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Development of bottom fauna in the man-made Volta Lake in Ghana

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With 7 figures in the text

The tropical Volta Lake in Ghana is by its surface area of 3,275 square miles the largest man-made lake of the world. The estimated shoreline of the complex dendritic shape is 4,500 miles. The main axis of about 250 miles length runs mainly through Guinea savanna, and borders the forest zone only in the south. The lake which was established in May 1964 is expected to reach its full size after the rainy season of 1968 or 1969.

Since 1964 the vertical distribution of bottom fauna has been studied, with the aim of assessing the changes in the biomass of macrobenthic fauna during the period of the filling of the lake and its stabilization. Since 1966 studies have been carried out at 5 stations in different parts of the lake. For sampling a Rigosha mud sampler was used as this was found to be the most suitable for use in this reservoir where vegetation was not cleared before flooding. Six samples, each of an area of 50 cm^2 were taken at a series of depths each time a collection was made. Samples were washed on a sieve of 0.4 mm mesh size, and fixed in 4 % formaldehyde.

Results

Changes in the bottom fauna reflect both the geographical position of the Volta Lake and the factors which influence it, such as the alternation of rainy and dry seasons.

The Volta Lake extends over more than 200 miles in a north-south direction. Climatic changes have therefore a definite impact upon the physical characteristics of the water, especially upon water temperature and water mixing. There are four seasons in each year; during the rainy season the water surface cools, and cooler water enters the lake with floods coming from the north where the largest rivers are situated. This season is followed by hot weather, resulting in the warming up of surface water and in stratification of the water masses. A temperature gradient develops along the north-south axis, with higher water temperatures in the north, and lower in the south, as a result of increasing continental climatic conditions in areas more distant from the ocean. Cooling breezes coming from the south reach only to Kete Krachi.

The next season starts at the end of December when dry Harmattan winds from the north result in surface cooling and in the formation of large waves, especially in open areas. This season lasts to the middle of February. Then follows the second hot season characterised by a pronounced stratification of water. Stratification is finally disturbed by the onset of new rains and floods.

That bottom organisms respond to these changes is indicated by their pattern of vertical distribution. During and immediately after the floods the benthos reaches deeper though its abundance is low. In the northern areas (Fig. 1) directly under the influence of flood waters with a marked flow of water lasting several months, the bottom fauna is more evenly distributed with depth and reaches right down to the deepest parts of the old now permanently drowned river bed (see A). After the rains the water stratifies and this is followed by stratification of benthos, now found predominantly in shallow depths (April 1966; January, April 1967, see B). In the next flood season the bottom fauna again penetrates to maximum depths to be succeeded by stratification. Similar trends in changes in the vertical distri-

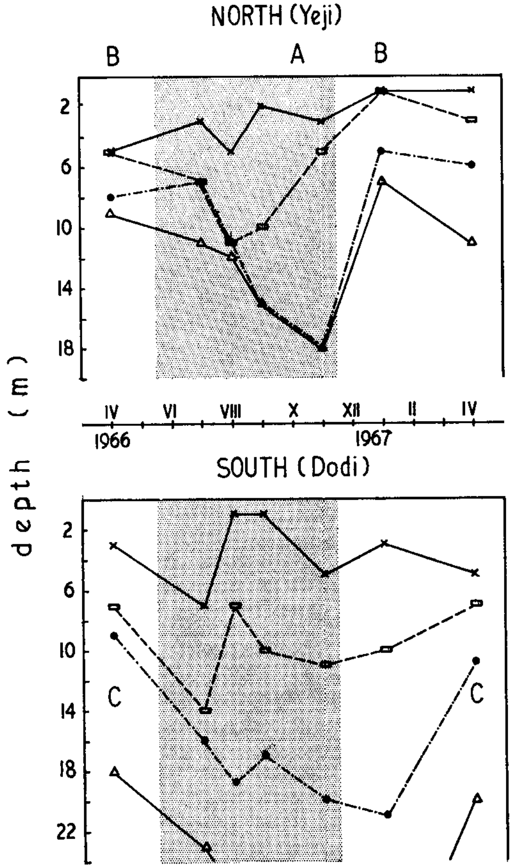

Fig. 1. Vertical distribution of bottom fauna. ×——× 50 % of the total biomass. □——□ 90 % of the total biomass. ●—.—.—● maximum depth of benthos distribution. △——△ isobar of 30 % saturation of oxygen. Shaded area indicates the months during which the water level was rising in the Volta Lake.

bution of the bottom fauna can be followed in the south at Dodi. Stabilization of water masses leads to the bottom fauna preferably occupying shallows (April 1966, April 1967, see C), while the rains result in a decrease in abundance of the bottom fauna, their penetration deeper and their more even distribution with depth (July 1966). A metalimnion, characterised by a sudden drop in oxygen concentration, develops during the stratification at 18 to 25 m depth but it has been found that this water stratum is not so stable as it was formerly expected, and rapid changes in oxygen concentration can occur within this layer (Viner, in press).

Seasonal changes in biomass show peaks during the time of the stratification of water, i. e. during the hot seasons, and low values during the periods of water mixing. These seasonal changes have also been found during investigations of aquatic invertebrates living on the submerged surfaces of *Ceratophyllum* and of *Pistia* (Petr 1968). It has been found that the fauna on *Ceratophyllum* growing at an average depth of 1 m show much more seasonal variation than the fauna on *Pistia* roots which extend just below the water surface. It is obvious that there exists a difference, in both physical and chemical properties, between the surface water and that from 1—2 m depth, and that this is the important and most probably the decisive factor which induces the changes in population of aquatic invertebrates both on *Ceratophyllum* and in the benthos.

During the first period of filling in 1964—1966 the oxygen distribution with depth seemed to be limiting the distribution of bottom fauna (Lawson et al., in press). In observations carried out close to the dam in 1964—1966 the bottom fauna was found predominantly down to a depth of 5 m only (Ewer 1966). The oxygen concentration at that depth, which fell in the littoral-sublittoral range, was usually below 30 % saturation. However, in deeper water profundal species seem to require a higher concentration of dissolved oxygen, than those of shallows. After floods, with improved oxygenation, the bottom fauna spreads deeper, but it has never been found to extend below 21 m depth.

The limiting effect of oxygen concentration on the vertical distribution of the bottom fauna can still be best observed in shallow bays. These bays have high primary and secondary productivity. Because of their shallowness diurnal mixing frequently occurs, resulting in a temporary but considerable depletion or even a complete absence of oxygen in the whole water mass. The presence or absence of chironomids seems to be dependent upon a minimum level of cumulative oxygen concentration. For chironomids of these littoral zones, a concentration of about 30 % saturation of oxygen seems to be critical. In the deeper waters of these areas, where oxygen saturation is 30 % or less, rich populations of *Chaoborus* have developed (Fig. 2).

The leading benthic organisms in the Volta Lake are larvae of chironomids, which between 1966 and 1968 formed 59.0 % of the total biomass for all stations. These were followed by nymphs of *Povilla adusta* Navas with 30.2 %. In shallows with an abundance of aquatic plants such as *Ceratophyllum, Pistia* and *Jussiaea,* the snail *Bulinus* formed a substantial part of the total biomass of benthos and has permanently established itself in this habitat (Fig. 3). This is of special interest as *Bulinus* is a vector of *Schistosoma* and its distribution along the shoreline of the Volta Lake has helped to increase the infestation of local human populations, especially of fishermen, by bilharzia (Paperna, in press). In some areas larvae of the caddis fly Ecnomus and Dipseudopsis ~~*Aethaloptera dispar* Brauer~~ are common in the benthos.

During the period 1966—1968 *Povilla* has colonized practically the entire lake (Fig. 4). These ephemeropteran nymphs were very often found in benthic samples and in some areas they greatly contributed to the total biomass of benthos (Fig. 5). The nymphs burrow into wood and especially attack flooded trees, which were not cleared before the lake was formed. These belts of trees often extend far off-shore and have provided additional substrates for organisms which would not otherwise be able to exists here on the deoxygenated bottom. Hiding during the day inside the wood, the nymphs come out during the night to feed on periphytic coatings of these trees. These new wood surfaces were of greatest importance during the first years, when the bottom water layers were deoxygenated even in shallows. During that period in areas with flooded trees the biomass of "Auf-

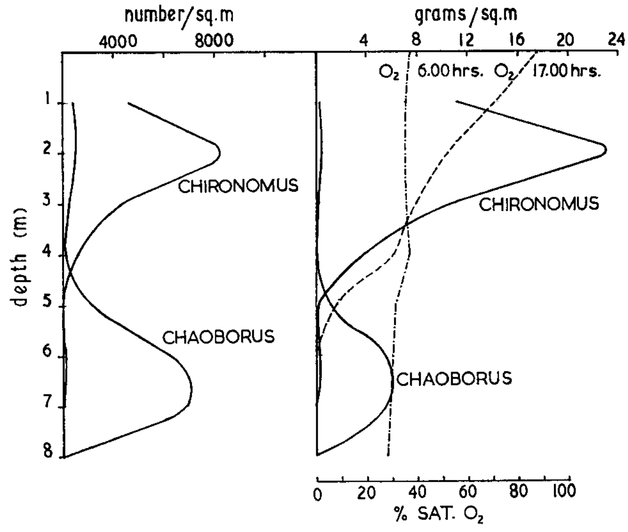

Fig. 2. Vertical distribution of chironomid and chaoborid larvae in relation to the oxygen concentration.

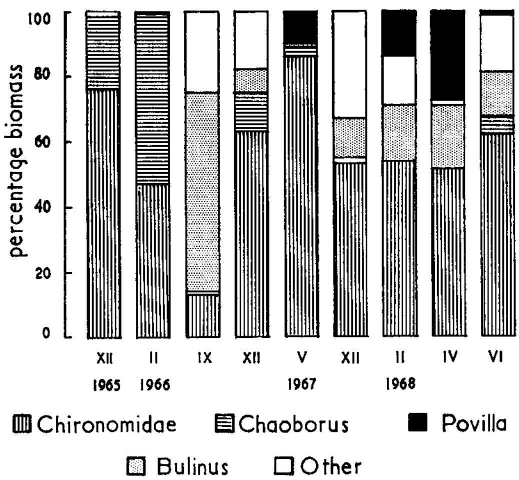

Fig. 3. Percentage biomass of the major groups of bottom fauna in a shallow bay in the south of the Volta Lake.

wuchs", in which term is here included the various invertebrate forms living free within the mat of sessile forms, vastly exceeded that of the bottom fauna.

The development of rich populations of *Povilla* in flooded trees has been reflected by changes in fish population of the Volta Lake, and by changes in their feeding regime. Fish which previously fed on the benthic and littoral fauna readily started to exploit invertebrates inhabiting the surfaces of flooded trees. Species which under riverine conditions had a rather broad range of food types, have been found to feed preferentially on the emerging stages of aquatic insects, mainly *Povilla*. In the north, at Yeji, *Povilla* almost disappeared from the benthos between 1967 and 1968 (c. f. Fig. 5). However, its importance in the diet of *Alestes bare-*

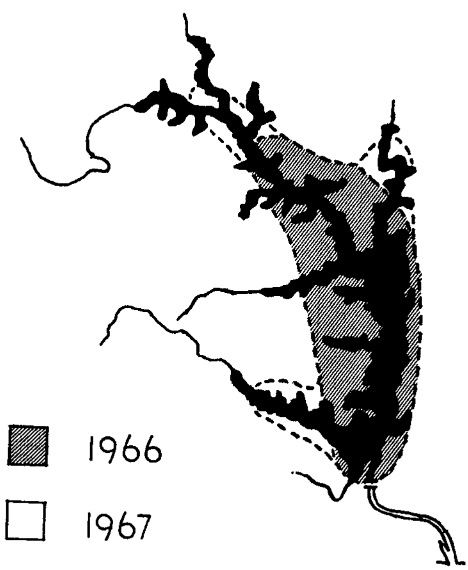

Fig. 4. Establishment of *Povilla* in the Volta Lake in 1966 and 1967.

mose JOANNIS, the most common fish of that area, increased during the same period from 8 % to 61 %. Since we have just seen that the quantity of *Povilla* in the benthos decreased, it follows that most of the *Povilla* nymphs consumed by the fish in the north and elsewhere in the lake must have originated from flooded trees.

In submerged wood *Povilla* constituted 91 % by biomass of all macroinvertebrates there present, while in the benthos it constituted only 10 % of the bottom fauna. The presence of an invertebrate consumer of periphyton such as *Povilla,* capable of rapid reproduction and distribution over new areas, helped the development of such insectivorous fish as *Alestes, Eutropius* and *Schilbe*, which formed in 1967 81 % in fish landings in the north. These fish generally decrease in abundance in newly formed lakes, as they prefer a riverine habitat.

The biomass of bottom fauna has been found to have decreased during the period 1966—1968 at all station, except that in the north of the lake (Fig. 6). The decrease in biomass recorded at all stations in more stabilized lacustrine conditions is minimized by the supply of nutrients from flooded land due to the increase in lake level in each year. The benthic productivity may be expected to be lower when the lake is completely full, and the only source of nutrients will be annual flood waters and those released by destruction of flooded trees. As the bottom fauna is found predominantly in depths down to 10 m, the productivity of the Volta Lake as a whole, i. e. including also the deeper sections, is much lower than

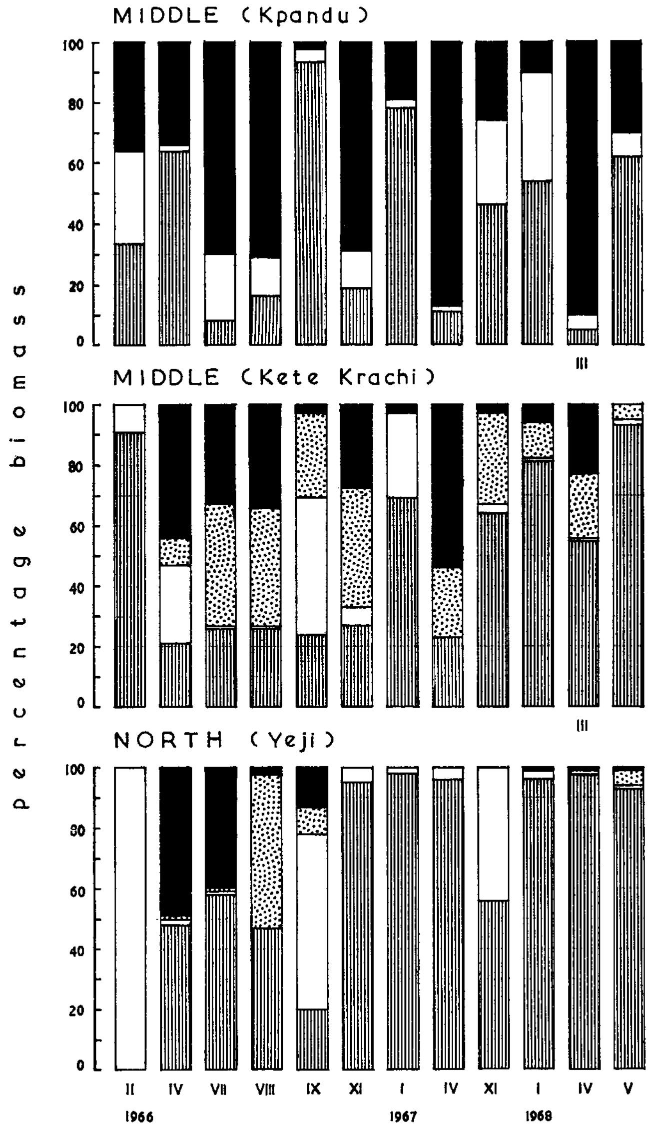

Fig. 5. Percentage biomass of the major groups of bottom fauna in the middle and northern parts of the Volta Lake. For symbols, see Fig. 3. Areas stipled — *Aethaloptera*.

that shown in the Fig. 6, which is calculated for the top 10 m of shore, where the majority of all organisms live. However, because of the higher number of generations of aquatic insects per year in tropical waters than in temperate waters, the productivity of the bottom fauna is much greater than it appears from its biomass.

The high standing crop of chironomids in shallows of the lake (c. f. Fig. 2) may be related to the abundance of the blue-green algal bloom of *Microcystis* and *Oscillatoria* which has continuously persisted in these areas. Rogers (1963) found

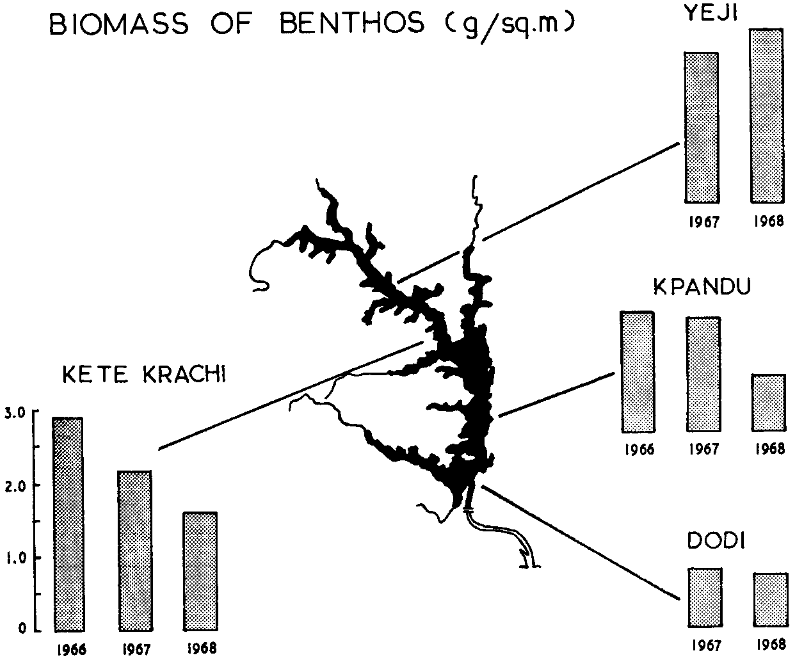

Fig. 6. Changes in the biomass of bottom fauna. For 1966 the averages are calculated from February and April values, for 1967 and 1968 from January and April (March) values.

that ponds having a dominant blue-green algal bloom produced more midges than ponds having a dominant bloom of green algae. However, the role of different types of soil being flooded must not be neglected. Differences in the standing crop of the benthic fauna at different stations reflect without doubt different types of substrates. Fine sand with almost no organic admixture supports a low biomass, while flooded alluvial soil, rich in organic matter mainly the remains of flooded plants, yields a much higher biomass.

Conclusions

With maturation of the new tropical man-made Volta Lake in Ghana, the bottom fauna has been found to be able to reach a maximum depth of 21 m. Initially the bottom fauna was limited by oxygen deficiency in relatively shallow waters to only a few meters depth; later, with the improved oxygen situation, it penetrated deeper. The major concentration of biomass has been found between a depth of 1 to 5 m, where 87.6 % of the total number of all organisms were collected in 1966—1968; this corresponds to 88.8 % of the total biomass.

The first stage of formation of the bottom fauna in the Volta Lake was characterized by a predominance of chironomids (Fig. 7). These responded to seasonal changes by peak occurrence before and at the end of floods. With maturation of the lake and smaller annual rises in the lake level the peaks of abundance have become much lower.

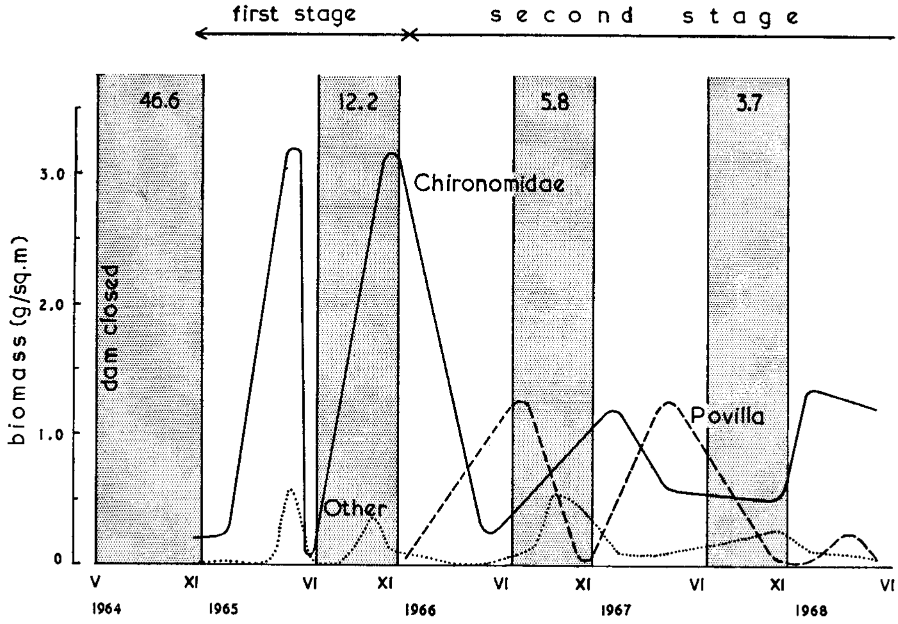

Fig. 7. The development of the benthos in the Volta Lake during its first four years. Shaded areas indicate the seasons with rising lake water level, figures show the rise in meters for flood period.

The second stage set in with the appearance of the burrowing nymphs of *Povilla,* which were first collected in benthos samples after the second floods. The proportion of *Povilla* in these samples rapidly increased, with peaks just before rains. The low abundance probably resulted from the fact that the freshly flooded plant material could not be as readily attacked by these wood burrowing nymphs, as it was after submergence for three or more months.

In temperate man-made lakes, during the first period of their formation, chironomids form the most important group of bottom organisms; this was true also in the Volta. Later oligochaetes and molluscs become the dominant forms of benthos with their biomass exceeding that of chironomids (MORDUKHAI-BOLTOVSKOI 1961). This is the second stage in formation of benthos of a temperate man-made lake. In the Volta Lake neither oligochaetes nor molluscs have great importance in the total biomass of the benthic fauna, except in so far as the latter group is abundant in areas with aquatic weeds.

The presence of a rich biomass of *Povilla* in the benthos is obviously closely related to the presence of numerous flooded trees, the proper habitat of these nymphs. With the disappearance of trees by their decay the biomass of *Povilla* in the benthos will decrease and chironomids will remain as the dominant group of the bottom fauna. This situation can be considered as the third stage of formation of the bottom fauna of a tropical man-made lake, such as Volta.

The biomass of the bottom fauna during the first four years was found to be several times lower in the Volta Lake than that of large man-made lakes of temperate climate during their first years of existence. However, since more generations of aquatic insects complete their life cycle within one year in tropical than in temperate waters, the productivity of the temporary bottom fauna per year can be estimated for both types of water body as being not greatly dissimilar.

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Discussion

VAN DER LINGEN: We have the same problems in Lake Kariba, and also find that benthos is very poor deeper than 5 m. Do you find differences in amount of benthos in areas where vegetation has developed and bare grounds?

PETR: Benthos was found to be less rich under *Pistia,* than that under *Ceratophyllum. Ceratophyllum* seems to encourage the bottom fauna by production of oxygen, and by the rich periphyton which develops on its surfaces. This plant can be used as a "ladder" by some benthic organisms as it has a close contact with the bottom. Benthic organisms can then actively feed upon the periphyton of *Ceratophyllum.* Below *Pistia* the oxygen concentration is rather low, lower than in the open water and this has evidently a negative impact on the bottom fauna below this plant. The biomass of benthos under *Ceratophyllum* is richer in molluscs, mainly gastropod *Bulinus,* than the surrounding bare grounds.

BRINKHURST: Have you tried other samplers — i. e. core tubes?

PETR: No. Our substrate seems to be too hard for core tubes.

ALLANSON: Have you found *Chaoborus* larvae in deoxygenated water?

PETR: *Chaoborus* larvae occur in shallow bays on soft muddy bottom, where temporary deoxygenation has been recorded. However, nocturnal mixings bring some oxygen to the bottom after the stratification during the daytime.