Dynamics of benthic invertebrates in a tropical man-made lake (Volta Lake 1964—1968) Standing crop and bathymetric distribution

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With 6 figures and 3 tables in the text

Abstract

During the first five years of filling of Volta Lake (in Ghana, West Africa) two major groups of invertebrates dominated the benthic fauna: ephemeropterans, especially the nymphs of *Povilla adusta* NAVAS, and chironomids, especially the larvae of *Nilodorum brevibucca* FREEMAN and *Chironomus* spp. Their later decline in numbers resulted in a decrease in the biomass of the benthic invertebrates in the lake.

The quantitative and qualitative changes in the benthic fauna in this lake seem to be determined to a large extent by changes in the substratum due to shoreline erosion. The lowering of the oxygen discontinuity and the prolongation of periods of high dissolved oxygen content in deep water helped the bottom fauna to occupy greater depths, but did not seem to prevent the decrease in the total standing crop of benthic invertebrates in the lacustrine sector during the process of lake ageing. The major inflows may be held responsible for maintaining a high biomass of the bottom fauna in areas under their direct influence.

Introduction

The damming of the Volta River in Ghana in 1964 presented a unique opportunity to determine whether or not the bottom of the new lake would be colonized by benthic organisms, and, if so, how long this process would take. It was important initially to know the answer to these questions in order to know whether the insectivorous fishes of riverine origin, especially benthic feeders, present in the new lake, would find enough food in the new environment.

A narrow epilimnion, which established itself soon after the closure of the dam in the gorge region close to the dam, was expected to prevent the bottom organisms from occupying the deep bottom. An exception to this would be *Chaoborus* larvae which are mobile and capable of surviving certain periods of time in deoxygenated mud. But even this organism did not establish itself in the gorge region (PETR 1972 a) although it appeared in large numbers in one other area of the lake. All the other bottom inverte-

brates established themselves in a narrow zone close to the lake margin. The
speed of colonization of this zone was rapid, with organisms reaching their
maximum density within four weeks of the innundation of this new sub-
strate (PETR 1971 a). It was soon discovered that the bottom fauna of the
marginal zone was only a small part of the total bottom invertebrates, the
majority of which developed dense populations in submerged bushes and
trees. This Aufwuchs-community, with its algae and dependent organisms,
was present on submerged parts of trees projecting into the epilimnion of
the lake. Often this occurred far off-shore in areas where no bottom fauna
could survive due to lack of dissolved oxygen (PETR 1970 a). During the
filling of the lake the Aufwuchs could be considered as being a more im-
portant source of food for fishes than the bottom fauna (PETR 1971 b).

The changing chemical conditions in the new lake were expected to
have an effect on the establishment of the bottom fauna during the filling.
One of the questions which arose was whether or not the higher dissolved
oxygen content in deep water would lead to an increase in the bottom fauna.
This question could not be answered from data obtained at Kariba Lake
where studies on the bottom fauna started only in the second phase of the
lake's history, i.e., after its maximum retention level had been reached.
Several other questions also arose such as: How do changes in substratum
due to shoreline erosion affect the composition of the bottom fauna and
standing crop of the benthos? Do changes in the dissolved oxygen content,
associated with seasons (especially with rains and floods), affect the total
biomass of the bottom fauna? Does a large water body such as Volta
Lake behave as a unit, or are there longitudinal differences in the biomass
of benthos.

This paper will investigate some of these questions.

The Lake and collection of samples

Volta Lake started to fill in May 1964 when the Akosombo dam in the
gorge area on the Lower Volta River was sealed. During the first year flood
water filled the lake to a level of about 50 m above the former river level
(Fig. 1). In the years which followed, flood waters entering the lake from
the end of June or from July until October—November, further enlarged
the lake, and increased its depth.

After floods in 1968 the lake reached a length of about 380 km, and it
covered about 8,000 km², with a maximum depth of about 80 m at the dam.
Detailed morphometric features of the lake are given by ENTZ (1969). In
1964—1966 the benthic fauna was first sampled about 3 km from the dam,
but from mid-1966 this station was abandoned. Five new stations were
established at the end of 1965 and at the beginning of 1966. These included:
a) transect at an island situated in the widest part of the lake (Dodi); b) a
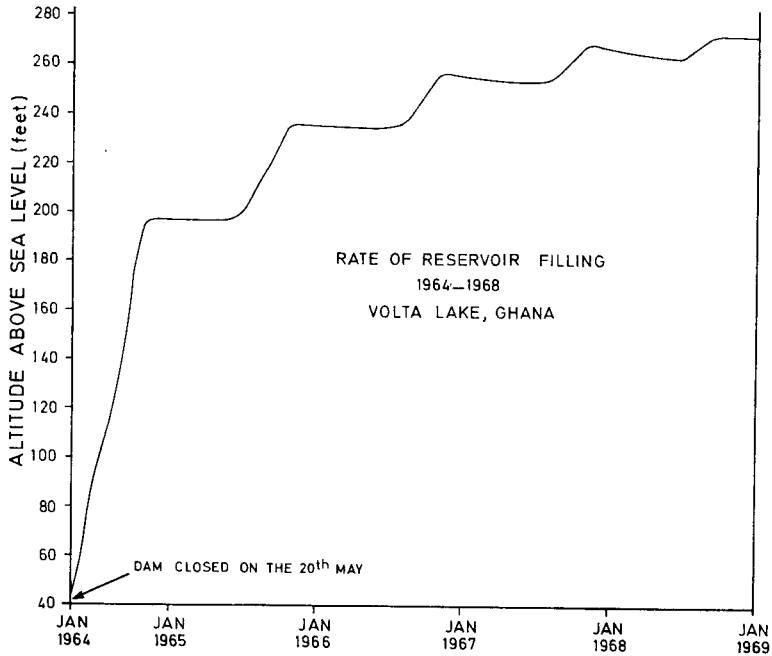
Fig. 1. Rate of reservoir filling 1964—1968, Volta Lake Ghana.

transect in the flooded Afram river valley in the south-west of the lake (Ampem); c) two stations in the mid-lake, i.e. at Kpandu and at Kete Krachi (the latter situated at the end of the northwestern limb); and d) one transect at the lake-river transition at Yeji. A full description of stations, with their geographical and some physico-chemical characteristics, as well as the sampling method is given in a previous paper (PETR 1972 b).

The sampling programme was often interrupted for unavoidable reasons, especially in 1967. In 1966 and 1968 the sites were visited at fairly regular intervals. Bottom samples were collected using a Marukawa sampler, which covers 50 cm² area. Six parallel samples were collected from each depth and pooled to represent one sample. To determine the degree of reliance which could be placed on this sampling method, six parallel samples from three depths (1 m, 5 m, 10 m) were collected at four stations. These were examined in order to determine the pattern of distribution of bottom organisms. A dispersion coefficient was calculated after RAVERA (1966) and ANDREWARTHA & BIRCH (1961). This applied only to chironomids as these formed a constant and substantial part of the bottom fauna of the lake.

The dispersion coefficient (A) was calculated as:

$$A = \frac{S\,(xi - \bar{x})^2}{\bar{x}\,(n - 1)} = \frac{\text{variance}}{\text{mean}}$$

where "xi" is the number of organisms for each sample, "x̄" their average and "n — l" the degrees of freedom. To test the significance of the deviation of this ratio from unity, the ratios of deviance to mean (B) were calculated as:

$$B = \frac{\bar{x}}{S\,(xi - \bar{x})^2} = \frac{deviance}{mean}$$

and these were compared in a chi-square test for n — l degrees of freedom. $X^2\,(0.05) = 11.07$.

Table 1. Mean values for dispersion coefficient (A), ratio of deviance to mean (B), mean (x̄) and variance (s²) based on six samples of chironomids.

Station	Depth (m)								
	\multicolumn{4}{c}{1}	\multicolumn{4}{c}{5}	\multicolumn{4}{c}{10}
	x̄	s²	A	B	x̄	s²	A	B	x̄	s²	A	B
Dodi	11	113	2.0	10.0	5	35	6.8	1.4	3	13	0.8	4.0
Kpandu	1	15	1.7	8.2	0.3	1	0.9	4.5	0	0	0	0
Kete Krachi	10	99	1.9	9.7	2	9	1.0	4.9	1	3	0.9	4.3
Yeji	9	39	0.9	4.2	5	22	0.9	4.4	4	355	18.7	93.4

The results (Table 1) suggest that six samples from each depth are a sufficient number to provide a reliable index of the pattern of distribution of chironomids in the bottom fauna at individual depths. Table 1 also shows that only at Yeji was the distribution of chironomids at 10 m depth clumped. At other depths, and at other stations there was no evidence that the chironomids were not distributed at random between the six samples collected from each depth.

Fig. 2 shows mean numbers of bottom fauna per square metre at each station with confidence interval estimates for different depths (P = 0.95). Each mean is based on six samples, each covering 50 cm² in January, 1968.

Samples were taken at 1—2 m intervals, starting at 1 m, and progressing at 2 m intervals until 11 m, and then progressing at 3 m intervals until 23—25 m. This was the last depth regularly sampled. On a few occasions 30 and 35 m depths were also sampled, but they never contained organisms.

The means for standing crop of the bottom fauna were computed from samples taken from 1 m to 9 m depth zone for each transect since the majority of all organisms occurred here. Collected invertebrates were preserved in 4 % formalin for later counting and wet weight.

Due to the irregularity in sampling, especially in 1967, the data were plotted on the basis of comparisons with the previous and following year samples, thus the trends and the magnitude of the changes could be estimated.
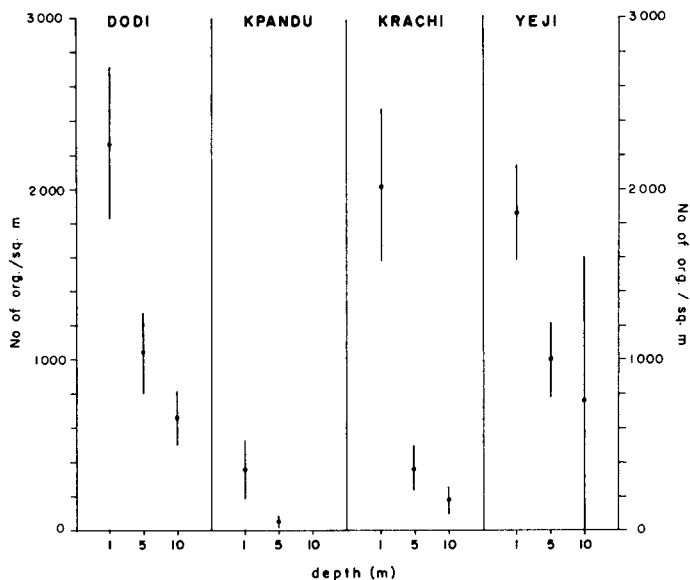
Fig. 2. Mean numbers of the bottom fauna per m² at 1 m, 5 m and 10 m depth at four stations, with confidence interval estimates for each depth (January 1968).

Results
Bottom fauna of the 1—9 m zone

For the purpose of following the seasonal and annual changes in standing crop benthic invertebrates were separated into three groups, i.e. Chironomidae, *Povilla* and Other invertebrates (Fig. 3).
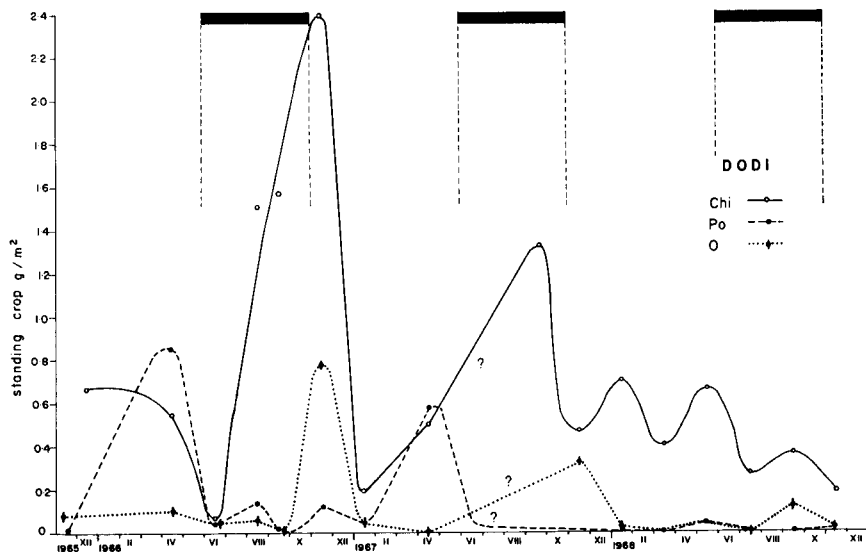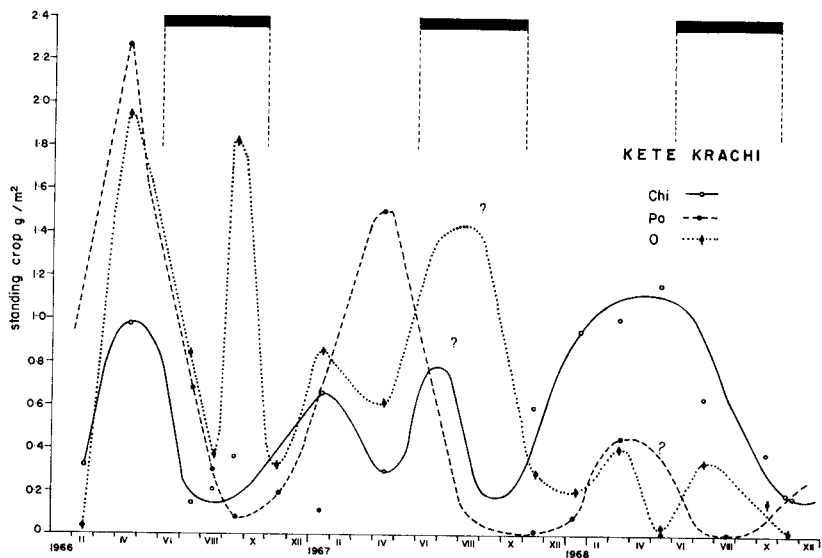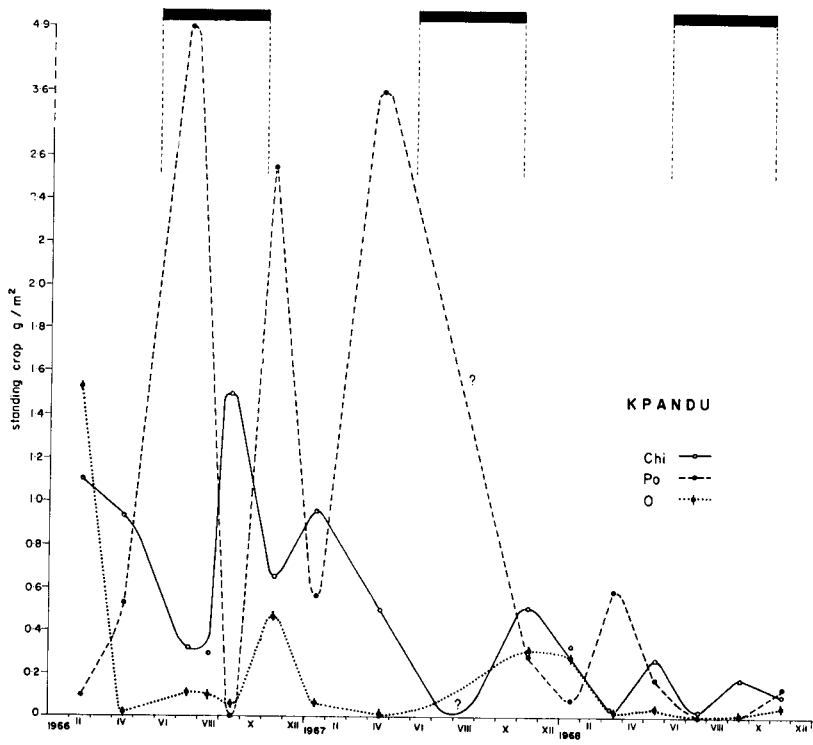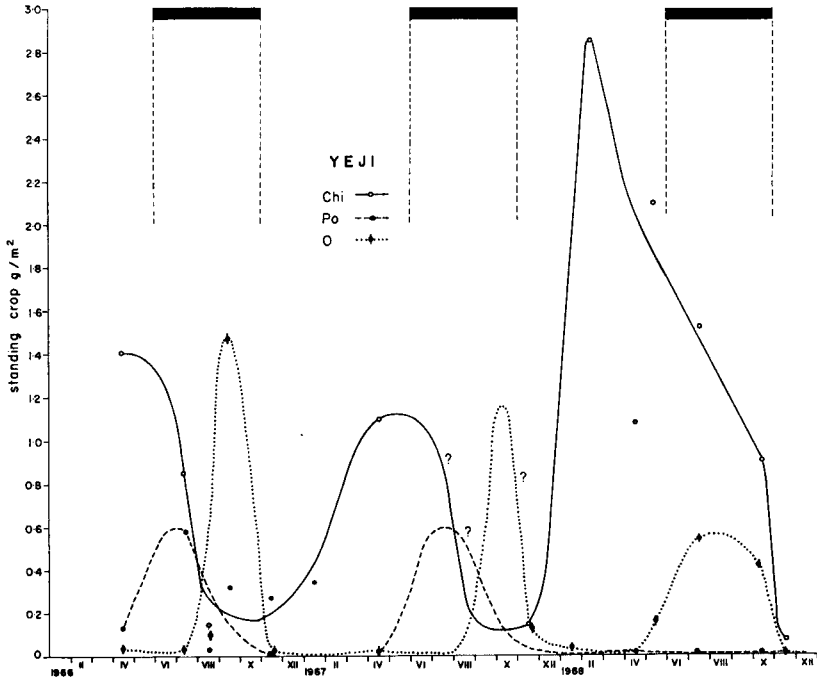
Fig. 3. Standing crop of Chironomidae (Chi), *Povilla* (Po), and all the other orga-
nisms (O) from 1965 to 1968: Dodi (a), Kpandu (b), Kete Krachi (c), Yeji (d).
The black bars indicate the length of the flood season.

The chironomids usually dominated the standing crop of the benthos.
In the area exposed to waves at Dodi Island, e.g., in November 1966,
during the first month after the lake level stabilized (Fig. 1), the peak in
chironomid standing crop reflected the presence of considerable numbers
of *Nilodorum* and *Chironomus* larvae (PETR 1972 b), predominantly in their
last instars. In the following two years the number of larvae of both genera
decreased, while an increase in the number of *Endochironomus* larvae (of
smaller size than the previous two species) was recorded. Thus, in 1967
the maximum standing crop of chironomids constituted only about half of
the 1966 peak, and the standing crop further decreased in 1968.

At Dodi, as well as at other stations of the lake, *Povilla* nymphs
reached their peak distribution and their maximum standing crop at the
end of dry seasons; they were very rare during floods. Their low numbers
and a correspondingly low biomass, especially during the second half of the
floods, seem to be associated with their demand for wood or grass particles
which have been submerged for several months, covered by Aufwuchs algae
and attacked by microorganisms. It is also possible that the generally low
dissolved oxygen content of the water during mixing may have an adverse

effect on the nymphs. *Povilla* seems to be limited·in depth distribution by the presence of periphytic and planktonic algae on which it feeds. These occur only in the shallow layer of water where there is sufficient light for photosynthesis. With the floods and rise in lake level, the old established bands of periphytic algae around the trunks of inundated trees become cut off from an adequate supply of light. Nevertheless, *Povilla* has been collected from depths of 10—15 m during the mixing periods, when planktonic algae are diluted, and the nymphs probably feed on that Aufwuchs algae which survive for several weeks below the compensation point. After the floods the build up of the population is slow, suggesting that freshly flooded wood is slowly being colonized by *Povilla*. However, *Povilla* nymphs were found in considerable numbers at the end of the floods in flooded grass which it seems to utilize as a habitat before the wood becomes suitable for colonization by the nymphs.

During 1966—1967 *Povilla* dominated the benthic invertebrate fauna at two stations in mid-lake. At Kpandu, the more southern station, the maximum standing crop of 4.9 g/m^2 for *Povilla* nymphs was recorded in mid-July, 1966. During the next year the maximum standing crop was 3.6 g/m^2 (April), and in 1968 only 0.6 g/m^2 (March). Similarly, a decrease in standing crop of *Povilla* inhabiting the bottom of the lake was recorded at Kete Krachi further north, where the maximum of 2.3 g/m^2 in 1966 was followed by 1.5 g/m^2 in 1967, and 0.5 g/m^2 in 1968. All of these peaks were recorded in March or April during the thermal and chemical stratification of the lake and well before the onset of rains and floods.

The chironomid populations of the two mid-lake stations differ considerably. The decrease in the maximum standing crop of chironomids at Kpandu from 1.5 g/m^2 to 0.2 g/m^2, during the period 1966—1968, shows a similarity to the situation further south close to the Akosombo dam (e.g. at Dodi Island). On the other hand, the Kete Krachi station during the same time period maintained a maximum standing crop of about 1.0 g/m^2, with a slightly higher standing crop in 1968 than in 1966. This station is situated at the end of the relatively narrow arm of the major inflow to the lake, and during floods it actually changes into a slow-flowing river. Further upstream, Yeji is more affected by floods. Here, unlike at Kete Krachi, the bottom fauna was always dominated by chironomid larvae, and as the lake filled up their standing crop increased reaching a maximum of 3.0 g/m^2 in 1968, compared with 1.4 g/m^2 in 1966.

A considerable number of species of organisms other than those mentioned above was recorded from the bottom fauna. Their numbers were usually low, and only in the shallows of Ampem did they contribute significantly to the standing crop. A gastropod (*Bulinus truncatus rohlfsi*) and anisopteran nymphs commonly resulted in a high standing crop, especially

towards the end of the floods. During that period the Odonata seemed to find suitable oviposition sites among the flooded grass, weeds, and macrophytes. There was abundant food present on these inundated areas, and other invertebrates such as oligochaetes and crustaceans, especially Ostracoda, were abundant. For snails the inundated grass served both as an oviposition site, and also as a food source since rich coatings of Aufwuchs algae developed there. However, the water level rose less and less as the lake filled, and this habitat became less common, being partially or completely destroyed. This was especially true of the destruction of submerged terrestrial plants, but it also applied to aquatic weeds such as *Ceratophyllum* and *Pistia*. These macrophytes developed in some littoral regions of the lake, especially in those protected from waves by the inundated trees. These plants disappeared with the erosion of shore-line. In the shallows at Ampem where the littoral zone is more gradually sloped, these plants remained abundant and consequently snails and dragonfly nymphs maintained their numbers, or as in the case of *Bulinus* the numbers actually increased in 1968 compared with 1966, (PETR not published). In the same area chaoborid larvae, once very common in muds down to about 10 m depth, became less abundant as the lake matured. The reason for this change has not been clearly defined (PETR 1972 a).

From 1966 to 1968 the standing crop of benthic invertebrates decreased at four out of the five stations (Fig. 4). The only increase in the standing crop was recorded for the river-lake transition at Yeji. At the end of the dry season 1968 large numbers of *Nilodorum* larvae were found in 1 m and 3 m depths (PETR 1972 b). During the dry season the water in shallows at Yeji frequently stratified, and as a result of this, the water was poor in oxygen. In November 1966 only 30 per cent saturation oxygen was recorded at 5 m. This limits the bottom fauna in this transect predominantly to shallow depths. It may be, however, that some bottom organisms such as *Endochironomus* and *Nilodorum* may reappear in the deep water of the now submerged river channel section, since oxygen is present here in abundance due to the river inflow into the lake (PETR 1972 a and 1972 b).

At different times different organisms may be responsible for the high standing crop. For example in November 1966 at Kpandu the high standing crop was a result of high numbers of *Povilla* nymphs, while at Dodi, during the same month, four chironomids such as *Nilodorum*, *Chironomus*, *Endochironomus* and *Cladotanytarsus pseudomancus* resulted in a high standing crop (PETR 1972 b).

In this 1—9 m depth zone the major quantitative changes in standing crop of bottom fauna during the period of filling may be summarized as follows: a) high standing crop of *Povilla* nymphs towards the end of dry season and before the major rise in water level during the floods, i.e., in
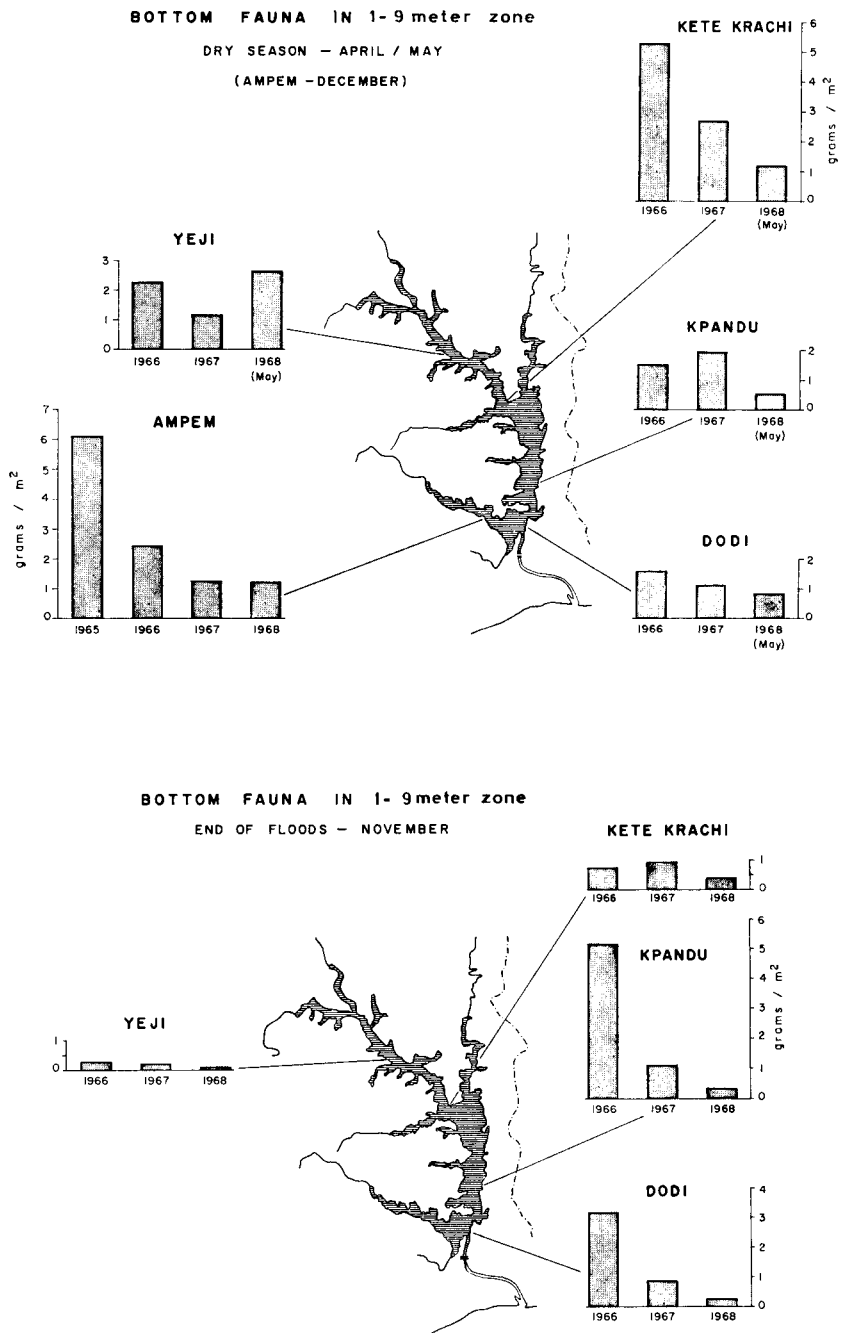
Fig. 4. Standing crop of the bottom fauna in the 1—9 m depth zone during the dry
season and the end of floods.

April to June; b) high standing crop of chironomid larvae towards the end of floods in September-November in the lacustrine south, but at the end of the dry season in April—June in the lake-river transition in the north-west; and c) a high standing crop of other organisms in September-November, during a small rise in water level, but before the water level starts receding, at the beginning of the maximum retention level.

### Bottom fauna of the profundal zone (11 m and deeper)

During the first two years the depth distribution of organisms was limited by poor oxygen conditions in deep water. With the oxygen discontinuity at 7—9 m (and often only at 3—5 m) in the gorge near the dam (station Ajena, VINER 1969) bottom invertebrates were only seldom found below the discontinuity. Until the floods of 1966, in this area no organism was found deeper than 11 m (PETR 1972 b).

Further north the oxygen discontinuity was deeper than in the gorge (VINER 1969) as a result of deep water mixing, due to the wind effect on the large expanse of the lake water surface. This favourably influenced the vertical distribution of the benthic fauna which was often collected down to 20 m.

At all stations, except one, the chironomids dominated the bottom fauna of the profundal zone and, thus, determined the distribution of the total bottom fauna (Fig. 5). In the south-west of the lake, at Ampem, the bottom fauna was rarely found below 11 m. When fauna was present it was represented mainly by chaoborid larvae (PETR 1972 a). This seemed to be related to frequent diurnal oxygen stratifications, resulting in complete depletion of oxygen in fairly shallow depths, making it impossible for chironomid larvae to live there. Chaoborid larvae can stay in deoxygenated bottom muds for a number of hours or even for longer periods of time. These were very common in Ampem area in 1966, but much less common in 1968. Several reasons for this change in the bottom fauna have been discussed (PETR 1972 a) and it is possible that the changes occurred as a result of an interaction of several factors such as: a) an irregular presence of zooplankton, the major food of these predatory larvae; b) changes in chemical composition of the bottom mud; and c) possibly improved oxygenation of water in this deep region.

In the northwestern limb at Kete Krachi and Yeji the deep water chironomids and the total bottom fauna increased in percentage abundance in 1968, compared with that for 1966. As mentioned above, the standing crop of the bottom fauna also increased in the shallowest zone, 1—3 m. At Yeji, both the shallowest and deepest areas were better oxygenated than the middle depth, where the low oxygen content of the water forced the bottom fauna to concentrate in adjacent, more highly oxygenated, waters. The small

TOTAL   BOTTOM   FAUNA

Percentage abundance by number

depth   zones   (m)

☐ 1 − 3   ☰ 5 − 9   ■ 11 − 25
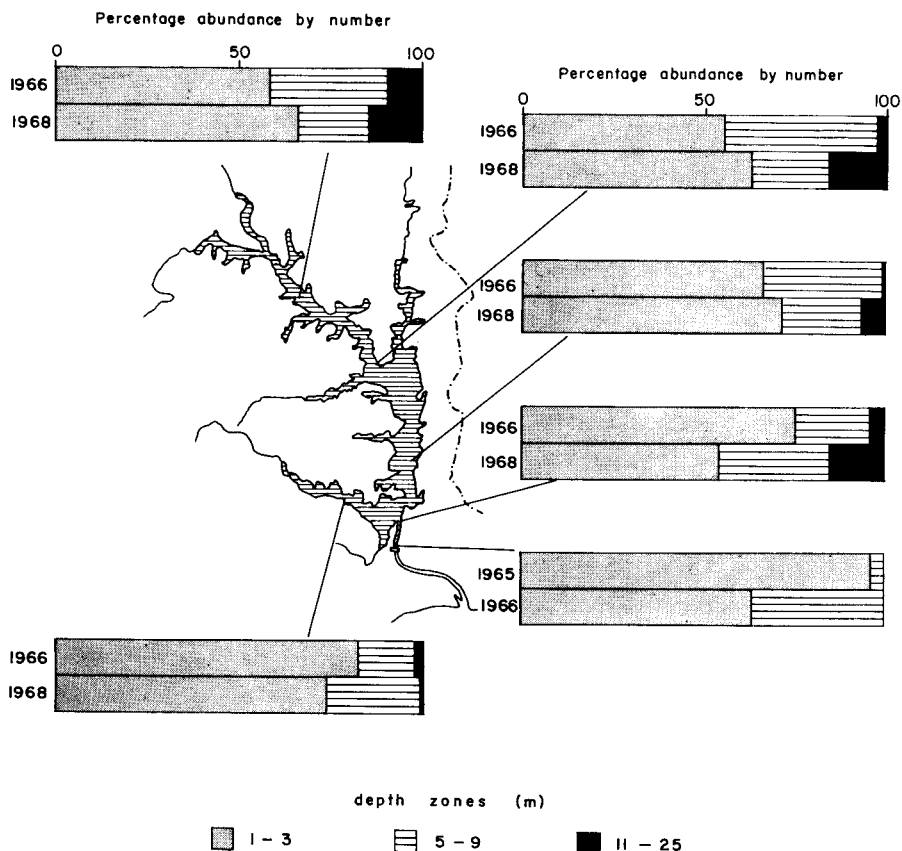
numbers of bottom invertebrates at Kete Krachi and Yeji in March 1968, and also from April to July, 1966 is evidently a result of stratification and the associated low oxygen concentration (Fig. 6).

At the open lake station at Dodi, in 1966, the oxygen discontinuity frequently developed at 17 m, and an occasional storm pushed it further down, but not deeper than 20 m (VINER 1969 and 1970). Two years later, in 1968, well-oxygenated water was found throughout the year below 17 m, and this resulted in fairly high numbers of bottom fauna in deep water (Fig. 5).

The tendency for female chironomids to deposit eggs close to the shore may be the major factor determining the low numbers of bottom invertebrates in deep waters at Kpandu. The deep water of 15—20 m depth is 1—3 km distant from the shore. In this region poor catches of chironomid
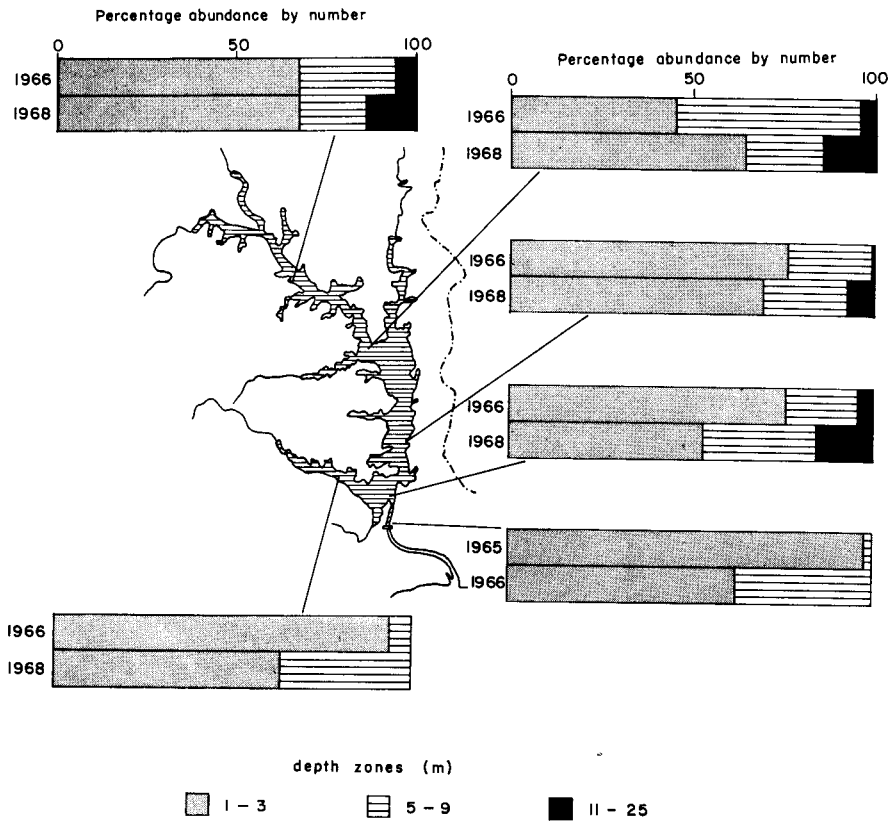
CHIRONOMIDAE

Fig. 5. Comparison of the total bottom fauna and Chironomidae at three different depth zones (percentage abundance by number) 1966 and 1968 (for Akosombo near the dam 1965 and 1966).

adults attracted to lights are typical (PETR 1970 b). The off-shore distance seems to be a limiting factor in these otherwise well and permanently oxygenated deep waters.

Discussion

The formation of a tropical man-made lake is characterized by the presence of a considerable amount of nutrients and organic matter. Some nutrients are washed into the lake by flood waters of the first and subsequent flood seasons, but the largest amount originates from the soil flooded by the rising water level. Large amounts of organic matter, such as grass and trees are being submerged, and during their decay a considerable amount of nutrient release occurs. The nutrients result in phytoplankton blooms

DODI - PROFUNDAL   KPANDU - PROFUNDAL

		A	B
x	1965	6	5
•	1966	24	14
□	1967	11	6
△	1968	24	17

		A	B
•	1966	11	5
□	1967	11	4
△	1968	23	6

a

b

KETE KRACHI- PROFUNDAL   YEJI - PROFUNDAL

		A	B
•	1966	15	8
□	1967	10	5
△	1968	22	17

		A	B
•	1966	9	6
□	1967	7	3
△	1968	20	13

c

d

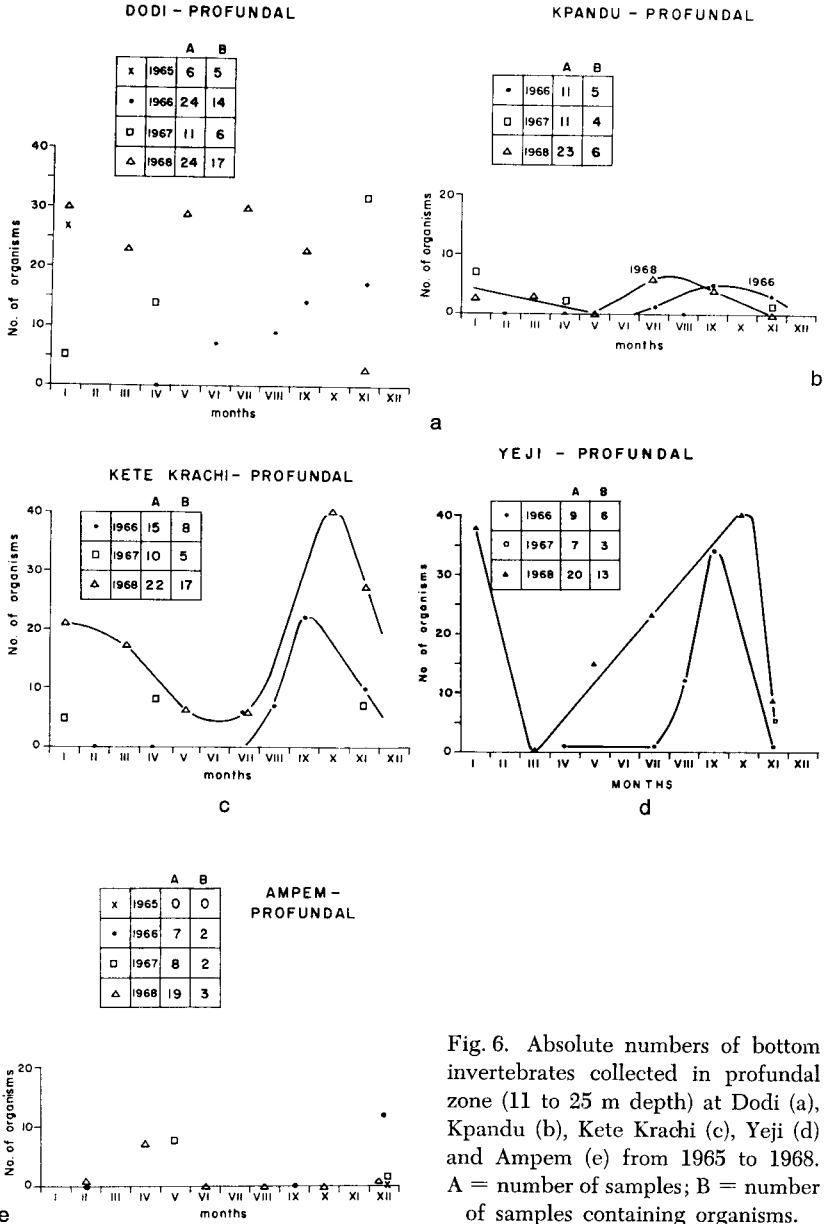|		A	B
x	1965	0	0
•	1966	7	2
□	1967	8	2
△	1968	19	3

AMPEM –
PROFUNDAL

Fig. 6. Absolute numbers of bottom
invertebrates collected in profundal
zone (11 to 25 m depth) at Dodi (a),
Kpandu (b), Kete Krachi (c), Yeji (d)
and Ampem (e) from 1965 to 1968.
A = number of samples; B = number
of samples containing organisms.

e

which develop under such conditions (BISWAS 1966). The organic matter
undergoes bacterial decomposition which requires a considerable amount
of oxygen. As a result, the dissolved oxygen present in water is rapidly used
up, leaving a thin layer of well-oxygenated water covering a large volume of
deoxygenated water.

This also occurred in the Volta Lake (EWER 1966; VINER 1970). During the first two years the depth of the epilimnion determined the vertical distribution of benthic invertebrates (PETR 1969). The third floods resulted in a further expansion of the lake and in an increase in the volume of water. A large surface area became open to the wind, resulting in deeper mixing and higher dissolved oxygen content. The thickness of the oxygenated layer (50—100 per cent saturation) reached 20—30 m (ENTZ 1969). Stratification periods became shorter and unstable. According to ENTZ (1969) a wind with a speed of 4—5 m/sec and two hour duration counterbalanced all the oxygen loss caused by decomposition within 24 hours. Higher dissolved oxygen content during the maturation of another man-made lake is also known from Lake Kariba. There, from 1960 until 1964 the hypolimnion became completely deoxygenated for shorter and shorter periods during stratification (COCHE 1968; HARDING 1966).

In Volta Lake the bottom fauna responded to these changes by developing in deep water. But it should be noted that even during long periods of mixing the bottom fauna never appeared below 24 m. This maximum depth distribution of the bottom fauna is probably a result of interaction of two factors: a) the length of the life cycle of chironomids which determines the distance a larva can travel before its larval stage is terminated; and b) predation of the larvae during their migration into deep water. The majority of females lay eggs along the shore (MACDONALD 1956; MACLACHLAN 1970). In some places a larva has to cover a distance of 1 to 3 km to reach 15 to 20 m. This must be done within 3 to 8 weeks which is the length of life cycles of various chironomids (PETR personal observation). The increased exposure of larvae to predators during their passage to deep water probably considerably reduces their chance for survival. This may be the reason why chironomid larvae were never collected from water deeper than 20—24 m, even when the dissolved oxygen content was high in this deep water for prolonged periods of time.

Changes in the substratum have a great effect on benthos. Flooded grass is grazed quickly by herbivorous fish such as *Tilapia zillii, T. melanopleura, Distichodus rostratus,* and by some omnivorous fish like *Synodontis* spp., *Alestes macrolepidotus* and *A. nurse.* Flooded vegetation is also destroyed by bacteria which attack fragments of bark und wood scattered on the bottom. All of this leads to a rapid decrease in numbers and biomass of burrowing mayfly, *Povilla,* which was a major contributor to the benthic fauna during the first 2—4 years. The nymph of this mayfly requires dead plant substance into which it can burrow. By doing this, it conceals and protects itself from predators. While inhabiting the burrows, it vibrates its external gills, and using brushes of pinnate setae on its mandibular tusks and forelegs, it selects food from the water current (HARTLAND-ROWE 1953).

The biomass of chironomids, especially *Nilodorum, Chironomus* and *Dicrotendipes* is also largely determined by the presence of a suitable substratum. Their larvae use fine mud particles for the construction of the tubes which they inhabit. When the inundated grass, bush and trees are destroyed by waves, etc., an increase in erosion results in small particles of substrate being washed out. As a result, suitable microhabitats for tubiculous larvae disappear. A substrate is left which usually contains a high concentration of sand particles and this is avoided by many larval chironomids and some other invertebrates. This was confirmed in experiments with *Nilodorum brevibucca* (McLachlan 1969 b).

This change in substratum during the ageing of the lake resulted in a sharp drop in the biomass of the bottom fauna. However, during the same time, the relative proportion of chironomids among all bottom invertebrates increased, and in 1968 they formed almost 80 per cent of the total number of benthic invertebrates, compared with only about 69 per cent in 1966 (Table 2).

Table 2. Percentage abundance of the major taxa in Volta Lake in 1966 and 1968.

	Chirono-midae	Povilla	Tricho-ptera	Oligo-chaeta	Chaobo-ridae	Other organisms
1966	69.2	14.2	2.4	6.1	3.2	4.9
1968	79.8	3.4	2.5	3.8	1.6	9.0

Volta Lake consists of several distinct sectors which differ in their limnology. For several months during floods the north-western limb of the lake becomes a river. Among other things, this results in a load of silt being brought into the lake and deposited over a considerable distance throughout the lake. With the silt comes a considerable amount of organic detritus. Throughout the year the inflow of cooler riverine water, rich in oxygen, results in good oxygenation of the water in the deeper regions of this part of the lake. This occurs even when the shallower regions are stratified and poor in oxygen at the bottom (Petr 1973 c). This inflowing water is evidently rich in nutrients, and this coupled with daily mixing of shallow water promotes rich growth of plankton. A similar situation to that just described, is also present in the south-western limb of the lake on the now permanently submerged agricultural and forest land of the Afram Valley. Here in shallows the situation is similar to that in the northern sector. But in the deep part, stratification may last for days and weeks, and the limited inflow from the Afram River is not sufficient to break down this stratification.

The difference between these two sectors and the main lake area is well illustrated by the differences in dominant species of the bottom fauna,

especially chironomids (PETR 1971 a and 1972 b). In the main limb the ageing of the lake within two to three years after being flooded has resulted in quantitative and qualitative changes which were later recorded in the north-western limb.

During their first years there are marked similarities in changes in the standing crop of benthic invertebrates of tropical and temperate man-made lakes. The maximum standing crop, and evidently the maximum productivity is achieved in the first two years after closing the dam. This period is followed by a depression of productivity.

Table 3 indicates the changes in the standing crop of Volga man-made lakes (MORDUKHAI-BOLTOVSKOI 1961) and in Volta Lake in the first five years.

Table 3. Changes in standing crop in a temperate and a tropical man-made lake during the first five years.

Year	Volga lakes standing crop (wet weight) g/m²	Volta Lake standing crop (wet weight) g/m²
1	1.5—15.0	3.2
2	5.0— 7.0	3.2—6.2
3	1.0— 5.0	1.6—5.5
5	less than 2.2	0.5—2.5

These data for the Volga lakes are calculated for whole transects, while those for Volta Lake relate only to the 1—9 m zone. In Volta Lake the spread of the fauna into deep water was initially prevented by the long-lasting deoxygenation. Such deoxygenation was recorded only exceptionally in the Volga reservoirs.

The rapid decrease in abundance of the bottom fauna in the second year of formation is common to all the Volga reservoirs. MORDUKHAI-BOLTOVSKOI (1961) suggested that the abundance of the bottom fauna would decrease even more rapidly if new land were not flooded. However, in the south of Volta Lake the gradual flooding of new soil each year had no beneficial effect on the bottom fauna and the standing crop continuously decreased throughout five years of filling. On the other hand, in the north of the lake, during the same time period the standing crop of the bottom fauna stayed at the same level, or even increased. The turbid inflow never passed the Kpandu section of the lake and ENTZ (1969) suggested that the floating coarse or colloidal particles, which were brought into the lake by three large rivers situated in the north, settled mechanically, precipitated, or settled by biochemical and biological processes, before the river water

could reach the Kpandu area. It is possible that the increased sedimenta-
tion in the north of the lake may have had an effect on the high standing
crop of bottom fauna there compared with that in the lacustrine environ-
ment of the south. In some new man-made lakes of the temperate zone the
rate of decrease of the biomass of the bottom fauna seems to be dependent
on the sedimentation rate (SOKOLOVA 1971).

Such longitudinal differentiation in the bottom fauna, as observed in
Volta Lake, has also been recorded from other large and small man-made
reservoirs, as well as natural lakes. RAVERA (1966) ascribes this to the fact
that detritus carried into a lake is rich in organic matter which can provide
a continuous supply of food that would support a high density of benthic
organisms. In areas under the direct influence of the Volta River the
standing crop was higher than elsewhere. Comparable patterns of changes
were recorded by MORDUKHAI-BOLTOVSKOI (1961) for the Kuybyshev reser-
voir on the Volga River. Similarly, the point of river-lake transition in the
Jebel Aulia reservoir on the White Nile is very rich in bottom fauna,
compared with the area near the dam (MONAKOV 1969). However, not all
rivers increase the productivity of man-made lakes. In Central Africa, the
Zambezi River feeding Lake Kariba is poor in nutrient content and low
in silt load (BEGG 1970).

Once the standing crop of the bottom fauna in the river-lake transition
zone has reached a point of stabilization, no further rapid change is likely
to occur. A value of 2 g/m² of standing crop of bottom fauna (wet formalin
weight) was found to be an average value for the 1—9 m depth zone. This
should be expected in this type of habitat, i.e., in tropical man-made lakes
in savanna-woodland regions. It is also possible that in the future, new
bottom organisms, such as molluscs and oligochaetes, now extremely rare,
may colonize the lake in large numbers. Since they live longer than chirono-
mids, they may also colonize the deepest water where a reasonably high
dissolved oxygen content may be expected in the near future (ENTZ 1969).
In sectors not influenced by rivers, the standing crop of the bottom fauna
will be probably less than 1 g/m².

Shoreline erosion during the filling of the lake assisted in particle size
sorting and silt deposition in deeper water, and this will certainly further
influence the bottom fauna of Volta Lake. The annual draw-down of 3 m
may not allow development of aquatic macrophytes along the shores with
a steep slope. Here the waves are much more active than on the gradually
sloping bottom. The differences in substratum can be expected to determine
the presence or absence of aquatic macrophytes. The experience from Lake
Kariba indicates that on mud flats, exposed during the drawdown, a dense
flush of terrestrial grasses develops which attracts large numbers of game.
When the water rises, dung and the remaining grass is flooded, and as a

result of such favourable nutrient conditions, the total biomass of chiro-
nomids in this area is 20 times higher than that of normal populations of
the bottom fauna (McLachlan 1969 a and 1969 c).

Very little game lives along the shores of Volta Lake, and the cattle
industry is negligible. So far, the growth of grass on the exposed muddy
areas has been weak. In some areas the draw-down area is cultivated. Even
without the presence of game, the annual flooding of exposed overgrown
areas may be expected to increase the productivity of the lake by providing
additional substrata which will support benthos and Aufwuchs during pe-
riods of high water. This will not be dissimilar to the situation before the
formation of the lake, when, during floods, the flood plains along the river
became the major spawning and feeding habitat for fish.

Summary

The initial high standing crop of benthic invertebrates in the Volta Lake was
followed by decline in numbers and biomass. This decrease was more consistent
in the areas near the dam, while only slight or no decrease was recorded in areas
under the influence of large rivers. Steeply sloping bottoms in the marginal zones
were found to be more affected by erosion forces. This resulted in translocation of
fine mud particles into deep water, and in the destruction of the littoral vegetation.
As a result, the standing crop of the bottom fauna in such areas decreased,
especially in the 1—9 m depth zone. The bottom fauna was richer in more pro-
tected areas, especially those with marginal vegetation. The ageing of the lake
resulted in a more regular presence of the bottom fauna in deep water. However,
bottom fauna was never found below the 24 m depth. It is suggested that the
distance which a chironomid larva travels along the bottom during its larval stage
limits its area of distribution. The standing crop data for Volta Lake are similar to
those of new man-made lakes in temperate zone during their formative period.

Zusammenfassung

In den ersten zwei Jahren des Bestehens des Volta-Stausees (Ghana, West-
Afrika) hat sich die Bodenfauna der seichten Gewässer durch eine relativ hohe Bio-
masse ausgezeichnet (3.2 g/m²—6.2 g/m²). Danach ist sie allmählich zurückgegan-
gen, insbesondere im südlichen Teil des Sees in der Nähe des Staudammes. Im
Norden des Sees, wo die Bodenfauna dem Einfluß einströmender Flüsse unter-
liegt, war ihre Biomasse fast gleichbleibend oder hat sich sogar erhöht (im Jahr
1966 1.4 g/m², 1968 3.0 g/m²). Das kann wahrscheinlich der Zufuhr organischen
und anorganischen Materials durch die Flüsse, insbesondere während der Flutzeit,
zugeschrieben werden.

Ein steil abfallender Boden des Litorals wird mehr von der Erosion beein-
flußt als ein langsam abfallender. Der erste Typus wird schneller erodiert, die
litorale Vegetation, die sich anfangs in den von toten überschwemmten Bäumen
geschützten Teilen des Sees gebildet hat, wird entwurzelt, die kleinen Boden-
partikeln ausgewaschen, um im tieferen Wasser abgesetzt zu werden. Unter dem
Einfluß dieser Veränderungen hat sich die Biomasse der litoralen Bodenfauna
vermindert. Auf den mehr geschützten und weniger steilen Böden wird die Bio-
masse von Bodenwirbellosen vermehrt, insbesondere dort, wo sich die Litoral-

pflanzen ausdehnen. Die Alterung des neuen Stausees und die damit verbundene
bessere Sauerstoffkonzentration in tieferem Wasser führt zu einem regelmäßigeren
Auftreten der Bodenfauna im tiefen Wasser. Das tritt jedoch keinesfalls durch eine
gesamterhöhte Biomasse der Bodenfauna des Sees in Erscheinung. Trotz der guten
und langdauernden Sauerstoffkonzentration im tiefen Wasser 3—5 Jahre nach dem
Schließen des Staudammes sind Bodentiere nie tiefer als in 24 m Tiefe entdeckt
worden. Es ist möglich, daß der kurze Lebenszyklus der Bodentiere die Verbrei-
tung dieser Organismen in den Tiefen durch die begrenzte Mobilität bestimmt.
Insbesondere gilt dies für die Chironomidenlarven, die fast 100 Prozent der Bo-
dentiere des tieferen Wassers ausmachen.

Die Biomasse von Bodenwirbellosen des Volta-Stausees während der ersten
5 Jahre gleicht ungefähr derjenigen europäischer Stauseen (UdSSR) im gleichen
Zeitraum.

Acknowledgments

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