The regulation of plant and animal species and communities in African shallow lakes and wetlands

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ABSTRACT

Shallow lakes and wetlands occur throughout Africa. According to latitude, altitude, and geographical situation within a major basin or craton, they are subject to a variable number of external forces, and within each of these forces, varying intensities of stress, at different time scales (diurnal, seasonal, and pluriannual). Their plant and animal communities have had a long history of experience with such changes, and different communities have evolved adaptations to different levels of change.

Eleven physical and chemical variables of interest are listed and commented upon. The reactions of biota to change in these and combinations of them are discussed, taking Lake Chad as an example of a shallow lake subject to strong seasonal and multiannual changes, and Lake George as one where diurnal changes are more important. Various other lakes and wetlands in other parts of Africa are then compared to these two examples, and a logical classification of lakes in order of increasing environmental stress is attempted. Complete desiccation is, of course, the ultimate form of stress for an aquatic organism, although osmotic stress at high salinities and, perhaps, high acidities (rare in Africa) are more selective and impoverish communities more strongly in the long run. Adaptations of biota to desiccation are numerous and widespread, and occur commonly in algae and higher plants, but also in invertebrates and vertebrates.

The capacity for recovery of shallow lakes following a major disturbance is therefore surprisingly high, but the first colonists are usually ubiquitous, euryosmotic, eurythermous organisms; specialists are much slower to recolonise, and may often be irreversibly lost to the system. Even minor disturbances, such as these caused by man bringing changes to major watersheds (like by dam building) may cause permanent changes in community structure, in the form of species replacements. Such subtle changes may not easily be predicted, and result from slight alterations in the delicate balance of nutrient partition, interference competition, grazing, and predation within species assemblages of plants and animals. Some shallow lakes and wetlands, with a great diversity of biota, appear to be able to maintain their diversity by a maximum physical diversification, and by moderate but predictable (repeatable) change in environmental variates such as temperature and salinity, which allow for the creation of additional niche space. Such top-diverse aquatic ecosystems occur in the transition zone between the seasonal (high-latitude) and aseasonal (equatorial) climate belts of Africa, i.e. the "Sahel" zone.

KEY WORDS : Africa — Shallow lakes — Floodplains — Swamps — Plants — Animals — Environmental variables — Community structure.

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RÉSUMÉ

LA RÉGULATION DES ESPÈCES ET COMMUNAUTÉS ANIMALES ET VÉGÉTALES
DANS LES LACS PLATS ET ZONES HUMIDES D'AFRIQUE

Le continent africain est riche en lacs plats et zones humides. En fonction de leur latitude, altitude, et position géographique au sein d'un bassin majeur ou craton, ils sont influencés par un nombre variables de forces extérieures, et, pour chacune de ces forces, à de variables intensités de stress à différentes échelles de temps (diurnales, saisonnières, et pluriannuelles). Leurs peuplements animaux et végétaux ont une longue expérience de ces changements, et différentes communautés ont développé des adaptations aux différents niveaux de changements.

Onze variables chimiques et physiques sont considérées dans cet article. Les réactions des biocénoses aux variations de ces facteurs, soit isolés, soit en combinaison, sont discutées. Le lac Tchad est choisi comme un exemple d'un lac plat sujet à de profonds changements saisonniers et multiannuels, et le lac George comme exemple d'un lac où les variations diurnes sont les plus importantes. D'autres lacs et zones humides dans d'autres secteurs de l'Afrique sont ensuite comparés à ces deux exemples, et une classification sur une échelle logique en ordre croissant de stress environnemental est proposée. La dessiccation complète est la forme ultime de stress, pour un organisme aquatique, bien que le stress osmotique à des salinités élevées et, peut-être, de hautes acidités (assez rares en Afrique) soient plus sélectifs, et appauvrissent davantage les communautés à longue échéance. Les adaptations des organismes à la dessiccation sont nombreuses et variées, et sont communes, aussi bien parmi les algues et les plantes que parmi les invertébrés et les vertébrés.

La capacité de récupération des lacs plats à la suite d'une perturbation majeure est donc étonnante, mais les premiers recolonisateurs sont habituellement des espèces ubiquistes, euryosmotiques et eurythermes. Les espèces spécialisées sont plus lentes à recoloniser, et sont souvent perdues définitivement pour le système. Mais même les perturbations mineures, telles que celles causées par l'homme en changeant les régimes fluviatiles (par la construction des barrages, par exemple) peuvent causer des changements permanents dans la structure des communautés, sous la forme de remplacements d'espèces par d'autres. De telles modifications subtiles ne sont souvent pas faciles à prédire, et résultent de légères altérations dans l'équilibre délicat de la répartition des nutriments, de la compétition, du broutage et de la prédation, au sein des communautés animales et des plantes. Certains lacs plats et zones humides à grande diversité biologique semblent capables de maintenir leur diversité grâce à une grande diversification du milieu physique, et par des variations modérées mais prédictibles (à répétition régulière) des variables de l'environnement tels que la température et la salinité. Ces dernières variations en fait créent des niches supplémentaires. De tels écosystèmes aquatiques à haute diversité existent dans le Sahel, la zone de transition entre les secteurs climatiques à saisons définies (hautes latitudes) et le secteur équatorial, sans saisonnalité marquée.

MOTS CLÉS : Afrique — Lacs plats — Plaines d'inondation — Marécages — Plantes — Animaux — Variables environnementales — Structure des communautés.

INTRODUCTION

The characteristics of shallow water bodies and wetlands as habitats for plants and animals include a high surface/volume ratio, a littoral zone which covers a substantial part of the total lake area, absence of a profundal zone and, except in some saline lakes, no or a transient and unpredictable stratification. Diurnal stratification may occur regularly, however.

The structure and functioning of such systems is influenced by the geology (geomorphology and geochemistry) of their basin, and by a number of climatic variables. Many of these interact with one another, often with an additive effect, and vary with time. Altough we naturally tend to discuss the state of systems in their present form (and the short period of observations available is to be equated with the present), climatic and geological events on a time scale of hundreds to a few thousands of years have been sufficient to significantly change most of these shallow lakes. The influence of past climatic changes on a single lake closely parallel present-day differences among lakes in a different geographical (hence climatological) situation. This should be kept in mind, as it provides a clue for a classification of shallow lakes.

Given an ideal flat continent and no influence

from the oceans, the amplitude of the external variables linked to climate should approximate zero on the equator, and increase steadily away from it. The (yearly) average of such variates is also determined by latitude (and by altitude), for example mean temperature and mean irradiation. Finally, most shallow lakes and floodplains receive much water from feeder rivers, and these often undergo variations in regime that depend on precipitation in areas considerable distances away, and subject to climatic conditions different from those of the lake itself.

The principal effect of cyclical or random change in environmental variables is to modify the network of relationships that exists between the organisms, the biota, of a lake. In a Darwinian sense, environmental change entails changes in natural selection. While selection may operate in various ways, interspecies competition (including nutrient limitation) and predation are among its best documented ways.

Environmentally induced changes in these two parameters of community structure may be subtle and take a long time to become visible to an observer of the behaviour of the system.

In the case, for example, where superiority and inferiority of a competing species-pair are regularly reversed by moderate cyclic variations of its external determinant(s), a system may appear complex, yet stable, on the time scale of human observation. When environmental change takes dramatic, non-cyclic or pseudo-cyclic, pluriannual dimensions, change in living communities may turn into sudden catastrophic events. Many biota have developed ingenious adaptations against such spaced and unpredictable changes but others have not. These adaptations define the resilience of a system, its capacity for absorbing shocks without collapsing. However, there are thresholds above which permanent damage occurs, and such events have both been witnessed during recent decades, and can be derived from palaeolimnological studies of many African shallow lakes.

As, it is hoped, will gradually become clear from the following pages, the interactions between external variables and biological variables ultimately merge into a never-ending chess-game between the abiological and biological components of lake systems.

EXTERNAL DETERMINANTS AND THEIR MODE OF ACTION

Water Level Fluctuation

The hydrological balance, the algebraic sum of the water inputs and losses of a lake, has several components which vary independently of each other. Evaporation proceeds throughout the year, with peaks in the warmest months, but precipitation and flooding may be sharply delimited in time, as in monsoonal climates. As a result, all lakes in semi-arid and arid climate belts that are not directly connected to the groundwater table will decrease in surface area as soon as the rains or the floods recede. Impact of this variation will depend on the proportion of the bed that dries out and gets exposed, on the length of this exposure, and on changes in absolute depth of the remaining lake. The world's record of evaporation (7.8 m. y^{-1}) has been measured in Unianga-Kebir, Chad, where local precipitation is 20-50 mm.y^{-1} (CAPOT-REY, 1961). Only groundwater-fed, saline lakes can exist here. As one moves equatorwards, evapo - (transpi)ration decreases, and precipitation increases. Some lakes in the Zaire basin are therefore close to an equilibrium between direct precipitation on the water surface, and evaporation therefrom.

Lake Tumba, for example (COMPÈRE and SYMOENS, 1987) even has a net outflow : precipitation 1 800 mm.y^{-1}, evaporation 1 300 mm.y^{-1}. Others, like Lakes Bangweulu, Mweru Wantipa, Moero, and Upemba probably present slight deficits, and are kept at (relatively) stable levels by riverine inputs. A wealth of data of this kind about African lake systems can be found in BURGIS and SYMOENS (1987).

Where flooding is seasonal in a reasonably predictable way, the portion of the lake bed that is alternatively exposed and inundated is exploited by biota which have become finely tuned to the alternating cycle of wetting and drying. An example are the meadows of the grass *Cynodon dactylon*, which have a growth phase during exposure, and a decomposition phase during inundation. In the Pongolo floodplain lakes, it was shown by FURNESS and BREEN (1982, 1985) that the length of each period is well defined, and that the amount of material (nutrients, energy) that is gained by a lake from the inundated and decomposing meadows is a function of the length of the preceding period of exposure.

On the equator, where rainfall is, in principle, aseasonal, water level variations must be expected to be minimal. This is true in the case of Lake George (see further) but not for the lakes of the equatorial lowland forest of Zaire, where water level varies by two meters per annum (MARLIER, 1958) because of the monsoonal regime of tributaries that spring in mountains far away from the equator.

Temperature

Animal and plant metabolism is temperature-dependent. Moreover, most species are tuned to an

optimum temperature, above and below which they function less well and eventually disappear temporarily or definitively. Therefore, not only the amplitude of temperature fluctuation over the year or the day is of ecological interest, but also the absolute maxima and minima. Where fluctuations are wide (5-35 °C), succession of algae and invertebrates, each adapted to a specific part of the interval occurs over the year. In vertebrates, such temperature fluctuations may determine the onset of reproduction, spawning migration, and beginning and arrest of feeding (CARMOUZE et al., 1983). In many shallow lakes, a temperature stimulus occurs in combination with other signals, such as flooding, a change in wind speed or wind direction, etc.

Where temperature is high and almost invariant, the ectothermic inhabitants of the system will show high metabolic rates, thus high primary production, growth rates, feeding rates, etc. In such conditions, nutrient depletion (but also nutrient regeneration), interspecies competition, and predation will proceed at higher (and uninterrupted) rates than elsewhere as well.

Salinity

Salinity, for all practical purposes the sum of 4 cations and 3 or 4 anions, is a complex variable. The chemical composition of the water of a lake depends on the geological nature of its bed and of that of the area where flood waters originate. It is also a function of the hydrological cycle of the system. Closed or endorheic basins act as sinks for dissolved salts and, with time, evolve into salt lakes. If evaporation consistently exceeds precipitation and flooding, such basins may temporarily dry out. Since this is the case of so many African shallow lakes, it is no wonder that their biota have evolved numerous adaptations to the problem of periodic desiccation (see further).

There is a gradation in intensity and length of desiccation from the Guinean to the Sahel and desert zones. Desert systems are dry for most of the year and sometimes for many consecutive years; lakes in the Guinean zone dry out only at well spaced intervals or not at all, and lakes in the Sahel zones of northern and Southern Africa take an intermediate position.

Permanent desert lakes are often situated in depressions that intersect with the groundwater table, and the water that evaporates from them is continually replenished. For examples from the Sahara, see DUMONT (1987). This type of lake is invariably saline. Some of them are saturated brines, in equilibrium with their precipitate.

Even in non-endorheic, permanent lakes, salinity may fluctuate on a seasonal basis and thus provide signals for biota to emerge, go dormant, migrate, etc. Minimum and maximum values should be given as much weight as the amplitude of fluctuation.

Some lakes in the monsoonal zone have a saline regulation. This is a system which causes salinity to fluctuate less than expected from evaporation losses. CARMOUZE et al., 1983, have studied the saline regulation of Lake Chad in great detail (see further).

Because of its composite nature, salinity may be dominated by different ions. The solubility of divalent cations is limited, and therefore monovalent cations (Na^+, K^+) are normally prevalent at higher salinities. Dominant anions are either chloride or bicarbonate and carbonate. Chloride waters have slightly alkaline pH-values. Bicarbonate-carbonate waters may have pH-values as high as 11, toxic to many species found in chloride waters. Hence, the flora and fauna found in the two types of saline waters are often quite different.

Salinity acts on biota through their ability to adjust the osmotic value of their body fluids to that of the external medium. At salt concentrations above seawater, buoyancy problems also appear. At high salinities, finally, trace elements can become sufficiently concentrated to have toxic or other selective effects. Such is the case with the high fluoride content in some saline lakes of the Rift valley (LA BARBERA and KILHAM, 1974).

Acidity

Swamps, whether rooted or floating, that surround shallow lakes, typically reduce the light that penetrates the water surface to about 10 % of its incident level (HOWARD-WILLIAMS and LENTON, 1975). Algal production is therefore reduced, and respiration prevails. Not only is carbon dioxide thus added to the water (see further), but the mass of the aquatic plants also liberates humic acids. The result is that the pH of swamps is considerably lower than that of open water.

Humic acids are chemically very diverse organic compounds (see HAYES et al., eds, 1989, for much recent information). The types liberated by Sphagnum, for example, not only acidify the water, but also remove ions from solution, and thereby reduce conductivity. Although Sphagnum bogs occur in several areas in Africa (e.g. the Drakensberg area, the plateaus of Rwandi and Burundi), they have been little studied. A bog-like situation is also found in the western arm of the Sudd-swamps, the Bahr el Ghazal, where Lake Ambadi is situated. This brown-water lake has a low conductivity and pH, and

shows a strong reduction in size and abundance of *Cyperus papyrus* and *Eichhornia crassipes* (DENNY, 1984), while its zooplankton is more scarce in numbers but more diverse in species than elsewhere in the Sudd (GREEN, 1984). Typical algal associations, with a dominance of desmids, have also been reported from this peculiar acid lake (GRÖNBLAD *et al.*, 1958).

Acid brown waters, presumably of the type found in the Varzea lakes of the Amazon (SIOLI, 1984), are also typical of the inundated forest zone of the middle Zaire. With pH-values in the range 4-5, they impose severe limitations on the types of animals, higher plants, and presumably also algae that can live there. An additional problem that faces animals in such an environment is the high oxygen demand of the humic material, producing anoxia during the night. Lake Tumba, the only lake in this area that has been studied (MARLIER, 1958), will be briefly discussed later.

Dissolved Gases

Oxygen has a moderate solubility in water, which decreases with temperature : warm water dissolves less oxygen than cold water (Henry's law). In shallow waters, well exposed to the wind, its vertical distribution is, as a rule, homogeneous to the bottom, regardless of salinity. Short-term stratification, however, commonly occurs in windless conditions. The bottom water, in close contact with reducing, organic sediments, can become depleted of oxygen. When more organic material settles to the bottom than there is oxygen to oxidize it, some of it will not decompose but fossilize. This process is more frequent in acid than in alkaline conditions, and may lead to peat formation.

Photosynthesis adds oxygen to the water, but respiration consumes it. The first process may lead to supersaturation during the day while the latter, being the only one that continues through the night, may lower the oxygen level to critical levels. If other external forces such as a low water level and strong winds stir the sediments and add reducing material to the water column, catastrophic mortalities will occur in the animal, and to a lesser extent, to the plant world of a lake.

When all oxygen is depleted, reducing processes prevail. Thus, for example, sulphate is reduced to sulphide. Hydrogen sulphide is a strongly smelling product, and its salts, the sulphides, are toxic although usually quite insoluble. In shallow waters, sulphides are normally only produced in organic sediments. If stirred up by wind action, they may, however, contribute to catastrophic mortalities.

CO_2 is another gas with biological significance. It

is less soluble than oxygen but reacts with the water molecule to form bicarbonate ions. In contrast to oxygen, it is produced by respiration and utilized by plants for photosynthesis. In lakes where flood waters have to percolate through dense vegetation belts before reaching the open water, this water may progressively become acidic and deoxygenated as a result of the intense respiration of the phytomass, and of decay of plant material that releases humic acids. Inflow of such water into a lake may cause massive mortalities among aquatic animals, especially fish.

Methane (CH_4) is bacterially produced under reducing circumstances in the sediment of many shallow lakes and marshes, from which it escapes into the atmosphere. It is a fairly inert gas, that is neither utilised by, nor toxic to, eucaryotic biota, but its presence is an indication of a marshy environment with an anoxic sediment.

Turbidity

Turbidity, either permanent or temporary, is linked to wind action, floods, depth, and the nature of the sediment. Its effects are important and manifold. They may be direct or indirect, along a sometimes complex chain of events. Its most obvious impact is on the underwater light climate (but dense stands of waterplants have the same effect). By reducing the absolute amount of light that penetrates to the water column, and by the selective absorption of long and of short wavelengths, the rate of primary production is affected. If a significant portion of the suspended particles are algae, they will actively photosynthesize in the upper layers, but the cells in the lower layers may be shaded so strongly (TALLING, 1960) that even during the day, respiration prevails here over oxygen production. Such lakes have sharply clinograde oxygen curves during windless days, and the water column may show a nightly oxygen deficit which, in cases like Lake George (see further), occasionally leads to complete deoxygenation of large areas of the lake, accompanied by massive fish kills.

The conventional delimitation of the lower limit of the euphotic zone in a watercolumn is the point where the incident light is reduced to 1 % of its surface value. If this level is situated above the sediments, no aquatic plants or algal mats will develop here. A benthic plant cover stabilizes the sediments and thereby reduces turbidity. Alternatively, a high turbidity will prevent benthic growth, and this, in turn, will tend to increase turbidity still further.

Turbidity may result from wind-induced resuspension of fine lake sediments. Where wide marginal

reedbelts occur, these will act as wind-breakers, and reduce turbidity, with the eventual development of a benthic plant cover in the open water as a result. Commonly, however, turbidity is due to the silt-load of flood waters. If the silt particles settle to the bottom more or less rapidly after reaching the lake, turbidity will have little effect on submerged aquatic plants. If not, benthic plants and algal mats will disappear, and at high turbidity, algal primary production will also be affected. Such a situation typically arises after forest clearing, followed by increased erosion in a river or lake catchment.

In clear waters, midday light levels are supraoptimal, and in such cases surface inhibition of photosynthesis occurs. Daily photosynthesis curves, integrated over time and depth, show that this depression can be quite substantial (TALLING, 1965). In turbid lakes, where turbulent mixing occurs, not only the absolute amount and spectral composition of light is affected, but there is a succession of algal cells carried from the aphotic to the euphotic zone. They remain in the euphotic zone for a short while, during which they photosynthesize, and are then replaced by other cells before their photosynthetic apparatus becomes inhibited.

Regardless of secondary production, standing stocks of zooplankton are usually much larger in turbid than in clear permanent lakes, because the feeding efficiency of visual plankton feeders such as fish is strongly depressed when underwater visibility is low. The community composition of zooplankton in turbid waters tends to shift to large species, which are too vulnerable (because they are more visible) to survive in clear water. In clear shallow lakes with fish, pelagial zooplankton is often completely absent and littoral zooplankton only occurs in sheltered areas, such as in submerged and fringing vegetation.

Because the bottom of turbid shallow lakes is often situated in the aphotic zone, anoxic conditions tend to develop here, especially where highly organic sediments occur, and the benthos of such muddy bottoms is poor in species. Typical inhabitants of such sediments are tubificids and *Branchiura sowerbyi* (Oligochaetes), which feed on organic detritus. The anterior part of their body is buried into the sediment, while the posterior part, containing respiratory pigments and sometimes gills, freely floats in the water above.

Turbidity also has direct physiological effects on animals, such as on the efficiency of the gas-exchange system in fish. In turbid water, many species revert from visual feeding to much less efficient filter feeding (ZARET, 1980). In turbid lakes, large zooplankters will thus resist extinction from predation much longer than in clear lakes. However, besides zooplankton, other suspended particles also collect on the gills and gill-rakers, which eventually become clogged. Thus, fish must spend extra time and energy cleaning their gill chamber; this cleaning time decreases the time available for searching food, and thus reduces the animals's feeding efficiency. Cases have been documented in lakes Chad and Chilwa where the gills of Cichlids and Cyprinids eventually became damaged or infected, and resulted in fish mortality. Other fish species, especially those capable of air-breathing like the catfishes of the genus *Clarias* may actively contribute to turbidity by continually stirring the sediments in search of benthic food. This effect is most significant at low water levels and conveys a competitive advantage to air-breathers in such conditions.

As suggested above, long periods of high turbidity change the zooplankton composition. For example, they tend to eliminate Cladocera. Like filter-feeding fish, these small Crustacea occasionally need to clean the filtering trunk limbs contained within their carapax. The higher and the more persistent the turbidity (but also the more filamentous algae and cyanobacteria, which have a similar effect, are present), the more time is spent cleaning. This amount of time, again, is not available for feeding. Rotifers, which have an external filtering apparatus (the corona), can feed continually even in the most turbid conditions. Less efficient in clear water, they often acquire a competitive advantage over Cladocera in lakes with a continuous high turbidity. Copepods, which catch and manipulate food items individually with their mouth parts (ALCARAZ et al., 1980; KOEHL, 1984) and hunt non-visually anyway, are also not disfavoured at high turbidity : the advantage of protection from visual predators likely far outweighs the disavantage of having to handle more particles.

Turbidity also plays a role in nutrient dynamics (mainly of nitrogen and phosphorus) which, in general, are not well known for African shallow lakes, swamps, and floodplains (GAUDET, 1976, 1977; HOWARD-WILLIAMS, 1979 b). However, FURNESS and BREEN (1982, 1985) recently called attention to the fact that in a flow-through situation such as that of the series of lakes found in the Pongolo floodplain, the suspensoid load of the incoming flood water provides an important input of allochtonous nutrients to the system, that compensates for various losses occurring between floods.

Wind

Wind action on lakes causes waves and sets up turbulent currents. In fact, laminar water currents do not normally occur in lakes (HUTCHINSON, 1957). Wave action is especially important in the littoral. It

may erode some lake shores, redeposit sediments along others, uproot and destroy existing marginal vegetation, and prevent young shoots from growing up.

By setting up currents, winds upset stratification, mix oxygen into undersaturated deep water, and stir up sediment. Wind is therefore an important co-determinant of turbidity. Winds also contribute to the creation and maintenance of a diversity of substrates in shallow lakes. This is the result of differential transportation and deposition of loose organic mud and debris from certain parts of a lake to others. Thus, sectors with sandy, loamy and clayey bottoms may be formed. The lightest particles (organic mud) will settle in areas protected from the turbulence generated by winds, i.e. behind or amidst aquatic plants, and in the deepest parts (with least turbulence) of the lake. These latter areas, as shown earlier, are least favourable for the development of benthic life.

Wind-driven currents have strong effects on zooplankton distribution. The circular currents in Lake George, for example, concentrate the plankton in the middle of this lake (see further). Limnetic zooplankton is naturally gregarious and tends to form swarms in the deepest parts of shallow lakes (DUMONT, 1967). Often, however, wind-driven currents are strong enough to disrupt such swarms, and the zooplankton may be swept towards the shore in great densities. Such near-shore aggregations are extremely vulnerable to predation by the numerous species of littoral and benthic fish.

Substratum Type

Substratum types are determined by the geology of the lake bed and by the nature and the amount of the sediment load of the inflowing water. Source, areas and granular size of imported sediments varies according to the seasonal flood regime of the inflowing rivers, or the runoff in a lake basin. Clearly, "development" in the sense of deforestation enhances erosion, and will greatly increase sediment input into a lake. Damming of inflowing rivers, conversely, prevents sediments (and the adsorbed plant nutrients) from reaching a lake and may thus upset its nutrient balance (FURNESS and BREEN, 1985). However, a differential susceptibility of certain parts of a lake to wind stress, and the lake's bathymetry itself are important determinants in creating zones with different sediment types within single lakes.

In a substratum uniformly composed of liquid organic mud, only anoxia-adapted organisms such as ciliates, worms (tubificids, Alma emini, nematods ...), some Crustacea (the cladoceran Ilyocryptus), some

dipterans (Chaoborus larvae, chironomid larvae) occur. All other sediment types are much richer. Sandy sediments, in particular, host a diverse benthic life, in which plants, but also Crustacea, insects, gastropod and bivalved molluscs, and fish are represented.

Geological Events

Our time scale of observations is usually too short to allow us to record effects of geological events upon the structure and functioning of shallow lakes, but there are exceptions to this rule. The Okavango delta, for example, is situated in an area of active rifting, where several earthquakes occur per year. The effect of these is that the drainage pattern of the different branches of the Okavango river within the delta is regularly altered, and that areas previously not flooded may become subject to flooding and vice versa. Similarly, the Lake Moero-Bangweulu area was tectonically tilted in the 1930' s, with an average increase in water level of about 2 m for a result.

Pleistocene Climate Changes

Pleistocene climate changes repeatedly modified the hydrological balance of African lacustrine environments. Some episodes had a much higher, and others a lower precipitation than today. Among other things, faunal and floral relics still testify to such changes, and these relics are therefore said to inhabit these lakes for historical reasons. Thus, the fauna and flora of the Sahara are mainly of northern origin, while that of the Sahel is of Afrotropical origin. In boundary regions, like Lake Chad and the lakes to the north of the internal delta of the Niger River, both types of biota mix, with a great species richness as a result.

Among higher plants, Cyperus papyrus is noteworthy. This species, widespread throughout the Eastern half of Africa, is still common in Lake Chad, which it may have reached during a holocene connection between the Nile and Chad basins. Apparently, it did not extend further west and did not colonise the Niger delta lakes, or at least could not maintain itself there. More examples of this kind can be found in DUMONT and VERHEYE (1984).

Man

In spite of parasite-borne health hazards, man in Africa has exploited shallow lake and floodplain environments since prehistory. Fishing was performed on interdunar lakes in the Sahara during the pluvials of the Upper Pleistocene (FAURE, 1969). Later, as agriculture and domestication evolved,

floodplains became even more valuable to the now settled human populations, e.g. along the River Nile. This type of exploitation is still continued, by the Dinka and Nuer tribes of the Sudd swamps for example. Here, cattle farming is combined with fishing on a seasonal basis : during the floods, people move their cattle to higher grounds, and return to the floodplain after the water has receded. Usually, such sediments fallen dry develop extensive meadows which provide excellent grazing and can also be used for agriculture. Such a shifting system is, in fact, found over most of Africa. It has been quantified by HEEG and BREEN (1982) for the Pongolo floodplain. In terms of biomass removed or utilized, not only the meadows (e.g. of *Cynodon dactylon*), but also other waterplants are important : *Phragmites* is widely used for roofing huts, while *Papyrus*, anciently used as a primitive form of paper, is still in use for boat and raft-construction on lakes Tana and Chad.

Fishing, by whatever means, has in the course of this century evolved into an activity of economic importance (WELCOMME, 1979). HEEG and BREEN (1982) state that the Pongolo fish stocks are underfished. This might well be an exceptional situation in todays' Africa, however. The annual yield of fish (mainly *Oreochromis niloticus*) in Lake George, for instance, removes more biomass than is produced. As a result, fish mature and reproduce at a smaller size and at an earlier age (BURGIS *et al.*, 1973). Similar facts were observed in Lake Chad (see case study). During the drought phase of the 1970's in this lake, fish populations became isolated in separate shallow lake basins and were in a comparatively short time overfished and completely eliminated by the local fishermen. Man as a determinant of shallow lake functioning is therefore rapidly evolering from a exploiter to an overexploiter.

Twentieth century technology is currently being more and more applied to African shallow lakes. Examples involve the damming of headwaters, such as the Logone, Pongolo, Volta, Senegal and Niger rivers. The objective of such interventions is to upscale local agriculture, subsistence agriculture and horticulture being the traditional forms of agriculture performed on floodplains. However, unless water release is carefully managed, the inundation cycle of the floodplain lakes gets distorted to a point where — at least in part — permanent drainage and loss of biota occurs.

Unless the cost of regulating the floodplain regime on a pseudo-natural basis can be offset by such products as fishery, tourism, and conservation (HEEG and BREEN, 1982), man will become more and more important as a deregulator of the functioning of such environments. Another striking example, in

which the drainage of a giant swamp is considered as of secondary importance against the gain of more water for downstream irrigation, is the Jonglei Canal Project (EL MOGHRABY, 1982). Pumping up water for irrigation or as a source of drinking water for major cities occurs in Lake Guiers, Senegal, and on the Nigerian side of Lake Chad.

Effects of river regulation by upstream damming on downstream lakes may sometimes be subtle. Thus, the creation, in 1968, of the Lake Kainji dam on the River Niger (4° 20'- 4° 45' E, 9° 50'- 10° 55' N) reduced the Niger floods in the delta area (NWADIARO and IDABOR, 1990), where thousands of shallow oxbow lakes occur. Most of these are only seasonally connected to the Niger, when floods fill the innumerable temporary canals and floodplains, and allow fish to perform their characteristic lateral (spawning) and longitudinal migrations (see section on Lake Chad for details on these movements). While many of these lakes remained broadly connected to the Niger after 1968, the largest, Lake Oguta (6° 41'- 6° 50' E, 5°41'-5°44' N, surface area 1,796 km², max. depth 9.0 m) lost part of its connection, a complex maize of river channels between the rivers Orashi and Niger. The result was a decline in ichthyobiomass, and lowered fisheries production, although fish diversity remained high (80 + species : NWADIARO, 1989). Pelagic zooplanktivores (e.g. young-of-year *Citharinus*, the upside-down catfish *Hemisynodontis membranaceus*, and the freshwater sardine *Pellonula leonensis*) were most strongly affected, ceased to migrate from the river to the lake and eventually disappeared or became exceedingly rare (see further, under "Lake Chad", for details on these seasonal fish movements). The zooplankton of this clearwater lake reacted by developing a dominance of a fairly large-sized calanoid, *Tropodiaptomus lateralis*, an endemic of the Niger system, but which had rarely been recorded throughout its basin previously (MAAS *et al.*, 1992). As elsewhere in tropical Africa, *Daphnia* remained absent (DUMONT, 1980), but apparently the Calanoid managed to co-exist well with the remaining planktivorous fish.

Perhaps another result of man's interference was the appearance of algal "jellies" (NWADIARO and IDABOR, 1990), mainly composed of Cyanobacteria, in the benthos. These interfered with the normal functioning of a number of benthic fish. They also seem to perform a limited degree of vertical migration, and may clogg fisherman's nets.

A final example of a deregulation is provided by artificial species introductions. The most notorious accidental introduction in Africa is that of *Eichhornia crassipes*, the South American water hyacinth, which has invaded river systems in Southern, Central, Western, and Eastern Africa as far north as
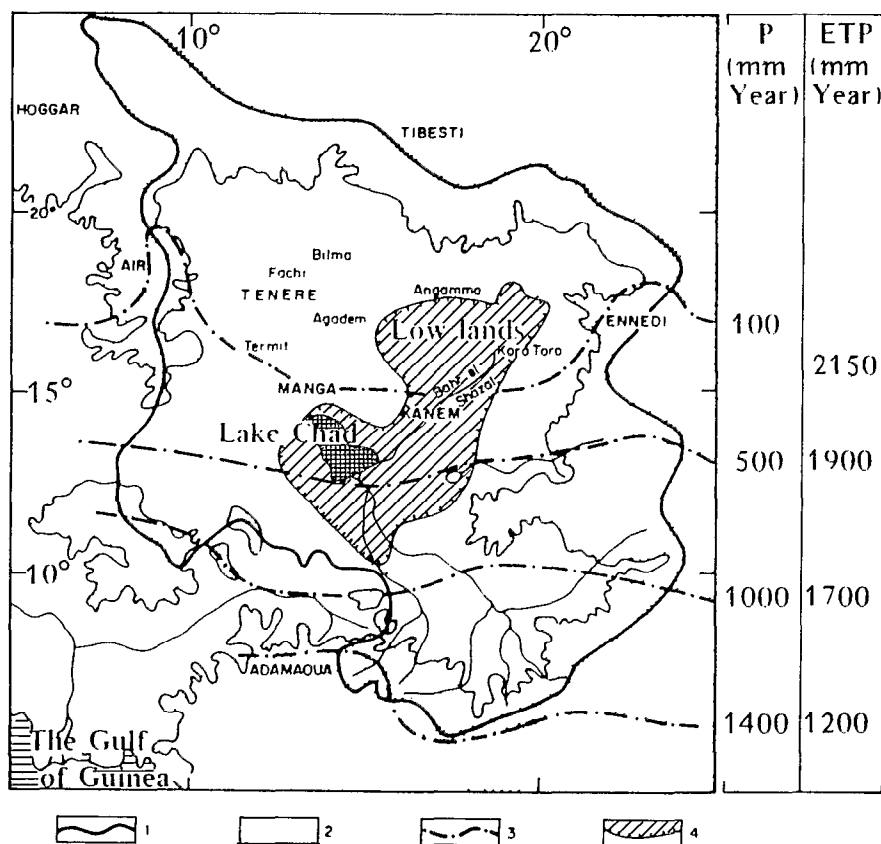
Fig. 1. — The basin of Lake Chad, with the extension of the present lake and its supposed holocene maximum (c. 6000 BP) (redrawn after CARMOUZE et al., 1983).

Bassin du lac Tchad, avec l'extension du lac actuel et son maximum holocène (c. 6000 BP) (d'après *CARMOUZE* et al., *1983).*

the White Nile. Apart from causing navigational problems by obstructing river channels, the broad leaves of this plant seal off the water surface and deoxygenate the underlying water, while increasing water losses by its huge evapotranspiration (OBEID, 1975).

Combating such pest species requires either new introductions, such as hyacinth-eating beetles of the genus *Neochetina* (BASHIR et al., 1984), or the use of synthetic pesticides, such as 2,4-D (BEBAWI and MOHAMED, 1984). While the biological method is to be preferred, care should be taken to introduce only host-specific grazers or predators.

The second procedure, large-scale spraying with synthetic organic compounds, is extensively used for purposes of public health, in controlling, for example, sleeping sickness and malaria. In the Okavango Delta, slowly degrading DDT, along with many other products, was still in use until recently (RUSSEL-SMITH, 1976). The long-term effects of such actions, and of the toxic residues which they carry

up and concentrate in a food-chain, have been only superficially considered by scientists in Africa. The danger that the economic argument will continue to prevail over the ecological one is always present.

CASE STUDIES

No single wetland or shallow lake combines all aspects of stability or change that one might wish to illustrate. Two contrasting examples have therefore been selected here : one with large and dramatic fluctuations in water level, and one with a stable water level.

Lake Chad (fig. 1)

Lake Chad has been monographed by CARMOUZE et al., 1983, and thereby a wealth of information from a multidisciplinary study of this lake, between
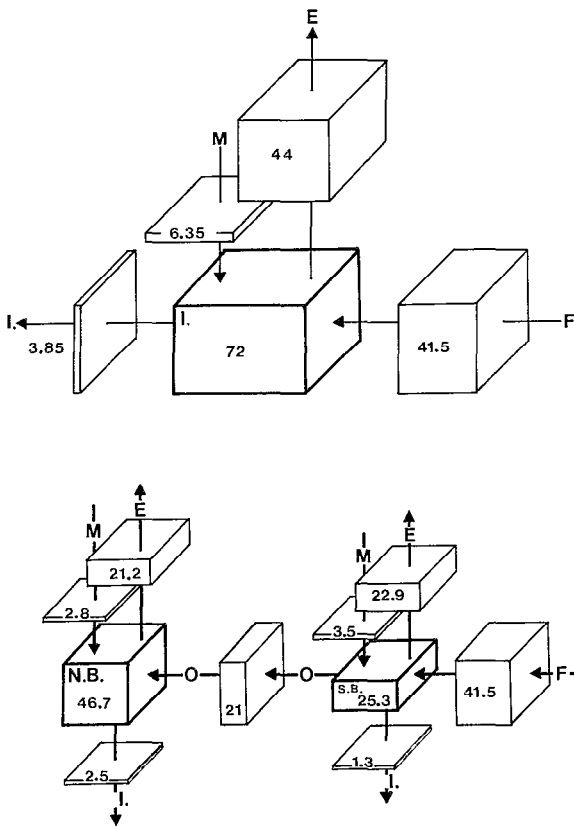
Fig. 2. — Average annual hydrological balance of Lake Chad.
a. Balance for the whole lake; b. balance for the north and
south basins taken separately (after CARMOUZE et al., 1983).

*Bilan hydrologique moyen du lac Tchad. a. Bilan du lac entier; b.
bilan pour les bassins nord et sud (d'après CARMOUZE et al.,
1983).*

1965 and 1978, has become available. While this research was taking place, the lake became subject to a major recession. Although after 1976 it seemed to stabilise at some new level, as of 1983, a new drought occurred. This second event has, however, not yet been sufficiently documented to form part of the present account, especially as things became complicated by upstream damming, and water extraction for irrigation.

Lake Chad is endorheic, situated in Sahel country (mean latitude 13° N), at an average altitude of 281.9 m. In 1965-68 it had a maximum depth of 12 m, and a mean depth of 4 m. The average yearly fluctuation in water level was about 1 m. Consequently, the margins of this 18,000 km² large lake fell dry in the course of the dry winter and were

flooded during summer monsoon. Inputs are from local precipitation (240 mm y⁻¹ at the northern tip of the lake, 550 mm at the southern tip, and occur between May and October, with half the total amount in August alone), and from the combined flow of the Logone-Chari rivers ($40,10^9$ m³, on average). Other contributions are negligible. The balance is achieved by the evaporation of 40-50 10^9 m³ of water on a lakewide basis (fig. 2). Two factors complicate this balance : 1) the lake is SE-NW oriented along a steep gradient in precipitation and receives most of its inflow from the south; 2) its basin is almost exactly split in half by a transverse threshold ("great barrier"), with most of the bed of the northern half c. 3 m below that of the southern half (fig. 3). This makes both halves almost as different as two separate lakes.

Indeed, even during wet years, the Chari (average ionic content 40-50 mg l⁻¹) discharges enormous amounts of salts into the lake(s). This causes electrical conductivity to increase by a factor 15 from the south to the north. Salinity increases also, but not all ions behave in the same way. Only the concentration of Na^+ increases in direct proportion to evaporative water loss. All other ions take part in a saline regulation of the lake. Some are chemically sedimented in the lake or along its margins, but the hydrological balance also includes important losses to the groundwater. In the north and north-east, which is the saltiest part of the lake, the loss in minerals through this "leak" is high and results in an increase of salinity much lower than if determined by evaporation alone. This saline regulation works in both directions. During the annual floods, a partial redissolution of precipitates smoothens the effects of dilution (CARMOUZE, 1983). The overall effect is to oppose and slow down change.

The major biotopes of the average Lake Chad are a mosaic of open water (38 %), archipelagoes (zones fragmented by emergent dune tops, forming innumerable islands, 23 %) and reed belts (39 %) (fig. 3b). However, as of 1972 a sequence of below-average floods provoked dramatic changes in lake area, depth, volume, chemistry, and biota, which lasted through 1978, when most observations were interrupted.

PHYSICAL ASPECTS OF A RECEDING LAKE : 1972-1977

CARMOUZE and LEMOALLE (1983) summarize the events as follows :

a. 1972-1973 : formation of the "Lesser Chad". After a flood of only 17.3 10^9 m³, which compensated for not more than 3 months of evaporation, the lake began to recede. By April 1973, the great barrier fell dry and the two basins became separated, with a deeper lake in the north, and two shallow
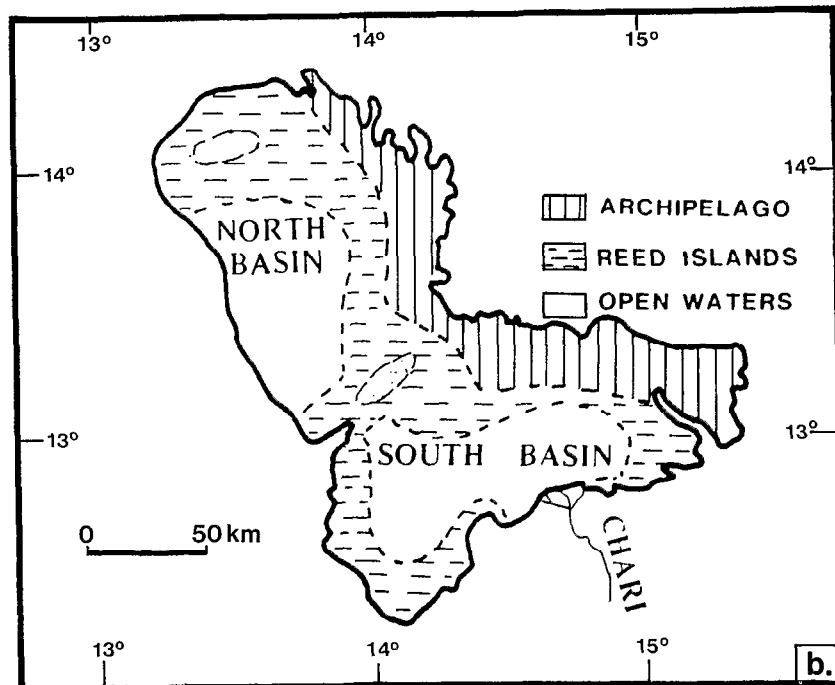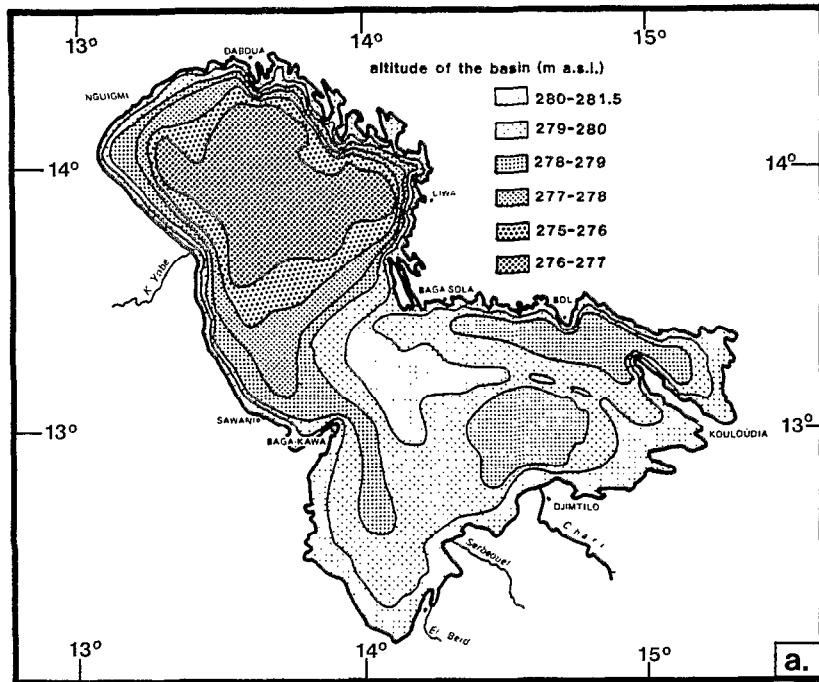
FIG. 3. — The two basins within Lake Chad. a. Altitude distribution within the compound basin ; b. ecological zones associated with the depth distribution of the lake (after CARMOUZE et al., 1983).

Les deux bassins du lac Tchad. a : Contours altitudinaux de l'ensemble du bassin ; b : zones écologiques associées à la distribution des zones de profondeur du lac (d'après CARMOUZE et al., 1983).
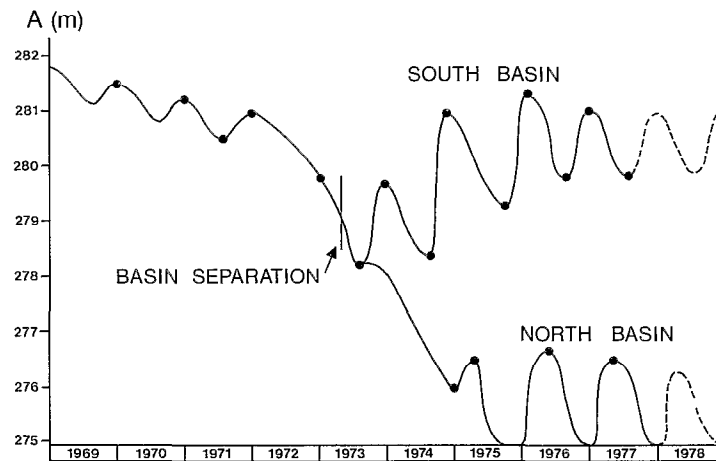
FIG. 4. — Effects of Lake Chad's recession during the 1970's. At first the two basins separate. Later, the north basin temporarily dries up while the south basin almost regains its original depth (CARMOUZE et al., 1983).

Effets de la récession du lac Tchad au cours des années 1970. D'abord, les deux bassins se séparent. Plus tard, le bassin nord s'assèche temporairement, tandis que le bassin sud regagne sa profondeur originale (CARMOUZE et al., 1983).

water surfaces in the south (fig. 4). Progressive contraction with a level loss of 1.6 m continued, and by August 1973, marsh plants began to proliferate on the dry parts of the lake bed.

b. 1973-1974 : a weak flood (18.4 10^9 m³) filled the south basin, but little water seeped through the thick vegetation of the central barrier to reach the northern lake, which soon started fragmenting. The situation worsened in 1974, turning the northern lake into a giant archipelago.

c. 1974-1975 : two floods of slightly below average volume (1975 : 30.5 10^9 m³; 1976 : 36.6 10^9 m³) restored a normal situation in the south basin. However, abundant vegetation on the central threshold prevented water movement to the north. The northern lake first dried up in 1975. Thereafter, it became an intermittent lake.

d. 1977-1978 : the 1977 flood was below average (28.7 10^9 m³), and because the southern basin withheld most, it was only slightly affected. The situation in the north remained unchanged.

EFFECTS ON BIOTA

Biota of the "Average Chad" (1968-1972) : Recurrent Small Fluctuations

Aquatic Plants (fig. 15)

Aquatic plants, covering about 12 % of the lake surface, were concentrated in shallow areas, where they could either root (emergent species), or receive enough light for photosynthesis (submerged species) : the river deltas (Chari, Yobe, El Beid) and a fringe around the main lake shore and its numerous islands. Floating islands, mainly composed of *Pista stratiotes* occurred everywhere, but most commonly in the south basin (ILTIS and LEMOALLE,

1983). Indeed, a north-south gradient caused by increasing salinity was evident : stenoionic species with low salinity tolerance *(Cyperus papyrus* and *Vossia cuspidata)* sharply declined northwards where generalists such as *Phragmites australis*, *Typha australis* and, finally, stenoionic species with high salinity requirements *(Cyperus laevigatus)* either replaced them or became much more common.

Algae

COMPÈRE (1967-1977) listed the extraordinary number of c. 1 000 algal species from Lake Chad. Major changes in this floral composition occurred with time, as the lake became affected by drought. The community composition was typically tropical but with qualitative and quantitative differences between the north and the south basins, ascribed to a different salinity tolerance (COMPÈRE and ILTIS, 1983). As salinity increased, nutrient salts also became more concentrated, and therefore, algae with low P and N tolerance remained restricted to the south basin. In addition, the zones with open water had predominantly limnetic species, smaller in number and specifically different from the diverse algal flora that was found in the periphyton of the aquatic plant belts. The result was a zonation within the lake, with two main archipelago zones (each with subzones), and two open water zones (fig. 5). The limnetic zones behaved like mesotrophic environments, while the archipelagoes were transitory to eutrophic environments. The influence of the inflow of water from the River Chari in the south was
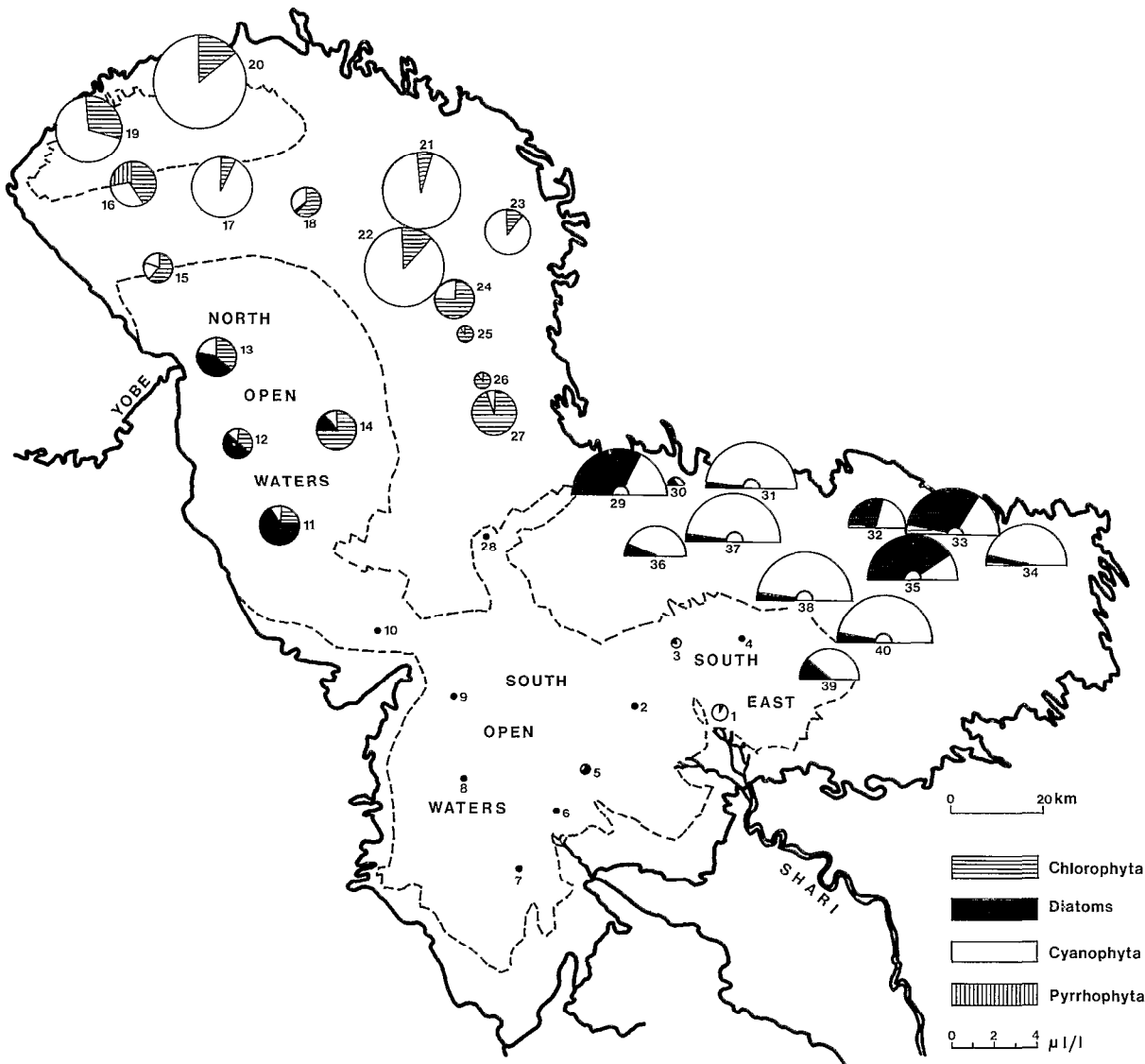
FIG. 5. — Taxonomic composition and relative proportions in the algal biomass of the phytoplankton of Lake Chad's different ecological zones (after CARMOUZE et al., 1983).

Composition taxinomique et proportions relatives de la biomasse algale du phytoplancton des différentes zones écologiques du lac Tchad (d'après CARMOUZE et al., 1983).

expressed by low standing crops. A combined increase in salinity, nutrients, and macrophyte cover progressively favoured cyanobacteria, non-diatom algae and an increase in biomass from south to north in the open water, but not in the vegetated archipelagoes. Seasonal variations were dependent on flooding rather than on temperature, and thus the Chari delta was most strongly affected (fig. 6), with a substantial increase in Chlorophyta during the months of flooding.

Zooplankton

Apart from the species-rich fauna found in association with the aquatic plants (see further), the limnetic Cladocera were represented by 8 limnetic, grazing species (SAINT-JEAN, 1983), and the copepods by at least 12 species, 7 cyclopoids and 5 calanoids. Only *Mesocyclops*-species, and *Thermocyclops incisus* are carnivorous as adults but herbivorous or omnivorous as copepodids. Thus, up to 17 species of
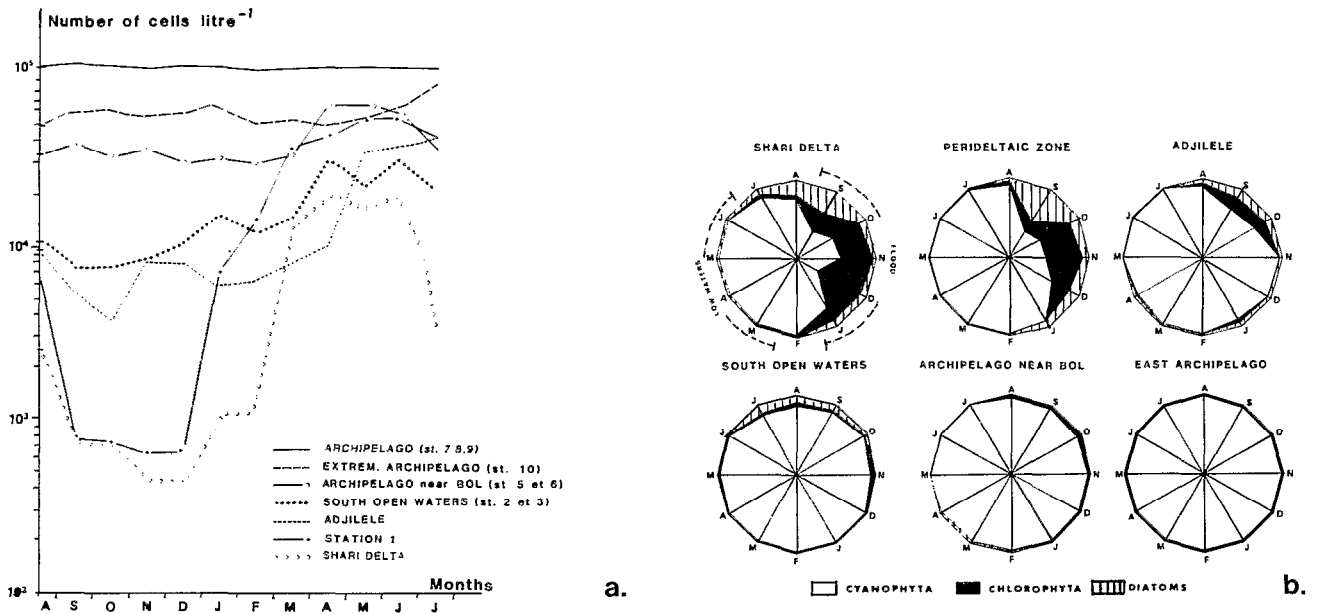
TABLE I

OLIGOCHAETES
  Alluroïdidae
Alluroïdes tanganykae
  Tubificidae
Aulodrilus remex, Euilodrilus sp.
  Naïdidae
Branchiodrilus cleistochaeta, Allonais paraguayensis ghanensis, Pristina synclites, Naïs sp.

Only Alluroïdidae and Tubificidae were abundant in the bottom substrata, while Naïdidae were found only occasionally, for they preferred the water grasses.

MOLLUSCS
  Prosobranchia
Melania tuberculata, Bellamya unicolor, Cleopatra bulimoïdes
  Lamellibranchia
Corbicula africana, Caelatura aegyptiaca, Caelatura terestiuscula, Pisidium pirothi, Eupera parasitica, Mutela dubia, Mutela rostrata

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The three species of Prosobranchs, as well as *C. africana* and *C. aegyptiaca,* were very abundant with a wide distribution. The other species were less numerous and more localized.

INSECTS
  Chironomids
   Chironominae
Chironomus formosipennis, Cryptochironomus stilifer, Cryptochironomus nudiforceps, Cryptochironomus dawulfianus, Cryptochironomus diceras, Tanytarsus nigrocinctus, Polypedilum fuscipenne, Polydepilum griseoguttatum, Polypedilum abyssiniae, Polypedilum longicrus, Cladotanytarsus lewisi, Cladotanytarsus .pseudomancus
   Tanypodinae
Ablabesmyia pictipes, Ablabesmyia dusoleili, Clinotanypus claripennis, Procladius brevipetiolatus
   Orthocladiinae
Cricotopus scottae
   Ephemeroptera
Cloeon fraudulentum, Eatonica schoutedeni, Coenomedes brevipes, Povilla adusta
   Trichoptera
Dipseudopsis capensis, Ecnomus dispar, Ecnomus sp.

---

ton by predation. Otherwise, only slight but persistent differences in standing crop between the southern and northern open waters existed. The northern, deeper water had a lower standing crop and production per unit volume, but not per unit surface (fig. 7) (SAINT-JEAN, 1983). In all these studies, relatively little attention was given to the rotifers (see further).

Benthos : worms, molluscs, and insects

No ecological studies exist on the microbenthos (bdelloids, nematods, ostracods, harpacticoids ...) of any African lake. In Lake Chad, the macrobenthos (oligochaetes, molluscs, chironomids, some non-dipteran insect larvae) have been well studied (table I :

some representative species) (LÉVÊQUE *el al.,* 1983). The grain size and organic content of the sediment were found to be of prime importance in the distribution of species across the lake bed. Five major sediment types were mud, peat, soft clay, granular clay (hereafter called pseudo-sand), and sand. On account of its organic acid content, peat was avoided by insects and worms alike. Worms and molluscs were most abundant on clayey bottoms, insects on sandy bottoms. Within oligochaetes, allurioids were absent from mud, but the tubificids, adapted to anoxia, replaced them here. Allurioids were most common on pseudo-sand.

For an extrapolation of these observations to the whole lake, and in contrast to findings in the zooplankton, substratum type had to be combined
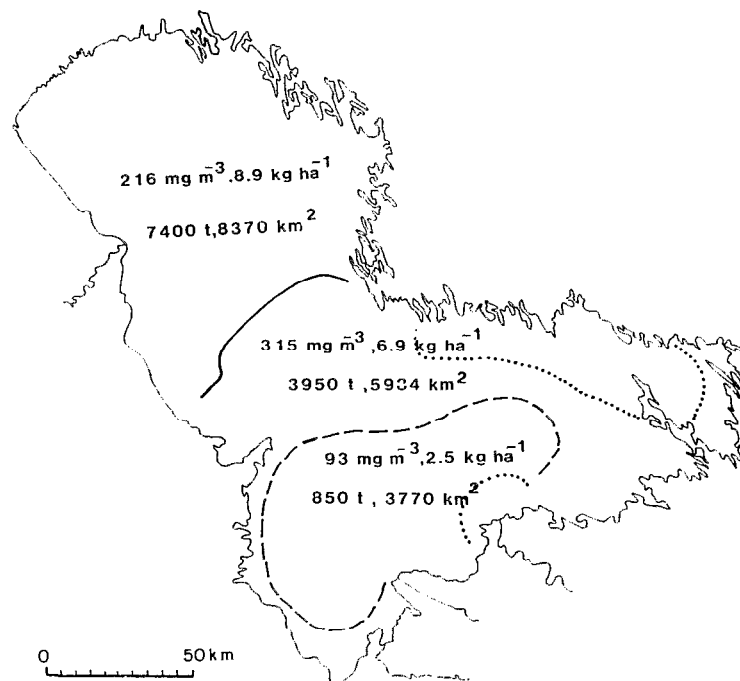
Fig. 7. — Zooplankton biomass per unit volume, unit surface, and integrated for each of three main areas of Lake Chad in 1971 (*from* CARMOUZE *et al.*, 1983).

Biomasse du zooplancton par unité de volume, de surface, et intégrée pour chacune des zones majeures du lac Tchad en 1971 (d'après CARMOUZE *et al., 1983).*

with salinity/conductivity. Empirically, Lévêque established that on clay bottoms, 420 μS cm⁻¹ was an important threshold value for oligochaetes. Below it, allurïoids were present, but above it tubificids replaced them. This separation was extremely clear (fig. 8) (CARMOUZE *et al.*, 1972) and indicates that in the absence of competitors, Tubificids will also colonize less organic and anoxic substrata.

Similar thresholds were identified for prosobranch gastropods : *Cleopatra, Bellamya,* and *Melanoides* sharply declined above 500 μS cm⁻¹ (LÉVÊQUE, 1972) (fig. 9). All benthic bivalves and gastropods disappeared above 750 μS cm⁻¹, regardless of substratum type, but their dead valves and shells showed that they had thrived here in times of lower salinities. While this applied to benthic species, pulmonate gastropods continued to occur among water plants at these and much higher salinities.·

Insects behaved differently, and a conductivity range of 200-1 000 μS cm⁻¹ seemed irrelevant to regulate their distribution across Lake Chad. At most, some became somewhat more or less abundant. Halophilic species began to appear at the

highest salinities in the north but were much more common in the natron ponds of the Kanem (e.g. *Cryptochironomus deribae, Chironomus caliplerus*).

Finally, temperature had significant effects on animals with annual life-cycles. Oligochaetes and Chironomids reached peak densities at the lowest yearly temperatures (fig. 10). This effect was less clear in Molluscs, which live longer than one year, although in some species (e.g. *Corbicula africana*) reproduction took place in the cold season only. In the absence of experimental work, the effect of temperature is difficult to isolate from that of water level and turbidity. The coldest water coincides in time with lowest water level, highest salinity, and highest turbidity (increased impact of wind) in the north ; in the south, considerable turbidity occurs during the summer floods. One important biotic factor to be remembered is, however, predation. In a lake with a distinct cold season like Lake Chad, vertebrate predators (mainly fish) have lower predation rates in winter. The apparent peak densities in preys recorded at that time may thus not reflect a direct impact of the environment, but an indirect
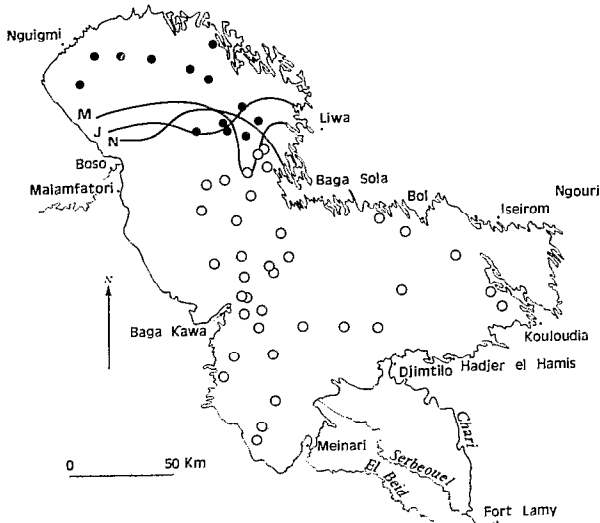
FIG. 8. — The distribution of allurioid oligochaetes on clay substrata in Lake Chad. The 420 µS cm⁻¹ boundary and its fluctuation (M, J, N) effectively limit the northward extent of this group, which is replaced, at higher salinities, by tubificid oligochaetes (see also fig. 11) (*from* CARMOUZE *et al.*, 1983).

Répartition des oligochètes Allurioides sur substrat d'argile du lac Tchad. La barrière de 420 µscm⁻¹ et la fluctuation (M, J, N) limite l'extension de ce groupe vers le nord, où il est remplacé par les Tubificidés à des salinités plus élevées (voir également fig. 11) (d'après CARMOUZE et al., 1983).

one, regulated by temperature-dependent predation pressure (DUMONT, 1982).

Based on a combination of factors (salinity, substratum type, and susceptibility to sediment resuspension), individual zones within Lake Chad were defined for major taxa. For oligochaetes, CARMOUZE *et al.* (1972), identified four main zones (fig. 11). LÉVÊQUE (1972) distinguished not less than 25 zones for molluscs, but later reduced these to 7 (fig. 12). They overlap with the four oligochaete zones, but are not identical with them. In insects, the changes with time were strong and not recurrent on a yearly basis. Based on the chironomids, six major zones were found, one of which was defined by flooded grasses and therefore contained only periphytic species such as *Cricotopus scottae*. In the course of the "normal" year 1970-1971, these zones, especially the northern ones, began to change. Zone 1 (defined by *Cladotanytarsus lewisi*) progressively declined, and eventually disappeared. Zone 3 (defined by *Clinotanypus clavipennis*) first expanded and later took the place of zone 1 (fig. 13).

The background of such events remains to be clarified, but it is noteworthy that the southern zones, with the lowest yearly amplitude in salinity and temperature, remained almost unaffected. Because chironomid species are so numerous in shallow lakes, niche overlap and therefore interspecies competition for limited resources must be

FIG. 9. — Frequency distribution of the molluscan genera *Melanoides, Cleopatra,* and *Bellamya* as a function of conductivity in Lake Chad (*from* CARMOUZE *et al.*, 1983).

Distribution des fréquences des genres de mollusques Melanoides, Cleopatra *et* Bellamya *en fonction de la conductivité du lac Tchad* (d'après CARMOUZE et al., 1983).

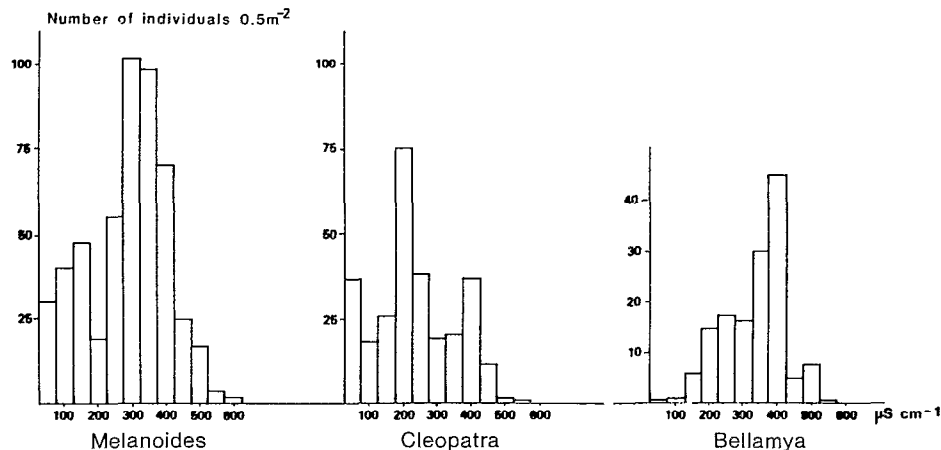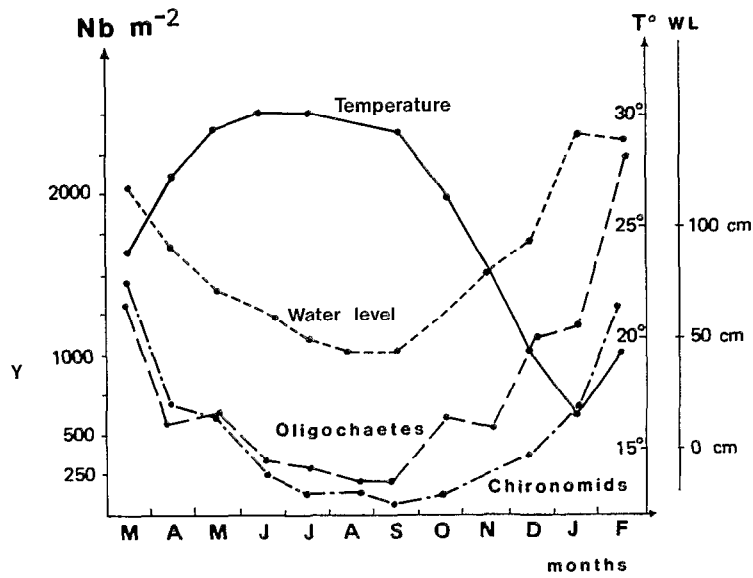Fig. 10. — Dependence of the standing crop of oligochaetes and chironomids on temperature variation in Lake Chad (1966-67).Note that water level behaves inversely to water temperature. Because of increased turbidity at low water, it may have increased the temperature effect (*from* CARMOUZE *et al.*, 1983).

*Évolution de l'effectif des oligochètes et chironomides en fonction des variations de la température du lac Tchad (1966-67). A noter que le niveau de l'eau varie en opposition avec la température. A cause d'une turbidité accrue aux eaux basses, ceci a pu avoir un effet supplémentaire sur celui de la température. (*d'après CARMOUZE et al., 1983).
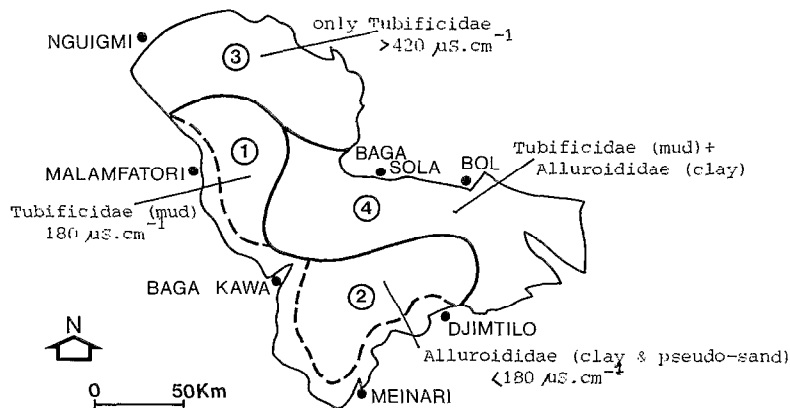
Fig. 11. — Distribution of oligochaetes in Lake Chad as a function of substratum type and conductivity (redrawn *from* CARMOUZE *et al.*, 1983).

*Distribution des oligochètes du lac Tchad en fonction du type de substrat et de la conductivité (*d'après CARMOUZE et al., 1983).
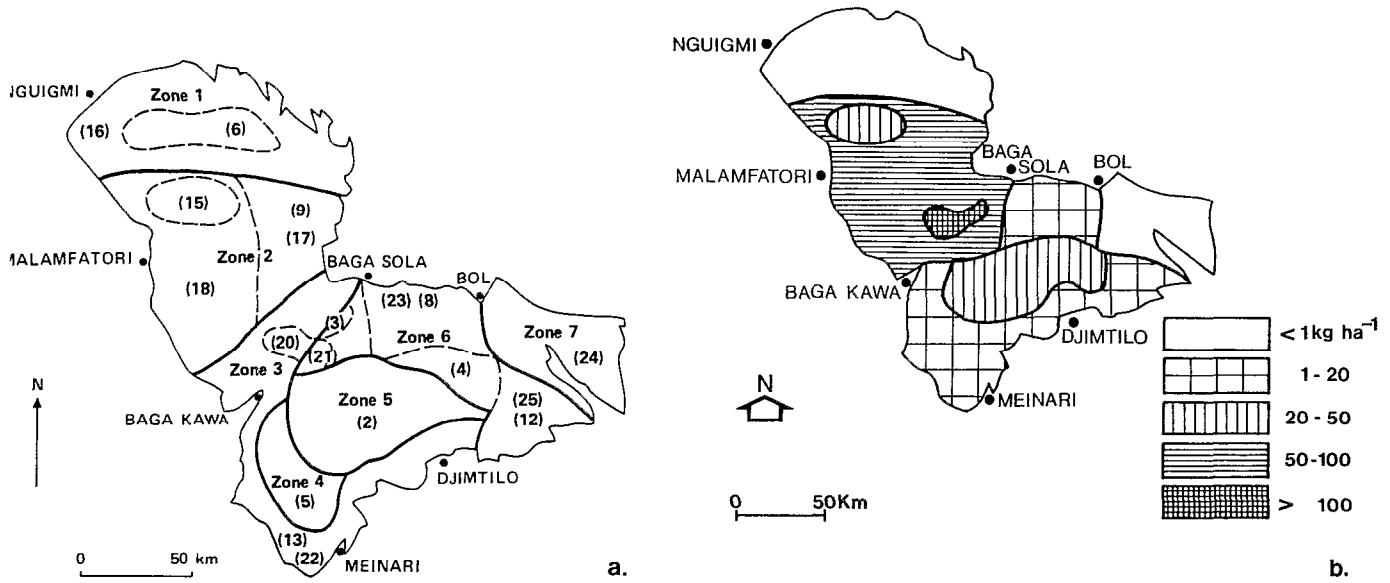
FIG. 12. — a. Detailed zonation (with subzones), mainly based on substratum type, for the Mollusca of Lake Chad ; b. distribution of molluscan biomass across Lake Chad (redrawn *from* CARMOUZE *et al.*, 1983).

a. Zonation détaillée des mollusques du lac Tchad, basée sur le type de substrat ; b. répartition de la biomasse des mollusques du lac Tchad (d'après CARMOUZE et al., 1983).

MARCH 1970   JULY 1970   NOVEMBER 1970   MARCH 1971
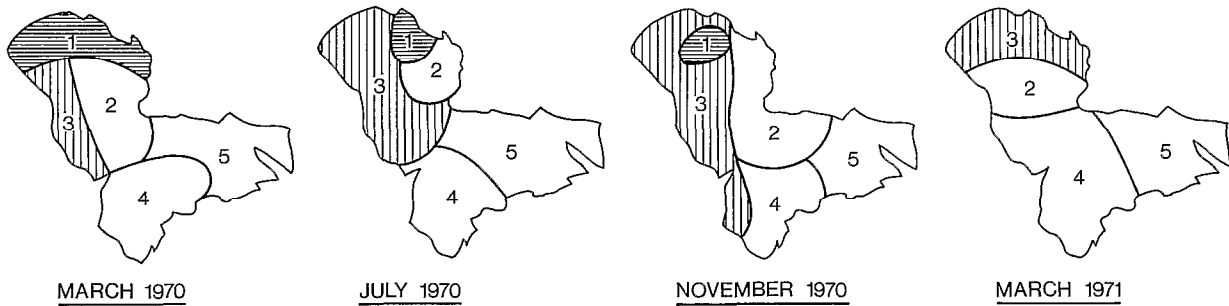
FIG. 13. — Zonation of chironomid larvae in Lake Chad (1970-91), based on dominance of species or of species associations. The zones shift, but not with an annual periodicity. This example illustrates the complex interactions between several variables in the lake (see also fig. 14) (redrawn *from* CARMOUZE et al., 1983).

Zonation des larves de chironomides du lac Tchad (1970-71), sur la base de la dominance d'espèces ou d'associations d'espèces. Les zones se déplacent, mais sans périodicité annuelle. Cet exemple illustre les interactions complexes entre plusieurs variables dans le lac (voir aussi fig. 14) (d'après CARMOUZE et al., 1983).

frequent. Subtle year-to-year differences in seasonal environmental changes may be sufficient to increase this overlap to proportions in which some species gain a strong advantage over others and eliminate them. In chironomids, this is enhanced by the fact that adults are aerial insects with good capabilities for dispersal and colonization. In other groups, which disperse more slowly, such as worms and

molluscs, similar visible reactions to small changes will not readily occur, and if changes become dramatic, such groups may not even have time to emigrate, and will die out (see further).

Expressing such patterns in quantitative terms (standing crops) showed that the allurioid worms remained high and relatively invariant throughout the year. In contrast, tubificids showed seasonal

predation lowest
MARCH 1970

predation very high
JULY 1970

predation declines
NOVEMBER 1970

☐	0 – 0.6 kg ha⁻¹
▦	0.6 – 1.2
▥	1.2 – 2.4
▤	> 2.4

☐	0 – 0.1 kg ha⁻¹
▦	0.1 – 0 5
▥	0.5 – 1.5
▤	> 1.5

OLIGOCHAETS
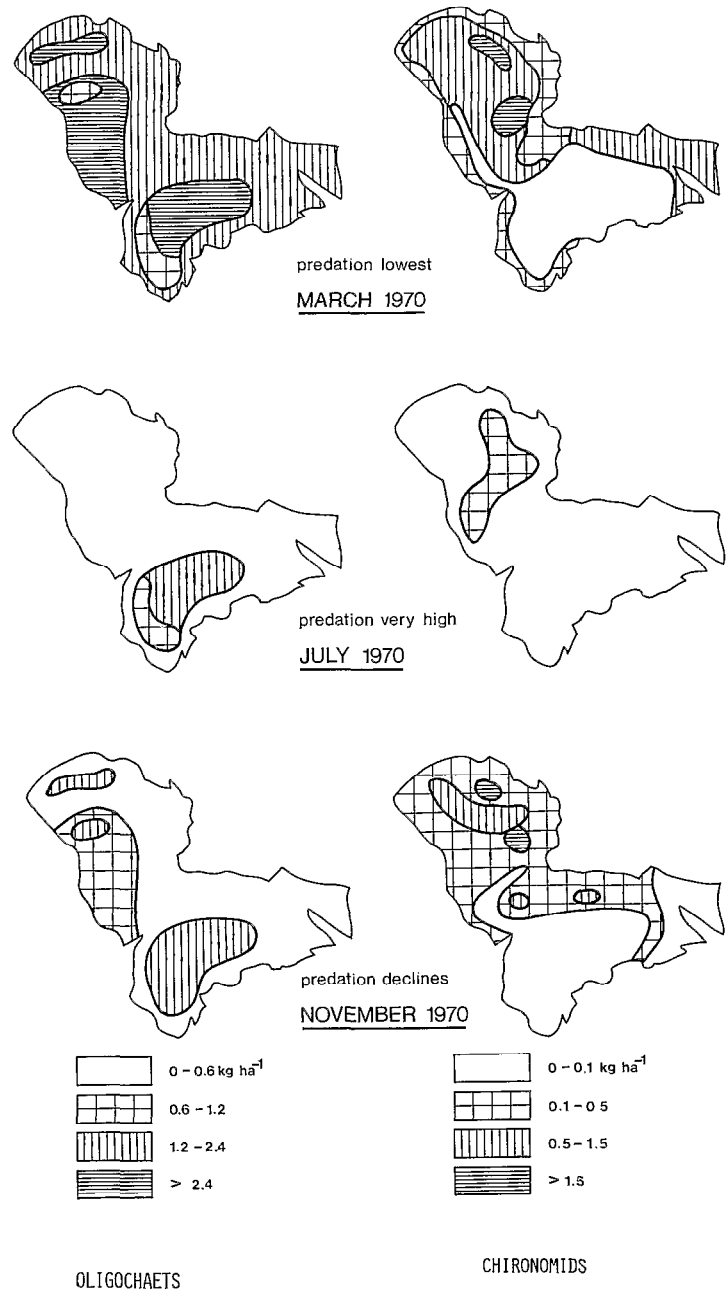
CHIRONOMIDS

FIG. 14. — Seasonal distribution of biomass of oligochaetes (left) and of chironomids (right) in Lake Chad (March-November, 1970). The standing crop of both groups is seen to be a function of fish predation, which reaches a maximum in summer. Note that the maximum numbers in both prey groups are displaced suggesting competition for space (modified *from* CARMOUZE *et al.*, 1983).

Répartition saisonnière de la biomasse des oligochètes (à gauche) et des chironomides (à droite) du lac Tchad (mars-novembre 1970). Les effectifs des deux groupes sont fonction de la prédation des poissons, qui atteint son maximum en été. A noter que les nombres maximaux des deux types de proies sont décalés, suggérant une compétition pour l'espace (modifié d'après CARMOUZE et al., 1983).
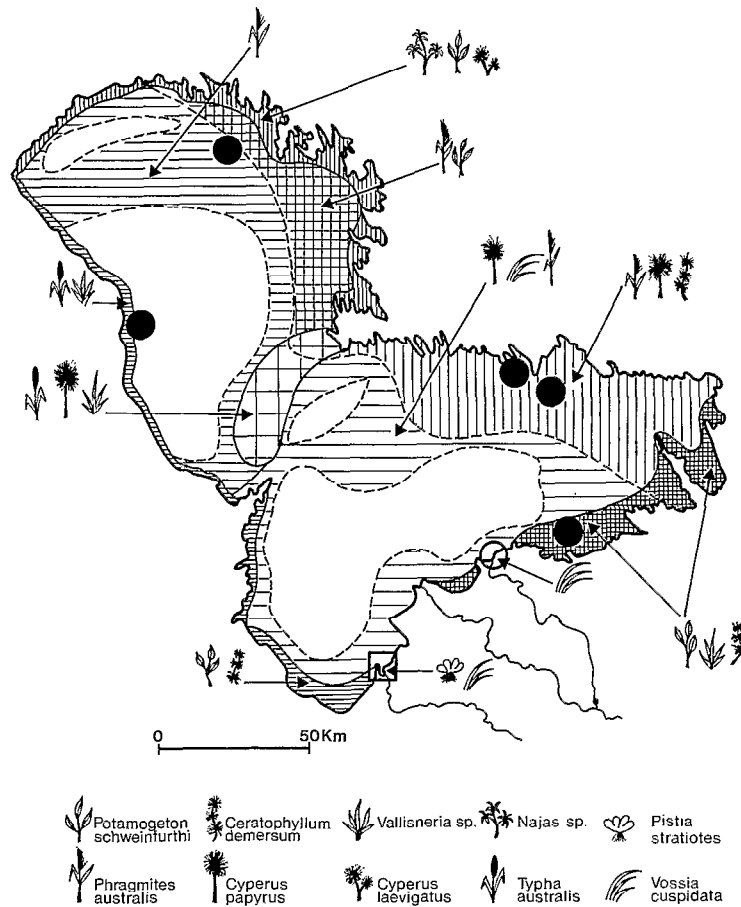
FIG. 15. — Distribution of submerged and emergent water plants in and around Lake Chad (*from* CARMOUZE *et al.*, 1983).

*Répartition des plantes submergées et émergées du lac Tchad (*d'après CARMOUZE et al., *1983).*

changes (fig. 14), which narrowly paralleled similar changes in chironomids (fig. 15). To the present writer, these changes represent the effect of intense fish predation during the summer months, but no proof of this exists, since no size classes have been studied (fish usually remove the largest sizes selectively).

Similar changes in mollusc biomass also occurred (LEVÊQUE, 1972). The highest values were associated with deep open water in the north basin, along the great barrier, and in the northern archipelago, and may be yet another reflection of local and temporal differences in susceptibility to fish predation.

Fauna associated with aquatic plants

The various emergent and submerged water plants of Lake Chad (fig. 15) harbour rich animal associations, ranging from ciliates to fish, amphibia, repti-

les, and mammals. *Potamogeton* and *Ceratophyllum*-dominated associations are by far the richest (figs 16, 17). Animals found here include Naididae among the Oligochaeta, Hirudinea, Nematoda, Rotifera, about 30 species of Cladocera, about 15 species of Cyclopoida and Harpacticoida, and the decapods *Caridina africana* and *Macrobrachium niloticum*. Among insects, chironomid larvae are a dominant group, with c. 60 species quantitatively important. Larvae of Odonata, Trichoptera and non-chironomid Diptera also occur commonly, while Coleoptera and Hemiptera are found here as larvae and as adults. Mollusca, finally, are represented by c. 10 species, all of which were quantitatively restricted to *Potamogeton* and *Ceratophyllum*. They include the bilharzia-transmitters *Bulinus truncatus*, *B. forskali*, and *Biomphalaria pfeifferi*.

There are no data on biomass and production of this tremendously varied community. Its diversity follows from a structural contrast with the monotonous sediment or open water environment. Branched macrophytes provide a three-dimensionally differentiated habitat, with good possibilities for shelter and mimicry, and in which vertical and horizontal gradients in light, temperature, oxygen, pH, and other variables occur. Table II illustrates some of the differences between the open water and the plant habitat. The fine leaves of *Ceratophyllum* and *Potamogeton* offer a much wider choice in microhabi-
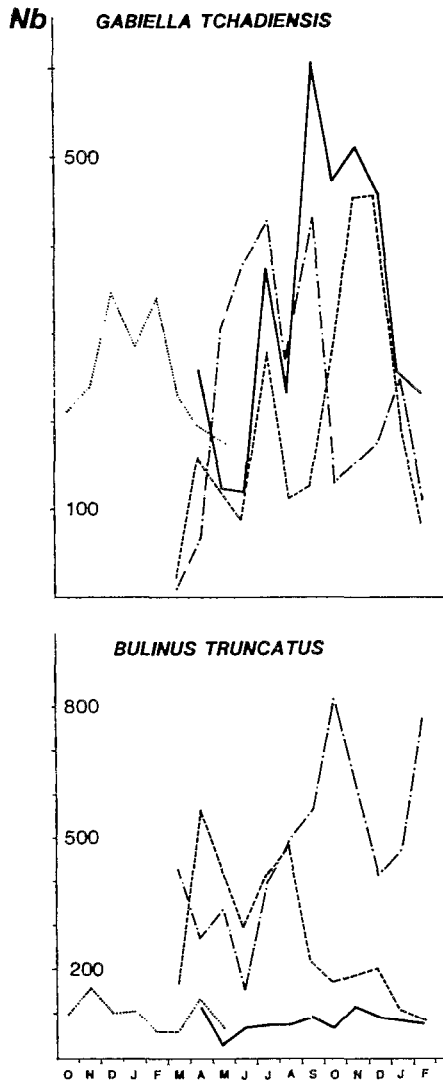
FIG. 16. — Seasonal variation of two Mollusca inhabiting the *Ceratophyllum* stands of lake Chad (N = numbers of specimens per 100 g plant dry weight). Note strong intersite variations, superposed on seasonal trends (*from* CARMOUZE *et al.*, 1983).

Variation saisonnière de deux mollusques habitant les herbiers de Ceratophyllum *du lac Tchad (N = nombre d'individus par 100 g. de poids sec). Les variations entre sites sont considérables, et se superposent aux tendances saisonnières (*d'après CARMOUZE et al., *1983).*
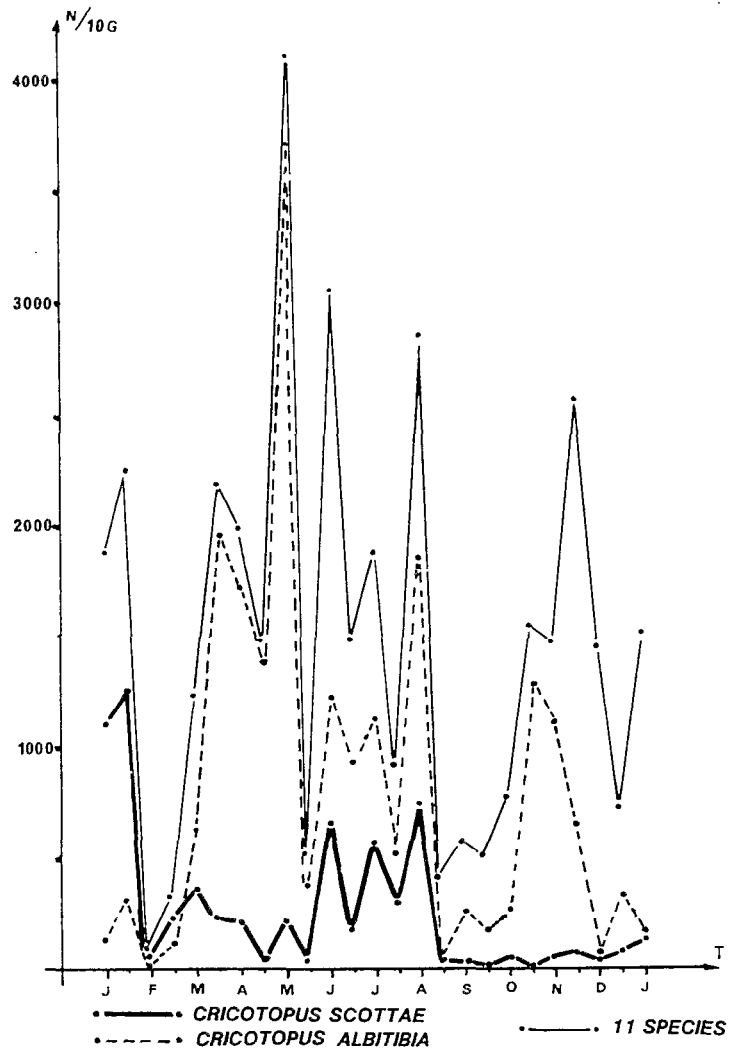
FIG. 17. — Complex seasonal fluctuations in chironomid density in *Potamogeton* stands in the Shari delta area (N = number of specimens per 10 g plant dry weight), involving the influence of external variables, but probably also of predation and voltinism.

Fluctuations saisonnières complexes des densités de chironomides dans les herbiers de Potamogeton *du delta du Chari (N = nombre d'individus par 10 g. de poids sec), résultant de l'influence de variables externes, ainsi que de la prédation et du voltinisme.*

TABLE II

Source of Differenciation	submerged macrophytes	open water
LIGHT		
- vertical gradient	x	x
- mosaic of brightness contrasts	x	-
- leaves with dark/bright sides	x	-
- horizontal gradient	x	-
- colour mosaic	xx	x
TEMPERATURE		
- vertical gradient	x	x
- horizontal mosaic	x	-
pH		
- vertical gradient	x	x
- horizontal gradient	x	-
CHEMICAL EXSUDATES		
- vertical gradient	x	-
- horizontal gradient	x	-

tats than the stems and roots of *Typha*, *Phragmites*, and Papyrus. They had up to four times more species than these plants with simple, linear leaves, and some of these species were not found elsewhere.

Large *Ceratophyllum* and *Potamogeton* beds also attract numerous Anura, which feed on the invertebrate fauna and reproduce here. Snakes like *Python* and *Grayia* in turn, feed on Anura and fish here. *Typha* and *Phragmites*-belts are sites where crocodiles, water turtles, and waterfowl aggregate, the latter especially for nest-building. The Sitatunga hides and feeds here, while the hippopotamus and water otter mainly find a daytime refuge here. Waterplants thus add significantly to the overall diversity of animals in a lake, marsh or wetland. Changes which lead to a disappearance of aquatic plants will thus automatically engender losses of animals, even terrestrial ones.

Weed-bed dwelling fish may be associated with plants in various ways. Some live here permanently, or occur in open spaces between beds of waterplants but sheltered from true open water, or feed or hide in macrophytes during part of the day or night only, or they may live here during their larval and juvenile stages and migrate to the open water later. Whatever the case, macrophytes provide an important habitat to the shallow lake ichthyofauna.

Seasonal variations studied in some of the invertebrates only were either absent, as in some molluscs (e.g. *Bulinus* : fig. 16), or present (e.g. in *Gyraulus costulatus* and numerous insect species). However, an example for chironomids (fig. 17) shows that such fluctuations are not simple and may result from a combination of such factors as voltinism, migration, predation pressure, competition, epizootic waves, and environmental fluctuations.

Fish of the Lake and the Floodplains

The fish fauna of Lake Chad is part of the so-called Soudanian fauna, which extends across Africa from the Nile to the Senegal. Like in its other biota, endemism is almost reduced to nil, an indication of the lake's geological youth and instability. Its fish fauna cannot be isolated from that of its feeder rivers and their floodplains. Extensive reproduction movements of adults from the lake to the river and floodplain are followed by return migrations of juveniles from the river to the lake (fig. 18). These seasonal movements are tuned to the flooding regime. Not all species that occur in the river (about 140) are found in the lake (about 85-90) but all species save one have been found in the river or its floodplain at one time or another. Some riverine species extend just to the river delta *(Polypterus bichir, Mormyrus hasselquisti, Auchenoglanis biscutatus ...)*, and this area was the richest of the lake (62 species recorded) (DURAND, 1983). Further north, this number declines, in the open water and waterplants alike. As in benthic molluscs, salinity was found to be of prime importance to this phenomenon. Electric fishes of the family Mormyridae disappeared above 300-400 μS cm^{-1}, and the continuing decline resulted in net-catches with as few as 9-12 species in the extreme north-east. The species that remained were found over the whole lake *(Lates niloticus, Distichodus rostratus, Sarotherodon galilaeus, Oreochromis niloticus,* and *Tilapia zillii, Epiplatys senegalensis, Eutropius niloticus, Hydrocynus forskalii, H. brevis, Synodontis schall, Labeo senegalensis)*. Another wide-ranging species, *Hemisynodontis membranaceus* was restricted to the south part of the north basin only.

Some species associations were typical of well-defined habitats. In the lower Chari, river-oyster beds are found which have fish species associated with them that do not occur elsewhere : *Petrocephalus simus, Nannocharax fasciatus, Synodontis filamentosus*. Some other species found in this association were much rarer elsewhere.

Another community of interest is that inhabiting periodically flooded depressions and temporary pools. In spite of the wide variation in duration of such environments, ranging from a few weeks to almost permanent flooding, characteristic species were found here. They include *Clarias spp., Ctenopoma spp., Protopterus annectens, Brienomyrus niger, Notobranchius spp.* and a few others. These are facultative or non-migrant species, with adaptations for air-breathing or capable of estivation in a cocoon or as an egg under conditions of complete drought (see further). They are the last survivors and the first colonists of aquatic systems that are periodically reduced to mud-pools or dry surfaces.
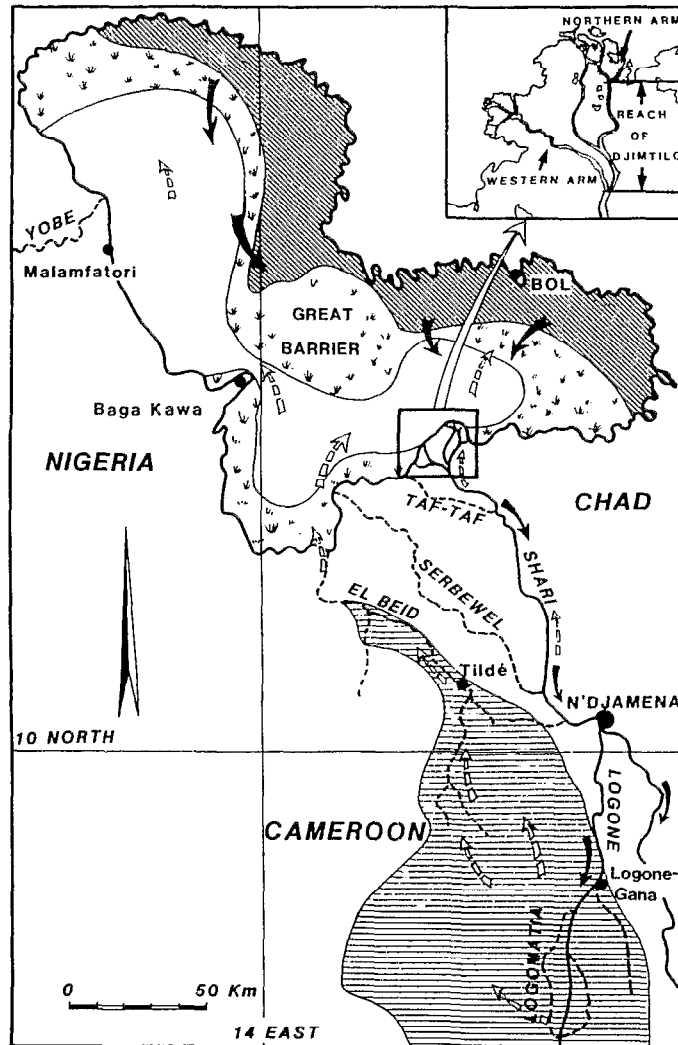
Fig. 18. — Seasonal migration of *Alestes baremoze* between Lake Chad and the Logone-Shari and its floodplain. Black arrows : adults. Open arrows : juveniles (*from* Carmouze *et al.*, 1983).

*Migration saisonnière d'*Alestes baremoze *entre le lac Tchad, le Logone-Chari et la plaine d'inondation. Flèches noires : adultes. Flèches blanches : juvéniles (*d'après *Carmouze et al., 1983).*

The Lesser Chad After 1972 : a Catastrophic Recession

Even before 1972, lake Chad cannot be described as particularly stable, as seen in some species successions that occurred. For example, between 1963 and 1968 there was a gradual replacement of the catfish *Schilbe mystus* by *Schilbe uranoscopus* (Mok, 1975), for unidentified reasons. However, as of 1973, the yearly hydrological deficit became catastrophical (figs 4, 19).

Physical and chemical changes associated with the separation of the two basins were relatively small in the south basin, which continued to be directly influenced by the inflow of the Chari waters, but profound in the north basin. They included a tenfold reduction in transparency (from about 90 cm to less than 10 cm) and a fivefold increase in conductivity during 1974, while the water level dropped by 3 m. After 1974, the south basin filled up to the 1972 level again, and regained much of its former physical and

chemical characteristics, but the north basin conti-
nued to contain only a series of temporary pools.

Aquatic Plants

The drying-up of the northern basin was so rapid
that water plants had no time to respond to it by a
succession of species. Moreover, incoming cattle
grazed on the young shoots that developed in areas
that had fallen dry, and thus the species that
remained were unpalatable or even poisonous (e.g.
Calotropis procera). Later, Typha australis recovered,
and the bush Aeschynomene elaphroxylon advanced
into the north basin from the south where it had
developed dense forests on the sediments fallen dry.
In its expansion in the south, it was accompanied by
Vossia cuspidata, forming meadows, and by Ipomoea
aquatica. Phragmites australis, Cyperus papyrus,
Polygonum senegalense and others declined. In May
1976, the total water area of the south basin was
c. 6000 km², and about 55% of this surface was
covered with waterplants. The cover in the north
basin at that time was of the same order of
magnitude, but water was almost absent. In all, the
aquatic vegetation cover expanded fivefold in
4 years time, but diversity declined dramatically.
Littoral, emergent species expanded, but submerged
species were almost eliminated. In the regulation of
these complex changes, the decisive events were
initially a decrease in transparency (eliminating
submerged waterplants), and increase in salinity
(eliminating such stenoionic species as Cyperus
papyrus). Emergent colonists of marshy surfaces, but
also algae were subsequently favoured. Although
from Lake Chad itself no such measurements are
available, we may infer from general limnological
knowledge that the well-known antagonism between
higher plants and algae (HASLER and JONES, 1940;
WIUM-ANDERSEN et al., 1982) was at work. This
mechanism has yet to be fully clarified, but involves
both the release of compounds that militate against
algae, and the uptake of excess (" luxury ") phospha-
te by higher plants, to keep it away from algae, and
prevent the buildup of waterblooms. Permanent
waterblooms indeed cause declines in populations of
waterplants by adding to the turbidity of the
environment, and by the algae releasing in their turn
compounds toxic to higher plants (WETZEL, 1975). In
moderate amounts, additions of organic matter and
of the nutrient salts they contain may be beneficial,
and even a condition to the proper functioning of a
wetland (FURNESS & BREEN, 1985). However, in the
north basin of Lake Chad, these inputs were too
massive and the changes too large for the previously
existing communities to absorb.

Algae

A generalized first response of the algal communi-
ties was an increase in biomass on a volume basis,

and a decrease in diversity, involving a shift in the
relative proportions of the different algal groups
present. As the drought worsened, three distinct
algal zones came into being (fig. 19) : the south, the
south-eastern archipelago, and the north. In the
south, euglenoids became more common than before.
The diatom Synedra berolinensis first appeared and
rapidly became abundant. During low waters, bio-
mass kept increasing and Cyanobacteria and Eugle-
noids increased in numbers; during floods, much
phytoplankton was washed away and diatoms beca-
me dominant. COMPÈRE and ILTIS (1983) describe
this community as riverine. The archipelago develo-
ped towards a swamp facies, dominated by Eugleno-
phytes. Biomass first increased, later decreased
again, but remained above pre-drought levels at all
times.

The northern basin showed the most spectacular
changes : biomass values (and chlorophyll content)
went up by two orders of magnitude. Extraordinary
values of up to 3.6 g m³ chl a were reached in August
just before the lake dried out. This evolution was
that of a freshwater lake transforming into a natron
pond. The phytoplankton community first simplified
to an assortment of Chlorophyceae and diatoms.
Above a threshold value of 2 g l⁻¹ salinity, Cyano-
bacteria took over from Diatoms. Such species as
Synechocystis minuscula, Anabaenopsis arnoldii, Os-
cillatoria spp. and Spirulina geitleri (often referred to
under the name Spirulina platensis) appeared en
masse.

As stated in a previous paragraph, the increase in
algal mass can be related to the decline in submerged
waterplants, and to increased turbidity, as evidenced
by the fact that these changes were much more
expressed in the north than in the south. As the
water volume in the north contracted, and thus
general salinity but, in particular, concentrations of
nutrients continued to increase, more and more algal
species and groups disappeared. Finally, the north
basin ended up with a strongly simplified commu-
nity consisting of few but very resistant and toxic
Cyanobacteria.

Zooplankton

For reasons of accessability, the zooplankton
studies during the reduction phase of the lake were
concentrated on the south-eastern archipelago,
which was transforming into a marsh. Profound
changes took place, and many species were lost from
the system. These included all Daphnia, Bosmina,
and later Tropodiaptomus and Thermodiaptomus.
Instead, littoral species such as Chydorus, Alona and
Macrothrix appeared in plankton samples. It has
been suggested that macrophytes release compounds
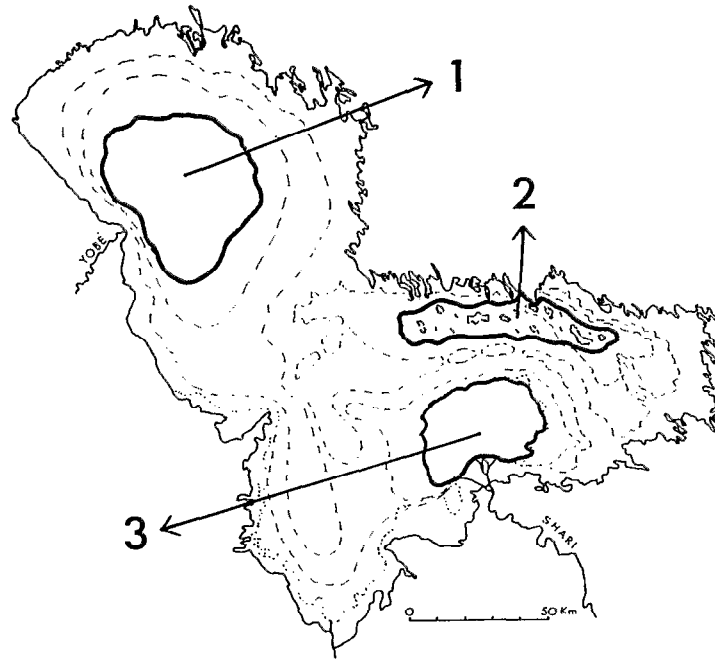
Fig. 19. — Recession of Lake Chad after 1972 and development, as of 1975, of different facies in the surviving parts of the lake, based upon aquatic plants and phytoplankton. 1. Evolution towards a natron pond; 2. towards a swamp; 3. towards a river delta (from CARMOUZE et al., 1983).

*Récession du lac Tchad après 1972 et développement, à partir de 1975, d'un faciès différent dans les parties survivantes du lac, basé sur les plantes aquatiques et le phytoplancton. 1. Evolution vers une mare natronée; 2. vers un marécage; 3. vers un delta de rivière (*d'après CARMOUZE *et al., 1983).*

that behave antagonistically towards limnetic Crustacea (PENNAK, 1973; DORGELO and HEYKOOP, 1985). Once the limnetic fauna has disappeared, previously littoral species can freely venture into the open water. If fascicles of Cyanobacteria are present here, providing resting-stations, their numbers may rise to appreciable levels.

In the northern basin, where *Daphnia* was commonest from the start, this species-group appears to have persisted for a long time during the contraction phase and so, apparently, did *Tropodiaptomus* and *Thermodiaptomus.* While *Daphnia* and other Cladocera may retreat from a habitat that is becoming unfavourable by going into diapause, it has not yet been established whether the African limnetic Diaptomids are capable of this as well. In Paradiaptomids *(Lovenula, Paradiaptomus, Metadiaptomus)* estivation has, conversely, long been known and, as the lake receded and salinity and turbidity increased, the latter group may have replaced the former *(Metadiaptomus mauretanicus, Paradiaptomus rex, P. schultzei, P. greeni* have been cited from the lake basin). As the Cladocera dwindled, rotifers replaced

them, as shown by the fact that the two remaining species *(Moina micrura, Diaphanosoma excisum)* did not increase above their pre-drought densities. However, in all only c. 30 rotifer species are on record from the Lake (POURRIOT, 1968; ROBINSON and ROBINSON, 1971). This is a surprisingly small number if compared to some other African and non-African sites (see further), and suggests that the inventory of littoral and periphytic species is far from complete. Other changes involved a replacement of *Thermocyclops incisus* by *Thermocyclops neglectus,* and a decline of raptorial feeders *(Mesocyclops).* The overall result was a considerable impoverishment of the zooplankton community. Possible mechanisms for this have been suggested earlier, and involve a different salinity tolerance, but also, in the case of the Cladocera, tipping the balance of competition in favour of efficient high-turbidity filter feeders, such as the rotifers. A reduction in diversity of algal food may also have contributed to the impoverishment of the zooplankton, as well as toxic effects of Cyanobacteria on certain crustaceans.

Benthos

The molluscs had slowly started to decline even before the catastrophic drought became obvious. As of 1973, this decline accelerated, especially on soft substrata. With the water level dropping, the muddy sediments became vulnerable to stirring, and *Melanoides tuberculata* replaced *Cleopatra bulimoides*, but later, at even lower water levels, *Melanoides* also declined. On sand and pseudo-sand, stability was greater than elsewhere, and the increased silt load (LEMOALLE, 1979) was disastrous to the filter-feeding bivalves only. Chironomids responded to lowering water levels by a reduction in number of species. Some species restricted to the North in the 1960's became dominant in the south-east in the late 1970's *(Cryptochironomus stilifer, Tanytarsus nigrocinctus)*. In the deltaic areas, changes were small, and species restricted to the inflowing river were not affected at all. The sequence of events, especially in the north, suggests that increased turbidity, and later increased salinity, were the main variables involved in the changes that took place.

Fauna associated with aquatic plants

Factors which determine the distribution of water plants automatically determine the distribution of their associated fauna. As the zone covered with waterplants increased from 12 % to 55 % of the total lake surface, the periphytic fauna may have expanded considerably, but most of this vegetation was marginal or restricted to wet sediments, and therefore of no great value to aquatic invertebrates. A special situation must have faced an open water predator like *Lates niloticus*, the nile perch, which lives among waterplants during part of its life only. Up to a length of 2 cm, the larva lives in the plankton and feeds on copepods and Cladocera. It then moves to the vegetation, and lives on insects and decapods. When it reaches a size of 15-20 cm, it turns to piscivory and moves to the open water, where it is known to be fairly tolerant of widely fluctuating environmental conditions, but needs much space. Initially, the drought thus favoured this species, but it soon suffered from both lack of hunting space and increased catchability by fishermen. As a result, it drastically declined.

Other fish

Most fish species reacted to the drought by mass mortality and a reduction in numbers of species. At first, some seasonally migrating species like *Alestes baremose* (fig. 18) ceased migrating, and retreated into the — then still deep — northern basin. This happened even before the two basins became separated. Later, loss of depth, high turbidity, and strong diurnal variations in dissolved oxygen (from 0 to 20 mg l^{-1} at 10 cm below the water surface),

combined with an increased fishing efficiency of the local fishermen, caused many fish populations to crash (BENECH *et al.*, 1976). Local extinctions were noted of such species as *Heterotis niloticus, Hydrocynus brevis, Tetraodon fahaka, Pollimyrus isodori, Mormyrus rume.* As they were lost, some surviving species assumed increasing quantitative importance. Lungfishes *(Polypterus senegalus)* with aerial respiration were among these, but also several *Tilapia* s.l. *(Oreochromis niloticus, O. aureus, S. galilaeus).*

In the latter three species, high initial mortalities occurred, but were more than compensated by a high reproduction, combined with a fair tolerance of low dissolved oxygen levels. Of these three species, *O. aureus* was adapted best. Its oxygen requirement was only 30 % of that of *S. galilaeus.*

Some Mochocidae with a good resistance to deoxygenation *(Synodontis schall, Brachysynodontis batensoda)* also increased in numbers at first (BENECH and LEK, 1981), because in spite of substantial mortalities, their abundance in the reduced water volume of the northern lake became higher than before.

By the end of 1974, the fish community had changed to a marshy facies, with air breathers *(Brienomyrus niger, Clarias* spp., and of course, lungfishes) as dominant elements. After the first drying up in 1975, *Clarias* became the single dominant fish.

The south-eastern archipelago, cut off from the southern basin by a barrier of waterplants several kilometers wide since April 1973, was initially much richer in fish species and biomass than before. This was a concentration effect, however, and it lasted only for a short time. Like in the north, hypoxia and CO_2-rich water filtering through the waterplants caused heavy mortalities. Increased vulnerability to fishing by the local people gave high fish yields of a short-time nature, but contributed to the depletion of the stocks of several species. A further factor is that for some feeding specialists, food became limiting.

The disappearance of Mollusca eliminated the malacophagous species, and when large-sized zooplankton became scarce, the planktivores also suffered. The surviving species combined good tolerance to hypoxia with feeding plasticity. One such plastic species is *Brachysynodontis batensoda*, normally a zooplankton eater, but which shifted to a detritus diet in the shrinking lake. It managed to survive, but that its new feeding mode was nothing but a starvation diet was demonstrated by the fact that its growth was arrested (BENECH, 1975). Because of all these events, the number of species dropped from 34 in early 1973 to 5-8 at the end of 1974.

In the south basin (the delta and "peri" delta),

%

0   10   20   30

Microcystis aeruginosa

M. flos-aquae

Anabaenopsis spp.

Lyngbya spp.

Aphanocapsa sp.   blue-green algae 80%

Chroococcus sp.

Synedra berolinensis

Nitzschia microcephala

Pediastrum sp.

Scenedesmus

Kirchneriella

other algae
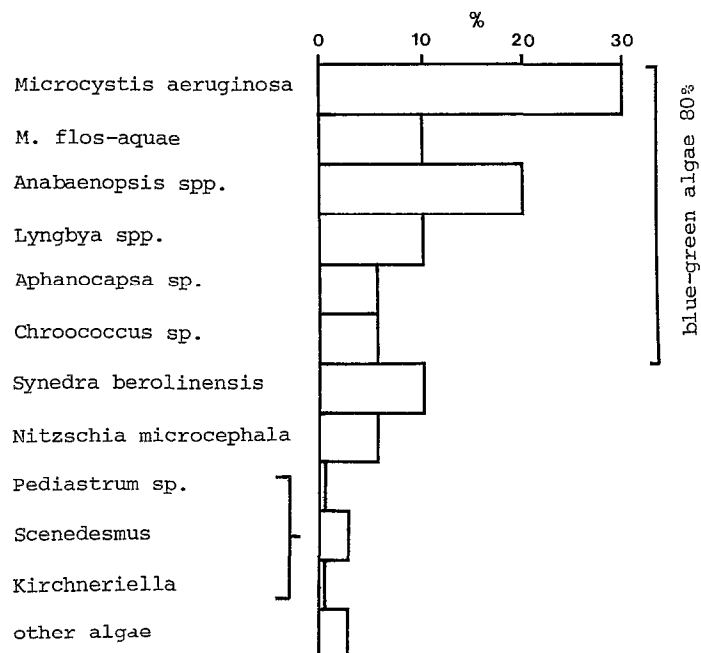
FIG. 20. — Phytoplankton composition and distribution of biomass between dominant taxa in the open waters of Lake George (from BURGIS et al., 1973).

Composition du phytoplancton et répartition de sa biomasse entre taxons dominants de l'eau libre au lac George (d'après BURGIS et al., 1973).

TABLE III

	herbivores	carnivores	detritivores
zooplankton	*Thermocyclops	Mesocyclops	
	crassus	"leuckarti"[1]	
	Cladocera	*Chaoborus spp.	
fish	*Tilapia nilotica	*Haplochromis	Tilapia leucosticta
		angustifrons	
	*Haplochromis	H. squamipinnis	
	nigripinnis	H. pappenheimi	
	T. leucosticta	Aplocheilichthys	
		Protopterus	
		Clarias	
		Bagrus	
benthos		Procladius	oligochaets
			Chironomus
			Procladius
			ostracods

(1) True M. leuckarti does not occur in Africa ; the local species is probably
    M. aequatorialis, or a related species.

changes were much less dramatic, and involved little extinction. Lake species that had retreated south replaced riverine species here, but before all, migratory behaviour was altered, because of lack of inundated areas for spawning and return pathways to the lake afterwards. Some former migrants lowered their age and size at first reproduction (e.g. *Alestes baremoze* : Durand, 1978), a response also recorded from the overexploited fish populations of Lake George (see hereafter).

A Comparison With Lake George

A detailed description of Lake George is given by TALLING (1992). Situated on the equator at an altitude of 910 m, it is small, has a maximum depth of 2.4 m, and almost constant water levels (amplitude 0.1 m a^{-1}) and annual solar energy input. Stratification occurs, but it builds up and breaks down on a diurnal time scale. The seasonal temperature amplitude is only 2 °C, and much smaller than the diurnal extremes (up to 10 °C). The hydrological balance is positive, and water leaves the lake towards lake Edward through the Kazinga channel.

In the early Pleistocene, it was part of a much larger (Kaiso) lake, which included lakes Edward and Albert, and had a fauna in which soudanian elements (*Lates niloticus, Hydrocynus*, the nile crocodile ...) were widespread. Faulting separated the individual lake beds, and in the Holocene (c. 8-10000 y BP), volcanic inflows into the lake caused many species extinctions. Finally, an arid climate phase caused Lake George to dry out completely. It emerged in its present form only around 4000 BP, and was recolonized from Lake Edward, by rivers that descend the Ruwenzori mountains, by passive dispersal of dormant stages, and by active immigration of party aerial biota (mainly insects).

The overall result is a lake which still shows little biotic diversity. The fish, for example, represent only an extract of the cichlid-flock of the fauna of Lake Edward (GREENWOOD, 1973, 1980).

THE PHYTOPLANKTON

The biomass of the open water of Lake George is phytoplankton-dominated : algae make up 95 % of the total biomass and 99 % of the plankton biomass (Tab. III) (BURGIS *et al.*, 1973). Cyanobacterial colonies predominate (fig. 20), with 5 taxa composing 75% of them *(Microcystis aeruginosa, M. flosaquae, Anabaenopsis spp, Lyngbya sp., Aphanocapsa sp.)*. Diatoms and Chlorophytes are of minor importance. The predominantly light winds from the north cause an anti-clockwise rotation of the lake water. While this does not break down the vertical stratification in temperature and oxygen, it is

sufficient to produce a pattern of concentric rings in phytoplankton densities. Another lake motion of interest is caused by short storms (mean duration 1 h, wind velocity more than 12.5 m sec^{-1}) which occur about once per 3 weeks. These storms cause a turbulent mixing of the water column and stir the bottom mud to a depth of 20 cm. There are also daily afternoon breezes which initiate the diurnal breakdown of vertical stratification (VINER and SMITH, 1973).

The phytoplankton responds to these physical disturbances as follows : with the onset of thermal stratification (c. 10 h 00), the uniformly distributed phytoplankton begins to sink. In the afternoon, it accumulates below the euphotic zone and begins to sediment to the bottom. Towards the evening, turbulent cooling restores an even vertical distribution.

Because of their gas vacuoles, which true algae do not have, Cyanobacteria can actively regulate their day-depth, eventually shade other algae, and thus acquire a competitive advantage over them. However, among viable algae found in the sediment down to a depth of 20 cm (fig. 21), Cyanobacteria were again dominant. After a storm, the numbers of *Microcystis* increased by a factor 2-7, while diatoms and chlorophytes did not. An ability to survive in conditions of anoxia and darkness therefore seems to be among the many biological advantages of the Cyanobacteria.

The standing crop is particularly high and stable over the year (and over the years), and fluctuates around 400 mg chl a m^{-2} or c. 30 g C m^{-2} (GANF and VINER, 1973), with slight diurnal departures of production from a mean value. Extremes observed were 20 and 40 g C m^{-2}. For a standing crop to stabilise at such a high level, a delicate balance between production and consumption or other losses of biomass is required (GANF and VINER, 1973).

Disturbances, such as the turbulent mixing of bottom mud and water during storms, considerably lowers the oxygen of the water column. This has little effect on the phytoplankton community (hence its composition and stability), but greatly affects the animal components of the system.

AQUATIC PLANTS

The shores of lake George are devoid of littoral water plants, except for Papyrus-swamps in the north, where rivers from the Ruwenzori debouch into the lake. The possible effects of deoxygenated water from these swamps flowing into the lake have not been investigated. In view of the tremendous primary production in the lake, any effect is likely to be of local importance only. Submerged species such as *Ceratophyllum* are limited to some river mouths;
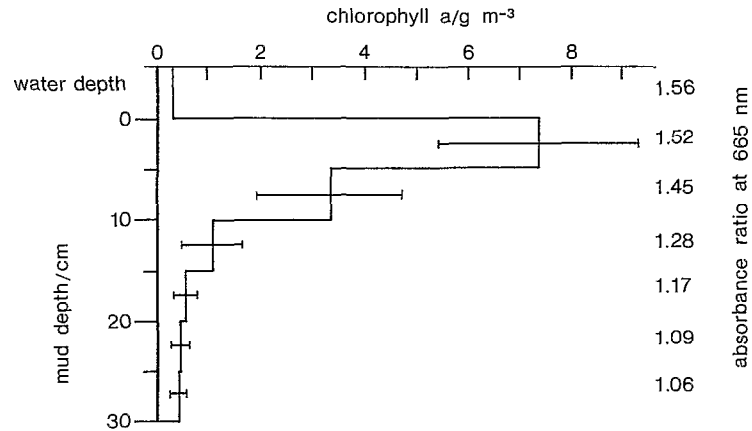
Fig. 21. — Algal biomass (expressed as chl a) floated out from liquid mud in lake George. At a depth of 10 cm, most of these algae were still viable, as shown by the absorbance ratio at 665 nm before and after acidification (right hand side of figure) (*from* Burgis *et al.*, 1973).

Biomasse algale (exprimée en Chl a) séparée par flottation du sédiment fluide du lac George. A la profondeur de 10 cm, la majorité des algues restait viable, ainsi que démontré par l'absorbance à 665 μm avant et après acidification (partie droite de la figure); d'après Burgis et al., *1973).*
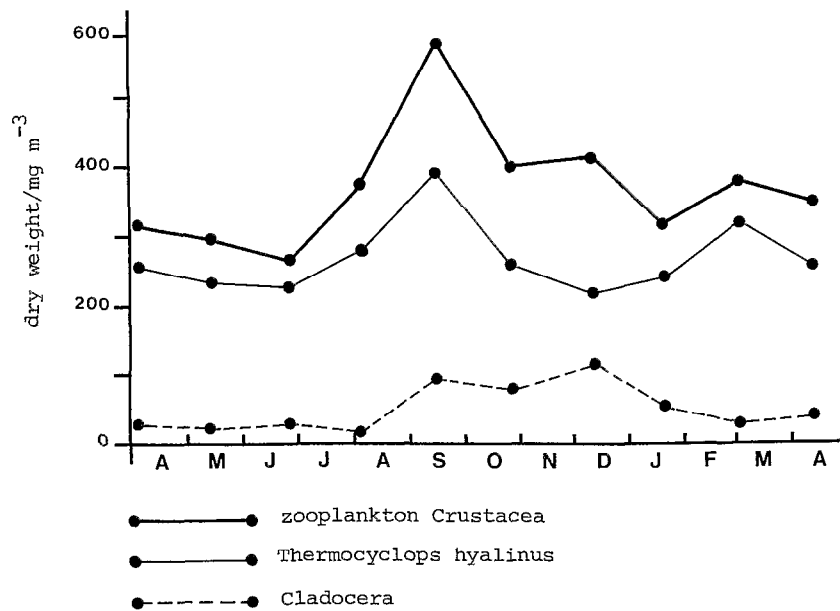
Fig. 22. — Seasonal variation in zooplankton biomass (Cladocera, *Thermocyclops crassus*, and sum of both) in Lake George. All species involved are mainly grazers, but note that the Cladocera are out of phase with the Copepods (*from* Burgis *et al.*, 1973).

Variation saisonnière de la biomasse du zooplancton (Cladocères, Thermocyclops crassus, *et la somme des deux) du lac George. Toutes ces espèces sont phytophages, mais les Cladocères sont déphasés par rapport aux copépodes (*d'après Burgis et al., *1973).*
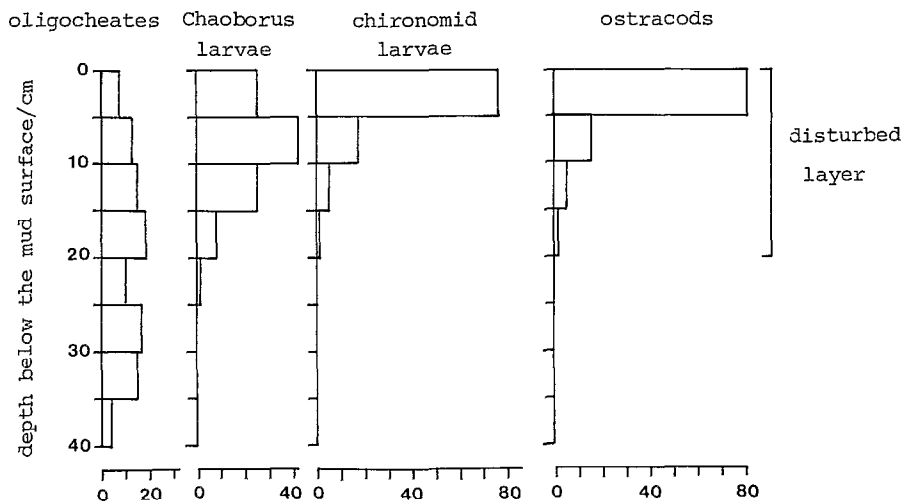
FIG. 23. — Percentage composition and depth distribution of the benthic fauna of Lake George (from BURGIS et al., 1973).

Composition (pourcentage) et distribution en profondeur de la faune benthique du lac George (d'après BURGIS et al., 1973).

mouths; floating species such as *Pistia stratiotes* are found locally along the western shore.

Although no studies were undertaken to explain this scarcity of water plants, it seems related to the eutrophic condition of the lake (abundant nutrients available to the phytoplankton), and the dominance of Cyanobacteria.

ZOOPLANKTON

The limnetic community is simple and composed of a herbivorous cylopoid, *Thermocyclops crassus*, and the carnivorous *Mesocyclops equatorialis*. Cladocera are present in moderate numbers : *Daphnia barbata, Moina micrura*, and *Ceriodaphnia cornuta*. The mean standing crop, c. 1 000 animals per liter, represents a low biomass, which is rather invariant over the year. Increases in Cladocera are out of phase with those in copepods (fig. 22), an indication of avoidance of competition between both groups.

Although Cladocera reproduce much faster (and parthenogenetically) than copepods, their number in lake George is only a fraction of that of the copepods. Moreover, they are all small species (max 1 mm). This is evidence of predatory removal of (larger) Cladocera by fish. Because adult cyclopoids are excellent swimmers, they avoid fish more efficiently than the slower Cladocera.

The horizontal distribution forms concentric rings with maximum density in the centre of the lake, even more clearly than in the phytoplankton (fig. 25). Planktivorous fish behave in the opposite

way, therefore these patterns may result from active avoidance of predators, active search for a food optimum, passive concentration by currents, or it may be the result of differential predation. Probably, a combination of several factors is at work.

Rotifera have been little studied. They increase in abundance and diversity near the swamps, where up to 15 species co-occur with littoral Cladocera (*Chydorus sp., Alona spp.*).

BENTHOS

Except at the lake margins, the substratum is a uniform, soft mud. The benthos found in its top 20 cm is composed of chironomid and Chaoborus larvae, and ostracods (fig. 23). Oligochaets even occur up to depths of 40 cm. This community is depauperate in species and groups, because of the deoxygenated and soft substrate. All species are detritivores, except one or two chironomids which are partly carnivorous, and *Chaoborus* which burrows into the mud during the day, but moves into the water column to feed on zooplankton at night.

Only close to the shore, on sand, clay, and gravel, is a richer community, composed of molluscs, nematods, and insects found. Its dependence on the nature of the substratum is similar to that in Lake Chad.

FISH

About 30 species of fish occur. More than half belong to the cichlid group of *Haplochromis* s.l., a
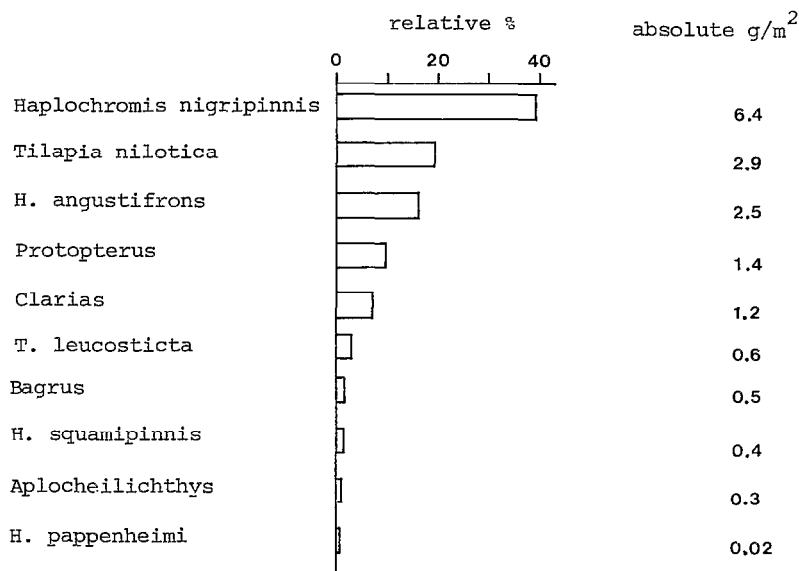
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                                    relative %           absolute g/m²

                                0      20     40

Haplochromis nigripinnis                                          6.4

Tilapia nilotica                                                 2.9

H. angustifrons                                                 2.5

Protopterus                                                     1.4

Clarias                                                         1.2

T. leucosticta                                                  0.6

Bagrus                                                          0.5

H. squamipinnis                                                 0.4

Aplocheilichthys                                               0.3

H. pappenheimi                                                 0.02
```

FIG. 24. — Relative and absolute mean biomass of the ten fish species, which occur lake-wide in Lake George (*from* BURGIS *et al.*, 1973).

*Biomasse moyenne relative et absolue des dix espèces de poissons réparties sur l'ensemble du lac George (*d'après BURGIS et al., 1973).

formerly giant genus now fragmented finely into numerous small genera by GREENWOOD (1980).

Only ten species are found lakewide in the open water, of which the two algivores *Enterochromis nigripennis* and *Oreochromis niloticus* account for 60 % of the biomass (fig. 24). *Oreochromis niloticus* is the principal component (up to 80 %) of the commercial fish yield of the lake, which amounts to some 5,000 t y⁻¹. This figure, the expression of man's effect as a top predator on the system, represents an overfishing. It stresses the fish to mature at smaller-than-normal sizes (BURGIS *el al.*, 1973), as in the case of the river-mouth populations of *Alestes* in the Chari during the droughts.

One of the remarkable things about the fishes of Lake George is that, with three exceptions, all are carnivores but with diets that vary species-wise. Although they are less extremely specialized than the inhabitants of ancient lakes like Tanganyika, Malawi, and Victoria, some are true food specialists. This situation reflects the condition that Lake George's ichthyofauna is composed of immigrants from Lake Edward, an ancient lake.

The ichthyomass is distributed in concentric rings across the lake, with peak densities near the shores (fig. 25), a result of species-specific habitat selection with few species (algivores and some piscivores preying on the algivores) in the lake centre, and most species in the more differentiated littoral. *Aplocheilichtys* shoals are associated with *Pistia*-rafts.

Of considerable interest is the occurrence, at intervals, of massive fish kills. These happen when the effects of storms combine with the nocturnal respiration of the biomass to produce deoxygenation of the water column. Because such mortalities rarely extend over more than half of the lake, populations usually recover rapidly. However, the situation is strikingly analogous to that of Lake Chad in its shrinking phase. It appears that at a critical depth (less than say, 3 m), wind stress and an organic sediment combine to form a powerful disruptive force in any shallow lake, in spite of constancy of all other variables.

Other Systems

The previous examples show the varying degree to which two categories of external variables, those related to climate, and those related to basin structure, interact with one another, and with the living world of shallow lakes. Beside great differences, many similarities in structure and functioning were found. The reduced Lake Chad, by losing much of its physical diversity, developed a flora and fauna that was becoming more and more related to that of Lake George.

To evaluate the generality of this conclusion, a brief look at some other systems is necessary. The lowland equatorial Lake Tumba (760 km²), situated
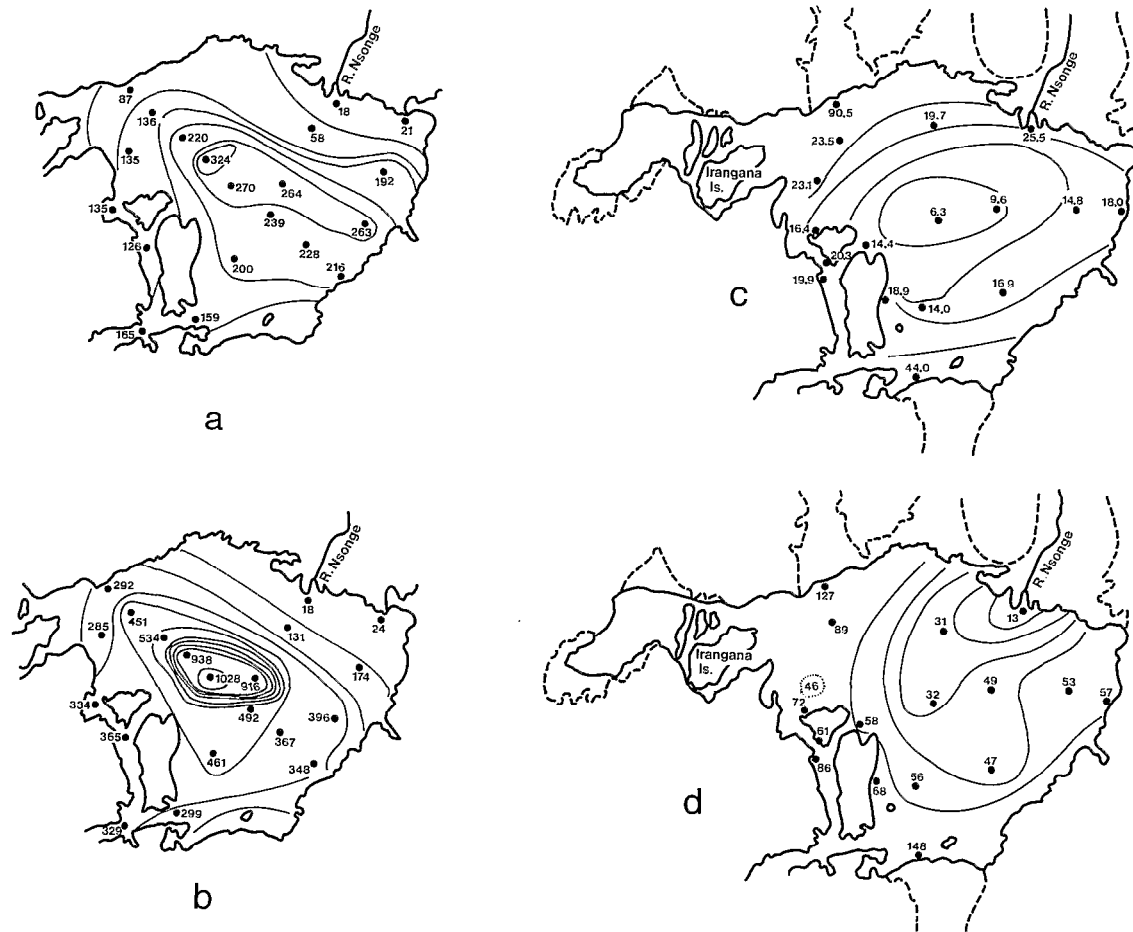
FIG. 25. — Concentric and centripetal distribution of biomass in Lake George. a. Phytoplankton (µg chl a l⁻¹); b. zooplankton (µg DW l⁻¹); c. pelagic fish (g FW m⁻²); d. fish density in 10³ ha⁻¹.

Répartition concentrique de la biomasse du lac George. a : Phytoplancton (µg Chl a 1⁻¹); b : zooplancton (µg PS 1⁻¹;, c : poissons pélagiques (g PF m⁻²); d : densité des poissons en 10³ ha⁻¹.

just south of the equator (maximum depth 3 m), has a water level fluctuation of 2 m y⁻¹. At high levels, it completely floods the surrounding forest of *Oubangia laurentii* trees. Its bottom is clayey and little diversified; water plants (floating meadows of *Echinochloa*) occur in sheltered bays, the only areas where a few centimeters of mud may accumulate. The water flowing in from the forest is brown, loaded with humic material, low in conductivity, and acidic (pH 4.5-5.0). Molluscs are therefore absent, and ostracods scarce. Open water zooplankton is sparse and without large copepods or Cladocera. Only in the floating meadows is some diversity in Crustacea and insect species found (MARLIER, 1958). To the fact that the open water is almost a desert, the c. 65

species of fish contribute a great deal, even though many occur only at the lake margins, in the flooded forest, and in the isthmus that leads to the Zaire river. Species with aerial respiration abound, and small species, mostly clupeids and characids, are unusually abundant. The latter are mostly zooplankton-eaters. Besides, plant-, insect-, seed-, and fish-eaters have been identified. In this dystrophic environment, cyprinids are absent, but mormyrids are plentiful.

One trait in common with shallow lakes elsewhere is that fish migrate into the inundated forest at high water levels to reproduce, and migrate back at receding lake levels.
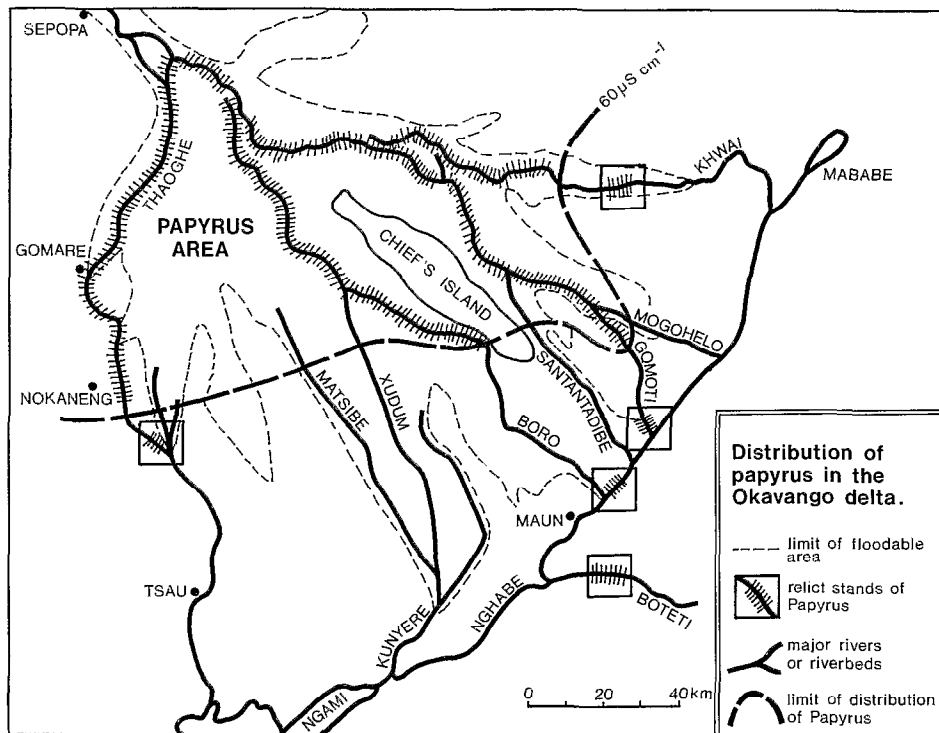
Fig. 26. — Distribution of *Papyrus* in the Okavango swamps (redrawn *from* SMITH, 1976).

Distribution des Papyrus *dans les marécages de l'Okavango (*d'après *SMITH, 1976).*

The salient factor regulating this lake, and differentiating it from many others, is open-water acidity derived from humic material. On the one hand, it eliminates all animal groups that depend on Calcium salts for forming an exoskeleton, while on the other hand, nighttime deoxygenation by oxidation of humic organic matter favours animals with additional (aerial) respiratory organs.

A system related to Lake Chad in many respects is the endorheic Okavango delta. The Okavango river discharges into a triangular, downfaulted, incipient rift valley (COOKE, 1976). Its salinity and conductivity are almost identical to that of the Chari river, but an estimated evaporation of 85% causes a strong increase in salinity southwards (from 50 µS cm⁻¹ in the river to as much as 5,000 µS cm⁻¹ in some pools at the distal margin of the delta).

The vegetation is zonally arranged, as a response to this gradient. The river banks above the delta have *Phragmites* and, in deeper waters, *Papyrus*. In the permanent swamps (up to 4 m deep), various submerged plants *(Nymphaea, Ceratophyllum, Utricularia)* abound. Like in Lake Chad, *Papyrus* disappears with increasing conductivity (60 µS cm⁻¹)

(fig. 26). Beside salinity, seasonal drying up may also be important in this species, however. GAUDET (1975) found that it only grows well in permanently waterlogged soils. Downstream of the *Papyrus* belt, only *Phragmites* remains. This salinity-tolerant plant even extends down to the Makgadikgadi salt pan area, where salt crusts testify to the rare floods that reach that far south. *Phragmites* is here found in damp depressions between the pans, but not in the pans themselves.

Algal diversity has not been studied, but primary production is low (THOMPSON, 1976). Swamps and riverside lakes along the Okavango in the Caprivi (unpublished data) contain a rich zooplankton, with the calanoid *Tropodiaptomus* cf. *kraepelini*, the cyclopoid genera *Thermocyclops* and *Mesocyclops*, and the Cladocera *Ceriodaphnia* cf. *cornuta, C. dubia, Bosmina longirostris, Diaphanosoma exisum, Moina micrura, Daphnia lumholtzi*, and *D. barbata*. During the dry period, when swamps and pools shrink back, this community is depleted by fish predation, and all but the smallest elements of the zooplankton survive (HART, 1986). This community is reminiscent of Lake Chad, of the internal delta of the Niger

FISH BIOMASS (%)

Hepsetus	7%
Serranochromis	11%
Clarias	5%
Schilbe	3%
Alestes + Barbus	3%
Haplochromis	7%
Synodontis	1%
Mormyrus	1%

Fish

Invertebrates   Plants + Algae

Organic
Detritus

Tilapias 60%
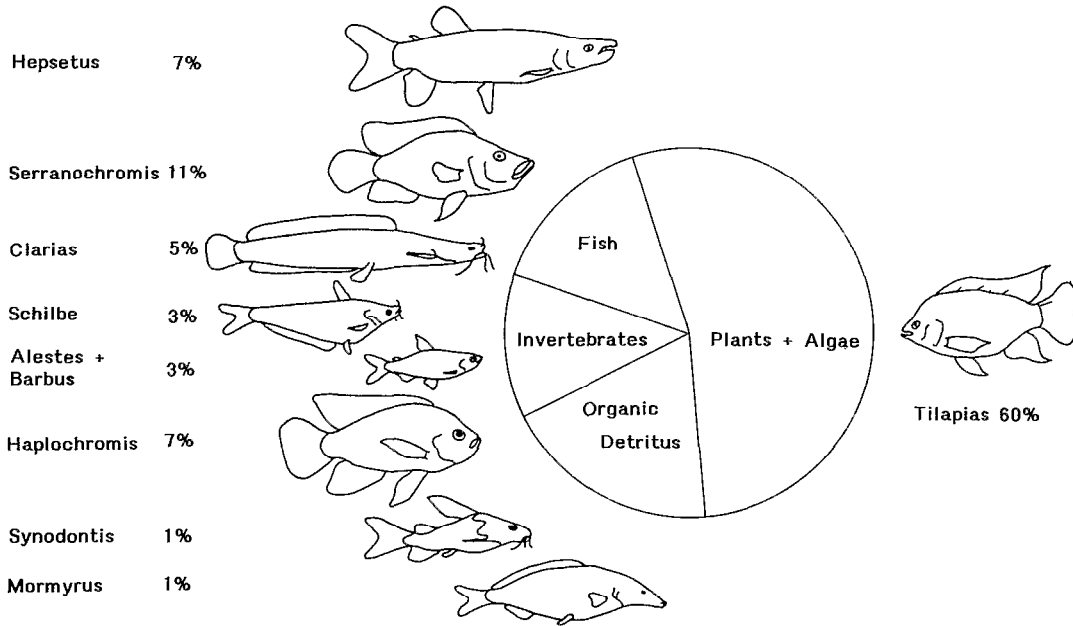
Fig. 27. — Percentage composition of the fish fauna of the Okavango delta and of their diet (*from* Fox, 1976).

*Composition (en pourcentages) de la faune ichtyologique du delta de l'Okavango et de son régime alimentaire (*d'après Fox, 1976).*

Area under flood

M J J A S O N D J F M A M

increasing temps   Rains

Mortality effect

Mean density of fish

Concentration effect

Dilution effect

Population growth
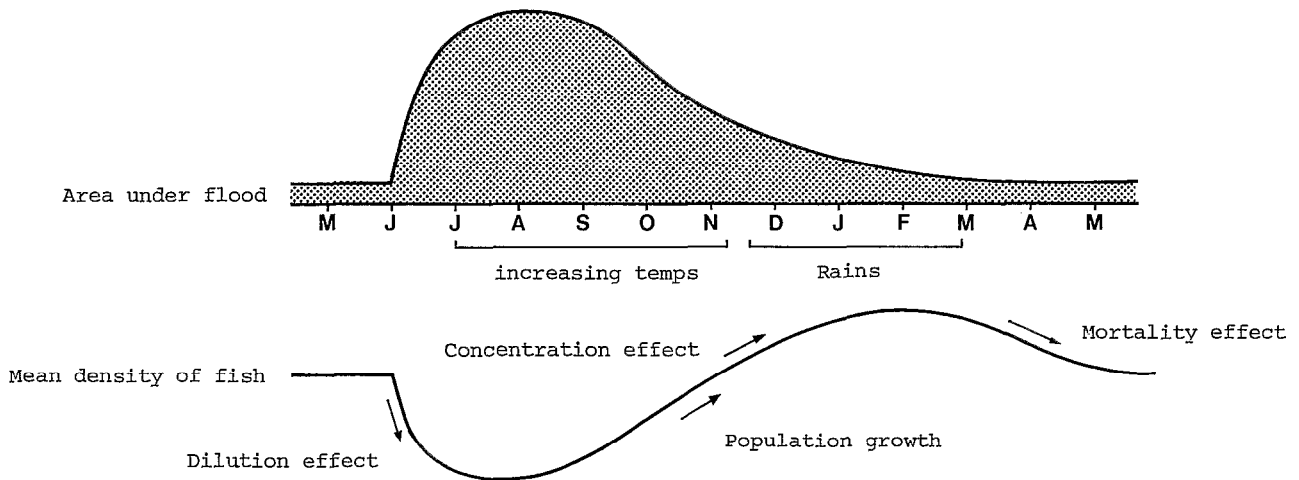
Fig. 28. — Scheme of the relationship between flooding regime and temperature variation, and the fish of the Okavango delta. Reproduction occurs during and after the rains. Heavy mortalities occur afterwards (*from* Fox, 1976).

*Schéma de la relation entre le régime d'inondation, la variation des températures et les poissons du delta de l'Okavango. La reproduction se situe pendant et après les pluies. De fortes mortalités se produisent ensuite (*d'après Fox, 1976).*

(DUMONT *et al.*, 1981), of the Sudd swamps (GREEN, 1984), and of the Pongolo floodplain (personal unpublished observations). Another point of agreement is the fish fauna. Over 80 species live in the delta proper (SKELTON *et al.*, 1985), and their ecological spectrum agrees with that of Lake Chad and of the internal as well as the lower Niger delta lakes. A few top predators occur, and further a variety of fish, invertebrate, and zooplankton eaters, but which are sufficiently adaptable to switch to completely different diets in times of change. Waterplant, algal, and periphyton feeders, mostly cichlids, compose about 50 % of all species (fig. 27). MERRON and BRUTON (1989) argue that, while the various tilapia, tigerfish, and african pike *(Hepsetus odae)* are currently overfished by professional fishermen and sport fishers, the smaller but prolific silver catfish, *Schilbe mystus*, is underexploited and that fishermen should be encouraged to use smaller-sized gill nets to catch more of this species, which lives in the open waters. The danger of removing even more, and smaller *tilapia* along with the *Schilbe* is small, because small-sized *tilapia* inhabit the dense plant communities lining the various channels and pools, not the pelagial, until they are at least two years old.

Lake Ngami, situated south of the delta proper and connected to it by an intermittent river channel varies in area from nil to 200 km², and its depth is 3.5 m when full. It can pass from full to dry in two years, and was dry for many years before 1951, and again in 1973-1974, when it was covered by a salt crust of variable thickness. No waterplants occur here.

Like in Lake Chad, massive spawning migrations of fish into the floodplains occur during floods. When floods reach lake Ngami, numerous species swim towards the lake or are washed into it. When its level drops and salinity increases, a rapid elimination of species takes place, and soon only few species tolerant of wide fluctuations of several variables (temperature, dissolved oxygen, and turbidity) remain : small *Barbus, Alestes* and *Clarias* spp. This evolution runs nicely parallel to that in the north basin of Lake Chad during the drought of the 1970's.

The relationship between flooding and fish populations in the delta is shown schematically in figure 28.

The internal delta of the river Niger, the Sudd swamps of the White Nile and, on a smaller scale, the Pongolo floodplain, are other mosaics of permanent and periodic swamps, lakes, and floodplains. They are not, however, in a terminal (endorheic) position, and their salinity problem is less acute. In the permanent Niger lakes, poverty of waterplants is striking, *Phragmites* being the dominant species everywhere. This may well be a comparatively recent phenomenon, and the result of cultural eutrophication. Cattle is indeed extremely numerous, and most shallow lakes have permanent cyanobacterial blooms. Curiously, *Papyrus* does not occur here. It may have recently disappeared or be absent for historical reasons (DUMONT and VERHEYE, 1984). The zooplankton is as rich as that of Lake Chad and composed of almost the same species (DUMONT *et al.*, 1981). About 120 species of fish occur, exploited intensely, and once again largely composed of the same species as in Lake Chad.

The terminal Niger delta, and especially its upper part, which is not influenced by the tides of the Atlantic Ocean, is another area rich in shallow lakes (mostly of oxbow origin) and wetlands (see earlier). Most of these have hardly been studied, but Lake Oguta is an exception (NWADIARO, 1987 ; NWADIARO and UMEHAN, 1985). The majority are shallow, productive, turbid, moderately acidic lakes, situated in primary forest, and support traditional fisheries. Since the mid 1980s, *Eichhornia* has invaded the area, and is locally becoming a problem. Most lakes have an extremely low standing crop of zooplankton, the result of cropping by fish, but a considerable diversity, especially in the littoral area. In one of these lakes, Iyi Efi, the protective umbrella of *Pistia* and other macrophytes sheltered a rotifer fauna of c. 140 species (SEGERS *et al.*, 1993), a world record.

Lake Chilwa, finally, bridges the gap between Lake Chad and Lake Ngami. The present lake level is about 5 m lower than 1,000 years ago. Even when full at its present average level (1962 : lake area 700 km², surrounding swamp 600 km², floodplain 650 km², max. depth 4 m, mean depth 2 m), it is relatively saline (conductivity 1,000-2,000 μS cm^{-1}, increasing from the marginal swamp towards the centre). It is endorheic and has a yearly water renewal of 60-80 %.

Thus, minor fluctuations in annual rainfall in its catchment cause level fluctuations of 0.5-1 m in the lake, and slightly stronger fluctuations cause the lake to dry out. An 8 year drought cycle has been detected by KALK *et al.* (1979), and the lake notably dried out in 1960 and 1968. The 1968 drought is best documented. It resulted from a decline that took 3 years, but it filled up again in one year of time thereafter.

In considering the biota of this lake, one cannot but equate the modern "normal" situation of the lake with that of Lake Chad in 1972-1978. Its swamps are indeed dominated by *Typha domingensis*, with patches of *Aeschynomene pfundii*. *Papyrus* is scarce and limited to the mouth of the inflowing rivers. Channels intersecting the *Typha*-stands are grown with *Ceratophyllum, Utricularia*, and other submerged species (HOWARD-WILLIAMS, 1979).

The Chilwa-full association is perfectly similar to the south basin of the lesser Lake Chad of 1976-1978. The analogy can be taken further if one considers the algae : in the inflowing rivers, diatoms and Chlorophyta are found, but in the lake, Cyanobacteria dominate (Moss, 1979). At average lake levels, such genera as *Anabaena* and *Anabaenopsis* abound, but at low levels, when conductivity exceeds 5,000 µS cm⁻¹, only *Spirulina geitleri* is left, in the same enormous quantities as in the saline pools north of Lake Chad, some natron lakes in the Rift valley, and the salt lakes of Ounianga in the Sahara (Léonard and Compère, 1967 ; Vareschi, 1978).

Since the bottom mud is fluid and anoxic, benthos is rare and composed of a few chironomid species, and of larvae of the beetle *Berosus* sp. These have long spiny expansions on the side of their body, which prevent them from sinking into anoxic mud. Mollusca are limited to the contact line between the lake and the swamp (*Aspatharia* sp., *Lanistes ovum*). A massive mortality in these species was recorded when the lake first contracted from the swamp. Further contraction was accompanied by increasing salinity. Between 5,000 and 10,000 µS cm⁻¹, most of the residual fauna died out (McLachlan, 1979).

The fish fauna of the lake is simple : *Barbus paludinosus*, *Clarias gariepinus* and *Oreochromis spiranus chilwae* are its only three open-water species (Furse *et al.*, 1979). The latter is the only endemic fish taxon of the lake : it evolved here after Lake Chilwa became separated from Lake Chiuta, situated north of it, some 9,000 years ago. Lake Chiuta, deeper and still a freshwater lake, has a much richer fauna, with about 35 fish species. Although it has not been studied in detail, it is logical to assume that this fauna was originally shared by both lakes, and that the impoverishment of Lake Chilwa over 9,000 years is paralleled by the changes that took place in Lake Chad in a period of 6 years. As could be expected, the food regime of the fishes of Lake Chilwa is generalised and opportunistic, *Barbus* and *Clarias* having a strong animal component, *Oreochromis* a plant component to it. All species are either adapted to low dissolved oxygen levels, or have accessory air-breathing organs.

In the Chilwa swamp, a much fresher environment, about 10 more fish species live, while still others (including several Mormyridae, which are notably intolerant of high salinities) are restricted to the inflowing rivers. The open-water species spawn in the swamp and the floodplain at high water level : whether upstream migrations occur is unknown. The aquatic plant world of the swamp is composed of *Typha* and of *Ceratophyllum*. The associated invertebrate fauna was similar to that of Lake Chad, and

showed the same preferences : *Typha* had the poorest and, because of its spatial differentiation, *Ceratophyllum* had the richest associations.

Whenever the lake dries out, some lagoons and river mouths act as refuges for the fish of the lake, but most of the stocks die. The species die in an orderly fashion, dictated by their tolerance to turbidity and anoxia : *O. s. chilwae* is lost first, followed by *Barbus*, while *Clarias* only disappears with the very last water. At low lake levels, it does in fact contribute to keeping a constant level of high turbidity, by actively stirring up the bottom mud while swimming and feeding.

When the lake fills up again, recolonization occurs at rates which are species-dependent. Most colonists are derived from relict populations that survived in the bordering swamps or rivers, but there exist other strategies as well, even among fish. Lungfish, for example, estivate inside a mud cocoon in the dry lake bed, and *Clarias* may dig into the sediment down to permanent damp layers and await the return of surface water here.

ADAPTATIONS OF BIOTA TO DESICCATION

Estivation, the technique employed by the fish cited above, is also used by several species of burrowing toads, by semi-aquatic turtles (Pelomedusidae), and even by crocodiles. Among invertebrates, some dragonfly larvae dig into the bottom mud, sometimes socially, while some cyclopoid copepods encyst in the copepodid stage, and gastropods such as *Bulinus* spp., *Biomphalaria* spp. may survive drought for many months by hermetically closing the opening of their shell. Like the large amphibious snails *Pila ovata* and *P. wernei*, which have a mantle cavity divided into a water and an air-breathing compartment, these species reduce their metabolism to a low level, and slowly continue to breath air in a dry environment (Beadle, 1981).

The most widespread adaptation, however, is the production of a dormant stage, which is not the animal itself, but a resting egg or an encysted embryo. Algae and Protozoa (cysts), Cladocera (epphipial eggs, which are usually sexual, rarely parthenogenetic), calanoid copepods (encysted eggs), sponges (gemmules) coelenterates (cysts and podocysts), ectoprocts (statoblasts), oligochaetes and leeches (egg cocoons), almost all groups of aquatic insects (drought-resistant eggs) have evolved this mechanism. In the crustacean orders Anostraca, Conchostraca, and Notostraca, many species produce eggs that even need a period of estivation before they are hatchable.

Some caution is in order, however. The faculty of cyst production and/or diapause, because present in some species of a group, is not necessarily shared by all species. For example, in calanoid copepods, the production of resting eggs has been demonstrated in many paradiaptomid genera *(Lovenula, Paradiaptomus, Metadiaptomus)*, but not in diaptomids *(Tropodiaptomus, Thermodiaptomus)*. The former abound in intermittent aquatic biotopes of the desert, semi-desert, and soudanian lowland zone of Africa. In the temperate climate zones of that continent (The Maghreb, South Africa, the East African plateau, and most African high-mountain lakes) these same species also live in permanent waters. This suggests that both groups avoid competition by a different habitat selection in areas where they co-occur. Temporary and high-mountain biotopes are, moreover, low-predation environments in which big, clumsy swimmers like Paradiaptomids are less vulnerable than elsewhere.

The capacity of producing drought-resisting eggs has also evolved in fish, especially in the family Cyprinodontidae. Most species of the genera *Notobranchius* and *Aphyosemion* are therefore restricted to rainpools, or to the most temporary pools of a given wetland. Following a flood, they develop quickly to reproducing adults. Their life cycle is limited to one year.

ADAPTATIONS TO HIGH SALINITIES, AND PARALLELS WITH MOUNTAIN LAKES

Ephemeral rainpools, high mountain lakes and bogs, and permanent salt-water lakes are extreme environments, and the first and the last type may be viewed upon as terminal stages of freshwater lakes. In contrast to rainpools, which may or may not be predictable in terms of flooding, permanent salt lakes are extremely predictable environments. They usually occur where a lake bed intersects with the groundwater table and has no or an intermittent outlet. In high-evaporation areas (up to 7 m in the Sahara), such lakes ultimately evolve into saturated brines. Many examples occur in deserts : the Dawada lakes in the Fezzan, the Ounianga lakes in northern Chad, Lake Oua en Namous, the salt lakes of the erg Rebiana and of Kufra in Libya, Lake Nukheila in Northern Sudan, etc.

The biota of such lakes are extremely limited in number of taxa, but population densities may be such that total biomass is as high as in high-diversity freshwater systems. Salt-water biota all have specific lower and upper salinity thresholds, but a reasonable number or salt-loving species begins to appear at conductivities of 2,000-3,000 μS cm^{-1}. As stated

earlier, there are two basic types of saline waters, and not all animals and plants are capable of living in both. The brine shrimp *Artemia* for example occurs almost exclusively in chloride-waters, but the blue-green " alga " *Spirulina geitleri* indifferently occurs in both chloride and soda lakes. In some rift lakes, at salinities between 3,000 and 18,000 μS cm^{-1}, it is grazed upon by the calanoid *Paradiaptomus africanus* (LA BARBERA and KILHAM, 1974). This invertebrate is thereby in competition with a bird, the lesser flamingo *(Phoeniconaias minor)*, and a cichlid fish, *Oreochromis alcalicus* (VARESCHI, 1978, 1979).

In certain areas, where these Cyanobacteria are exploited by man, the copepod is likely consumed along with the algal cake. This is certainly the case in the Dawada-lakes of the Libyan Fezzan, where both *Artemia* and *Spirulina* are harvested and consumed as a cake by the local human population (MONOD, 1969). Another use of *Spirulina* from salt lakes was noticed in Lake Malha, North-Western Sudan (personal observation), where an algal slurry is mixed with salt deposits and the resulting cake is fed to camels.

The rotifer *Brachionus plicatilis* indifferently occurs in both types of salt lakes too, but because of the possibility of cryptic (non-morphological) speciation in this animal, it is possible that more than one species is involved. In the genus *Hexarthra*, conversely, distinct species have been claimed to inhabit chloride *(H. fennica)* and sodawaters *(H. jenkinae)*, but here the species status of both taxa has been challenged.

Detailed lists of salinity tolerance intervals for numerous animal and plant species are given by HAMMER (1986), while the underlying physiology, i.e. the mechanism of osmotic regulation that is involved, is treated at length by BAYLY, 1972. Some typical species of African saline lakes, occurring from about half seawater strength to almost saturation are the harpacticoid copepods *Nitocra lacustris* and *Cletocamptus* spp ; the midge larva *Aedes detritis* ; brine flies of the genus *Ephydra* ; larvae of *Stratiomyidae* ; larvae and adults of the beetle *Potamonectes cerysyi*, the cladoceran *Moina mongolica* and the ostracods *Heterocypris salina* and *H. barbara*. Cyanobacterial mats, encrusted with diatoms, line the bottom of many clear salt lakes. Submerged waterplants are absent, but the sedge *Cyperus laevigatus* typically grows along the margin of such lakes.

A species that combines life in saline and temporary environments is the Anostracan *Branchinectella salina*.

High-mountain lakes, with their low evaporation, low turbidity (because of lack of organic productivi-

GEOLOGY

water chemistry

toxicity

POPULATION PARAMETERS

②

pH

shape of basin

① Allochtonous sediment (largely inorganic)

salinity

osmotic regulation

water level fluctuation

③ ④

depth

turbidity

estivation encystation

PHYSIOLOGY: METABOLISM

BALANCE OF COMPETITION AND PREDATION

water balance

②

precipitation evaporation

winds

respiration

primary production

post-mortem decomposition

dissolved oxygen

CLIMATE

temperature

Autochtonous sediment (largely organic)

COMMUNITY STRUCTURE AND DIVERSITY ZONATION

④

Pleistocene History

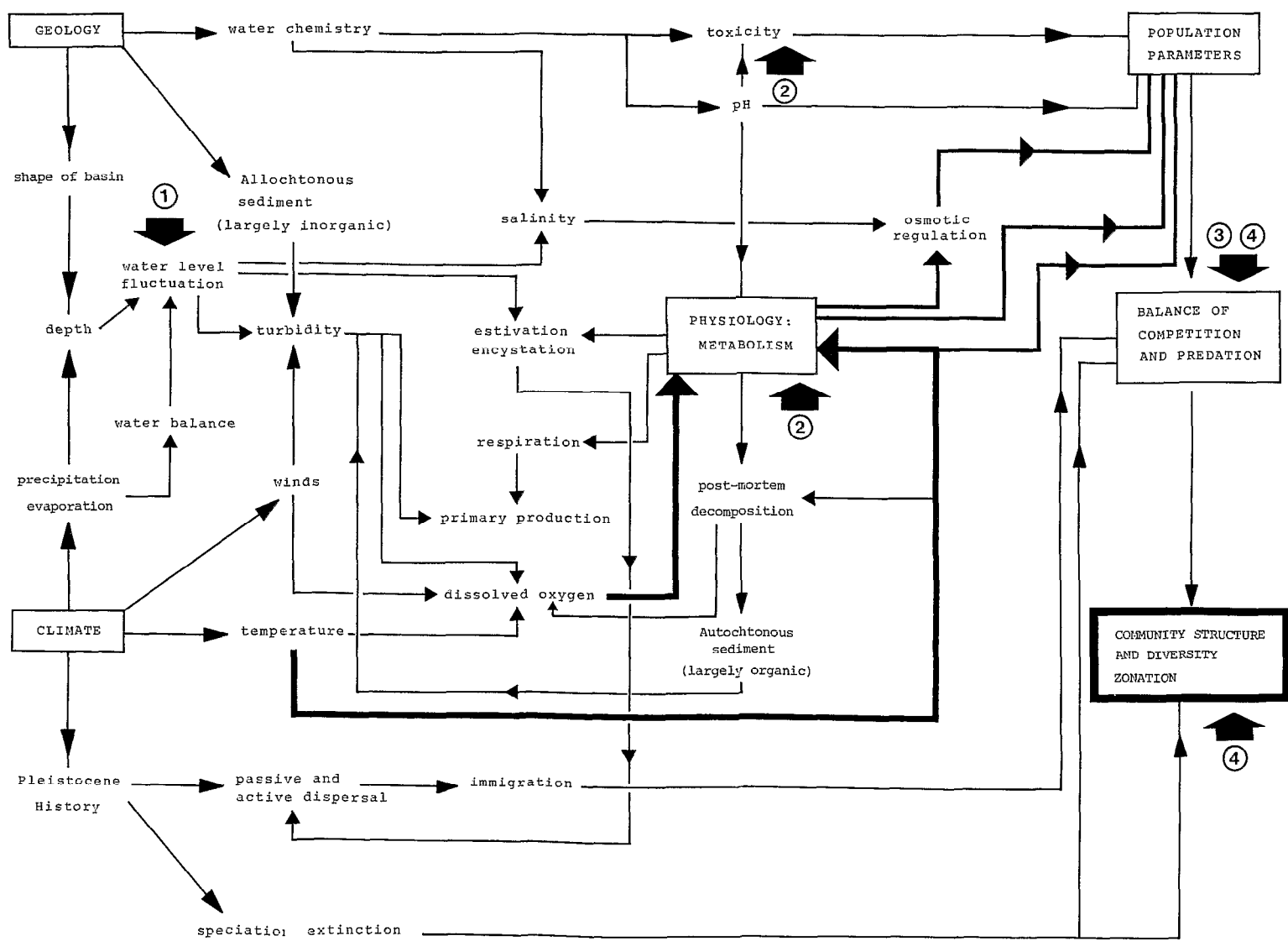passive and active dispersal

immigration

speciation extinction

Fig. 29. — Scheme illustrating the complex interplay of external variables (left) with the biota of shallow lakes, their physiological response (centre) and the results on diversity and zonation (right). Human interference may occur at all levels (black arrows). 1. Flood control modifies the geological variables; 2. pollution either alters the metabolism of species or acts via toxicity; 3. fisheries represent man's impact as a predator on the system, but by selective removal of species, competition is also affected; 4. species introductions (or extinctions) directly change community structure by adding or substracting species, and indirectly modify competition and predation in the preexisting community. If most of the abiotic and biotic variables have been quantified, mathematical modelling of the system becomes possible.

Schéma illustrant les interactions complexes entre les variables externes (à gauche) et les composantes biologiques des lacs plats, leur réponse physiologique (au centre) et les effets sur la diversité et la zonation (à droite). L'interférence humaine peut se situer à tous les niveaux (flèches noires). 1. Le contrôle des crues modifie les variables géologiques; 2. la pollution change le métabolisme des espèces ou agit par toxicité; 3. la pêche et les pêcheries représentent l'impact de l'homme comme prédateur sur le système, mais par prélèvement sélectif d'espèces, la compétition est également affectée; 4. L'introduction (ou l'extinction) d'espèces change directement la structure des communautés par addition ou soustraction d'espèces, et modifie indirectement la compétition et la prédation au sein de la communauté. Si la plupart des variables abiotiques et biotiques sont quantifiées, une modélisation mathématique devient possible.

ty), low mineral content, and high precipitation, have extremely simplified but stable communities. These usually lack aquatic vertebrates and water-plants, have few insects and crustaceans, and benthic algal growth is dominant over planktonic life. Usually, a deep-red pigmented calanoid, sometimes accompanied by a brown-black coloured *Daphnia*-species compose the true zooplankton. A good example of how historical reasons may account for a particular species array is found here. In the East African mountain lakes, the dominant copepod is *Lovenula falcifera*. In the Ethiopian high mountain lakes, conversely, an *Arctodiaptomus* is found (LOF-FLER, 1968, 1978). The second genus is of northern origin, and invaded Africa at a time of lower temperatures and higher precipitation than today, presumably around 12,000 BP. It has not been replaced by African species in the north eastern high mountains, but it has not reached the eastern mountains either, or was driven out of them again.

SYNOPSIS

The shallow lakes and floodplains of a broad zone situated between the desert and the equator in Africa can be arranged in a logical order of increasing environmental stress. The general case is shown schematically in figure 29. For a given geological setting, stress increases as flooding becomes more unpredictable, and the hydrological balance more and more distorted. Geographically, stress should increase with distance from the equator, but the situation is complicated by the fact that some major shallow lakes are fed by north-south oriented rivers. It is also remarkable that in systems which are today under severe pressure, dry out regularly or only have water at intervals, we have evidence that in former, more humid times, much less stress occurred. The time scale of such changes is of the order of a few thousands of years, but the decisive events may have taken only decades to develop, as shown by the dramatic changes of Lake Chad in the 1970's.

The biota of lakes subjected to increasing stress respond by local extinctions, but not in a linear way. The first signs of reaction to change are shifts in abundance of species within communities. Such events are most commonly explained as disruptions in the delicate resource partitioning between the components of plant and animal communities. Given enough time, some species will therefore be eliminated from their environment, but often, lakes return to their original situation before this happens. Where such minor periodic changes (with a period of the order of several to some tens of years) occur,

environmental change may even provide an extra dimension to the niches present. Diversity may then increase *vis-a-vis* systems that remain invariant through time. Examples of such lakes are to be found in the internal delta of the Niger, and in the Sudds swamps. They show a great diversity at all levels. In their zooplankton, and probably in their phytoplankton as well, this is further enhanced by differential grazing and predation. In competing species, the superior one is often more intensely preyed upon (or grazed upon) than the inferior one, and thereby incapable of eliminating its competitor. A periodic oscillation and long-term coexistence of the competitors with their predators is the result.

However, as soon as changes overshoot certain thresholds, effects quickly become dramatic. Such thresholds may be certain salinity values, but depth is even more critical : wind-exposed lakes in which average depth falls below 2-3 m become so turbid and deoxygenated that whole segments of their biota get wiped out. A rapid selection for opportunists and generalists, capable of feeding on a wide variety of food types, and resistant to high salinity and low dissolved oxygen takes place. Phytoplankton communities shift to associations of Cyanobacteria. Higher plants are reduced to *Phragmites*. If salinity increases above, say, 5,000 μS cm^{-1}, a further selection takes place : only true salt-water species remain. In all, an impoverishment in community richness by about two orders of magnitude occurs, until one ends up with truly extreme environments. These are exceedingly simple, but also exceedingly resistant to further change. Examples are high mountain lakes, salt lakes, and pans. A comparatively little known type of shallow lake is that in the equatorial lowlands of Africa, amidst permanently flooded forest. In these lakes, acidity is the factor which is selective for many plants and animals.

Resilience and capacity for recovery following a major disturbance is dependent upon the availability of refuges, such as perennial swamps around a dry lake, but more often feeder rivers. Here relict populations of the lake's species may survive. They later recolonize the lake, at different speeds, the generalists-opportunists coming first, the surviving specialists following later and at a slower pace. Many species, mostly invertebrates and a minority among the vertebrates, escape extinction by diapausing or producing resting stages (gametes, embryos) or cysts. This switching from active to latent or pseudo-latent life may last for many years, but hatching occurs as soon as conditions return to normal.

After a major disturbance, or a series of small disturbances, it is unlikely that a lake will quickly regain all of its former diversity, unless the ecosystem was truncated in the first place, and consisting

of few species that actually benefit from major changes.

That long periods of stability in shallow lakes are truly exceptional is shown by the fact that such lakes have almost no endemic taxa. Finally, a lake, after a disturbance, will not necessarily return to its original physical and chemical state but may stabilize at some new level. Its biota will react accordingly, and if the new level is less favourable than before, the biotic component of the system will tend to simplify. This is what happened to Lake Chilwa ·sometime during the last 1,000 years, and possibly to Lake Chad at the present time.

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