from 13 000 years BP the depressions of the basin were occupied by several lakes that were maintained for more than ten thousand years. However the existence of eolian sands and of layers with dessication cracks between the lacustrine series prove that these lakes also encountered several periods of drought.

The present endorheic lake occupies a 25 000 km^2 basin between 12° and 14° 20′ N and 13° and 15° 20′ E. During the 'Normal Chad' period (water level higher than 280 m) the area of water varied between 15 000 and 21 500 km^2.

The lake is divided into two basins of fairly equal area and of shallow mean depth: 3 to 5 m for the north basin; 0.75 to 2.75 m for the south basin. Each of these basins is subdivided into three main regions that correspond to three habitat types: the open water; the reed islands which are islands of vegetation (*Cyperus papyrus* and *Phragmites*) colonizing shallows; the archipelagoes whose islands correspond to emergent crests of an immersed erg. The two basins are connected by a vast zone of reed islands called the 'Great Barrier'.

17.1.1.2 *The climate.* Situated in the intertropical convergence zone, the lake is subjected to a Sahelian type of climate. The dry winds from the northeast (harmattan) blow from October to April, while the humid winds from the southwest occur between May and September. The winds blow especially between 06 and 12 a.m. and the speed is on average greater than 5m/s for 6 hours per day.

The rainy season begins in May–June and ends in October with 50% of the precipitation occurring in August. The mean annual rainfall increases from the north to the south of the lake, from 150 to 250 mm. Annual variability is high.

The mean annual air temperature is 28°C while the monthly average varies from 29° to 32°C between March and October and from 22° to 24°C between December and February. The minimum diurnal differences occur in August (7° to 9°C) and maxima in January (16° to 17°C):

On the edge of the lake, at Bol, the humidity of the air reaches a maximum in August (72 to 81%) and a minimum in February–March (23 to 31%). The evaporation is considerable, between 2.05 and 2.20 m/year.

The mean annual total incident radiation is 2310×10^4 joules $m^{-2} \cdot day^{-1}$

with a minimum of 2140×10^4 in January and a maximum of 2580×10^4 in March. The seasonal variations are thus low. The mean insolation is about 280 hours a month.

17.1.1.3 *The fluvial system and the hydrological regulation of the lake.* From the hydrological and biological point of view (fishes in particular), the lacustrine environment essentially depends on the fluvial system. The hydrographic system consists mainly of the Shari and the Logone which flows into the Shari near N'Djamena, 250 km from the lake. These two rivers have a tropical regime characterized by an annual flood (September to December) and a well-marked period of low water (from March to June). Due to these seasonal variations 40 to 50% of the flow occur during the four months of the flood. At this time some of the water leave the river bed to flood vast flat plains. The floodplain of North Cameroon (or Yaéré) (5000 km^2) is fed by the overflowing of the left bank of the Logone in September–October and the waters recede from December to February, drained by the El Beid which flows northwards into the south of the lake. The overflows of the right bank of the Logone give rise to the 'Grand Courant' which contributes to the flooding of a large plain between the Logone and the Shari.

The fluvial water (between 20 and 50×10^9 m^3 with a mean of 40×10^9 m^3) represents 86–87% of the total supply to the lake; the rest comes from rain. These supplies are counterbalanced by losses of 92% due to evaporation and 8% by seepage losses. The volume of the lake is maintained at a low level between 40 and 85×10^9 m^3. The annual turnover of the lake water is very important with an average of 2/3 being renewed each year. Because of this rapid turnover time the lake does not efficiently absorb the irregularities of annual supplies.

Water movements are under the influence of the wind regime and fluvial water supplies. At the end of the low water in June, the monsoon winds favour a general displacement of the southern waters towards the north and movement begins in the north basin at the level of the northeastern part of the 'Great Barrier'. In August this is accentuated by a push from the waters of the Shari flood which then begins. The lake receives 50% of its fluvial supplies in October and November, when the harmattan begins, displacing the overflowing zone towards the south of the 'Great Barrier'. At the maximum of the flood the waters then penetrate into the north basin along the southeast coast and drive back all the residual water in the direction of the Northeastern Archipelago and Reed Islands. The flood waters also begin to invade the reed islands and the archipelago in the south basin. From the end of January there is no longer a flow of water into the north basin and the last supplies of the Shari that spread out in the south basin involve a general displacement of water towards the periphery. From April to June, there is no notable water circulation.

17.1.1.4 *The physical characteristics of the waters.* The mean annual temperature ranges between 25.5° and 27.5°C. During the cold season (December to February) the water temperature varies from 17° to 21°C whereas in the warm season (May–June) it is generally over 30°C. The average diurnal difference is about 2°C. A thermal stratification can develop over the day during rare periods when the wind does not blow. Thus Lake Chad is a tropical polymictic lake.

The oxygen distribution is homogenous over the water column in the early morning when the concentration approached saturation. There is an increase of surface oxygen tension over the course of the day (120% saturation) and a diurnal stratification appears during calm periods.

Transparency varies according to the season, the region of the lake and the water level. At the 282 m level, in the open waters of the south basin, it is maximal in December–January (1 m) and minimal in August (20 cm) when the Shari flood waters arrive loaded with silt. However, in the archipelago of the south basin the seasonal variations are less marked. In the entire north basin the transparencies range between 60 and 90 cm.

17.1.1.5 *The chemical characteristics of the waters and salinity regulation.* Lake Chad waters are fresh, but their salinity changes, according to the regions considered. The salinity of the Shari water that enters the lake is about 60–65 mg l^{-1} (or about 50 µS cm^{-1}). The relative importance of the different elements is 48.4% HCO_3, 6.3% Ca, 2.95% Mg, 4.6% Na, 2.86% K and 34.8% SiO_4H_4. Salinity increases with distance from the delta: the open waters of the south basin are 1.2 to 1.5 times more concentrated than those of the Shari while those of the archipelago in the north basin are 10 to 20 times higher. On average, the waters of the north basin (625 mg l^{-1}) are four times more saline than those of the south basin, which are themselves two and a half times more saline than those of the Shari. The chemical composition changes with the concentration: HCO_3 and Na become predominant at the expense of SiO_4H_4, Ca and Mg and their relative importance in the north basin is 61.4% HCO_3, 7% Ca, 3.8% Mg; 9.9% Na, 4.5% K and 5.25% SiO_4H_4. Seasonal variations are more accentuated in the regions close to the Shari delta than in the archipelago.

The pH of the river water varied from 7 to 8; in the lake, the pH does not exceed 8 in the south basin, and 8.9 in the north basin.

These results show that Lake Chad is not a basin of high salt concentration as might be assumed, *a priori*, from both its lack of surface outlet and the fact that it is subjected to strong evaporation. With an average conductivity of 450 µS, it falls in the middle of the list of major African lakes classified according to increasing conductivity (Talling and Talling 1965; Symoens 1968). It is on an average more saline than Lake Victoria, George, Malawi and less than Lakes Tanganyika, Albert, Kivu and Turkana.

Moreover, the salinity of the water during the 'Normal Chad' period changes only slightly from one year to another. So, between the severe 1972 recession and the large flood of 1957, the average salinity decreased by 30%. By comparison, the salinity of Lake Chilwa can triple from year to year (Kalk 1979).

These apparent contradictions result from several factors which combine to maintain the dissolved salt stocks proportionally close to those of the water volume.

(a) The low salinity of the water is maintained by three factors:

— the low salinity of the river water (50–60 mg l^{-1}) is half the mean salinity of the lake water;

— climato-geographical regulation results from a combination of water transfer factors (river supplies, rain, evaporation, seepage) to give an 11-fold concentration of the river water which is not very high for a closed lake in an arid zone. This is because seepage losses are relatively important (7.5% of the total annual water losses);

— considerable biogeochemical sedimentation of SiO_4H_4, Ca, Na, HCo_3/CO_3, and, to a lesser degree, K^+ occurs in the lake itself. This geochemical precipitation comes from the neoformation of smectites and the precipitation of calcite. The clayey neoformations are favoured by a relatively high concentration of dissolved silica from the river waters (20 mg l^{-1}) and by some supplies of solids rich in iron and aluminium hydroxides. SiO_4H_4, Ca and Mg are sedimented. The precipitation of calcite is favoured by the fact that the anions are only represented by HCO_3^- and CO_3^{--}; saturation is thus quickly reached and calcite forms in some environments of relatively low salinity (700–900 mg l^{-1}). Biochemical sedimentation, mainly due to molluscs and macrophytes, mainly involves Ca, HCO_3, Mg and K.

All these processes of chemical sedimentation lead to a 45% decrease from the value that the salinity would reach by climato-geographical regulation only. Given that the different elements are sedimented to different degrees, the chemical composition of the water evolves towards sodium-bicarbonate facies (cf. Chapter 4).

(b) The attenuation of temporal fluctuations in salinity

At the time of the flood, the volume of the lake increases more quickly than the salt stocks in all the salt concentration basins. This causes a decrease of the water while during its recession the inverse happens. Usually these effects are poorly dampened in a shallow lake. In Lake Chad, however, salinity fluctuations are attenuated by two principal mechanisms. The first results from the morphology of the south basin as the erg bordering it from the southeast to the southwest favours the isolation of ponds which rapidly dry up when the water subside. This results in important losses of salty waters in the marginal zones. Thus at recession, the lowering of salt stocks is accelerated and the increase of salinity is diminished in proportion. The increase of salinity during the fall in water level from 1967 to 1972 was attenuated by 18%, due to this mechanism.

In contrast, during a flood, some of the salts deposited during the preceding dry phase are partially redissolved. The difference between the increase in salt stocks and that of water volume is reduced and thus the decrease of the water's salinity is attenuated.

The second mechanism concerns the rate of biogeochemical sedimentation. It tends to increase during flood subsidence and to decrease during a flood. In both cases this mechanism attenuates the difference between the change of the lake volume and the salinity. The increase in salinity was reduced by 15% during the contraction of 1967–1972 due to this mechanism.

The combination of these two mechanisms dampens variations in salinity very efficiently:

— during the contraction of 1967–1972, the average salinity of the waters was 67% of the value which would have been obtained without these two mechanisms;

— during the expansion period from 1945 to 1957, the salinity only reached 50% of the value expected without these mechanisms.

It should finally be noted that 60% of the salts deposited in the marginal zones are dissolved when water returns. In other words, each flood-recession cycle involves a definite loss of dissolved salts. This appears to be a supplementary means of elimination of salts supplied by the rivers which contributes to the maintenance of a low mean salinity.

17.1.1.6 *Sedimentology*. Four main types of sediment are found:

— mud, the most abundant sediment in the lake is a structureless material generally present in a fine and homogenous suspension. The water content is 2.5 to 5 times the dry weight which includes a significant organic fraction (10 to 15%) with a mean C and N content of 20 and 8% respectively. Peat is frequently found at the edge of vegetation fringes where decomposing organic matter is very abundant;

— clay can be in a soft and structureless, a more or less structured, or in a granular form. Its water content varies between 40 and 130% of dry weight and its organic fraction does not exceed 5%. This sediment is well represented in the open waters and to a lesser extent in the archipelago where it occupies an average of 30% of the bottom surface;

— the pseudo-sands are granules, from 0.2 to 0.3 mm mean diameter, composed of goethite and nontronite. They are especially abundant in the open waters adjacent to the Shari delta.

— part of the sand comes from the flooded erg of the north (0.25 mm size, quartz) and another part from fluvial supplies (micaceous sand of small size: 0.16 mm). The latter are mainly localized in the coastal zone adjacent to the delta.

17.1.2 *The organisms*

17.1.2.1 *The phytoplankton.* More than 1000 species and taxa were identified in Lake Chad where the algal flora was dominated qualitatively by the Desmids and the Diatoms whereas the Cyanophycea played a very important role quantitatively (30 to 50% of algal biovolume in 1971–1972).

During the 'Normal Chad' period four regions were distinguished which were characterized by the dominance of species or groups of species:

- the open waters of the north where the Desmids (*Closterium aciculare*) were predominant for the major part of the year; *Pediastrum, Botryococcus* and *Microcystis* were abundant while the diatom *Melosira granulata* were absent;
- the northeastern archipelago where Cyanophycea (*Anabaena* and *Microcystis*) were dominant but *Closterium, Pediastrum* and *Botryococcus* were still abundant. In the open waters of the south and the southeast, which are under the influence of the Shari flood, the diatoms *Melosira granulata* and *Surirella muelleri* make up the bulk of the phytoplankton;
- the eastern and southeastern archipelago where the Cyanophycea, *Microcystis* and *Anabaena* were abundant and occasionally *Surirella, Pediastrum* and *Melosira.*

The highest densities were observed in the archipelagoes (1.4 to 2 $\mu l\ l^{-1}$) and they were much lower in the open waters of the south and the southeast (0.03 to 0.22 $\mu l\ l^{-1}$). The total biomass was estimated at 40 800 tons fresh weight for the lake in 1971, or 6200 tons dry weight if a conversion factor of 15% is used. From the primary production measurements made over several years in the eastern archipelago, a model was established to estimate the hourly production around midday (Lemoalle 1973). The mean gross daily production in this region was 4.2 g $O_2\ m^{-2}\ day^{-1}$ or 550 g $Cm^{-2}\ year^{-1}$. It was a little lower in the southern open waters and a little higher in the north basin.

17.1.2.2 *The macrophytes.* Twelve plant associations were really important in Lake Chad where the aquatic plants occupied about 2400 km^2 during the period of 'Normal Chad'. *Vossia cuspidata* which was very abundant in the Shari delta as well as *Cyperus papyrus* in the south basin disappeared progressively towards the north, as a function of salinity, whereas *Typha australis* appeared. *Phragmites australis* was well represented everywhere and there was also much submerged vegetation containing *Potamogeton, Ceratophyllum, Vallisneria, Utricularia* and *Nymphea.* The biomass of the aerial parts was estimated, in dry weight at 31 t ha^{-1} for *Phragmites*, 28 t ha^{-1} for *Cyperus papyrus*, 17.5 t ha^{-1} for *Vossia* and 15.5 t ha^{-1} for *Typha.* The total biomass for the entire lake was calculated at 7.2×10^6 t for the aerial parts of these four species and at 13×10^6 t (also dry weight) for the roots.

The annual production of macrophytes was not studied, but it was certainly important and probably roughly similar to the biomass of the aerial parts.

17.1.2.3 *The zooplankton*. The population of planktonic crustacea in Lake Chad was fairly rich as 8 species of Cladocera and 4 species of Copepods were well represented. In comparison only four species were abundant in Lake Chilwa (Kalk 1979), Lake Turkana (Ferguson 1975) and Lake Naivasha (Litterick et al. 1974) and two in Lake George (Burgis 1974). There were also several Rotifer species (Pourriot 1968) but they only represented a small percentage of the zooplankton biomass.

There is a seasonal fluctuation in the density of organisms which is strongly influenced by the Shari flood, in the open waters of the south basin (Gras et al. 1967). In the zones that are well protected from the influence of the flood, the minimum density is also observed during the cold season and a maximum in April–May.

There were no notable variations in the zooplankton population structure over the lake as a whole. Nevertheless, three major ecological zones can be distinguished during the period or 'Normal Chad' based on the density of organisms and the seasonal cycle of abundance. The open waters of the south and the southeast were the poorest (95 ind. l^{-1}, 110 g m^{-3}) and the quantitative variations there, were very high over the course of the year. In the archipelago and the reed islands of the southern basin, the seasonal variations were very reduced and the density was higher (318 ind. l^{-1}; 333 mg m^{-3}). Finally, in the northern basin where the seasonal variations were also low, the density was intermediate (224 ind. l^{-1}, 216 mg m^{-3}).

The total biomass of zooplankton crustacea was estimated at 12 200 tons, dry weight, during 1971 or an average of 0.81 g m^{-2}. This biomass was unevenly distributed: 0.9 g m^{-2} in the northern basin which had 60% of the stock, 0.7 g m^{-2} in the eastern archipelago and 0.25 g m^{-2} in the eastern and southeastern open waters.

The duration of development of the embryonic stages, determined *in vitro* ranged between 1 and 1.5 days at 30°C, and 1.4 and 2 days at 25°C, for both the Cladocera and the Copepoda. The post embryonic development was more rapid in Cladocera. Juvenile development varied between 1.2 and 2.3 days at 30°C in *Moina micrura, Diaphanosma excisum* and *Ceriodaphnia cornuta* and between 2.9 and 4.4 days in *Bosmina longirostris* and the three species of *Daphnia*. In the Copepods, juvenile development at 30°C lasted about 6 days in the Cyclopoids, 11 days in *Thermodiaptomus galebi* and 18 to 25 days in *Tropodiaptomus incognitus*.

The annual P/B ratio of the major species was determined over the course of a year of observations in the eastern archipelago. On average it was 23 for the Calanoids, 63 for the Cyclopoids and 113 for the Cladocera (191 for *Moina*, 151 for *Diaphanosoma*, 151 for *Ceriodaphnia* and 72 to 76 for *Daphnia* and *Bosmina*). The annual production was estimated at about 860 000 tons in 1971 (47 g m^{-2} dry weight, or 260 kcal m^{-2}).

17.1.2.4 *The zoobenthos.* The benthic fauna was essentially composed of three groups of invertebrates: oligochaetes and molluscs, represented by a small number of species, and many species of insect larvae.

The distribution of the oligochaetes and the molluscs depended especially on the nature of the sediment although the chemical composition of the water could have had an influence on the distribution of some species. The insects appear to be less sensitive to these ecological factors but they had, like the oligochaetes, a seasonal cycle of abundance with a maximum during the cold season and a minimum at the end of the warm season.

The benthic biomass expressed as dry weight (shell not included for the molluscs) was estimated at 71 000 tons for the entire lake in 1970, or 3.7 g m^{-2} on the average. Molluscs represented the bulk of the biomass, over 90% or 3.3 g m^{-2} on the average. They were particularly represented by three species of Prosobranchs: *Melania tuberculata* numerically dominant in the northern basin, *Cleopatra bulimoides*, abundant in the southern basin and *Bellamya unicolor* which represented 40% of the benthic biomass. The molluscs were particularly abundant in the open waters and the archipelago of the northern basin as well as near the 'Great Barrier' where the biomass was between 4.8 and 7.2 g m^{-2}. They were rare in the northern and the eastern part of the lake where the biomass was respectively 0.02 and 1.1 g m^{-2}.

The Oligochaetes were essentially represented by the Tubificids (*Aulodrilus remex* and *Euilodrilus* sp.) in the north basin, whereas the Alluroididae (*Alluroides tanganyikae*) were dominant in the open waters of the south and the southeast. Their average biomass of 0.3 g m^{-2} generally varied between 0.1 and 0.2 g m^{-2} except in the open waters of the north where they reached 0.8 g m^{-2}. Finally, the insects were relatively poorly represented in the benthic biomass with a mean of 0.1 g m^{-2}.

Only the production of benthic molluscs has been studied over the course of a seasonal cycle in different biotopes and different regions of the lake (Lévêque 1973). The mean annual $P/\bar{B}$ ratio was estimated at 5.8 for *Bellamya unicolor*; 4.4 for *Melania tuberculata*; 2.6 for *Cleopatra bulimoides* and *Corbicula africana*; 2 for *Caelatura aegyptiaca*. The annual production was 279 000 tons of dry organic matter in 1967–1970 or 14.5 g m^{-2} year or 58 Kcal m^{-2} year on average. The Prosobranchs and more particularly *Bellamya* were responsible for the major part of this production. The shell production was about 100 g m^{-2} year.

The biomass of worms and benthic insects was low but the corresponding production was probably quite significant. In fact, biological cycles in the tropics are short and the more short-lived the organisms, the higher their P/B ratios (Lévêque et àl. 1976). In these conditions, a production of about 5 g m^{-2} year for these two groups is a likely value and the total benthic production was probably close to 20 g m^{-2} year or 85 Kcal m^{-2} $year^{-1}$.

17.1.2.5 *The fish.* Among the one hundred and forty species of fish identified by Blache (1964) in the Chad basin, one hundred and twenty were observed in Lake Chad and the lower reaches of its tributaries. Most of these species also occur in the basins of the Nile and/or the Niger. There is no endemism with the exception of *Alestes dageti* which is found only in Lake Chad.

The lacustrine species are represented in the fluvial system but many fluvial species are not found in the lake. The fluvial system is actually the permanent environment from which the recolonization of the lacustrine environment starts following the periodic drying of the latter.

The distribution of these species in the lake depended on both the distance from the fluvial system and on the type of habitat (open water, archipelago, reed islands ...). There were fewer species in the north basin than in the south basin, several of these disappeared north of the line from Baga Sola to Malamfatori probably because of the increase in salinity of the water. This was particularly so in the case of the Mormyridae and *Schilbe uranoscopus.*

The archipelago zones of the south basin were characterized by the abundance of *Alestes baremoze* and *A. dentex*, Cichlidae and *Heterotis niloticus.* These species were rare or absent in the open waters where some small planktivorous fish serving as food for the predators (*Hydrocynus, Lates*, etc. ...) are found. The largest number of species were found in the southern border of the lake and the delta region because of the proximity of the fluvial system. In particular, the presence of *Ichtyoborus besse, Siluranodon auritus* and *Polypterus senegalus* was noted as they are fluvial species which were absent from the rest of the lake.

In the rivers as in the lake, the seasonal variations in catches related to species abundance proved the importance of migration, which were of two main types: longitudinal spawning migrations and lateral migrations linked mostly in searching for food. Taking into account their possible migratory behaviour and knowledge of their distribution, it was possible to differentiate several species groups from those whose distribution was widespread, to those which were only found in particular environments or circumstances. Four species appeared to be really ubiquitous: *Lates niloticus, Labeo senegalensis, Distichodus rostratus*, and *Hemisynodontis membranaceus*. Some other apparently ubiquitous species are only found in permanent environments: *Micralestes acutidens, Hydrocynus forskalii, Eutropius niloticus. Alestes dageti* only frequented the lake whereas some species, such as *Alestes nurse, Ichtyborus besse*, were caught only in the rivers and their temporary annexes. Several species were restricted to the flooded zones and to their more permanent surrounding: *Clarias* sp., *Synodontis nigrita, Brienomyrus niger, Ctenopoma* spp. The extreme and well-known example of the dipnoid, *Protopterus annectens*, should also be mentioned. It was very common in all the zones of temporary flooding along with *Nothobranchus*, whose very short cycle includes the laying of long-lived eggs, which was generally caught in isolated temporary ponds.

The relative abundance estimated using gill nets showed that the mean catches over the course of an annual cycle were much lower in the south basin than in the north basin. The open waters of the south basin were also much poorer than the archipelago where some direct biomass estimates were made. The use of ichthyotoxins gave mean biomass figures of about 500 kg ha^{-1} with a range of 110 to 820 kg ha^{-1}.

The beach seine fishing gave much lower values of about 90 to 100 kg ha^{-1}. This was essentially due to differences between the environments sampled as the coastal coves were richer than the open waters of the archipelago, and also to the beach seining itself which must have involved a certain underestimation of biomasses.

Some similar sampling was also carried out in the rivers where clear differences were again found for similar reasons. The average biomasses obtained with beach seines in the Shari upstream of the confluence with the Logone, was near 120 kg ha^{-1} whereas by poison fishing in a secondary arm of the river in the same region the mean figure for biomass was about 2400 kg ha^{-1}.

The characteristically diverse traditional fishing techniques, the dominance of river fishing over lake fishing and the very moderate level of exploitation before 1960, were totally modified after 1963. This was due to the introduction of nylon gill nets which resulted in a decrease in the importance of traditional techniques, a very rapid increase of fishing effort, and an increase of fishing in the lake. Most of the catches (80 to 90%) were made with large mesh nets (80 to 120 mm). Before the contraction of the lake, the fishing was most developed in the north basin and concentrated on *Lates niloticus, Heterotis niloticus, Citharinus* spp., *Distichodus rostratus, Labeo* spp., *Gymnarchus niloticus* and *Hemisynodontis membranaceus.*

The catch per unit effort decreased considerably from about 15 kg 100 m^{-2} $night^{-1}$ in 1963 to 1.5 in 1967–1969 and 1.0 in 1971 whereas the total catches increased from 30 000 tons in 1963, to 46 800 tons in 1970, and 86 300 tons in 1971. Fishing effort thus multiplied by about 40 between 1963 and 1971.

The stock of *Alestes baremoze*, a fluvio-lacustrine migratory species was studied most intensively (Durand 1978). Total catches of this species were estimated at 6360 tons in 1969, 8280 tons in 1970 and 4970 tons in 1971. Exploitation was almost exclusively fluvial during this period with lacustrine catches not exceeding 5%. In a 'Greater Lake Chad' the optimal mean catches could reach 9000 to 11 000 tons depending on fluvial or fluvio-lacustrine exploitation.

Some active traditional fishing still occurred during recession of the river at the outlets of floodplains, the most important being that on the El Beid which connects the North Cameroon floodplains to Lake Chad, where about 1200 tons of fish, almost exclusively a few months old, were caught. This corresponds to a yield of 4 kg ha^{-1} for all the flooded zones.

The total catches before the drying period were estimated at 60 000 tons in

1969, 65 000 tons in 1970 and 115 000 in 1971 for the fluvio-lacustrine environment. Although the lake had then been exploited more than previously, there was apparently no overexploitation. In 1972, the fishing rose to 165 000 tons or 104 kg ha^{-1} $year^{-1}$. Some similar values (100 to 130 kg ha^{-1} $year^{-1}$) were found from 1974 to 1977 in the south basin which by then represented the only lacustrine environment.

From these observations, the mean sustainable yield could be about 90 kg ha^{-1} or 180 000 tons from a large Lake Chad with an area of 20 000 km^2.

17.1.2.6 *Trophic relations*

Planktonic Crustacea. The principal Cladoceran species fed on unicellular or colonial planktonic algae whose size is between 4 μ and 30 μ. However they did not usually consume the Cyanophycean, *Anabaena flos-aquae* which represented a major part of the phytoplankton. This species was however important in the diet of *Tropodiaptomus incognitus* and of *Thermocyclops neglectus* but irregularly, depending on the abundance and the state of the colonies.

Fishes. From the study of their stomach contents (Lauzanne 1976), the principal fish species could be classified into major consumer groups according to their trophic level. If the first level was represented by primary food sources (algae and detritus), three other levels could be recognized.

The second was formed by the primary consumers, includes the phytoplankton filter-feeders (*Sarotherodon galilaeus*), detritivores which fed on the bottom organic film made up mostly of sedimental algae (*Labeo senegalensis, L. coubie, Distichodus rostratus, Citharinus citharus* and *C. distichodoides*) and phytophages which consume higher plants (*Alestes macrolepidotus*).

The third level includes the secondary consumers among which were the strict zooplanktivores (*Alestes baremoze* and *Hemisynodontis membranaceus*), predominantly zooplanktophagous species (*Brachysynodontis batensoda* and *Alestes dentex*). Several benthophagous species also belonged to this category which exclusively or essentially fed on benthic invertebrates: *Synodontis schall, S. clarias, Hyperopisus bebe* and *Heterotis niloticus.*

The fourth level is made up of top consumers; some were strictly ichthyophagous (*Lates niloticus, Hydrocynus brevis*), whereas others had a more varied diet of fish, shrimp or insect larvae (*Schilbe uranoscopus, Eutropius niloticus, Bagrus bayad, Hydrocynus forskalii*).

Food was abundant and varied in Lake Chad. The adult fish belonged to a well-determined trophic level but their diet was subject to slight modifications according to habitat and season. The benthophagous species of the open waters of the south basin seemed to have a simplified diet in comparison to those of the archipelago due to the absence or scarcity of food sources such as shrimps, insect larvae or macrophytes in the open waters. Conversely the benthic feeders of the open waters consumed molluscs in greater abundance than those of the archipelago where molluscs were not so common.

Some changes of trophic level were observed during the period of growth. Thus most of the terminal consumers (level 4) were initially secondary consumers (level 3) during their young stage.

The trophic relations between fishes of level two and three were relatively direct and most of the food consumed by the fish of a given level came from the immediately lower level, forming a food chain. The problem was more complex for the less-strictly ichthyophagous terminal consumers whose food came from all trophic levels and even from some sources outside the aquatic ecosystem (terrestrial insects).

The importance of different consumer groups was variable according to the region of the lake. In the eastern archipelago mostly planktophagous and especially zooplanktophagous species were found, representing 44% of the ichthyomass. In the eastern open waters the terminal consumers dominated (64% of the biomass) due to the decreased importance of terrestrial insects and the abundance of small zooplankton feeders such as *Micralestes acutidens* and *Pollimyrus isidori* which appeared to have a high production. The benthophagous species do not represent a significant biomass and did not appear to play a role in the nutrition of terminal consumers in the archipelago or in the open waters.

The conversion rate of food has been determined quantitatively for three species of fish belonging to three different trophic levels. In fresh weight or energetic equivalents these rates are respectively 3.1 and 18.9 for *Sarotherodon galilaeus* (phytoplanktophagous), 8.8 and 44.8 for *Alestes baremoze* (zooplanktophagous), and 26.4 and 27.3 for *Lates niloticus* (ichthyophagous).

17.1.3 *Matter and energy budgets*

From the various results given above many aspects of transfer and yield can be estimated for the Lake Chad ecosystem. These data will then be compared to those obtained in some other aquatic ecosystems, both tropical and temperate.

17.1.3.1 *Lake Chad.* It has long been argued whether the body of water corresponding to Lake Chad is really a lake and some authors consider that its relatively low volume, uniformly flat morphology and its endorheic character make it nothing more than an area inundated by river waters. Daget (1967) considered Lake Chad more similar to floodplains of tropical rivers than to true lakes. The absence of an endemic fauna could be an argument in favour of this hypothesis. However, this absence results from the frequent drying of the lake and its recolonization which is carried out by some organisms sheltered in the lower reaches of rivers and the few permanent waters of the south basin.

In view of recent research this hypothesis must now be modified because the main characteristic of these zones is a very marked seasonal rhythm of flooding and drying, and also because some clearly lacustrine characters appear in the north basin of Lake Chad during the period called 'Normal Chad'. This north basin which is deeper and partially sheltered from the Shari flood, represents a much more stable environment than the south basin which can be considered as a transitional environment where the fluvial influences impose marked seasonal rhythms.

This distinction between the south and north basin is also evident in their populations since the two basins are ecologically different. In fact the zonation is more complex because it varied according to the taxonomic group considered, and their ecological requirements. However, taking into account the lacustrine habitats (open waters and archipelagoes), it is possible to consider only four major, relatively homogenous, areas on the basis of biomass and production. The corresponding data expressed in kg per hectare for biomasses and in kg ha^{-1} $year^{-1}$ for production are presented in Table 1.

The phytoplankton biomasses were particularly low in the open waters of the south basin and about 70 times more important in the archipelagoes of the north basin; the archipelagoes of the south basin and the open waters of the north basin are at an intermediate level. Primary production is only known through the values for the southeastern archipelago; thus 550 g C m^{-2} $year^{-1}$

Table 1 Biomass (kg ha^{-1}, dry weight) and productions (kg ha^{-1} $year^{-1}$) in the four main natural regions of Lake Chad.

		South basin		North basin	
		Open water	Archipelago	Open water	Archipelago
Phytoplankton					
	$\bar{B}$	0.09	4.13	3.84	7.28
Gross	P.P.		18 000		
Macrophytes					
	$\bar{B}$	←	11 000		→
	P	←	?		→
Zooplankton					
Copepods		2.5	6.9	8.9	
Cladocera	$\bar{B}$				
Copepods		159	438	732	
Cladocera	P				
Benthos					
Molluscs	$\bar{B}$	25.8	10.6	64.2	33.6
Worms	$\bar{B}$	2.0	0.8	8.0	1.8
Insects	$\bar{B}$	0.1	0.6	2.1	1.8
Molluscs	P	77	30	353	136

corresponds to an approximate value of 1800 kg ha^{-1} (net production) of phytoplankton. No regional values are available for the macrophytes but their average biomass for the entire lake is 11 000 kg ha^{-1}.

The same relative poverty of zooplankton was found for the open waters of the south basin but less marked than for the phytoplankton. The north basin as a whole is the richest environment. The high turnover rates (from 60 to 80 on the average) lead to fairly high production.

The results obtained for the principal benthic groups were more heterogenous. The open waters of the south basin were very poor in insects whereas in the entire north basin, the biomasses were 20 times greater. Molluscs and worms had equally high biomasses and production in the north basin, but in each of the two basins the biomasses of open waters were twice those of the archipelagoes. The production could only be calculated for the molluscs whose average turnover rate varies between 2 and 6.

The mean values obtained in the four main lacustrine zones were used to calculate some average values for the entire lake, taking into account the relative areas of the zones (Table 2). The energy equivalents have been calculated by taking as mean calorific values (cal g^{-1} dry weight), 3000 for the phytoplankton, 4300 for the macrophytes, 5600 for the zooplankton and 1400 (cal g^{-1} fresh weight) for the fish.

The production of macrophytes has not been measured, but Thomson (1975)

Table 2 Lake Chad: biomasses and energy budgets.

		Mean annual biomass and productions (kg ha^{-1}, dry weight)	Energy equivalents (Kcal m^{-2})	Total biomass and productions (tons, dry weight)
Incident energy			201.5×10^4	
Phytoplankton	B	3.4	1	6200
	P	(1800)[a]	(540)[a]	3.2×10^6
Macrophytes	B or P	(11 000)	(4730)[b]	(20×10^6)
Zooplankton	B	6.8	3.8[c]	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)[d]	(450 000 f.w.)

[a] Gross P.P. = 550 g C m^{-2} yr^{-1}; net P.P. is assumed to be 10% of gross P.P.; 1 g C = 3.3 d. w; 3000 cal g^{-1} d.w.
[b] 4300 cal g^{-1} d.w.
[c] 5600 cal g^{-1} d.w.
[d] 1500 cal g^{-1} f.w.
N.B.: fresh weight is used for fish.

estimated the production of *Papyrus* (stems and roots) at about 100 tons of dry matter per hectare and per year in some Uganda swamps. If these results were extrapolated to other macrophytes (*Phragmites* in particular), they may represent a net production similar to the biomass, which is considerable. This net production is equivalent to the gross production of phytoplankton.

Moreover, it is probable that the production of phytoperiphyton which has not been measured, is also very important as is generally the case in shallow lakes (Wetzel 1979). The total primary productivity from all sources is thus very high in Lake Chad.*

If it is supposed that the turnover rate of the worms and the insects, which only represent 10% of the biomass, is close to that of molluscs, the benthic production is estimated to be about 2.5 times lower than the zooplankton production, although the benthic biomass is five times higher than the biomass of planktonic crustaceans. This is due to the fact that the planktonic organisms have much shorter generation times than the benthic organisms and thus a much higher rate of production.

We do not have an exact estimate of the biomass of fishes, but we saw (in Chapter 13) that the mean sustained yield must be about 100 kg ha^{-1} $year^{-1}$ and it can reasonably be supposed that the biomass must be between 200 and 300 kg ha^{-1}.**

The only data available on fish production concern the common zooplanktophagous species *Alestes baremoze* for which the P/B ratio is close to 1 with a mean longevity of about 5 years. By supposing that this value is reasonable the biological production would be approximately equal to the biomass of the fish or about 450 000 tons per year for the entire, the energetic equivalent of which is 37.5 kcal m^{-2} $year^{-1}$.

The incoming solar energy measured at N'Djamena is 201.5×10^4 Kcal m^{-2} $year^{-1}$ and the total transfer of energy in the lake would therefore be as follows: gross phytoplankton production represented 0.25% of the solar energy and the macrophyte production would be of the same order of magnitude. The zooplankton production corresponded to only 0.013% and benthic production to 0.0045%. Finally the production of all the fish can be calculated at 0.002% of the total incident energy.

The relative importance of plant and animal production can also be compared. By supposing that the entire primary production (phytoplankton, macrophytes and phytoperiphyton) is about 6000 Kcal m^{-2} $year^{-1}$, secondary production represents 6.5% and the fish production 0.6% of this value.

* Bacterial activity, has not been studied but it must probably be very important in Lake Chad, given the abundance of plant detritus and decomposition. We do not know the role of these organisms in the remineralization of nutritive elements.

** Some close links exist between rivers and the lake for several species of fish which make seasonal spawning migrations. The values used here are for the entire fisheries (lake and lower reaches of rivers) but the lacustrine part is by far more predominant.

Finally, the ichthyological production represents about 10% of the secondary production.

We will see later a comparison of these values with results obtained from other lakes. It is nevertheless evident that Lake Chad is a rich ecosystem primarily due to certain factors favourable to a high productivity.

The shallow depth initially allows the development of a vast littoral zone colonized by several emergent or submerged macrophytes. In Lake Chilwa, Howard-Williams and Lenton (1975) showed the fundamental role played by this littoral zone in the functioning and regulation of shallow lakes. It provides some specific habitats for plants and animals, contributes greatly to autotrophic production and constitutes an important source of food and detritus for the deeper zones. The shallow depth also allows good oxygenation of the bottom water favouring the development of fairly dense benthic populations and the aerobic decomposition of organic detritus. Conversely the stirring of water by wind disturbs the sediment below shallow water and fine particles are resuspended decreasing transparency and thus the euphotic layer. In addition, disturbance of the sediment is unfavourable to the maintenance of a rich benthic fauna.

The high solar energy input in the tropics and its lack of seasonal variation compared with higher latitudes are also surely favourable to autotrophic production. But the role of salinity regulation must also be noted. Its effects are such that the spatio-temporal variations of salinity and ionic composition do not induce fundamental modifications of the communities. It is, however, impossible to know if a much higher salinity would have only negative effects. It is probable that, as the type of changes noted in the north basin of the lake would suggest, as long as concentrations were not too high, there would be a decrease in population diversity by selection of well-adapted species, and an increase in biomass and production of those remaining.

In conclusion, let us recall that one of the reasons for expecting a high productivity should be *a priori*, the stability of the lacustrine ecosystem and this depends on its hydrological regulation. This is not, however, the case in Lake Chad as the normal lacustrine volume is only twice the average yearly fluvial supplies which is highly variable.

17.1.3.2 *Comparison with other lacustrine ecosystems*

(a) *Lake George*. Among the African tropical lakes, Lake George is the only one which has been studied in detail during the I.B.P.. The main results are given in Table 3 (after Burgis 1978).

Both Lake Chad and Lake George are shallow lakes with very low mean depth. Due to their location global incident radiation is high and of the same order of magnitude although slightly lower at Lake George, because of greater cloudiness. However they differ in several ways. Firstly Lake Chad is of the endorheic type and its area 80 times greater than that of Lake George which has

Table 3 Comparison of characteristics and productivity of some tropical (Lake Chad and Lake George) and temperate lakes.

Lakes	Latitude	Altitude a.s.l. (m)	area (km²)	Z̄ (m)	Solar energy Kcal m⁻² yr⁻¹ (× 10⁴)	Gross P.P. Kcal m⁻² yr⁻¹	Zooplankton Kcal m⁻² yr⁻¹		Zoobenthos Kcal m⁻² yr⁻¹		
							B̄	P	B̄	P	
George	0	913	250	2.4	172	19 710	5.2	200	3.3		Burgis (1978)
Chad	12–14	282	20 000	4.0	201.5	5040	3.8	265	15.3	90	this study
Findley	47		0.1	7.8		25	1	5	3	7	Wissmar and Wetzel (1978)
Mirror	43		0.15	5.8		380	3	21	9	30	
Marion	49	300	0.1	2.4		50	2			34	
Lawrence	42		0.05	12.0		430					
Wingra	43	97	1.4	2.4		4300	20	230	2	22	
Kiev (reservoir)	50	103	992	4.0		3590	8.1	206	44.1	156.6	Gak (1972)
Baikal	51–55	455	31 500	730	105.6	875	9.4	88.6			Moskalenko (1972)
Naroch	54		80	9.0		1975	4.0	75	5.5	13.0	Winberg et al. (1972)
Myastro	54		13.1	5.4		2260	10.1	161	0.9	4.0	
Batorin	54		6.2	3.0		2329	10.0	192	2.7	12.9	
Mikolajskie	54		4.6	11.0		4140		430		120	Kajak et al (1972)
Taltowisko	54		3.3	14.0		4370		400		200	
Sniardwy	54		109.7	5.9		3300		110		50	
Flosek	54		0.04	3.0		2200		470		0.5	
Warniak	54		0.4	1.2		1600		—		140	
Esrom	56		17.3	12.3		2440		100		103	Jonasson (1972, 1977, 1979)
Loch Leven	56	107	13.3	3.9	93	6000 to 9000		100	95	386	Morgan (1974)
Rybinsk (reservoir)	59	102	4300	5.4		650	1.6	78	3.3	12.8	Winberg (1972)
Krasnoe	66		9	6.6		1570	5	111	4.6	19.4	
Pääjärvi	61	78	13.4	14				55.0		19.2	Sarvala (1978)
Øvre Heimdalsvatn	61	1090	0.8	4.7	94.9	(110)		11.0		12.2	Larsson (1978)
Red Lake	64		9.1	6.6		1093	5.7	98.3	4.8	20.4	Andronikova (1972)
Myvatn	65	277	37	2	79	1180		40		160	Jonasson (1979)
Krivoe	66		0.5	12.0		160	1.2	12.5	1.7	2.2	Alimov et al. (1972) and Winberg (1972)
Krugloe	65		0.1	2.1		55	0.8	10	2.7	5.2	

an outlet. But the most important is the climatic difference as the seasonal variations of different climatic factors are very muted in Lake George due to its location under the equator (Burgis et al. 1973). This results in an exceptionally constant physico-chemical environment for an aquatic ecosystem (Greenwood 1976; Burgis 1978), which is evidently not the case in Lake Chad where considerable differences are observed from one season to another such as the variation in water temperature from 18°C during the cold season to 32°C during the warm season. Populations were relatively stable over the course of the year in Lake George whereas some marked seasonal variations were observed in Lake Chad.

One of the major characteristics of Lake George was the importance of phytoplankton in the biomasses and in the trophic cycles of aquatic organisms. Composed mainly of Cyanophacea (80%), the phytoplankton represented an average biomass of 300 Kcal m^{-2} and they made up 98% of the planktonic biomass and 90% of the total biomass exluding the macrophytes. In Lake Chad the phytoplankton biomass was considerably lower (0.34 g m^{-2} in dry weight or about 1 Kcal m^{-2}) and only represented about 30% in dry weight or 20% in calories of the plankton biomass. This low proportion of phytoplankton in the plankton biomass is remarkable. The difference between the algal biomass (from 1 to 300) was not reflected in the values of primary production since the ratio of gross primary production between Lake George and Lake Chad was only about 4. Thus, it may be deduced that algal population cycles were much more rapid in Lake Chad and that turnover rates eighty times higher on an average, reduced the tremendous gap between the two lakes biomasses.

The zooplankton biomass was of the same order of magnitude in the two lakes: 3.8 Kcal m^{-2} in Lake Chad, 5.2 in Lake George (of which 3.7 is for planktonic Crustacea and 1.5 for *Chaoborus*). But only one Copepod species (*Thermocyclops hyalinus*) is dominant in the latter whereas seven species of Cladocera and Copepods are well represented in the zooplankton populations of Lake Chad.

The benthos of Lake George was poor (about 3 Kcal m^{-2}) probably due to the very high fluidity of the mud which was the most common sediment and which was not a good substrate for the establishment and maintenance of benthic species especially molluscs. The latter represent by contrast most of the benthic biomass of Lake Chad estimated at an average of 15.3 Kcal m^{-2}.

The predominance of phytoplankton in the total biomass of Lake George was reflected in the composition of fish populations. They were dominated by some herbivorous species that are able to use the Cyanophycea. Thus two species (*Sarotherodon niloticus* and *Haplochromis nigripinnis*) which represented 60% of the ichthyomass fed directly on the phytoplankton. However, in Lake Chad secondary (mostly zooplanktophagous and benthophagous) or terminal (ichthyophagous) consumers were dominant in the biomass.

Thus there were some fundamental differences between the two lakes although they both are tropical and shallow. In Lake George, the environmental conditions as well as the populations and the productivity of the ecosystem were stable over the course of the year. The phytoplankton biomass was high but the production relatively low and the animal biomass was dominated by a few essentially herbivorous species. The trophic cycles are thus short, but it appears that the efficiencies are low (Burgis 1978).

In Lake Chad, however, the ecological factors showed some annual and yearly variations that were sometimes considerable. The phytoplankton biomass was fairly low but the production relatively high. The fauna was more diverse and several species were well represented in the herbivorous zooplankton. The trophic chains to fish were generally longer with a high proportion of secondary consumers and ichthyophagous species. These trophic structures explain that although it is very productive, Lake Chad has average fish yields lower than Lake George: 100 to 120 kg ha^{-1} year^{-1} instead of 140 kg ha^{-1} year^{-1} (Burgis and Dunn 1978).

(b) *Middle and high latitude lakes.* We compared the observations made on Lake Chad to some data collected in other lakes and reservoirs belonging to various regions of the earth, mostly located in temperate zones (Table 3).

In 1973, Brylinski and Mann compiled data gathered from 55 lakes and reservoirs for the International Biological Program. The analysis of these results show that the amount of solar energy available appears to have a greater influence on production, on a global scale, than the amount of available nutrients. The latitude, which integrates the duration of light, the temperature of the air, the duration of the growing season etc. appears to explain a large part of the statistical variability. On the other hand, when comparing the same latitudes, the quantity of available nutrients has a very considerable influence.

In reality the most productive lakes must be those for which the vegetative period is the longest, thus allowing the development and maintenance of a diversified population of primary producers. This duration of vegetative period increases from arctic zones where it is reduced to some months, towards the tropics. The ultimate state is exemplified by Lake George located on the equator where the environmental conditions are relatively constant throughout the year. Lake Chad is at 14°N, and there is a well-marked seasonal cycle with a cold season from November to February during which a notable slackening is observed.

The influence of latitude between the extremes of arctic and tropical lakes is clearly seen in the data in Table 3, but some very diverse values are found for temperate lakes. Thus Loch Leven which receives half of the incident energy, has a gross primary phytoplankton productivity approaching that of Lake Chad. Some Polish lakes also have a gross primary productivity approaching that of Lake Chad (Kajak et al. 1972).

The zooplankton biomass was not particularly high in Lake Chad (6.8 kg ha^{-1}) in dry weight or 3.8 Kcal m^{-2}) but the production was fairly high although it stayed lower than that observed in some temperate Polish lakes. The P/$\bar{B}$ ratios calculated (annual mean of 65 for the zooplankton) are, however, much higher than those which have been observed until now and have been reviewed by Waters (1977). These high P/$\bar{B}$ values are probably partially related to the fact that the growing period and thus the production, last throughout the year in Lake Chad. The mean benthic biomass of 37 kg ha^{-1} is fairly high but not exceptional since some very high values have been observed in several temperate lakes (Larsson 1973; Jonasson 1972). In most cases, however, the high biomasses are due to some Chironomid larvae, whereas, in Lake Chad, the molluscs are largely dominant. The benthic production estimated at 180 kg ha^{-1} $year^{-1}$ of dry weight (90 Kcal m^{-2} $year^{-1}$) is also among the mean values of several temperate lakes having higher production (Table 3, and Waters 1977). However, as for the zooplankton, the P/$\bar{B}$ ratios of Lake Chad molluscs are fairly high and it is probably the same for the insects and the Chironomids, in particular, whose life cycles are often shorter than one month.

Terminal production cannot be estimated through the average fishing yield of 100 to 120 kg ha^{-1} but it is an index of a high productivity. This is all the more true as, unlike Lake George, it is not dominated by short food chains and phytoplankton-feeding species. The zooplanktophagous and ichthyophagous species have a particularly important place. The high terminal production could be explained by the average or high productivity at all trophic levels and by a major diversification of terminal consumers, which use most of the available trophic resources.

In conclusion, if Lake Chad does not appear as an exceptionally rich lake in each of its major biological components, it appears that it is an example of a system where most of the classic trophic levels (phytoplankton, macrophytes, zooplankton, benthos and fish) are very well represented. The organic degradation of plants and animals and the rapid recycling of nutrients is probably one of the main explanations of the richness of this lacustrine ecosystem. Due to the diversity of trophic pathways and species composition it shows a remarkable plasticity which allows it to adapt to environmental changes and to maintain a high productivity.

17.2 Modification of Lake Chad during a period of drought (1972–1978)

In all the preceding chapters, we have only considered two major periods offering the greatest contrast by calling one 'Normal Chad', from 1965 to 1972 and the other a drying state or 'Lesser Chad', from 1972–1973.

The end of this last period cannot be ascertained because it continues in 1981, and may still continue for several years. Comparisons between the two periods explain the changes in the ecosystem but we should not forget that it did not remain stable and unvarying between 1965 and 1972. The water level progressively dropped more than two meters, involving a decrease to nearly half of the original volume. This evolution, though gradual had consequences for the populations and we must take it into account in order to understand the evolution of the ecosystem during this period of drought.

17.2.1 *Hydrology and environment*

17.2.1.1 *The hydrological evolution.* The habitats of the lake were completely transformed at the time of the exceptionally low floods of the Shari in 1972/1973 (17×10^9 m^3 against 40×10^9 m^3 on the average). In April 1973 the 'Great Barrier' dried up and from this period the south and north basins had completely different hydrological regimes.

The drying of the whole lake worsened with the Shari flood of 1973–1974 which was nearly as low as that of the preceding year (18.4×10^9 m^3). However, it did allow reflooding of a large part of the south basin which had been divided in April–May 1973 by the drying out of the southeastern reed islands. Nevertheless this region was dried out again in May 1974. As the Shari waters hardly crossed the 'Great Barrier', the north basin continued to dry and from July 1973 to July 1974, the water level fell by 0.90 m, leading to the appearance of shallows in the open waters of the North.

During 1974–1975, the Shari flood was much higher (30.5×10^9 m^3) though still far from the median flood volume. The height of the water level at Bol, by the end of 1974, was close to that registered at the end of 1971.

Following this period, the south basin had a 'new average situation' close to that of 'Normal Chad', that is, without a hydrological break between the open waters and the archipelago at low water period. However, this new situation differed from the preceding one by the more marked seasonal fluctuations in water level and the presence of more abundant vegetation. Unlike the south basin, the north basin was no longer fed normally. The development of a thick plant cover at the 'Great Barrier' during the very low water period of 1974 was an obstacle to the passage of flood waters. The inundated areas were very rapidly reduced to no more than a few ponds in the center of the basin by May 1975, but these ponds dried up completely by October.

The 1975–76 flood which was close to the median flood with 36.6×10^9 m^3 caused a clear rise in water level in the south basin and the variations of the water level at Bol were close to those registered in 1971–72. In spite of this, the vegetation of the 'Great Barrier' again restricted penetration of flood waters into the north basin and the latter was only partially reflooded in the south but dried rapidly before the flood receded. During 1976–77 and 1977–78 the Shari floods were low, sufficient to maintain the new hydrological situation of the south basin, but insufficient for a permanent reflooding of the north basin, even in the south.

On the whole, two periods can be distinguished over the course of this severe drought. The first began at the end of 1972 during a flood that was insufficient to feed the north basin and whose most spectacular consequence was the separation of the two basins in May 1973. It ended with the complete drying of the north basin at the end of 1975. The following period corresponded to a 'Lesser Chad' limited to the south basin and receiving a fluvial water supply sufficient to maintain it in a situation close to that characteristic of 'Normal Chad'. This is the present situation.

17.2.1.2 *Evolution of the physical and chemical characteristics of the water.* A slow evolution of the abiotic characteristics of the environment was accelerated, from 1973. Three regions of the lake were isolated and evolved differently: the open waters of the south basin, the region of the southeast archipelago and the north basin.

(a) The drying period

The open waters of the south were the least modified because they receive the Shari waters. However from the 1973 low water to the flood at the end of 1973 this environment had considerable seasonal modifications in that its area and its volume almost doubled (2500 $km^2 - 1200\ km^2$ and $7.5 \times 10^9\ m^3 - 4.5 \times 10^9 m^3$). The mean annual salinity increased only slightly (10%) but the seasonal differences were more pronounced than during the period of 'Normal Chad' in that salinity varied from 45 to 110 mg l^{-1} against 45 to 70 mg l^{-1} during 'Normal Chad'. A similar seasonal variation was registered in 1974 but with less amplitude.

From April–May 1973 the archipelago of the south basin was isolated from the open waters. Deprived of supplies the habitat was rapidly subdivided and some ponds isolated. The salinity of the water increased rapidly reaching values that were four times higher (530 mg l^{-1}) five months later. Moreover, the development of vegetation modified the relative composition of this salinity by reducing the percentage of potassium and dissolved silica; pH values stayed between 6.9 and 8.2. In some bays and channels that were well sheltered from the wind by the presence of macrophytes newly developed during the decrease in water level, a stratification was established as the water warmed up in February–March and it was maintained until the arrival of the flood in September. During this period, these areas behaved as warm monomictic lakes. Under these conditions oxygen levels fell and during the cold season the oxygen content at the surface was 12% of saturation during the day, but was more variable during the warm season (between 5 and 60%). The hypolimnion generally stayed anoxic. In 1974–75 similar seasonal variations were registered.

The north basin was cut off from the south basin in April–May 1973 and became progressively dried out. During this period which was complete in

September–October 1975, the transparency of the water rapidly decreased to reach very low Secchi disc values of about 10 cm; its oxygen content was very variable and marked by some frequent periods of anoxia; and the salinity tripled from mid-1973 to the beginning of 1974, going from 1000 to 3000 mg l^{-1} (or from 1200 to 3700 μS cm^{-1}). This is a low value for waters on the way to drying up and it can partly be explained by an increase in chemical sedimentation (the salinity would be about 4000 mg l^{-1} without it) and probably by communication with the open water and the diluting effect of the underlying aquifer. The waters became very alkaline, and the pH increased to 9.2. The 1974–75 flood fed only a very small area of the north basin next to the 'Great Barrier', and transformed it into a marsh. As the flood waters spread the transparency of the water rose to 30–60 cm, the anoxia temporarily disappeared and the salinity again fell to a normal value. A few months later this region dried up once more as the drying process was repeated.

(b) The 'Lesser Lake Chad'

During the 1974–75 flood the open water of the south basin returned to normal conditions. The hydrochemical characteristics again became close to those of 'Normal Chad' with the mean salinity equal to 70 mg l^{-1} (against 60 mg l^{-1} for 'Normal Chad'). On the other hand, the seasonal variation was more pronounced with the maximum salinity in June equal to 110 mg l^{-1} against 75 mg l^{-1} during a normal period and the minimum salinity in September equal to 43 mg l^{-1} against 47 mg l^{-1}.

In the archipelago of the south basin the characteristics of the water were also close to those of the 'Normal Chad' period but with more severe seasonal fluctuations mostly due to the vegetation which remained abundant.

17.2.2 *The populations*

The analysis of changes in the animal and plant populations was very uneven. During the first period (1972–75) the information gathered was relatively complete since it includes some observations on the phytoplankton, macrophytes and fish for the entire drying period and for the beginning of this period on molluscs, insects and zooplankton. On the other hand, the beginning of a 'Lesser Lake Chad' can be described only through some partial data on the macrophytes and some fairly rich data on the fish populations and stocks.

17.2.2.1 *The populations during the drying period (1972–1975).* The drying period extends from 1972 to mid-1975 for the north basin of the lake and led to its total drying up. It ceased towards the end of 1974 in the south basin which was by then reduced to 1500 km^2 of open water and some areas of water in the archipelago, when the river flooded in November 1974. The collection of data was particularly difficult during the drying phase since the low water level and the development of plants often made communications impossible.

(a) The macrophytes

The evolution of the vegetation was characterized by a general increase in the south basin and showed various degrees of development depending on the species. The most spectacular development was that of *Aeschynomene* (*A. elaphroxylon* very dominant). The 'Ambatch' were true forests which invaded zones on the way to drying; prairies of *Vossia cuspidata*, formerly fairly localized, where found in all regions of open water and reed islands of the south basin. In contrast, *Typha australis* decreased in area.

In the north basin, the vegetation could not have a comparable development because of the very rapid retreat of the water. But plant formations that were formerly present returned and were accentuated by the grazing of herds. Only some small plants of *Aeschynomene elaphroxylon* and some stands of *Typha australis* were noted.

(b) The phytoplankton

In the Southeastern Open Water the plankton evolved towards a fluvial type increasingly marked by a high index of diversity, higher densities and some considerable differences between low water and flood periods. A considerable development of Euglenoids was noted at low water. The phytoplankton composition remained the same (with the exception of *Synedra berolinensis*, a diatom absent, or rare until then) and this region was, as a whole, the least modified during the drying period.

In the archipelago of the south basin, isolation led to some areas of water that were cut off or only temporarily linked to each other. The phytoplankton biomasses were, in general, much higher than before (7 to 8 mg l^{-1}) and decreased rapidly with the arrival of the flood water, filtering through the vegetation barrier of reed islands. This group of ponds became a marsh in which the Euglenophytes predominated while the Cyanophytes were less prevalent.

In the north basin, as in other regions of the south basin, the period preceding its isolation showed a clear increase in algal biomasses. Soon after it became isolated, biovolume increased considerably: 179 $\mu l\ l^{-1}$ in November 1974 corresponding to 1658 mg of chlorophyll *a* in the central basin. After dilution by some temporary water supplies, the amount of chlorophyll reached 3600 mg m^{-3} before the completion of drying. Some species characteristic of saline lakes of Kanem (Iltis 1974) appeared at the end of 1974 and in 1975, and the population was almost entirely composed of Chlorophycea and Diatoms with the latter predominating. At the end of this period the remaining water bodies in the north basin became more like saline ponds with a marked concentration of dissolved salts (3–5 g l^{-1}) and a high pH (9.1 to 9.5).

(c) The benthos

The observations on the benthic molluscs were mostly made before the drying period, from 1967 to 1972, in the south basin of the lake. In the archipelago, there was a general decrease of the number of abundant species. First, *Melania tuberculata* became dominant everywhere except on the mud substrate but the molluscs became generally scarce throughout the archipelago after 1972. In the open water the data obtained in 1972 showed a clear decrease in density of molluscs on the blue clay whereas the population of the pseudo-sand had not changed since 1968.

The aquatic insect populations also showed some evidence of pronounced evolution. In the Southeastern Archipelago the dominant species changed and above all there was a clear decrease in the number of species collected between 1965 and 1974. The species that were abundant and characteristic of the northern lake in 1970 (*Cryptochironomus stilifer* and *Tanytarsus nigrocinctus*) became dominant in 1972 and 1974 in the archipelago of the south basins and in 1974 *T. nigrocinctus* became equally abundant in the Shari delta.

It is likely that the main factor controlling the benthic populations is the partial resuspension of superficial layer of loose sediments. This resuspension is itself linked to the decrease in water level since it makes the water close to the substrate more and more sensitive to disturbance, thus creating environmental conditions that are unfavourable to the development of molluscs (very loose substrates). This effect had probably occurred early in the slow process of lake level decrease between 1967 and 1970. This hypothesis is corroborated by the contrasting stability of populations on the pseudo-sand substrates which include very few fine particles. This explanation is probably also valid for the oligochaetes and the insects, with the latter having the additional advantage of considerable powers of dispersion (either active or passive) which must also be a factor in the very rapid evolution of their populations.

(d) The zooplankton

The evolution of the zooplankton populations can be followed mostly in the southeastern archipelago. Until 1972, their general characteristics stayed the same with the total biomass about 300 mg m^{-3} and a diverse population dominated by copedods. In 1972, the first signs of change were noted with a decrease in density of *Bosmina* and a considerable increase of *Thermodiaptomus* and of littoral Cladocera. In 1973 the changes were still more noticeable with the reduction in Cladocera to *Moina* and *Diaphanosoma* only, increasing dominance of *Thermocyclops neglectus* and spectacular increase of rotifers whose densities reached 2500 to 4000 individuals per liter against 50 to 100 between 1965 and 1971. Their demographic structures also changed with a relative increase in adult biomass in spite of which the total biomass was not modified and stayed at about 300 mg m^{-3} until August 1973. The effects of the isolation of the archipelago were were then felt and biomass decreased rapidly with the disappearance of Diaptomids.

The period 1974–75 in the Southeastern Archipelago was characterized by low biomasses (55 mg m^{-3} on average), the disappearance of *Mesocyclops leuckarti* and lower abundance than expected of littoral forms. The two species of Cladocera maintained densities that they had during the high water period. The main reason for this general decrease in density was probably a more or less permanent deficit of oxygen, causing increased mortalities and/or lower reproduction.

In the open water of the south basin, during 1973 and 1974, the population seemed to retain its previous general characteristics, both of densities, which stayed in the same range, and of population diversity since seven species were well represented. Due to lack of data we cannot characterize the changes in the north basin, but the population was well diversified (9 species) and abundant (500 mg m^{-3}) at the beginning of the period. Later changes must have had some analogy with those of the Southeastern Archipelago in its isolated phase, but it must have been more strongly modified by the much higher conductivities prevailing in the north than in the south.

The factors influencing zooplankton abundance can be reduced to two: on the one hand the abundance and availability of phytoplankton for the phytoplanktophagous microcrustaceans and on the other hand the importance of the zooplanktophagous predators. The abundance of algae never seems to be a limiting factor, except seasonally in the impoverished waters, close to the Shari delta, because no correlation was found between the variation in abundance of phyto- and zooplankton. The regulation of densities therefore, must essentially be a function of the presence of abundant predators and of the important pelagic food webs. The long-term stability of densities would then be explained by their independence from predation pressure as long as the conditions for zooplankton nutrition remain favourable.

(e) The fishes

During the drying phase, three distinct processes of change can be described from experimental data. In the north basin the changes at the end of 1974 favoured three groups of species for different reasons: *Sarotherodon* suffered considerable mortality but still proliferated due to its high reproductive capacity. The survival of *S. aureus* is the most obvious as it is most resistant to lack of oxygen. The second group includes *Polypterus* species (mainly *P. senegalus*) which can supplement branchial with aerial respiration; whether they spawned or not is unknown. The third group included the Mochocidae whose importance increased although they did not reproduce, due to the concentration of the water and their better resistance to the worsening environmental conditions. In the final phase, the *Synodontis* disappeared and in the marsh the *Sarotherodon* and *Polypterus* populations were joined by *Brienomyrus niger* (which must have an accessory mode of aerial respiration, Bénech and Lek 1980) and especially *Clarias*, which dominates the biomass.

From the beginning of 1973 to the end of 1974, the Southeastern Archipelago was completely isolated and the periodic water supplies it received did not carry any fishes, since the flood waters had to cross a dense barrier vegetation of several kilometers wide. The deep water pelagic species, mainly predators and zooplanktophagous species, disappeared first. Two types of severe mass mortality occurred due to phenomena leading to hypoxic conditions: first the storms occurring during the rainy season brought about a rapid resuspension of reducing compounds; secondly the arrival of the flood waters which were very poor in oxygen and relatively acid (enrichment of dissolved free CO_2) after passing through the vegetation barrier.

Only the species with a particular resistance to hypoxia remained until the end of 1979 after the flood. These were the species possessing the possibility of aerial respiration (*Polypterus, Clarias, Brienomyrus*); they also included species with tolerance of low oxygen concentrations, such as *Distichodus rostratus, Brachsynodontis batensoda, Sarotherodon niloticus* that were checked experimentally by Bénech and Lek (1980). In total only seven species were found at the beginning of 1975.

The zone in contact with the rivers: the open water of the south basin were characterized by their permanent connection with the Shari and in 1973–74 by the appearance of a new feature of large vegetation belts which developed. Thus the rivers appeared to be a refuge for those stocks of the south basin which suffered from the changes in environmental conditions.

The observations in the delta region during 1972–73, are much more instructive however, because they reflect the evolution of the fluvio-lacustrine exchanges at the beginning of the drying period. In 1972 and 1973 there was a diminution in the catches, signifying that their migration behaviour was already disturbed and that the northern basin also acted as a temporary refuge. This quantitative decrease was accompanied by changes in the composition of the populations from which *Alestes baremoze* and *A. dentex* disappeared and previously abundant species, such as *Distichodus rostratus, Citharinus* spp. etc., were replaced by species such as *Synodontis clarias* and *S. frontosus*, etc.. These changes showed the relative weakness of the south basin stocks which were then the only ones to sustain the delta fisheries.

The changes in the aquatic environments during the drying period were accompanied by a parallel change in the total fisheries catches in the Lake Chad region. This phase corresponded to the exhaustion of stocks, especially in the north basin (cf. Fig. 3, Chapter 13). It was followed by a considerable increase in the total catches which tripled between 1970 and 1976, reaching a maximum figure of 200 000 tons.

In conclusion, the decline of the water level during the drying phase, acted on the fish populations by reducing the water volume and thus by increasing natural and fishing mortality. There was also a considerable variation in dissolved oxygen content due to various causes such as the decomposition of higher plants and the resuspension of reducing compounds. These phenomena promoted the dominance of marshy species adapted especially to hypoxia and able to survive in unstable environments.

17.2.2.2 *The 'Lesser Lake Chad' (1975–1978).* The drying phase was at its height during August–September, 1974. Half of the north basin was then dry while the south basin was greatly reduced after the very low second flood of 1973. The total water area hardly exceeded 6000 km^2 (cf. Fig. 20, Chapter 13); With the fluvial flood of 1974, the south basin was reflooded and has since remained the only permanent lacustrine environment.

In the north basin the drying was accentuated and resulted in a complete drying in October, 1975. Since then there were periodic resurgences of water during which half the southern part of the north basin was transformed into a vast marsh.

Some observations have been made during this period, on higher plants but the main point here also concerns the fishes. Data collection was very difficult in all the marsh zones, where the shallow water and the development of vegetation hampered normal movement.

(a) The macrophytes

In 1974 areas of the south basin which have been dry for one or two years were reflooded and there followed seasonal variations in water level similar to those of the lake, but with a bigger amplitude. The evolution of the vegetation can be summarized as follows:

— total disappearance of certain species such as *Ipomea aquatica, Lemma perpusilla* and two of the three species of *Aeschynomene: A. afraspera*, and *A. pfundii*;
— considerable regression of other species such as *Cyperus papyrus* and *Typha australis*;
— stabilization of the areas covered by the Ambadjs (*Aeschynomene elaphroxylon*);
— the massive appearance of *Pistia stratiotes, Nymphea lotus* and the development of *Vossia cuspidata.*

At the end of 1976 two species dominate the aquatic vegetation of the south basin: *Aeschynomene elaphroxylon* and *Vossia cuspidata.*

In the north basin, existing local vegetation disappeared during the drying and the young shoots were heavily grazed. Two species were still common just before the drying: *Typha australis* and *Aeschynomene elaphroxylon* (heavily grazed small plants). These two species were found after 1975 in the south and *Typha* in the depressions that functioned as temporary ponds.

(b) The fishes

The gross changes in the vegetation of the north basin were followed by aerial observations, but this was hardly possible for fish populations. One can only say that these marshy zones are not similar to the classical flooded zones, because the populations there are very specific. They are dominated by *Clarias* and secondarily by *Protopterus*, a well-adapted species, as well as individuals of various other species, depending on the years and the quantity of excess water from the south basin. From the fishery statistics of 1976 and 1977 it seems that the productivity of these temporary environments was very high.

The fish populations of the permanent environments (south basin and rivers) between 1976 and 1978 are much better known. The species richness of the south basin increased after a minimum following the flood of 1974, without reaching the 1973 level: 20 species at the end of 1975 instead of 34. The seasonal water level variations were lower than during the drying phase, although still greater than those observed at the establishment of 'Normal Chad'. The higher mean levels prevented the resuspension of the sediment fraction during storms, eliminating one of the causes of oxygen shortage. However, the other cause of anoxia remained with the arrival of the hypoxic flood waters. There was however still a periodic reappearance of species sensitive to the shortage of oxygen, that must have come with the rising water from the nearby open water through the partially degraded vegetation. These recolonizations were noted for *Schilbe*, *Siluranodon* ... and some pelagic species such as *Alestes baremoze* and *A. dentex*.

The establishment of a new fish community with increasing diversity (the Shannon index went from 0.92 in 1975 to 1.89 in 1977) was seen in the open water of the south basin between 1975 and 1977. This new lake population was analyzed from data covering a complete annual cycle (1976–1977) obtained on the delta. From this, three trends appear:

- species abundant before the drying whose stocks did not recover or did so very slowly, in the context of 'Lesser Chad': e.g. *Citharinus* spp., *A. baremoze* and *A. dentex*;
- initially rare species which became abundant such as *Schilbe uranoscopus, Distichodus brevipinnis, Gymnarchus niloticus, Brienomyrus niger*;
- species that were as abundant before as after the drying whether through rapid recovery of their stocks, e.g. *Synodontis schall, Hydrocynus forskalii* or *Eutropius niloticus*, or not having had any clear decline, e.g. *Brachysynodontis batensoda.*

These modifications of population composition and the relative importance of the principal species depended on complex interspecific competition. Here, fundamental biological characters such as reproductive behaviour, fecundity, feeding adaptability as well as the size of the stock to survive the drying etc., played a major role. The seasonal fisheries for juveniles in the El Beid, followed from 1974 to 1978, showed the variability of recruitment after 1973 with an apparently anarchic succession of abundant species such as *Sarotherodon* niloticus in 1974–75, *Marcusenius cyprinoides* in 1975–76, etc. However the species diversity increased slowly and the relative abundance seems to have stabilized progressively.

During the establishment phase of the 'Lesser Chad', fishing activities were kept at a high level and the total catches remained above 100 000 tons from 1975 to 1977. The composition of the catches changed noticeably but the yield per hectare remained high from 100 to 120 kg ha^{-1}. This indicates that the new ecosystem stabilized around 'Lesser Chad' also included conditions favourable to considerable terminal production such as normal floods causing inundation of the plains and favourable to the survival of young fry, and a permanent lacustrine environment with diverse habitats.

17.2.3 *Conclusions*

A period of high waters in 1963 was followed by one of relative stability. From 1972 the level of Lake Chad lowered rapidly, as a result of the drought and the north basin dried up in 1975. After this drying period a period called 'Lesser Chad' occurred during which only the south basin remained under water.

The drying period included some rapid changes in habitats and populations. Three major zones could be distinguished which had different fates: the north basin which dried, the eastern archipelago which underwent an initial drying before being reflooded, and the region close to the Shari delta in relation to the fluvial system, which showed some fluvio-lacustrine characteristics throughout. A considerable development of macrophytes and the appearance of marshy conditions was however observed in all these regions from time to time.

The instability of environmental conditions which characterized the drying phase generally included the disappearance of several species from the populations. However, some others developed, especially those which were well adapted to the new environmental conditions, such as marsh fish species and algal species of meso-carbonated waters. Hence due to its floral and faunal richness the ecosystem rapidly recovered and found new ways of functioning. This enables overall productivity to remain fairly high including the yields of fish.

The period of 'Lesser Chad' was characterized by a relative stability. The new lake was not however a homologue of the old one because it was clearly more limited (40% of the area) than the 'Normal Chad'. The seasonal variations were, moreover, much more marked due to the smaller volume of water and the influence of the fluvial system was therefore increased. Thus the lake was effectively a simple expansion of the fluvial system. During this period, some of the water brought in by the rivers, temporarily invade the southern part of the north basin where an abundant marsh fauna developed.

Unfortunately it was not possible to study the disturbances in the populations since the drying period in detail, but we have gathered the most spectacular aspects. This kind of ecosystem where the ecological conditions are subject to considerable variations are of particular interest because they comprise experimental natural environments which could be used for modelling attempts. Moreover, such environments are fairly abundant not only, in Sudanian Africa (southern zone of Sudan, central delta of the Niger, etc.) but also south of the equator (Lake Chilwa, delta of the Okavango, for example). Some of these are actually in danger, especially due to management projects, and knowledge of their functioning is necessary to assist all attempts at protection.

References

Alimov, A. F., Boullion, V. V., Finogenova, N. P., Ivanova, M. B., Kuzmitskaya, N. K., Nikulina, V. N., Ozeretskovskaya, N. G. and Zharova, T. V., 1972. Biological productivity of lakes Krivoe and Krugloe. In: Z. Kajak and A. Hillbricht-Ilkowska (eds.), Productivity Problems of Freshwaters, pp. 39–56, Warsaw and Krakow, Polish Scientific Publishers.

Andronikova, I. N., Drabkova, V. G., Kuzmenko, K. N., Michailova, N. F., and Stravinskaya, E. A., 1972. Biological productivity of the main communities of the Red Lake. In: Z. Kajak and A· Hillbricht-Ilkowska (eds.), Productivity Problems of Freshwaters, pp. 57–71, Warsaw and Krakow, Polish Scientific Publishers.

Bénech, V. and Lek, S., 1981. Résistance à l'hypoxie et observations écologiques pour seize espèces de poissons du Tchad. Rev. Hydrobiol. trop. 14: 153–168.

Blache, J., 1964. Les poissons du bassin du Tchad et du bassin adjacent du Mayo-Kebi. Mém. ORSTOM No. 4, 483 pp.

Brylinsky, M. and Mann, K. H., 1973. An analysis of factors governing productivity in lakes and reservoirs. Limnol. Oceanogr. 18: 1–14.

Burgis, M. J., 1974. Revised estimates for the biomass and production of zooplankton in Lake George, Uganda. Freshwat. Biol. 4: 535–541.

Burgis, M. J., 1978. Case studies of lake ecosystems at different latitude: the tropics. The Lake George ecosystem. Verh. int. Ver. Limnol. 20: 1139–1152.

Burgis, M. J., Darlington, J. E. P. C., Dunn, I. G., Ganf, G. G., Gwahaba, J. J. and McGowan, L. M., 1973. The biomass and distribution of organisms in Lake George, Uganda. Proc. r. Soc., B, 184: 271–278.

Burgis, M. and Dunn, I. G., 1978. Production in three contrasting ecosystems. In S.D. Gerking (ed.), Ecology of Freshwater Fish Production, pp. 137–158, Blackwell Scientific Publications.

Daget, J., 1967. Introduction à l'étude hydrobiologique du lac Tchad. C. R. Somm. Séanc. Soc. Biogéogr. Paris, 380: 6–10.

Durand, J. R., 1978. Biologie et dynamique des populations *d'Alestes baremoze* du lac Tchad. Trav. Doc. ORSTOM, No. 98, 332 pp.

Ferguson, A. J. D., 1975. Invertebrate production in Lake Turkana (Rudolf); Symposium on the Hydrobiology and Fisheries of Lake Turkana, 25–29th May 1975, 28 pp., mimeo.

Gak, D. Z., Gurvich, V. V., Korelyakova, I. L., Kostikova, L. E., Konstantinova, N. A., Olivari, G. A., Priimachenko, A. D., Tseeb, Y. Y., Vladimirova, K. S. and Zimbalevskaya, L. N., 1972. Productivity of aquatic organisms communities of different trophic levels in Kiev Reservoir. In Z. Kajak and A. Hillbricht-Ilkowska (eds.), Productivity Problems of Freshwaters, pp. 447–455, Warsaw and Krakow, Polish Scientific Publishers.

Gras, R., Iltis, A. and Lévêque-Duwat, S., 1967. Le plancton du Bas-Chari et de la partie Est du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 1: 25–96.

Greenwood, P. H., 1976. Lake George, Uganda. Phil. Trans. r. Soc. Lond. (B) 274: 375–391.

Howard Williams, C. and Lenton, G., 1975. The role of the littoral zone in the functioning of a shallow lake ecosystem. Freshwat. Biol. 5: 445–459.

Iltis, A., 1974. Phytoplankton des eaux natronées du Kanem (Tchad); VIII-Classification des

milieux étudiés et espèces caractéristiques. Cah. ORSTOM Sér. Hydrobiol. 8: 81–91.
Jonasson, P. M., 1972. Ecology and Production of the Profundal Benthos in Relation to Phytoplankton in Lake Esrom. Oikos, suppl. 14: 1–148.
Jonasson, P. M., 1977. Lake Esrom Research 1867–1977. Folia limnol. Scand. 17: 67–89.
Jonasson, P. M., 1979. The Lake Myvatn ecosystem, Iceland. Oikos 32: 289–305.
Kajak, Z., Hillbricht-Ilkowska, A. and Pieczynska, E., 1972. The production processes in several Polish Lakes. In: Z. Kajak and A. Hillbricht-Ilkowska (eds.), Productivity Problems of Freshwaters, pp. 129–147, Warsaw and Krakow, Polish Scientific Publishers.
Kalk, M., 1979. Zooplankton in Lake Chilwa: adaptations to changes. In M. Kalk, A. J., McLachlan and C. Howard-Williams (eds.), Lake Chilwa, studies of change in a tropical ecosystem, pp. 125–141, Monographiae Biologicae, Vol. 35, Dr. W. Junk Publishers, The Hague.
Kalk, M. and Schulten-Senden, C. M., 1977. Zooplankton in an endorheic lake (Lake Chilwa, Malawi) during drying and recovery phases. J. limnol. Soc. sth. Afr. 3: 1–7.
Larsson, G. L., 1973. A limnological study of a high mountain lake in Mount Rainier Park, Washington State, USA. Arch. Hydrobiol. 72: 10–48.
Larsson, P., Brittain, J. E., Lien, L., Lillehammer, A. and Tangen, K., 1978. The lake ecosystem of Øvre Heimdalsvatn. Holarct. Ecol. 1: 304–320.
Lauzanne, L., 1976. Régimes alimentaires et relations trophiques des poissons du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 10: 267–310.
Lemoalle, J., 1973. L'énergie lumineuse et l'activité photosynthétique du phytoplancton dans le lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 7: 95–116.
Lévêque, C., 1973a. Dynamique des peuplements, biologie et estimation de la production des mollusques benthiques du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 7: 117–147.
Lévêque, C., 1973b. Bilans énergétiques des populations naturelles de mollusques benthiques du lac Tchad. Cah. ORSTOM Sér. Hydrobiol. 7: 151–165.
Lévêque, C., Durand, J. R. and Ecoutin, J. M., 1977. Relations entre le rapport P/B et la longévité des organismes. Cah. ORSTOM Sér. Hydrobiol. 11: 17–32.
Litterick, M. R., Gaudet, J. J., Kalff, J. and Melack, J. M., 1979. The limnology of an African lake: Lake Naivasha, Kenya. Paper presented to the Workshop on African Limnology, Nairobi, December 1979, 73 pp., mimeo.
Morgan, N. C., 1974. Historical background to the International Biological Programme project at Loch Leven, Kinross. Proc. R. Soc. Edinb. (B) 74: 45–55.
Morgan, N. C. and McClusky, D. S., 1974. A summary of the Loch Leven IBP results in relation to lake management and future research. Proc. r. Soc. Edinb., 74: 407–416.
Moskalenko, B. K. and Votinsev, K. K., 1972. Biological productivity and balance of organic substance and energy in Lake Baikal. In: Z. Kajak and A. Hillbricht-Ilkowska (eds.), Productivity Problems of Freshwaters, pp. 207–226, Warsaw and Krakow, Polish Scientific Publishers.
Pourriot, R., 1968. Rotifères du lac Tchad. Bull. IFAN, A, 52: 535–543.
Rigler, F. H., 1978. Limnology in the high Artic: a case study of Char Lake. Verh. int. Ver. Limnol. 20: 127–140.
Sarvala, J., 1978. An ecological energy budget of the Lake Paajarvi. Lammi Notes 1: 12–16.
Symoens, J. J., 1968. La minéralisation des eaux naturelles. Exploration Hydrobiologique du bassin du lac Bangweolo et du Luapula, Vol. 2, fasc. 1, 199 pp.
Talling, J. F. and Talling, I. B., 1965. The chemical composition of African lake waters. Int. Rev. Ges. Hydrobiol. 50: 241–263.
Thompson, K., 1975. Productivity of *Cyperus papyrus*. In Cooper, (ed.), Photosynthesis and Productivity in Different Environments, Cambridge University Press.
Thompson, K., 1976. The primary productivity of African wetlands with particular reference to the Okavango Delta. Proc. Symp. Okavango Delta: 67–79, Botswana, Gaborone.
Waters, T. F., 1977. Secondary production in inland waters. Advances in Ecological Research 10: 91–165.

Wetzel, R. G., 1979. The role of littoral zone and detritus in lake metabolism. Arch. Hydrobiol. Beih. 13: 145–161.

Winberg, G. G., 1972. Some interim results of Soviet IBP investigations on lakes. In Z. Kajak and A. Hillbricht-Ilkowska (eds.), Productivity Problems in Freshwaters pp. 363–381, Warsaw and Krakow, Polish Scientific Publishers.

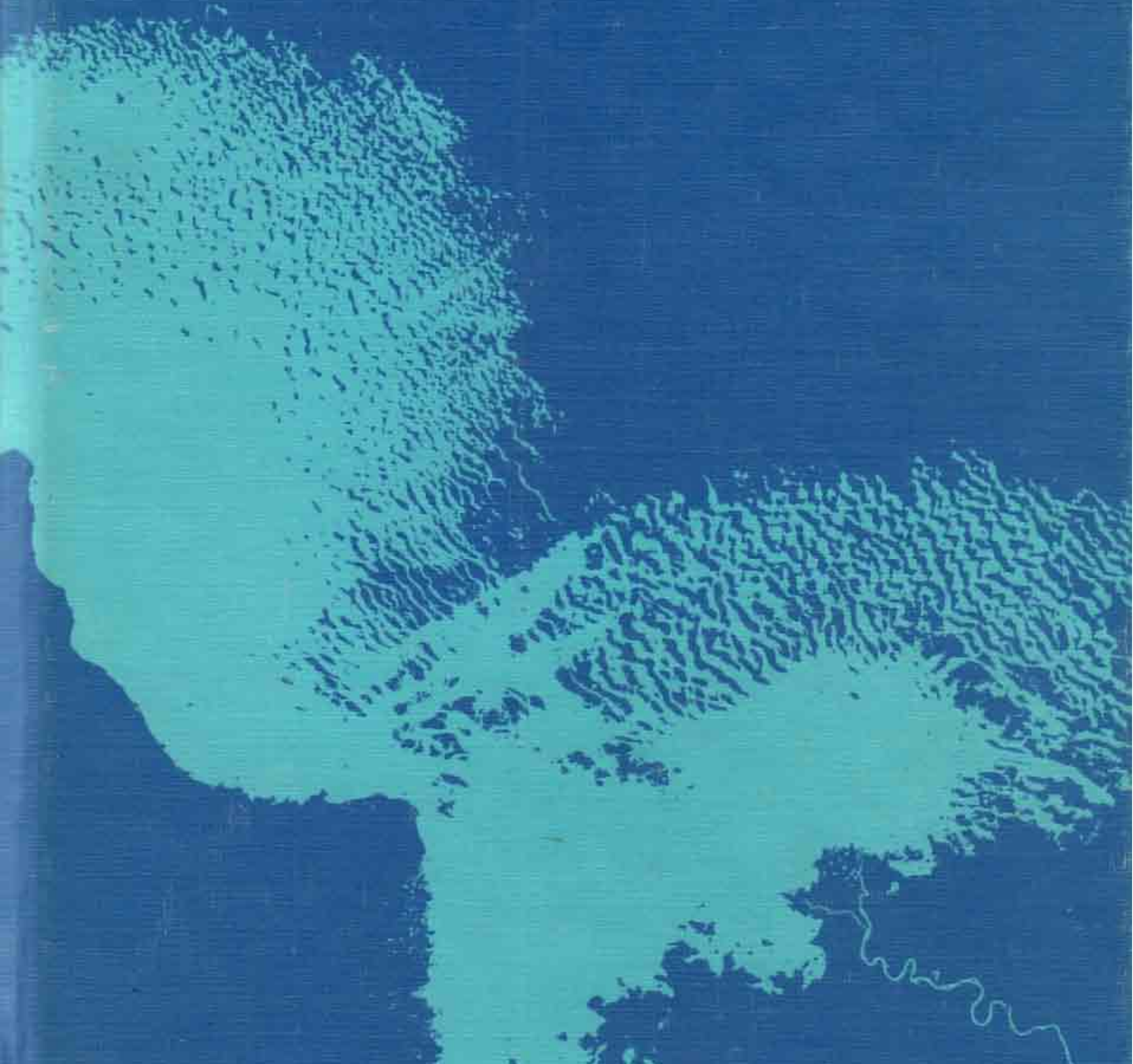
Winberg, G. G., Babitsky, V. A., Gavrilov, S. A., Gladky, G. V., Zakharenkov, I. S., Kovalevskaya, R. Z., Mikheeva, T. M., Nevyadomskaya, P. S., Ostapenya, A. P., Petrovich, P. G., Potaenko, J. S. and Yakushko, O. F., 1972. Biological productivity of different types of lakes. In Z. Kajak and A. Hillbricht-Ilkowska (eds.), Productivity Problems of Freshwaters, pp. 383–404, Warsaw and Krakow, Polish Scientific Publishers.

Wissmar, R. C. and Wetzel, R. G., 1978. Analysis of five north American lake ecosystems. VI- Consumer community structure and production. Verh. int. Ver. Limnol. 20: 587–597.

LAKE CHAD

ecology and productivity
of a shallow tropical ecosystem

edited by J.-P. Carmouze J.-R. Durand C. Lévêque



W. Junk Publishers

LAKE CHAD

Ecology and Productivity of a Shallow Tropical Ecosystem

Edited by

J.-P. CARMOUZE, J.-R. DURAND and C. LÉVÊQUE

1983 **Dr W. JUNK PUBLISHERS**
a member of the KLUWER ACADEMIC PUBLISHERS GROUP
THE HAGUE / BOSTON / LANCASTER

Distributors

for the United States and Canada: Kluwer Boston, Inc., 190 Old Derby Street, Hingham, MA 02043, USA
for all other countries: Kluwer Academic Publishers Group, Distribution Center, P.O.Box 322, 3300 AH Dordrecht, The Netherlands

Library of Congress Cataloging in Publication Data

Main entry under title:

Lake Chad.

(Monographiae biologicae ; v. 53)
Includes bibliographies and index.
1. Lake ecology--Chad, Lake. 2. Biological productivity--Chad, Lake. 3. Chad, Lake. I. Carmouze, Jean-Pierre. II. Durand, Jean René. III. Lévêque, C. IV. Series.
QP1.P37 vol.53 574s [574.5'26322'096743] 83-4288
[QH195.C46]
ISBN 90-6193-106-1

ISBN 90-6193-106-1 (this volume)

Cover design: Max Velthuijs

PRINTED IN THE NETHERLANDS