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**Benthic fauna of a tropical man-made lake  
(Volta Lake, Ghana 1965-1968)**

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With one map, 21 figures and 5 tables in the text

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\* ) This investigation was carried out when the author was a member of the Volta Basin Research Project of the University of Ghana.

### Abstract

Quantitative and qualitative changes in the individual taxa of the bottom fauna were followed in the Volta man-made lake over the filling period 1965—1968. The changes in the individual invertebrate taxa during this period are considered in relation to the changing environmental factors, such as oxygen content, substratum, degree of exposure to waves, and establishment of littoral aquatic macrophytes. The ecology of chironomids, ephemeropteran nymphs and chaoborid larvae is discussed in this paper in detail.

### Introduction

After the closing of the Akosombo dam on the Volta River in Ghana in 1964, the largest African man-made lake started to form. During the long filling period research was carried out on various aspects of limnology (BISWAS, E. R. I. 1969; BISWAS, S. 1966, 1969; EWER 1966; LAWSON et al. 1969; PETR 1971 a; VINER 1970 a, 1970 b) and on the formation of the fish fauna (PETR 1967, 1968 a; REYNOLDS 1970). The development and changes in the bottom fauna were among the investigated topics.

The newly flooded land was found to be rapidly colonized by bottom fauna, especially by chironomids (PETR 1971 a). Other bottom organisms, such as nymphs of the burrowing mayfly *Povilla adusta* NAVAS, later experienced a great expansion, and greatly influenced the bottom fauna population (PETR 1969). Since the establishment of the lake, the bottom fauna has undergone changes in its species composition and abundance, resulting in a decrease of the initial relatively high biomass (PETR 1969).

The present paper deals with the ecology of the individual taxa of the bottom fauna, based on qualitative and quantitative sampling. Observations on chironomids were carried out in detail as these animals dominated the bottom fauna numerically and in many cases also by weight.

### Description of the lake and sampling stations

The Volta Lake extends from  $9^{\circ} 10' \text{ N}$  to  $6^{\circ} 15' \text{ N}$ , and from  $30' \text{ E}$  to  $1^{\circ} 30' \text{ W}$  (map). Its total length in 1969 was about 380 km, and it covered about 8,000 km<sup>2</sup>. Its maximum depth was about 80 m. Detailed morphometric data for the lake at its maximum level of 84 m above sea level have been prepared by ENTZ (1969).

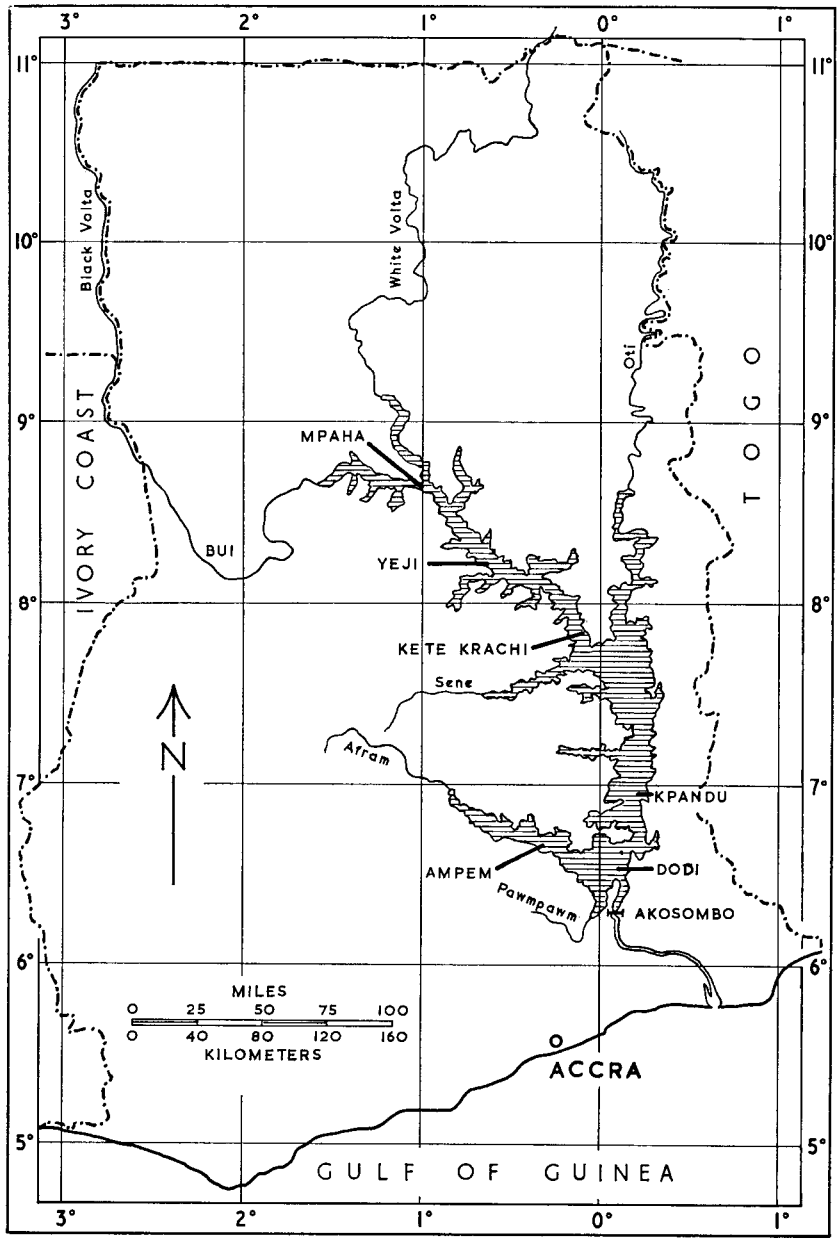
Despite its great length the Volta Lake extends through only one major vegetational zone, that of the Guinea savanna though this varies from a relatively moist type in the south at the edge of a tropical forest, to a relatively dry type in the north. This habitat, characterized by a large number of trees at the edge of a tropical forest was drowned during the formation of the lake (LAWSON et al. 1969).

The climate of Ghana is tropical and strongly influenced by southerly monsoons. Southerly winds predominate. Most of the Volta basin lies in the single-peak-rainfall zone, in which the rainy season maximum is in July, August and September. The rains, followed by floods, are succeeded by a dry hot season which extends over a period of seven to eight months. In December-February the effect of the dry season is accentuated by a period of harmattan wind of very low humidity, blowing from the north and north-east. The post-harmattan dry period ends with rains.

The effect of regular winds and of strong stormy winds on some limnological aspects of the Volta Lake was studied by VINER (1970 a, 1970 b). The seasonality of the climate was reflected especially in the periods of water mixing and water stratification, resulting in oxygenation and deoxygenation of deeper water layers. The effects of these changes upon the quantity and composition of the invertebrate fauna will be discussed later.

Water samples for physico-chemical analysis and samples of the bottom fauna were collected at six stations. The sites were selected so as to cover a large range of lake habitats: shallows distant from large rivers and therefore not directly affected by flood water; bottom under the direct influence of floods; bottom in close contact with water masses of the open lake; and areas partly protected by flooded trees. The gorge area close to the Akosombo dam, where the limnological studies on the new lake were initiated was also included, though the research there was terminated in July 1966.

**Akosombo:** This station, the first to be established, was situated about 3 km distance from the dam. The landscape in this area is hilly, with an abundance of forests. The river banks were cleared of trees before being flooded by rising water. The gradient of the shores above and below water level is steep, where the original river passed through a gorge. The bottom consists predominantly of rocks and large stones, separated by small



Map showing sampling stations and extent of the Volta Lake in Ghana.

patches of sandy and silty substrate. This station was sampled from November 1964 till July 1966.

During this period the percentage saturation of oxygen in the bottom water layers rapidly decreased with depth and seldom exceeded 35 per cent, usually being even less below 5 m. Oxygen was practically absent at 7 m and deeper (PETR 1970 d).

**Dodi:** A station was established in December 1965 on this island close to the former confluence of the Afram and Volta rivers. A few other islands are situated about 2 km distance from Dodi Island, and the mainland shore is about 5 km away. Dodi Island is about 1.5 km long and 700 wide, rising approximately 50 m above the lake. The shores exposed to waves are rocky, but belt of flooded trees surrounds the island and this is broader on the non-exposed sides.

A discontinuity, with a sudden drop in oxygen percentage saturation, was recorded in the bottom layers three times in 1966 at depths of 17 m and 20 m (PETR 1970 d). After June 1966 until the end of 1968 the discontinuity, when present, was always below 25 m depth, from where no organisms were ever found.

**Kpand u:** A low mountain range about 3 km distance inland is covered by forest, but the shore is typical savanna. The relatively shallow gradient of the flooded land resulted in a belt of dead and partly submerged trees extending for about 2 km into the lake. The flooded soil has a high proportion of silt and clay (PETR 1972).

Until August 1966 a well established oxygen discontinuity was present between 9 and 14 m depth. After this date the water in the bottom layers in all sampled depths was well oxygenated, although on several occasions the decaying flooded terrestrial vegetation was observed to result in a reduction of the oxygen content of water in shallows (PETR 1970 d).

**Kete Krachi:** This station as well as the one at Yeji is situated in fairly dry savanna. The number of flooded trees in this area is small and the bottom is sandy with some clay and silt. Scattered submerged trees extend for about 1 km off-shore because of the slight gradient of the lake bottom.

The changes in oxygen concentration at the bottom during the investigation period were similar to those at Kpand u. An oxygen discontinuity was present between 7 and 14 m until July 1966; later on, the bottom water layers were always well oxygenated.

**Yeji:** When this station was established in April, 1966, the flooded area was not very extensive. Before being flooded, parts of the land were cultivated. The soil particles are predominantly clay, silt and very fine sand. The bottom of the old river consists of coarse sand. Before the lake was established, extensive areas of land above the old river channel were regu-

larly inundated during flood seasons, and after the retreat of water into the river channel during the dry season, swamps persisted till the next floods. Numerous dead trees now rise above these former flood plains and the adjacent areas.

Owing to the small depth and the direct effect of the inflowing river, the water was usually well oxygenated down to the bottom. Later on, with increasing depth and with further areas of river bank being flooded, extensive shallows developed and the water was often stratified. While the bottom layers of these shallows were often deoxygenated, water in the deepest part of this area, e. g. the former river channel had a high oxygen content due to the inflow of the riverine water (PETR in press).

*A m p e m*: An inclined plain of agricultural land descends gradually to the lake. Towards the SSW, about 3 km distance from the lake shore, the plain is fringed by a range of forested mountains. The bottom of the lake has slight gradient and there is a relatively shallow bay here in an area which was cleared of trees before being flooded. An uncleared area of partly flooded trees lies about 1 km off-shore. The bottom consists predominantly of clay and silt, and has a high content of organic matter.

The oxygen content of the water seems to be determined mainly by two factors. Firstly, the large amount of organic matter present at this station (PETR in press) resulted in the rapid utilization of oxygen in the deep water and often led to poor oxygenation of water in shallows. Secondly, in these shallows, the high concentration of algae in the first few meters seems to have been responsible for a marked oxygen gradient which developed during the day, with the bottom often remaining deoxygenated during the afternoon. Later on, with the night cooling of the surface water, the stratification broke down, and oxygen concentrations of the water became low but evenly distributed with depth.

As the lake gradually filled the depth of the oxygen discontinuity during the stratification periods gradually became greater at all stations. The reason for this seems to be the larger surface area of water exposed to winds; the rapid destruction of flooded trees at the water surface also increased the area open to wind action.

### Material and methods

The regularity of sampling was determined by the availability of the research vessel. As this was often under repair, the frequency of sampling was variable at individual stations. In 1967, for example, only three visits could be paid to the lake stations. Sometimes stormy winds and heavy waves made sampling extremely difficult, especially among submerged trees.

For sampling the bottom fauna a Japanese Marukawa bottom sampler was used at all stations. This sampler closes on contact with the substratum. Being heavy and of small size it easily penetrates through the branches of the submerged

vegetation to reach the bottom. Large bottom samplers of Ekman-Birge type, used initially during the testing of the equipment, were found to be unsuitable for sampling bottoms rich in flooded vegetation, as the samplers never closed properly. They also were easily entangled in the submerged vegetation.

Often it was necessary to adjust the sampled depths because of the presence of obstacles on the bottom. During periods of lake-level rise the bottom at 1—3 m could sometimes not be sampled because of the dense cover of flooded grass. Stony and rocky bottoms, particularly abundant at Akosombo were also avoided. The rise in the water level during floods and its retreat during dry seasons resulted in shifting of the sampling points, the criterion for a sampling point being the depth measured from the water surface. During the first two years the depth sampling intervals were smaller than later on since at that time the bottom fauna was concentrated predominantly in the shallows.

From 1967 on with the bottom fauna occurring deeper, the following depths were selected for sampling, though not all of them were always sampled: 1, 3, 5, 7, 9, 11, 14, 17, 20 and 25 m. On a few occasions 30 and 35 m depths were also sampled.

At each site six samples, covering a total area of 300 cm<sup>2</sup>, were collected from each depth investigated. Samples were washed on a brass sieve of 0.4 mm mesh, and preserved in 4% formaldehyde solution. The number of organisms present in each taxon was counted and their biomass determined by weighing on a torsion balance, after drying on blotting paper for 3—5 minutes, according to the quantity of material present.

Chironomid larvae were mounted in Euparal for identification on the basis of their labial plates and antennae. Some larvae were reared and their pupae and adults obtained. Photographs of the mouth parts of larval types not in the literature are reproduced in Fig. 20 a—h. The taxonomic structure of the family Chironomidae used in this paper follows FREEMAN'S interpretation (1957). The nomenclature follows that used by JOHANSEN (1937).

### Part I. Bottom fauna other than Chironomidae

This section will deal with the occurrence and habitat preferences of invertebrates other than Chironomidae, and with changes in their abundance and depth distribution at various stations in 1965—1968 (Table 1).

The following abbreviations will be used for individual stations: AK = Akosombo, A = Ampem, D = Dodi, KP = Kpandu, KK = Kete Krachi, Y = Yeji. The figure following the letter gives the total number of organisms collected at each locality.

#### COELENTERATA (KK-1).

*Limnognathia* sp. Only one specimen was collected from a depth of 8 m during the flood peak in September 1966. It may well be that the specimen was caught from free water during the lowering of the sampler to the bottom. The water temperature at the surface was 30.4° C and at 8 m depth 27.8° C, this corresponding to 126 and 17 per cent oxygen saturation respectively. This is the only record of *Limnognathia* in the Volta Lake between May 1964, when the dam was closed, and 1970. In the

Table 1. Occurrence of invertebrates other than Chironomidae in bottom samples at various stations in 1965—1968.

Station	Yej	Krachi	Kpandu	Dodi	Ampem	Alkosombo	Year
	(river-lake transition)	(± open, mid-lake)	(± open, mid-lake)	(open to waves)	(protected shallows)	(gorge at the dam)	
	1966 67 68	1966 67 68	1966 67 68	1965 66 67 68	1965 66 67 68	1965 1966	
COELENTERATA							
<i>Limnocooida</i> sp.	—	+	—	—	—	—	
ANNELIDA							
Oligochaeta							
Naididae							
<i>Allonais</i> spp.	+	+	+	+	+	+	
<i>Branchiodrilus</i> spp.	—	—	—	—	—	—	
<i>Dero digitata</i> MÜLLER	+	—	—	—	—	—	
<i>Aulophorus</i> spp.	—	—	—	—	—	—	
Hirudinea	+	—	+	+	+	+	
MOLLUSCA							
Gastropoda							
<i>Bulinus truncatus rohlfsi</i> (AUDOUIN)	—	+	—	+	+	—	
<i>B. forskali</i> (EHRENBERT)	+	—	+	—	+	—	
<i>Anisus coretus</i> (BLAINVILLE)	+	—	+	—	—	—	
<i>Ferrissia</i> sp.	+	—	—	—	—	+	
Lamellibranchia							
<i>Pisidium</i> sp.	—	—	—	—	—	—	
CRUSTACEA							
Cladocera							
<i>Ilyocryptus sordidus</i> (LIEVIN)	+	—	—	—	+	—	
<i>Ceriodaphnia</i> sp.	—	—	—	—	—	—	



Organism	Station		Year		Akosombo (gorge at the dam)			Ampem (protected shallows)			Dodi (open to waves)			Kpandu (± open, mid-lake)			Kete Kradii (± open, mid-lake)			Yeji (river-lake transition)		
			1965	1966	1965	1966	1967	1968	1965	1966	1967	1968	1965	1966	1967	1968	1966	1967	1968	1966	1967	1968
Copepoda			+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ostracoda			+	+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cyclestheria hislopi</i> BAIRD			+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
HYDRACARINA			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
EPHEMEROPTERA			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pocilla adusta</i> NAVAS			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Caenis</i> spp.			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cloeon</i> spp.			+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
ODONATA			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Zygoptera			+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Anisoptera			+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
HEMIPTERA			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Micronecta</i> spp.			+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Gerris</i> sp.			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TRICHOPTERA			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Dipseudopsis njalana</i> ULMER			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Orthotrichia smaeni</i>			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
JACQUEMART			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ecnomus</i> spp.			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
COLEOPTERA			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dytiscidae			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
DIPTERA			+	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(other than Chironomidae)			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chaoboridae			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ceratopogonidae			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
LEPIDOPTERA			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pyralidae			—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TOTAL			15	6	6	5	10	10	17	11	6	7	16	8	7	14	8	12	13	6	10	10

man-made Lake Kariba in Central Africa *Limnocyclus tanganyicae* GUNTHER was found for the first time on the 23rd February 1960, i.e. 15 months after the dam was closed, and by September 1960 medusae were observed to be widespread there (PITMAN 1965). So far there are no records from the two other large African man-made lakes, i.e. Lake Kainji in Nigeria, and Lake Nasser in Egypt.

In West Africa *Limnocyclus* has been reported from Mali (DAGET 1950), Nigeria (BROWN 1908, GREEN 1960), Ivory Coast (MONOD cit. in PITMAN 1965), Senegal (LELOUP 1951) and Mauritania (DEKEYSER 1955).

The taxonomy of the genus is not clear, with three species in the genus mentioned by GREEN (1960), but only one by LELOUP (1951) and KRAMP (1964). Therefore no attempt has been made to identify further than genus the single specimen collected from the Volta Lake.

ANNELIDA (AK-199, D-37, KP-70, KK-91, Y-147, A-151).

Both Oligochaeta and Hirudinea were regularly collected from the bottom.

Oligochaeta (AK-194, D-36, KP-64, KK-88, Y-147, A-150).

Naididae. This is the only family of Oligochaeta found in bottom samples. The species which I collected from aquatic plants of the Volta Lake (PETR 1968b) have been described by HRABE (1966) and BRINKHURST (1966) and later revised by BRINKHURST (1970). In general, the Naididae tended to decrease in numbers with rains and floods, and during these periods they were generally found deeper than during the stratification of the lake. Among the bottom invertebrates, the oligochaetes, together with the chironomids, were found at the greatest depths.

*Allonais* (D-33, KP-62, KK-65, Y-119, A-133).

HRABE (1966) identified one species from *Pistia* and *Ceratophyllum* of the Volta Lake as *A. paraguayensis ghanensis*. BRINKHURST (1970) is of the opinion that *A. paraguayensis* (MICHAELSEN) is an extremely variable species in which all sorts of sub-species could be described, but that they are all linked by intermediate forms.

*Allonais* is the most common annelid in the bottom fauna, and any change in its abundance results in a change in total oligochaete fauna. It prefers aquatic plants and flooded grass being least common on sandy substrata and bottoms exposed to waves. In localities protected from waves and with an abundance of aquatic plants these oligochaetes were common (Ampem). In certain places a decrease in its numbers coincided with the littoral zone becoming more exposed to waves. Rains and floods resulted in a fall in abundance of *Allonais* (July, August 1966; September, October 1968). Naididae present in aquatic plants in 1965 responded to seasonal changes in a similar way (PETR 1968b).

*Branchiodrilus* (KK-9, Y-16, A-6).

Two species have been identified from the aquatic plants: *B. cleistochaeta* I. O. DAHL (HRABE 1966) and *B. hortensis* (STEPHENSON) (BRINKHURST 1966). These species were not separated in routine investigation of the bottom fauna. *Branchiodrilus* was found at greater depths during floods than during the dry season, suggesting that oxygen may be a limiting factor in its distribution in depth.

*Dero digitata* (MICHAELSEN) (D-3, KP-2, KK-4, Y-4, A-9).

It is the only species of *Dero* so far collected from the lake. As with *Branchiodrilus*, stratification limits the distribution of *Dero* to shallows.

*Aulophorus* (KK-5, Y-4, A-1).

This is the least abundant naidid. On aquatic plants from Akosombo it was represented by two species, e. g. *A. flabelliger* STEPHENSON and *A. pectinatus* STEPHENSON.

*Aulophorus*, though abundant on *Pistia* at Akosombo in 1965 (PETR 1968b) was rarely found in bottom samples. It reached a maximum depth at the end of floods when it was collected from 14 m (Yeji, November 1968).

HIRUDINEA (AK-5, D-1, KP-6, KK-3, A-1).

This group was not further identified. Soos (personal communication) has identified the following species collected from aquatic weeds: *Batracobdella nilotica* (JOH.), *Helobdella conifera* (MOORE) and *Batracobdella tricarinata* (BL.) (PETR 1968b). Leeches occurred usually in the first three m depth. Their vertical distribution seems to be determined by the abundance of food as suggested by their preference for the littoral zone with aquatic plants. During floods, when the lake level rises, the depth of rooted plants such as *Ceratophyllum* increases, and leeches are found deepest (at Kpandu at 6 m in September 1966, and at 7 m in July 1968).

MOLLUSCA (AK-6, D-3, KP-4, KK-1, Y-5, A-62).

Molluscs are poorly represented in the Volta Lake, both by number of species and by the number of specimens found. They occur predominantly in areas with an abundance of aquatic plants such as *Ceratophyllum* and *Pistia* (PETR 1968b). On the bottom they were usually confined to the first five m of depth, with a preference for very shallow water of 0.5–1 m. Their occurrence seems to be also determined by the availability of food such as periphytic algae and organic detritus. A high oxygen saturation of the water seems to be essential for their existence. The absence of molluscs in the north during floods may be related to a high content of inorganic matter in suspension, which may interfere with the reproduction of *Bulinus* sp., as suggested by HARRISON & FARINA (1965).

The dominant molluscs were snails. Only one specimen of a lamellibranch was collected in the bottom fauna.

Gastropoda (AK-6, D-3, KP-4, KK-1, Y-4, A-62).

*Bulinus truncatus rohlfsi* (AUDOUIN) (D-2, KP-2, KK-1, Y-3, A-5).

The presence of this species is closely correlated with the presence of aquatic weeds, especially *Ceratophyllum*. Rich underwater meadows of *Ceratophyllum* resulted in an abundance of *Bulinus* in bottom samples in shallows at Ampem. At other stations this species was very rare. PAPERNA (1969) who was following the incidence of this snail in the Volta Lake in relation to the infestation of the human population with bilharzia collected this snail from other habitats on the lake, including areas free of aquatic weeds. *B. truncatus* is limited to the first 5 m depth. Only empty shells were collected from deeper water. Its absence from deeper zones may be due to the absence of host plants and of the periphytic algae on which it feeds in the Volta Lake. In Lake Victoria, however, *B. truncatus trigonus* is found also in deep water below the euphotic zone (Paperna personal communication).

The absence of *B. truncatus* from bottom samples at most stations in 1968 indicates that its numbers may be gradually decreasing in places without aquatic plants. This decrease seems to run parallel with the gradual disappearance from the bottom of organic debris especially that of plant origin.

*Bulinus forskali* (EHRENBERG) (AK-1, KP-1, A-3).

This species was common at Akosombo in aquatic weeds in 1965, but only one specimen was collected from the bottom of that area. *B. forskali* like *B. truncatus* prefers shallow water and was found deeper only during the rise of the water level. As with the other species, the presence of *B. forskali* seems to be closely correlated with the presence of *Ceratophyllum* in the water. *B. forskali* was collected from a maximum depth of 6 m.

*Anisus coretus* (BLAINVILLE) (AK-1, D-1, KP-1).

The reason for the rare occurrence of this gastropod in bottom samples seems to be its fragility which makes it easily destroyed during the sampling and washing processes. It was collected from 0.5 m to 4 m depth.

*Ferrissia* sp. (AK-4, Y-1).

*Ferrissia* is a minute gastropod found firmly attached to the substratum, from which it can be distinguished only with difficulty. *Ferrissia* was collected from 0.5 m to 3 m depth.

*Lamellibranchia* (Y-1).

*Pisidium* sp. (Y-1).

The small size and the shape of *Pisidium* makes it difficult to distinguish it from substratum. At Yeji it was collected in August 1966 from the sandy bottom of the main river channel. The species may be restricted to the permanently well oxygenated river bed which is close to the major inflowing river in this part of the lake.

## CRUSTACEA (AK-52, D-10, KP-7, KK-14, Y-9, A-170).

The number of crustaceans was low. Ostracoda and Conchostraca were most common, while Cladocera and Copepoda occurred very seldom. One of the reasons for the low numbers of the latter two taxa in bottom samples may be that they were probably often overlooked owing to their small size.

## Cladocera (AK-2, KK-1, A-5).

*Ilyocryptus sordidus* (LIEVIN) (Macrothricidae) (AK-2, KK-1, A-4).

This is a common littoral species abundant mainly among aquatic plants. On the bottom it was collected from 1 m to 3 m depth.

*Ceriodaphnia* sp. (A-1).

One specimen was collected at Ampem from 1 m depth.

## Copepoda (AK-1, D-1).

Copepoda were not further identified. They were collected from 1 m and 2 m depth.

## Ostracoda (D-3, KP-2, KK-11, Y-8, A-107).

Ostracoda are common organisms of the littoral zone and of aquatic plants (PERR 1968b). This probably explains why they were most abundant at Ampem, the one locality rich in aquatic plants, and rare elsewhere. Only material collected from *Ceratophyllum* and *Pistia* has been identified (PERR 1968b). Their maximum depth distribution was 12 m, but the majority of specimens were collected from 1—3 m depth.

## Conchostraca (D-6, KP-5, KK-2, Y-1, A-58).

Conchostraca are represented by only one species, *Cyclestheria hislopi* BAIRD. *Cyclestheria* is parthenogenetic, and specimens with eggs or embryos in their brood chamber occurred in samples throughout the year. Thus in the Volta Lake *C. hislopi* breeds all the year round. This contrasts with NAIR's (1969) record from India (Kerala) where the same species is a perennial breeder with its peak period in January.

*Cyclestheria* shows a preference for the protected littoral zone with an abundance of aquatic plants, and its gradual disappearance from most of the sampling stations, as recorded especially in 1967—1968, coincides with the shallows being more open to waves.

## HYDRACARINA (D-9, KP-4, KK-1, A-157).

According to Cook (personal communication), who published an account of the Liberian water mites (Cook 1966), almost all specimens collected from the Volta Lake are new species. Hydracarina are much more abundant on aquatic weeds than on the bottom of the lake. Their abundance on the bottom increases with occasional admixture of plants in bottom samples, such as was observed at Ampem. This abundance is likely to be greater in places where there are large numbers of Entomostraca as they feed predominantly on these animals (Table 2).

Table 2. Total number of Hydracarina and Entomostraca at five stations.

	Dodi	Kpandu	Kete Krachi	Yeji	Ampem
Hydracarina	9	4	1	0	157
Entomostraca	10	77	14	9	170

Hydracarina were collected down to 7 m depth.

EPHEMEROPTERA (AK-11, D-211, KP-333, KK-143, Y-115, A-89).

There seems to be only three genera present in the bottom fauna of the Volta Lake: *Povilla adusta* NAVAS is the dominant species, whereas *Caenis* sp. and *Cloeon* spp. are much less common.

*Povilla adusta* NAVAS (D-195, KP-298, KK-136, Y-105, A-84).

This species dominated not only the Ephemeroptera but sometimes also the total bottom fauna. In the benthos *Povilla* nymphs were first collected in December 1965 at Dodi. In the first half of 1966 they were found at Kpandu, Kete Krachi and Yeji, in July 1966 at Akosombo, and only in May 1967 at Ampem. They were, however, recorded at Ampem before that time from fish stomachs collected by REYNOLDS (1970), which suggests that *Povilla* had already been there before it was found for the first time in a bottom sample. Adults were collected for the first time at Ampem in May 1967, when the first nymphs were found in bottom samples. Later on the adults were regularly attracted to lights at the majority of stations (PETR 1970 a).

Nymphs were found in pieces of wood and grass collected from the bottom, as well as freely moving on the surface. The presence of nymphs in grass stems can be compared with the habitat they occupy in Lake Victoria and other large African natural lakes where they are common in dead submerged parts of papyrus and some other aquatic plants.

The depth distribution of *Povilla* on the bottom varies with the oxygen saturation of the water and shows a seasonal pattern in a manner similar to that observed in other organisms. The maximum depth distribution of *Povilla* was recorded during periods of water mixing (Fig. 1). Although the zone which formerly constituted the epilimnion is poorly oxygenated during mixing when compared with the period of stratification, the oxygen is nevertheless evenly distributed down to the maximum depth of the lake. As a result, although organisms may be distributed deeper, their total number may fall. *Povilla* does not seem to be able to adapt itself to these environmental changes; its abundance greatly decreases after the beginning of the vertical mixing of water in the lake (PETR 1969). This probably reflects an intolerance to water of low oxygen concentration, but also other factors are involved (PETR 1970 b). Certainly the survival of *Povilla* nymphs in the laboratory was found to be markedly affected by oxygen concentration.

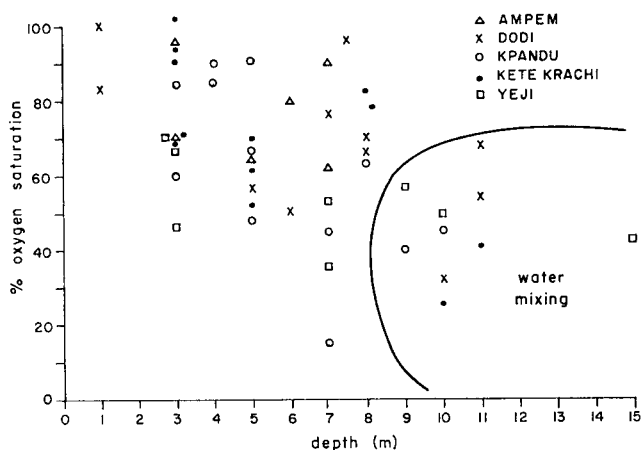


Fig. 1. The maximum depth distribution of *Povilla adusta* nymphs in relation to the percentage oxygen saturation of water during the period 1966 to 1968.

*Povilla* nymphs were especially abundant on the bottom in 1966 and 1967. Later, however, they were much less common. This may be a result of a gradual decomposition of the small wood particles and flooded grass which *Povilla* inhabits.

The biology of *Povilla* in the lake is discussed in details in a separate paper (PETR 1970 a).

*Caenis* sp. (D-16, KP-36, KK-7, Y-10).

Nymphs of *Caenis* have not been identified further. They were present during both the stratification and mixing periods and reached a maximum depth of 5 m. The small number of specimens collected does not allow any conclusions to be drawn about long term changes in their abundance at the bottom. At most stations they were collected in all years, except at Kete Krachi where they ceased to appear in samples after 1967. No adult *Caenis* were attracted to light.

*Cloeon* spp. (AK-11, A-5).

Nymphs probably belong to *Cloeon smaeleni* GILLIES and *Cloeon* sp., such as suggested by PETERS (personal communication). Because of their quick movements they seem to be able to escape the approaching sampler. The assumption that they are much more common at the bottom than it appears from the samples collected is supported by their abundance as adults in light catches, especially at Kete Krachi and Yeji. The nymphs occupy shallows down to 3 m depth, and seem to be associated with aquatic plants, from which they were commonly collected (PETR 1968 b).

ODONATA (AK-1, D-8, KP-6, KK-8, Y-1, A-34).

Among the odonatan nymphs, Anisoptera were more abundant than Zygoptera. The small number of zygopteran nymphs present on the bottom is probably due to their preference for aquatic plants (PETR 1968 b).

Anisoptera (AK-1, D-4, KP-6, KK-8, Y-1, A-10).

Anisopteran nymphs usually appeared as single specimens, preferring the shallows down to 3 m depth, with a maximum at 10 m. The commonest species is *Parazyxoma flavicans* (MARTIN), collected at all stations except Akosombo. *Brachythemis leucosticta* (BURM.) and *Trithemis* sp. were found at Ampem in shallows rich in aquatic weeds. The latter was also present in shallows in the north at Yeji.

Zygoptera (D-4, A-24).

In order of their abundance the following Zygoptera were found at Ampem: *Pseudagrion massaicum* SJOESTEDT, *Pseudagrion* sp., *Ischnura senegalensis* RAMB. *Pseudagrion massaicum* was also collected at Dodi. The presence of zygopteran nymphs seems to be related to the abundance of aquatic plants, especially *Ceratophyllum*, as found during observations of the fauna of aquatic plants at Akosombo in 1965 (PETR 1968 b).

HEMIPTERA (AK-2, D-1, KK-1, A-4).

A small number of *Micronecta* sp. was collected in bottom samples. The low frequency of occurrence of this organism in bottom samples is probably because *Micronecta* like *Cloeon* is quick enough to escape the approaching sampler. *Micronecta* which feeds on microscopic organisms and organic detritus on the bottom, is commonly found in the littoral to 3 m depth. On one occasion it was collected from 12 m at Dodi. *Micronecta* are attracted to lights, sometimes in large numbers.

One nymph of *Gerris* sp. was collected from 8 m at Ampem.

TRICHOPTERA (D-43, KP-56, KK-76, Y-34).

Of the four species of trichopteran larvae identified from bottom samples, *Ecnomus ulmeri* MOSELY (D-37, KP-17, KK-28, Y-16) and *Dipseudopsis njalana* ULMER (D-5, KP-28, KK-48, Y-18) were the most abundant, occurring regularly at four stations. The other two species were *Ecnomus* sp. (KP-5) and *Orthotrichia smaeleni* JACQUEMART (KP-1, D-1). Trichopteran adults attracted to light have been identified by GIBBS and by MARLIER (personal communication). The dominant species was *Dipseudopsis njalana*, followed by *Ecnomus* spp., the latter including *E. ulmeri* and *Ecnomus* sp. The following Trichoptera were also recorded as adults: *Amphipsyche berneri* KIMMINS, *A. senegalensis* (BRAUER), *Orthotrichia smaeleni*, *Polymorphanisus* sp. and *Oecetis* sp. The abundance of adults in light catches cannot be correlated with the abundance of larvae in bottom samples as the adults evidently originated from the larvae inhabiting trees, bottom and aquatic plants.

During the time of water mixing (September—November; January) *Ecnomus* and *Dipseudopsis* larvae are usually found deeper than during the period of stratification, although the oxygen saturation of water during



the mixing period may be lower (Table 3). The larvae are possibly more sensitive to large diurnal changes in oxygen (which may, as at Ampem, result in its complete depletion at the bottom) than to a relatively low, but constant oxygen saturation of the water.

*Dipseudopsis* larvae and *Ecnomus* larvae are about equally abundant in bottom samples from all stations except Dodi. The reason why *Dipseudopsis* was much less common than *Ecnomus* at this latter station may be connected with substratum preference. It is possible that *Dipseudopsis* avoids the sandy substratum common there.

Table 3. The maximum depth distribution of trichopteran larvae in relation to the percentage saturation of oxygen (A = date, B = maximum depth in m, C = percentage saturation of oxygen).

<i>Ecnomus</i>											
Dodi			Kpandu			Kete Krachi			Yeji		
A	B	C	A	B	C	A	B	C	A	B	C
XII/65	0.5	92	VII/66	1	87	IV/66	3	52	IV/66	2	42
IV/66	7	76	VIII	3	90	VII	3	90	VII	2.5	54
VIII	1	56	XI	5	90	XI/67	1	81	VIII	9	52
IX	3	45	XI/67	5	34	I/68	3	69	IV/68	1	80
XI	17	76	V/68	1	97	III	1	99	V	3	46
XI/67	11	59	VII	11	68	V	11	73	XI	5	46
I/68	3	86	IX	3	87	VII	9	58			
III	11	72				X	3	71			
V	3	80				XI	11	96			
VII	3	73									
IX	3	91									
XI	9	97									
<i>Dipseudopsis</i>											
XII/65	6	76	VII/66	1	87	IV/66	7	40	VII/66	11	48
IV/66	6	92	VIII	1	98	VII	7	77	IX	15	42
XI/67	3	65	XI	7	80	VIII	6	80	I/68	8	62
I/68	8	78	I/67	7.5	50	IX	12	25	V	5	65
III	3	65	IV	3	103	XI	8	83	VII	7	49
			XI	7	45	IV/67	5	93	X	11	52
			V/68	3	85	XI	8	85			
			IX	17	80	I/68	3	69			
			XI	5	67	III	3	102			
						V	5	80			
						VII	7	80			
						X	9	73			
						XI	5	70			

COLEOPTERA (AK-2, KK-1, A-1).

Coleoptera, although common on aquatic weeds (PETR 1968b) were scarcely found on the bottom. Three dytiscid larvae and one adult were collected from 0.5 m to 5 m depth.

DIPTERA (except Chironomidae) (KP-2, KK-17, Y-17, A—945).

Chaoboridae (KP-2, KK-17, Y-17, A-908).

The following species, arranged in order of their abundance were identified as adults: *Chaoborus (Neochaoborus) anomalus* EDWARDS, *C. (Sayomyia) ceratopogones* THEOBALD, *C. (S) pallidipes* THEOBALD.

The larvae of *C. anomalus* were dominant among the chaoborids at all localities. The larvae collected from the bottom belong to the third and fourth instars, as the first and second instar larvae of *C. anomalus* are planktonic (MACDONALD 1956). Their maximum density at the bottom was 9767/m<sup>2</sup> in 7 m (Ampem, December 1965), which is four times more than recorded by MACDONALD in Lake Victoria in Ekuna Bay. Chaoborid larvae reached a maximum depth of 20 m (Kete Krachi) which is close to the maximum depth of chironomid distribution. At Ampem, where they were among the most abundant organisms, chaoborids were usually collected from depths where the water was poor in oxygen or completely deoxygenated. It is known that chaoborid larvae, unlike most other bottom-living organisms, can exist for a considerable period in deoxygenated conditions and are abundant in those lakes in which the deeper water becomes depleted of oxygen (THIENEMANN 1922; FINDENEGG 1955; MACDONALD 1956; STAHL 1966).

It has been suggested that the presence and abundance of chaoborid larvae in various parts of the Volta Lake is to a large extent determined by the presence of suitable substratum (PETR 1972). In the Volta Lake, chaoborid larvae were found to be most abundant at Ampem, where the soil has a large proportion of clay and silt, i. e., small particles, and the highest organic content of all stations investigated. It is known that chaoborid larvae prefer to burrow in this type of substratum. In some other African lakes, such as Victoria (MACDONALD 1956) and George (DUNN et al. 1969) the larvae occupy soft, often very fine, flocculent mud rich in organic matter, with a readily disturbed mud-water interface. This mud contains a large proportion of dead or dying planktonic algae, especially bluegreens. Diurnal changes in the oxygen saturation of the bottom water layers, in a range from 0 to 40 % or more seem to be a further condition favoured by the larvae.

Another possible reason for the presence or absence of the larvae could be the distribution of the chaoborid prey the copepod zooplankton. The latter was regularly present and numerous at Ampem, while undergoing sudden quantitative changes during short periods of time elsewhere,

especially at Akosombo (PROSZYNSKA 1969) from where chaoborid larvae were absent.

The decrease in abundance of chaoborid larvae in bottom samples in areas distant from large inflows may be associated with the mineralization of organic matter in the bottom and with a consequent better oxygenation of deeper water. However, the numbers of chaoborids were gradually increasing in areas close to the large inflows. It has been suggested that the increase there is associated with a later flooding of the soil and with a periodical sedimentation which is taking place during and after floods in this area, and which does not occur further downlake (PETR 1972).

*Ceratopogonidae* (A-1).

From the bottom samples only one larva was collected, which was not further identified. The larvae were, however, common in aquatic plants (PETR 1968b). As adults they were occasionally attracted to light.

*Lepidoptera* (D-1).

*Pyrallididae* (D-1).

One specimen of a pyralidid larva was collected from 14 m at Doti (May 1968). The larva was not further identified.

## Part II: Chironomidae

Chironomid larvae established themselves in the new lake within a very short period (PETR 1971b) and were one of the major constituents of the bottom fauna. The seasonal as well as the yearly changes in species composition, quantitative representation and depth distribution were followed during the first years of the impoundment and are discussed in this paper.

Altogether 21 larval types have been distinguished (Table 4). These belong to three subfamilies: Tanypodinae, Orthoclaadiinae and Chironominae.

## Results

*Tanypodinae* (Figs. 2 and 3).

Tanypodinae formed usually less than one per cent of the total chironomid larvae collected from the bottom. Their percentage occurrence in relation to other subfamilies of Chironomidae decreased during the period of filling, as is evident from the data for 1968, compared with those for 1966. These larvae are predators and this decrease seems to be a reflection of the decreasing occurrence of their prey. Where food organisms, including oligochaetes and other chironomid larvae, were abundant, as in weed islands, the percentage of Tanypodinae among Chironomidae was very high. Thus for example, they formed 41 % of the total at Ampem in March 1968. WHYTE (personal communication) has recorded an even higher pro-

portion of Tanypodinae on aquatic plants in Lake Bosumtwi, where they formed some 45 % of the total chironomid fauna.

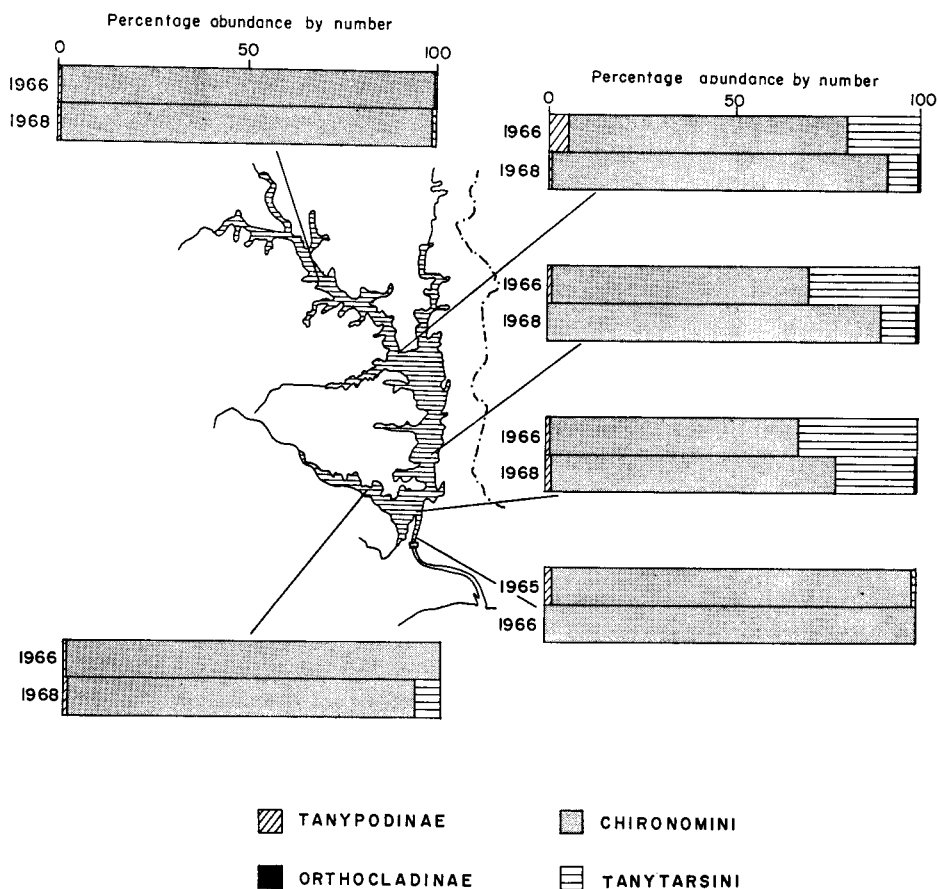


Fig. 2. Percentage abundance by number of major taxa of chironomid larvae in 1966 and 1968 (except at Akosombo where the data are for 1965 and 1966).

As predators tanypodine larvae are common in places such as the roots of the aquatic plants, and the shallows of the littoral zone which offer an abundance of food. Exceptionally they may reach deeper, and on two occasions they were collected from well oxygenated waters at a depth of 20 m (Fig. 3). Well oxygenated water together with an abundance of food organisms seem to represent two basic requirements of these larvae. In Lake Kariba MCLACHLAN (1969 a) collected the larvae of *Procladius* from depths of 20 m or less. The larvae of *Ablabesmyia nilotica* JOHANSEN were found to be associated with trees and aquatic vegetation, those of *A. appendiculata* KIEFER were most common in mud.

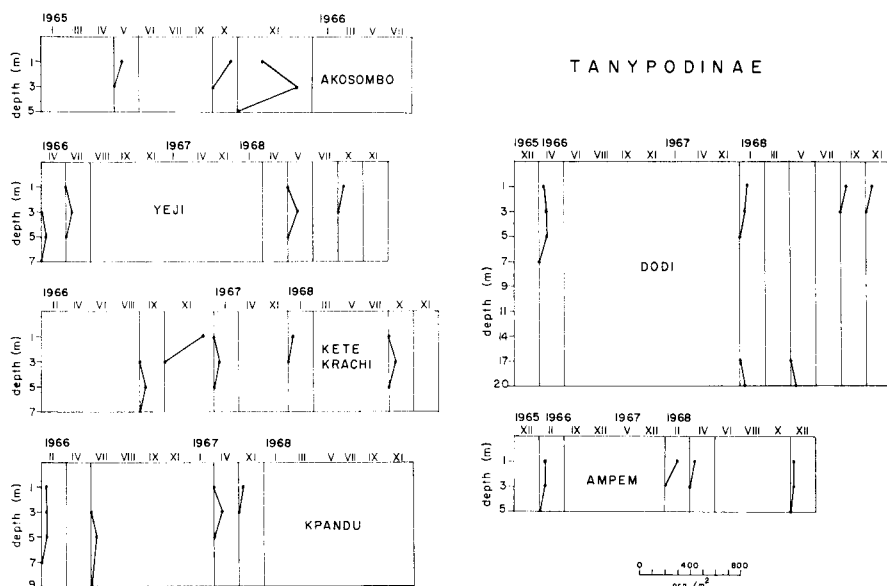


Fig. 3. Abundance and depth distribution of Tanypodinae larvae.

The majority of the larvae collected belong to *Ablabesmyia* though a few larvae of *Procladius* were also present. McLACHLAN (1969 a) who described the larvae *A. appendiculata* and *A. nilotica* mentions the difficulty of distinguishing between them. From the various collections made, I have identified the following as adults: *A. nilotica*, *A. dusoleili* GOETGHEBUER, *A. appendiculata*, *A. melaleuca* GOETGHEBUER, *A. pictipes* KIEFFER, *Tanypus fuscus* FREEMAN, *Clinotanypus maculatus* FREEMAN, *C. claripennis* KIEFFER, *Procladius maculosus* FREEMAN.

#### Orthoclaadiinae (D-6, KK-1, Y-1; Figs. 2 and 4).

Orthoclaadiinae was the least common subfamily of Chironomidae, and was never recorded from poorly oxygenated water, such as at Akosombo and Ampem. When the lake was almost full in 1968 they became more common, most probably due to improved oxygenation of water, but they never reached one per cent of the total of Chironomidae (Fig. 2). The absence of Orthoclaadiinae as adults from light catches seems to reflect their scarcity as larvae.

Though the material was poor in numbers the distribution of *Cricotopus*, the only genus identified from the larval stage, suggests a preference for well oxygenated water. This genus was collected from 1 to 20 m depth in water from 52 to 102 % oxygen saturation (Table 5). The preference of *Cricotopus* for environments with a high oxygen content is also suggested by its great abundance in the Black Volta rapids (PETR 1970 b), and on the bark of flooded trees exposed to waves (PETR 1970 a), although it is com-

Table 4. Occurrence of Chironomidae in bottom samples at various stations in 1965—1968.

Station	Akosombo (gorge at the dam)		Ampem (protected shallows)		Dodi (open to waves)		Kpandu (± open, mid-lake)		Kete Kradhi (± open, mid-lake)		Yeji (river-lake transition)	
Year	1965	1966	1965	66	67	68	1966	67	68	1966	67	68
Organism												
Tanypodinae	+	—	+	—	+	—	+	—	+	+	—	+
Orthocladiinae	—	—	—	—	—	—	—	—	—	+	—	—
<i>Chironomus</i> *	+	+	+	+	+	+	+	+	+	+	+	+
<i>Dicortendipes chloronotus</i>	—	—	—	—	+	+	+	+	+	—	—	—
<i>Dicortendipes multispinosus</i>	+	—	+	—	+	+	+	+	+	—	+	+
<i>Dicortendipes</i> sp. 1	—	+	+	+	+	—	+	+	+	+	—	+
<i>Dicortendipes</i> sp. 2	—	—	—	—	—	—	—	—	—	+	—	+
<i>Endochironomus</i>	+	—	—	—	+	+	+	+	+	+	—	+
<i>Nilodorum</i> *	+	+	+	+	+	+	+	+	+	+	+	+
<i>Cryptochironomus lindneri</i>	—	—	—	—	+	+	+	+	+	+	—	+
<i>Cryptochironomus</i> cf. <i>dewulfianus</i>	—	—	—	—	+	+	+	+	+	+	—	+
<i>Cryptochironomus nudiforceps</i>	—	—	—	—	+	+	+	+	+	+	—	+
<i>Polypedium</i> type 1	—	—	—	—	+	+	+	+	+	+	—	+
<i>Polypedium</i> sp. 1	+	+	+	+	—	—	+	+	+	+	+	—
<i>Stictochironomus calfrarius</i>	+	+	—	—	+	+	+	+	+	+	—	+
<i>Tanytarsus nigrocinctus</i>	—	—	—	—	—	+	+	+	—	+	+	—
<i>Tanytarsus</i> cf. <i>balteatus</i>	—	—	—	—	—	+	+	+	+	—	—	+
<i>Tanytarsus</i> ex gr. <i>lauterborni</i> sp. II	—	—	—	—	+	+	—	—	—	—	—	—
<i>Cladotanytarsus pseudomancus</i>	—	—	—	—	+	+	+	+	+	—	—	+
Total	8	7	5	7	5	15	17	13	17	15	13	14

\* Within these genera two types of larvae were distinguished.

pletely absent on less exposed trees. MACDONALD (1956) has suggested that high water temperature may limit the occurrence of *Cricotopus*, for, in East Africa, the various species were found to be relatively rare in Lake Victoria compared with the cold streams of the Kenyan Highlands. In the Volta Basin the proportion of Orthocladiinae among the chironomids in the rapids of the Black Volta River is much greater than in the lake. However, there is no marked difference in water temperature between the

Table 5. Distribution of *Cricotopus* in the Volta Lake.

Number of <i>Cricotopus</i> larvae collected	Date	Station	Depth (m)	Percentage sat. oxygen	Temperature (° C)
1	10. I. 1968	Dodi	20	77	28.0
2	16. IX. 1968	Dodi	1	102	30.0
2	16. IX. 1968	Dodi	3	91	29.4
1	19. XI. 1968	Dodi	14	78	28.8
1	23. XI. 1968	Kete Krachi	1	88	29.6
1	6. VIII. 1966	Yeji	7	52	28.4

rapids and the lake, and both are at a higher temperature normally found in Lake Victoria. This suggests that it is oxygen content of the water rather than temperature which is the major factor controlling the abundance and distribution of *Cricotopus*.

#### Chironominae.

Compared with other subfamily of Chironomidae this subfamily is represented by a large number of species in the Volta Lake. This is in accord with findings from other parts of tropical Africa where the majority of the species of Chironomidae fall into this subfamily (FREEMAN 1957). In the Volta Lake, 18 taxa of Chironominae were distinguished in larval stages out of the 21 species and types identified as Chironomidae.

Specific names have not been given to the "types", as their larvae were not reared to adults, and for some of the "types" such as *Nilodorum*, *Chironomus*, *Polypedilum* type 1 complex of closely related species. A more detailed examination of the larvae of the "types" mentioned might help to differentiate them eventually into particular species, but in the time available the matter could not be investigated in more detail. From a study of *Nilodorum* larvae it is suspected that there may be a considerable degree of anatomical variation within a species; this further complicates the clear definition of species characteristics.

*Chironomini* (Fig. 2).

This tribe greatly dominates other chironomid taxa. Many species of the tribe can tolerate quite considerable changes of oxygen concentration in the water. Their percentage occurrence was found to be highest in localities where considerable changes in oxygen saturation were recorded; in better oxygenated areas, characterized by the presence of Tanytarsini, the percentage occurrence of Chironomini was lower though they still dominated the family Chironomidae. The maturation of the lake, resulting in a better oxygenation especially of protected areas, such as Ampem and Yeji, resulted in slightly lower percentage abundances of Chironomini, due to an increase in the numbers of Tanytarsini. At stations in close contact with open lake waters the proportion of this tribe among Chironomidae increased, as is evident when the data for 1968 are compared with those for 1966 (Dodi, Kpandu, Kete Krachi, Fig. 2).

*Chironomus* (Fig. 4).

Owing to the large number of larvae collected, it was not possible to dissect and mount all specimens for detailed examination. Within the genus *Chironomus* two types were distinguished, *Chironomus* sp. 1 and *Chironomus* sp. 2 (Fig. 20b and Fig. 20c). From *C.* sp. 1 the adults of *C. formosipennis* KIEFFER were reared, and from *C.* sp. 2 those of *C. imicola* KIEFFER. From a larva similar to the *C.* sp. 2 from Lake Bosumtwi WHYTE (personal communication) has reared adults of *Dicrotendipes fusconotatus* KIEFFER. It is probable that, as observed with *Chironomus* larvae, in temperate waters one or both types of larvae include several different species.

The following adults were attracted to light, in order of their abundance: *C. formosipennis* KIEFFER, *C. imicola* KIEFFER, *C. transvaalensis* KIEFFER, *C. alluaudi* KIEFFER, *C. calipterus* KIEFFER, and *C. scotti* KIEFFER (PETR 1970c).

About half of the total number of *Chironomus* larvae collected were dissected and mounted. The results suggested that both larval types were present at all stations, and that both larval types have a similar range of depth distribution. High concentrations of larvae seem to be closely related to high organic matter content and abundance of organic debris in the flooded soil. The larvae seem to prefer muddy bottoms to sandy substrata, as indicated by their great abundance at Ampem, compared with that at Dodi.

The distribution of the larvae with depth appears therefore to be determined by an oxygen gradient in water. During stratification of the water the larvae were limited to the shallows where they occurred in great numbers, and during the rains and floods they extended to greater depths. However, they seem to be capable of withstanding considerable diurnal changes in oxygen concentration in the bottom layers, as shown by their abundance at Ampem.



Each period of floods, with the subsequent rise of the lake level, resulted in a temporary increase in the quantity of dissolved material as a result of new organic matter being introduced into the lake waters from freshly flooded soil. Indirectly this led to an increase in the population of *Chironomus* each year during the rise in lake level. By 1968, however, the lake was almost full, the quantity of organic matter introduced annually into the water was much smaller and correlated with this a decline in abundance of *Chironomus* was observed.

*Dicrotendipes multispinosus* FREEMAN (Fig. 5).

The adults of this species were reared from the larval stage (Fig. 20 d). The adults were commonly attracted to light (PETR 1970 c).

The larva was commonest at Kpandu and Kete Krachi where it reached maximum depth distribution during the floods. Its vertical distribution seems to depend on the oxygen concentration, with peak abundance in well oxygenated water.

*Dicrotendipes chloronotus* KIEFFER (Fig. 6).

The adults of this species were reared from the larval stage. The larva is described by McLACHLAN (1969 a).

The flooding of new soil was found to be followed by an increased abundance of the larvae of *D. chloronotus* at the bottom, where they reached their peak at the end of floods. This seems to be closely connected with the availability of fine soil and organic particles suspended in water as these are used by the larvae both for building their tubes and as food. The peak occurrence of adults in light catches preceded that of the larvae at the bottom.

No larvae of *D. chloronotus* were collected from flooded trees (PETR 1970 a) but this may be due to this species having a periodicity in its occurrence, with an absence of larvae at the bottom in May, the month when the samples from flooded trees were collected.

There was a decrease in abundance of these larvae during the present observations. While very abundant near the dam at Akosombo in 1965, they were found only in small numbers at all stations in 1968. It is suggested that this may be connected with a gradual decrease in organic matter, both at the bottom and suspended in the water (PETR 1971 b).

*Dicrotendipes* sp. 1 (Fig. 7).

This larva is somewhat similar to that of the *Dicrotendipes* sp. 2, with a difference in its labial plate, the first lateral tooth being flanked by a very short tooth (Fig. 20 e).

The distribution of the larvae seems to be more influenced by oxygen than by the substratum as they were collected on sandy substrata as well as from clay and silt. There is no indication of any significant preference for particular seasons, as they occurred in samples taken both during the

rains and floods and the dry season. Their maximum depth distribution was recorded during the water mixing period, correlated with the better oxygenation of deep layers.

*Dicrotendipes* sp. 2 (Fig. 8).

This larva was described from Lake Edward by CHRISPEELS (1959) as *Limnochironomus* sp. 2. DEJOUX (personal communication) suggested that the larva belongs to *Dicrotendipes* sp. (Fig. 20f).

The distribution of the larvae with depth seems to be closely related to their preference for well oxygenated water as they were found predominantly in the first 9 m depth. Their preference for water of high oxygen content seems to be reflected also in the fact that they appeared for the first time in the Gorge Region at Akosombo when the water there became better oxygenated in May to July 1966. When deeper water became better oxygenated in the shallows at Ampem during and after the floods of 1967, the larvae started to appear regularly in deeper water in this area. They may prefer muddy substrata to other types; the type of substratum seems however, to be of only secondary importance for their distribution. Their occurrence does not seem to be influenced by the annual cycle of changes in water conditions associated with dry and rainy seasons.

For the following species of *Dicrotendipes* identified as adults the larvae are not known: *D. sudanicus* FREEMAN, *D. kribiicola* KIEFFER, and *D. cordatus* KIEFFER.

*Endochironomus* (Fig. 9).

This larva was described by CHRISPEELS (1959) from Lake Edward as *Endochironomus* ex. gr. *singnaticornis*. In the Volta Lake it prefers well oxygenated water as is evident from its marked abundance in the best oxygenated bottom layers at Dodi. It seems to display no special preference for shallows or depth provided the water at the bottom is well oxygenated. With the development of an oxygen gradient the larva was generally found in shallower water than it was during the periods of mixing. The larva may possibly prefer sand to other types of substrata; the absence of sand, however, does not seem to limit its distribution.

As the lake continued to fill the percentage abundance of *Endochironomus* among other chironomids greatly increased and by 1968 this larva had become one of the major chironomid species in areas closely connected with the open lake (PETR 1971b). It continued to be completely absent from sheltered localities with water of a eutrophic character such as Ampem.

*Nilodorum* (Fig. 10).

The larvae of this genus, together with those of *Chironomus*, were the most abundant chironomids of the Volta Lake. Four species of *Nilodorum* were identified from the adults: *N. fractilobus* KIEFFER, *N. brevibucca* KIEFF-

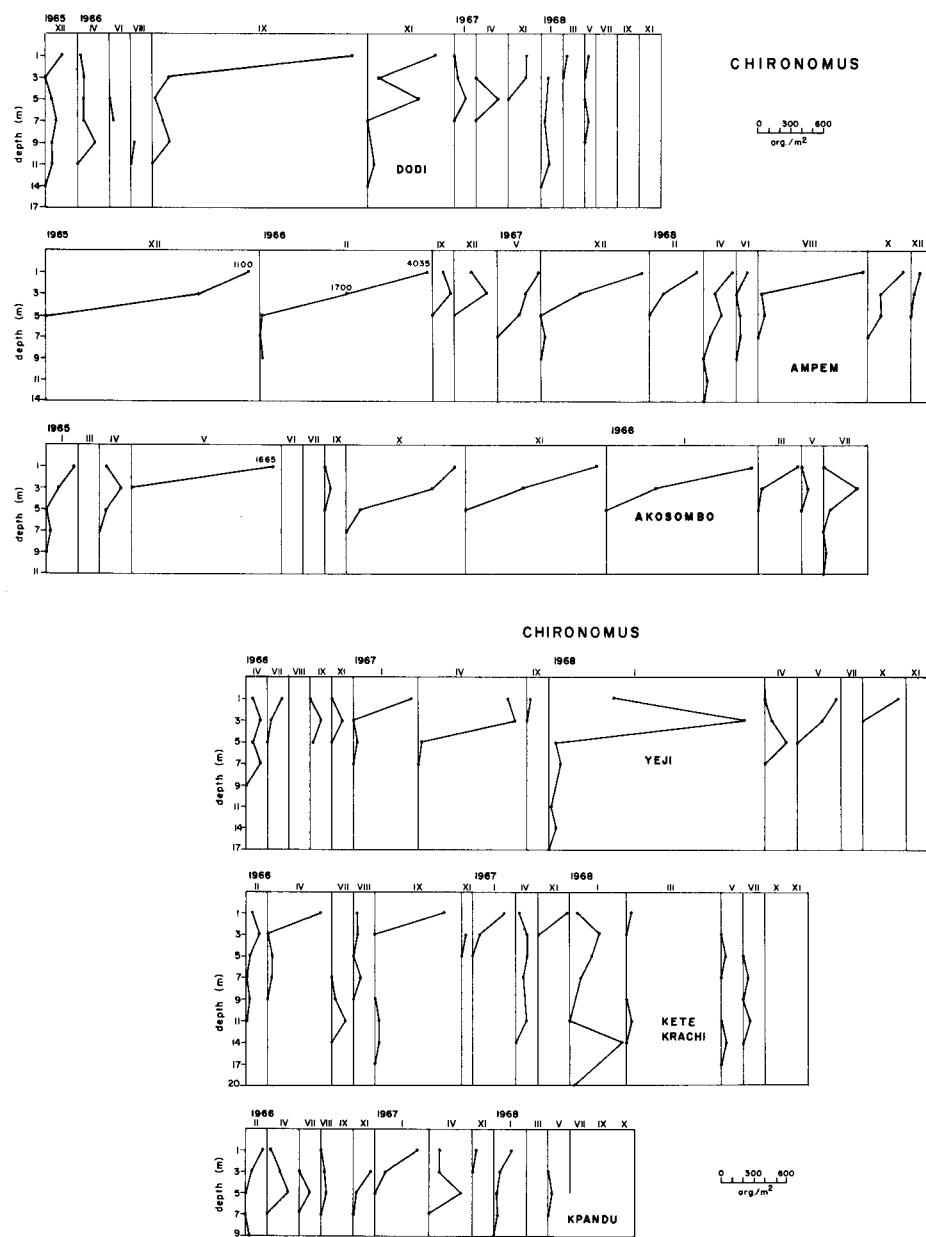


Fig. 4. Abundance and depth distribution of *Chironomus* spp. larvae.

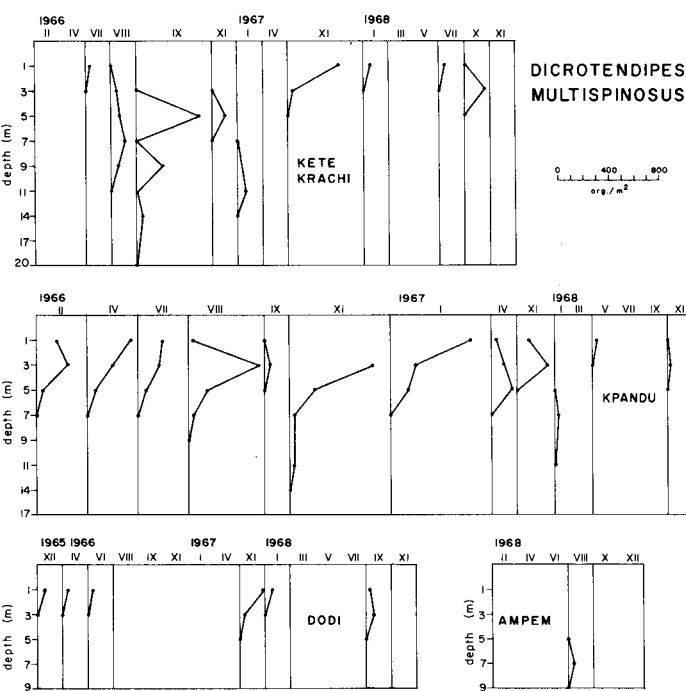


Fig. 5. Abundance and depth distribution of *Dicrotendipes multispinosus* larvae.

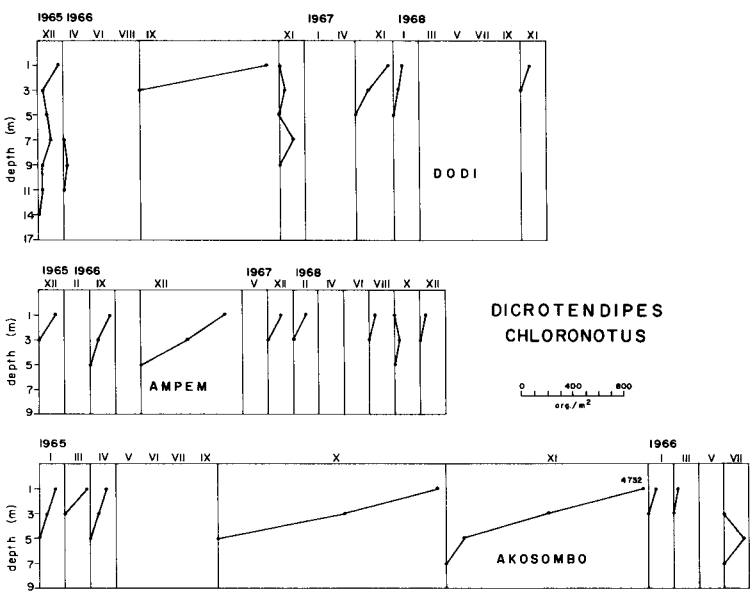


Fig. 6a

DICROTENDIPES CHLORONOTUS

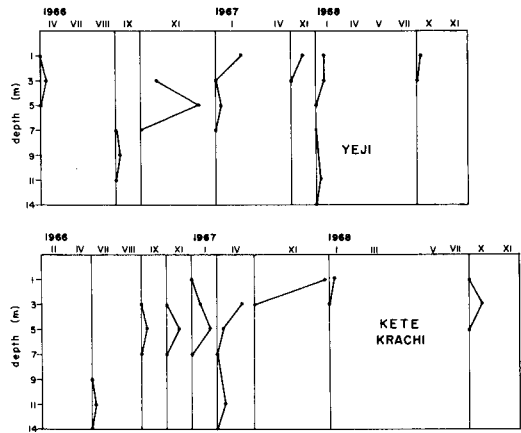


Fig. 6b

Fig. 6. Abundance and depth distribution of *Dicrotendipes chloronotus* larvae.

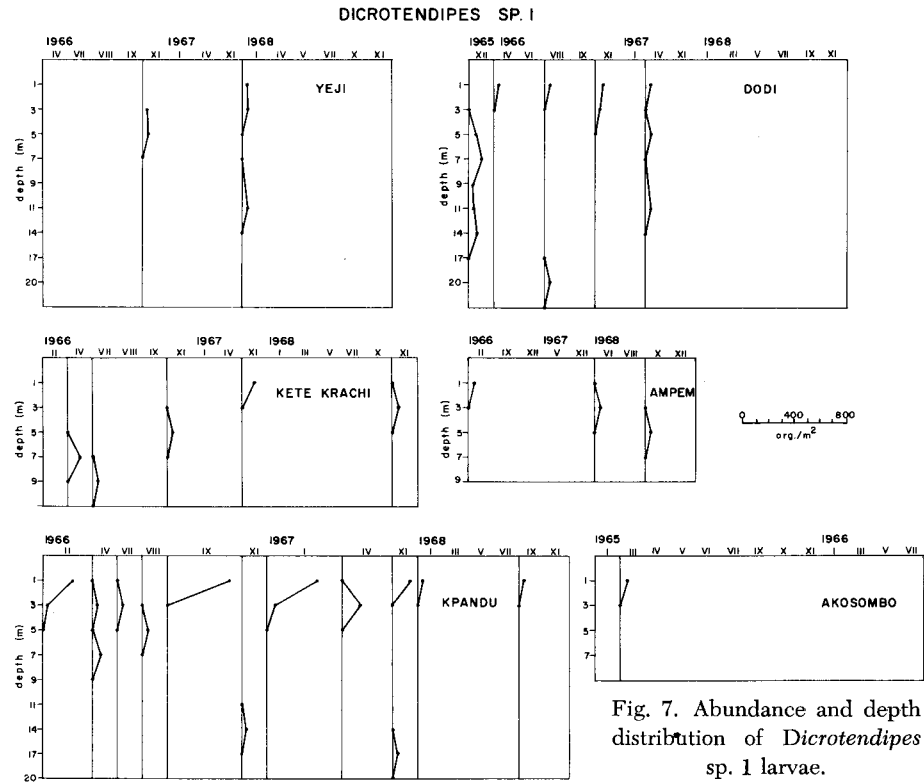


Fig. 7. Abundance and depth distribution of *Dicrotendipes* sp. 1 larvae.

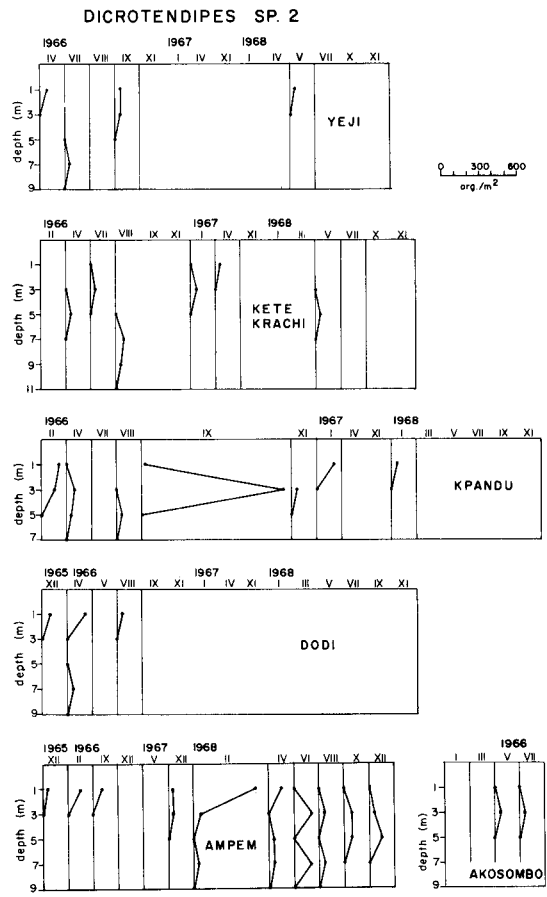


Fig. 8. Abundance and depth distribution of *Dicrotendipes* sp. 2 larvae.

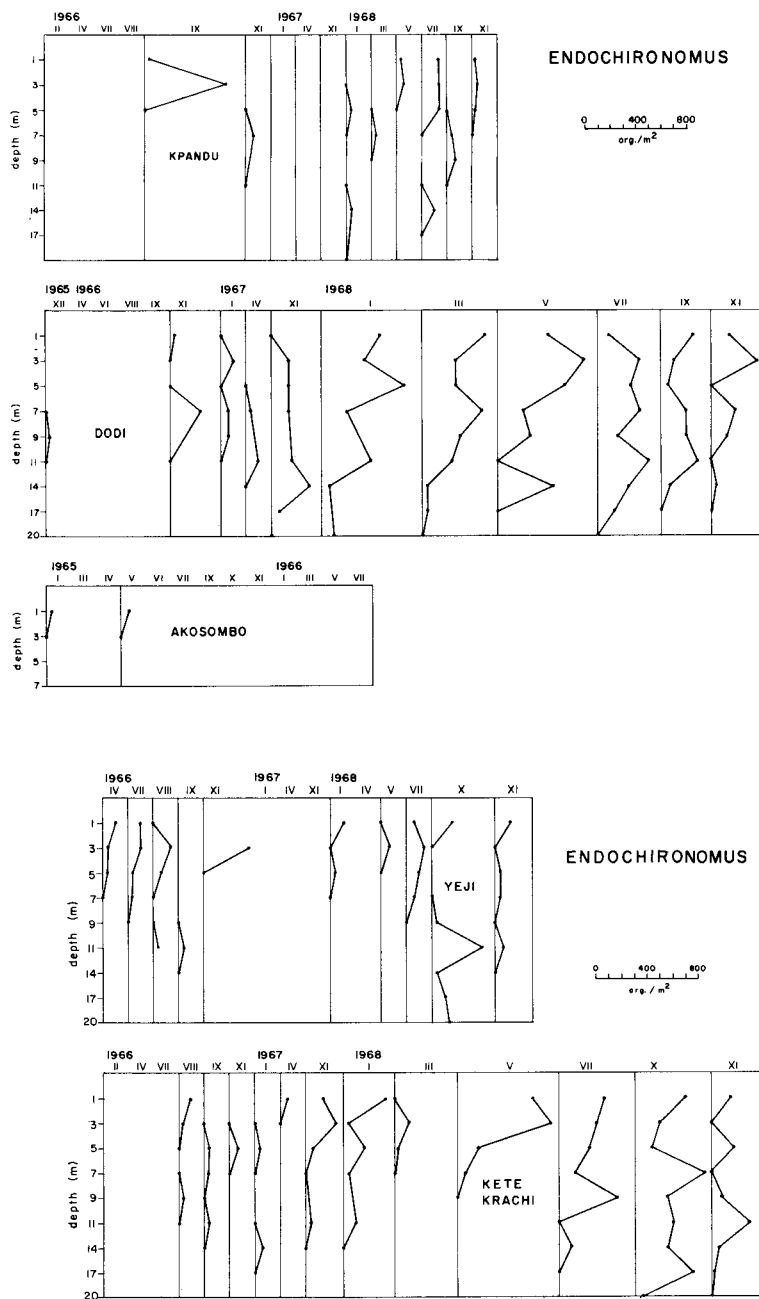


Fig. 9. Abundance and depth distribution of *Endochironomus* larvae.

## NILODORUM

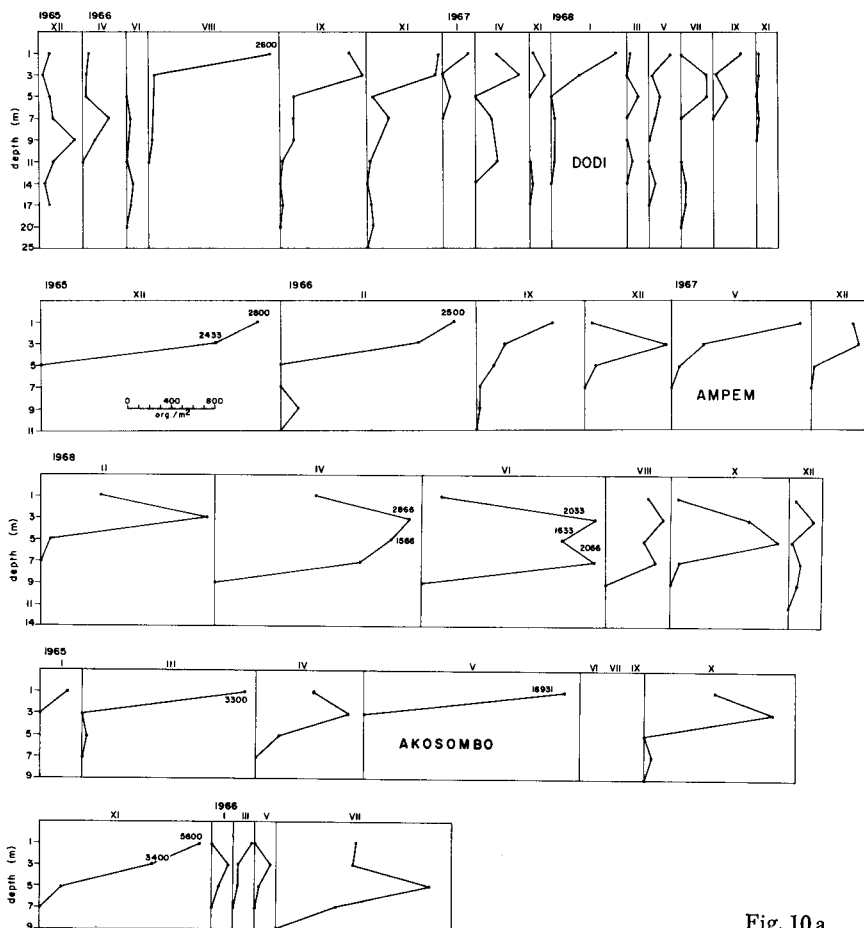


Fig. 10a

## CRYPTOCHIRONOMUS CF. DEWULFIANUS

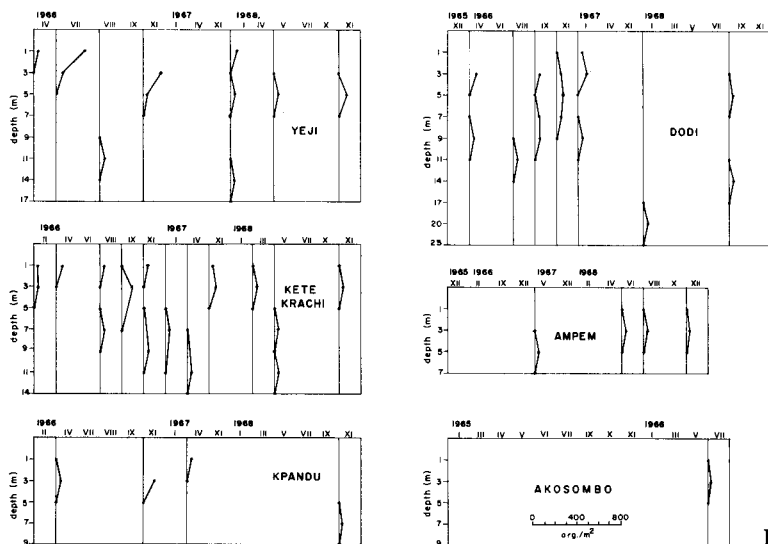


Fig. 11



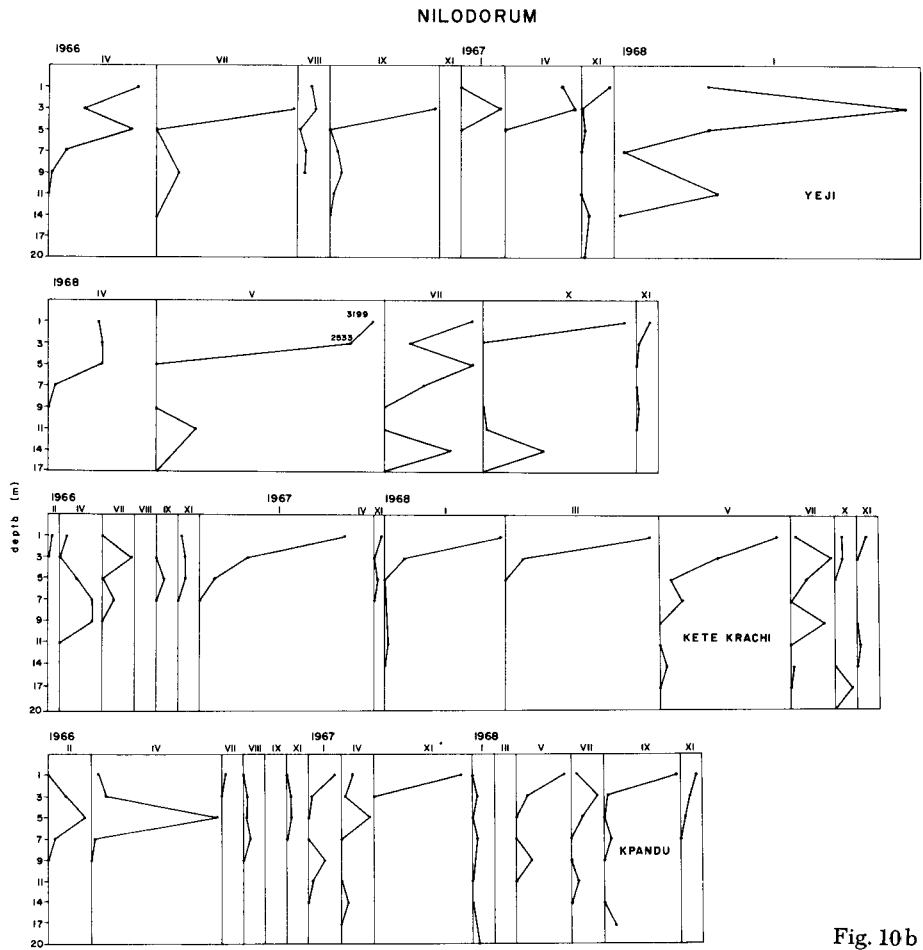
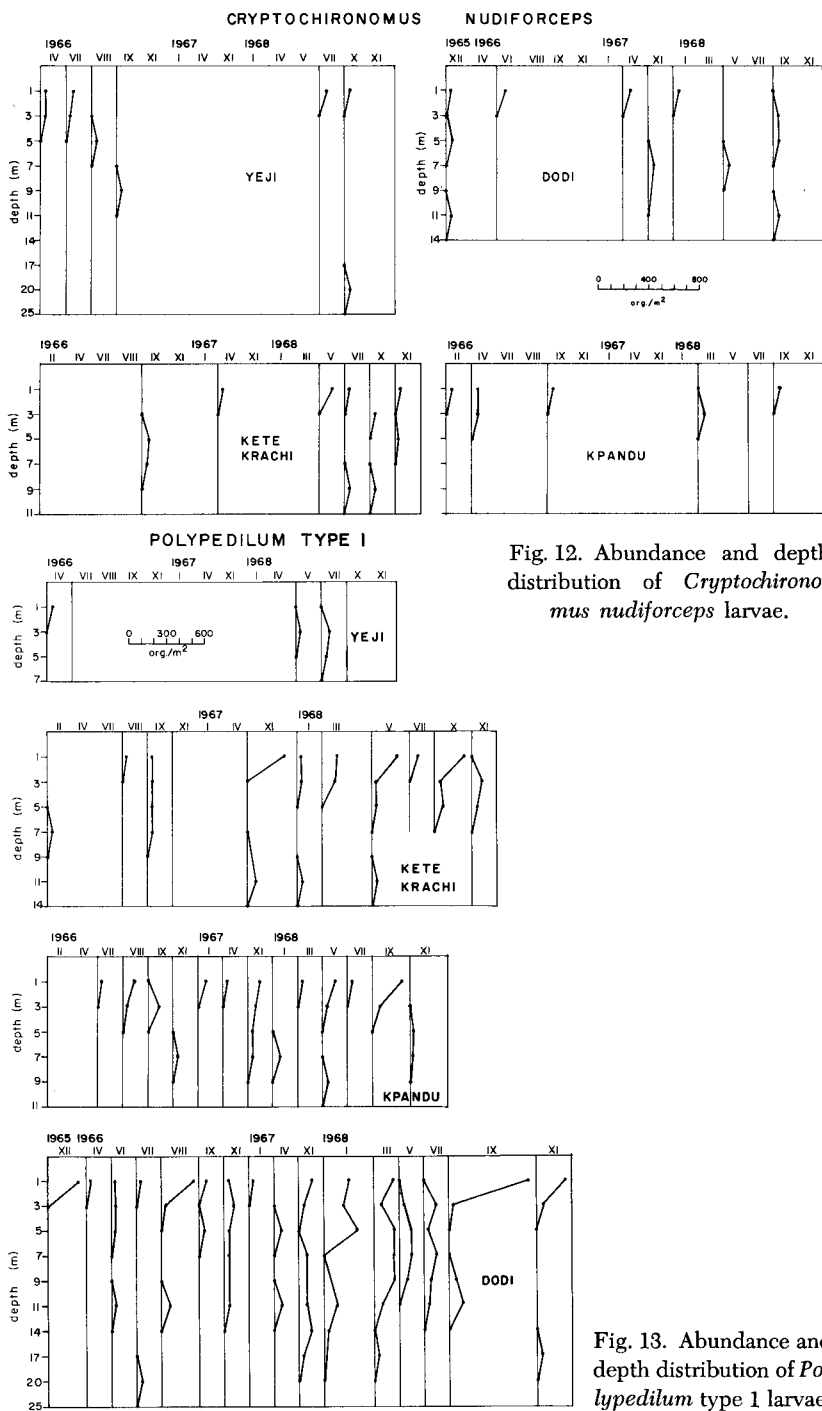


Fig. 10b

Fig. 10. Abundance and depth distribution of *Nilodorum* spp. larvae.

Fig. 11. Abundance and depth distribution of *Cryptochironomus* cf. *dewulfianus* larvae.



FER, *N. rugosum* FREEMAN, *N. brevipalpis* KIEFFER. They were not separated in their larval stages, and from reared larvae only the adults of *N. brevibucca* and *N. fractilobus* were obtained. The small differences in the dentition of the labial plate and other minute differences cannot be applied for routine distinguishing of the species. Furthermore, McLACHLAN (1969 a), in describing the anatomy of *N. fractilobus* from Lake Kariba, has pointed out that environmental differences can profoundly affect the anatomy of the larvae of this genus. If the quantitative distribution of the different species of *Nilodorum* in light catches reflects their quantitative distribution in the water, then *Nilodorum fractilobus* and *N. brevibucca* are the dominant species.

The number of larvae of this genus in the substratum seems to depend on its composition and on the degree of its exposure to waves. The larvae of *Nilodorum* require fine soil particles to build their tubes. Where these are present, as in shallows and sheltered areas with muddy substrata, they are very common. Where the bottom consists largely of sand and is exposed to waves, as at Dodi, they are much less abundant. Waves seem to limit the distribution of *Nilodorum* larvae by interfering with their tube building and feeding activities. This was observed on flooded trees where *Nilodorum* was common in areas protected from waves, but their abundance decreased in trees more exposed to waves, while they were practically absent from submerged trees exposed to wave action (PETR 1970 a). The substrate preference of *N. brevibucca* for fine rather than coarser particles has been confirmed by experiment (McLACHLAN 1969 b).

The larvae seem to be well adapted to diurnal oxygen changes such as those occurring at Ampem, but like the other chironomids they withdraw to better oxygenated substrata when an oxygen gradient results in oxygen depletion in the deeper water layers. At that time the larvae are usually more abundant than during the mixing periods. It is possible that there is less general water movement during the stratification and that this "stability" leads to an increase in their population density.

At Yeji, where an intermediate water layer of low oxygen content develops between the oxygenated littoral and the riverine channel section (PETR in press), the depth distribution curve for *Nilodorum* larvae showed two peaks of abundance correlated with the level of oxygenation. This was observed in most of the sampling months in 1968. In April 1968 only one peak was found; at that time the deepest water layer was completely devoid of oxygen. At Kete Krachi the maximum depth of the transect represented by the flooded riverine channel was not sampled, but the zone above the riverine channel also developed a double peaked distribution of *Nilodorum* with depth, especially in 1967 and 1968. It is thus possible that different

species of *Nilodorum* occur at different depths and that the peaks are due to different species.

The abundance of *N. fractilobus* adults has decreased as the lake has filled, while that of *N. brevibucca* has increased. *Nilodorum* larvae have become less abundant at localities in close contact with open water such as Dodi and Kpandu than elsewhere.

In general *Nilodorum* can be expected to be abundant in any environment where there is a substratum consisting of fine soil particles and an abundance of organic detritus as food and in which the bottom water is moderately to well oxygenated although a quite considerable diurnal change in percentage oxygen saturation can be tolerated.

*Cryptochironomus lindneri* FREEMAN (D-12, KP-5, KK-12, Y-11).

The adults were reared from larvae which have been described by McLACHLAN (1969a). The larvae, which are predators, were scarce. The adults seem to emerge throughout the year, with a maximum emergence during the rains in July and August, thus preceding the appearance of larvae collected in bottom samples. Because of the scarcity of the larvae nothing can be said about their substratum preference.

*Cryptochironomus* cf. *dewulfianus* (Fig. 11).

This larva was identified by DEJOUX (personal communication). A similar larva was described by McLACHLAN (1969a) from Lake Kariba as *Chironomus* (*Cryptochironomus*) sp. 4.

The shape of the mandibles suggests that the larva is a predator. The distribution pattern of the larva in samples does not suggest any substrate preference, larvae having been collected from all stations. Their absence from Akosombo until July 1966 suggests that they require well oxygenated water. This idea seems to be supported also by their distribution at Ampem, where they were limited from 3 m to 5 m depth while elsewhere they were commonly found deeper, being collected from a maximum depth of 20 m in well oxygenated waters at Dodi. The larvae seem to avoid very shallow water of 1 m depth; the reason for this can be only guessed. The large diurnal temperature variation of very shallow water may perhaps be detrimental for these larvae.

No seasonal preference was observed, the larvae being collected in all months in different areas of the lake.

Adults of *Cryptochironomus dewulfianus* GOETCHEBUER were found in light catches only once, in December 1967 when 16 males were collected in the upper north of the lake at Mpaha. It is possible that elsewhere the species was represented in samples by females which cannot be identified.

*Cryptochironomus nudiforceps* KIEFFER (Fig. 12).

The larva has been described from Lake Kariba by McLACHLAN (1969a). The larvae appear to prefer well oxygenated water as suggested

by their absence at Akosombo and Ampem. They did not show a preference for any particular type of substratum, being collected from both sandy and clay bottoms. The maximum depth distribution of the larvae coincided with the height of floods (Yeji, October 1968). The occurrence of larvae followed the presence of adults in light catches. The larvae were more common during the floods, while the adults were common before the floods.

The larvae of the following species of *Cryptochironomus* collected as adults are not known: *C. dicerus* KIEFFER, *C. forcipatus* FREEMAN and *C. acutus* GOETGHEBUER.

*Polypedilum* type 1 (Fig. 13).

The larvae of *Polypedilum* type 1 (Fig. 20 g) were not further identified. *P. deletum* GOETGHEBUER and *P. griseoguttatum* KIEFFER were obtained as adults by rearing the larvae. The anatomy of these larvae has been described by McLACHLAN (1969 a) who distinguished between the larvae of the above mentioned species.

The larvae prefer exposed localities open to offshore water to those with no exchange between inshore and offshore water. This is possibly due to a requirement for a high oxygen concentration. Their maximum depth distribution was recorded from the well oxygenated bottom at Dodi (20 m) where the larvae regularly occurred. Their presence or absence seems to be determined more by their high oxygen preference than by a substratum preference. As the lake matured the larvae became more frequent at Kete Krachi; this is probably a reflection of the better oxygenation of the bottom in that area.

*Polypedilum* sp. 1 (Fig. 14).

DEJOUX (personal communication) has suggested that this larva (Fig. 20 h) belongs to the genus *Polypedilum*. The larvae are among the smallest collected from the Volta Lake. The shape of their mandibles suggest that they are predators and feed on other Metazoa. Their marked abundance in the benthos at Akosombo in 1965, where they were also very common on *Pistia* roots (PETR 1970 d), as well as their regular presence at Ampem suggest that they may tolerate a low oxygenation of their habitat; nevertheless they were collected predominantly from 1 m to 3 m depth which is usually well oxygenated. The reason for their abundance at these depths may, however, be the presence of a rich food supply rather than a suitable substratum or oxygen concentration.

Seven species of *Polypedilum* were identified from adults attracted to lights. These were in order of their abundance: *P. longicrus* KIEFFER, *P. griseoguttatum* KIEFFER, *P. deletum* GOETGHEBUER, *P. fuscipenne* KIEFFER, *P. brunneicornis* KIEFFER, *P. annulatum* FREEMAN and *P. dewulfi* GOETGHEBUER.

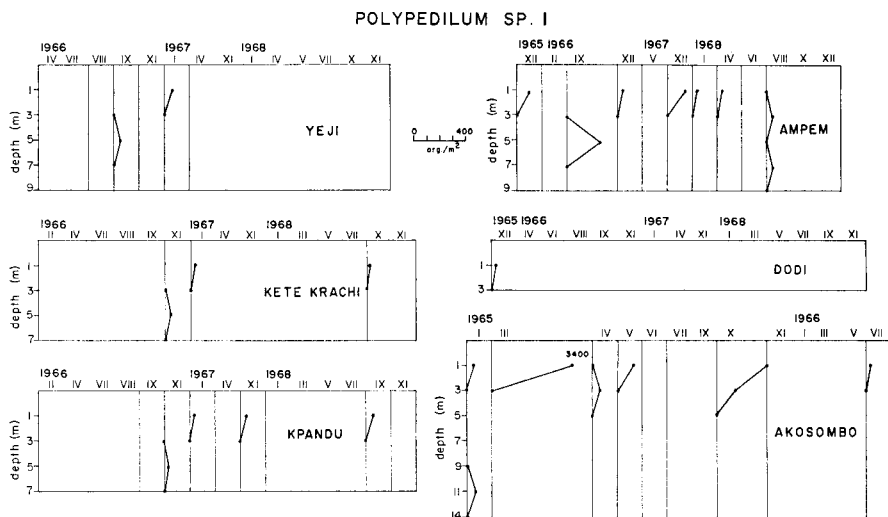


Fig. 14. Abundance and depth distribution of *Polypedilum* sp. I larvae.

*Stictochironomus cafferarius* KIEFFER (Fig. 15).

The species was identified from an adult reared from the larva. The larva is described by McLACHLAN (1969 a). The larvae would appear to require a well oxygenated bottom, as suggested by their absence from Ampem and relative scarcity at Akosombo, both stations with poorly oxygenated water. It is possible that the complete absence of the larvae at Ampem is determined by the diurnal changes in oxygen saturation which may limit their establishment in such areas. In the Volta Lake the larvae were found to prefer a mixed sandy and muddy bottom, although in Lake Kariba McLACHLAN (1969 a) considered this species to be a characteristic member of the mud habitat in shallows. KUGLER & CHEN (1968) found it among the most common species of the sublittoral zone in Lake Tiberias.

The absence of the larva at Ampem, its low numbers at Yeji and Kpandu, and its abundance at Kete Krachi is in accordance with the numbers of adults collected at light. The peak abundance of adults in light catches was before and during the rains (PETR 1970 c).

*Tanytarsini* (Fig. 2).

*Tanytarsini* are typical of oligotrophic lakes of the Palaearctic region; their great relative abundance among these chironomids in these lakes was recognised by THIENEMANN (1925) who correlated it with the permanently high oxygen saturation of water. In the Volta Lake the abundance of the *Tanytarsini* larvae differed according to the degree of oxygenation of a particular area. In permanently well-oxygenated waters they were common, while on bottoms characterised by considerable fluctuations of oxygen saturation their abundance was low or they were absent. As the lake became

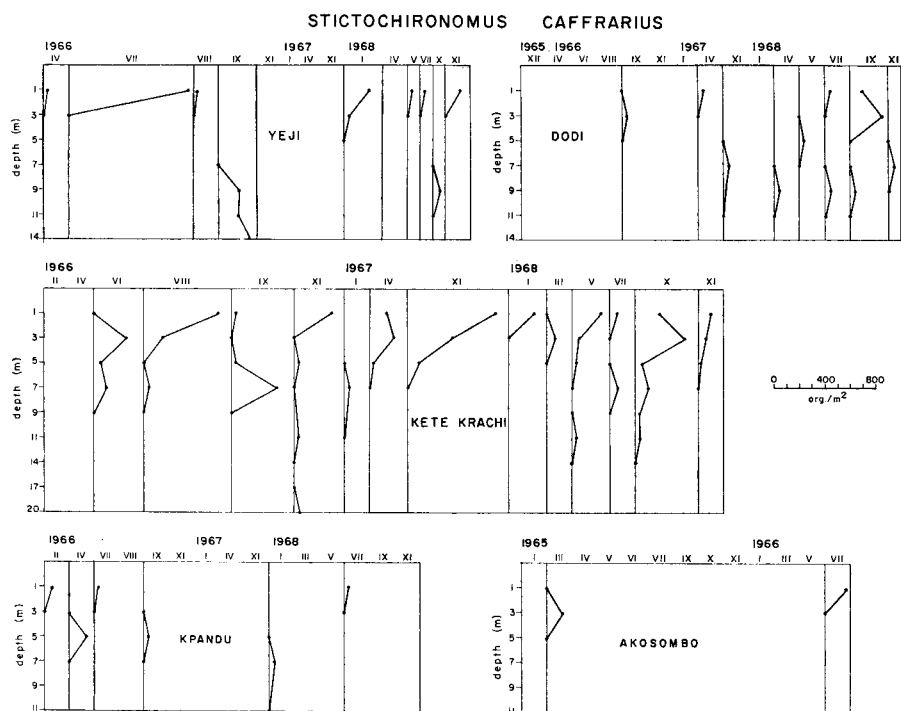


Fig. 15: Abundance and depth distribution of *Stictochironomus cafferarius* larvae.

fuller their proportion among other chironomids generally decreased despite the improved oxygenation of the water, as shown when the data for 1968 are compared with those for 1966 (Fig. 2). This suggests that better oxygenation of water above a certain level does not necessarily result in greater abundance of Tanytarsini among the Chironomidae. However, in eutrophic areas such as at Ampem, better oxygenation of water did result in the Tanytarsini becoming more abundant.

*Tanytarsus nigrocinctus* FREEMAN (Fig. 16).

The larva is described by DEJOUX (1968) who collected it in the delta of the River Chari, entering Lake Chad. The larva constructs tubes of sand and organic detritus. In the Volta Lake the larvae prefer the littoral to other zones. This may be due to their high oxygen requirement, as during floods with oxygenated water reaching deeper, this species is found in deeper areas (Kpandu, Dodi). Adults were collected in light catches only at Kete Krachi (PETR 1970 c). This species was probably present elsewhere as females which cannot, however, be identified.

*Tanytarsus* cf. *balteatus* (Fig. 17).

Like the previous species, *T. cf. balteatus* seems to require a permanently high oxygen saturation of water next to the bottom, without consi-

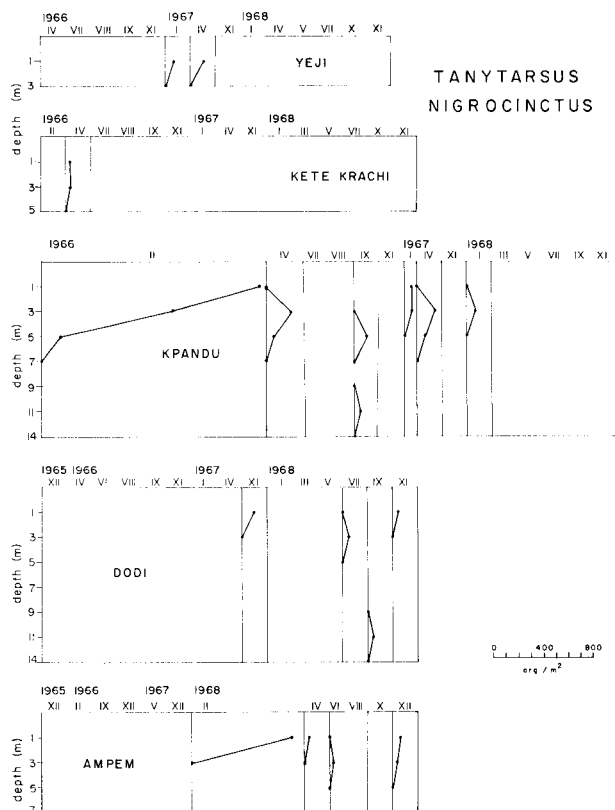


Fig. 16. Abundance and depth distribution of *Tanytarsus nigrocinctus* larvae.

derable diurnal changes. The poorly oxygenated water at Akosombo, Ampem and in shallows of Yeji had no larvae of this type, or they were very scarce in bottom samples. On the other hand, the well oxygenated locality at Dodi had the maximum depth distribution of these larvae.

It is not known whether the larvae show a preference for a particular type of substratum for while its distribution extended over mixed sandy-muddy substrata, pure muddy bottom were characterized by poorly oxygenated water and therefore, also by the absence of the larvae. A muddy substrate is described as typical for these larvae in Lake Kariba (McLACHLAN 1969 a).

The record of these larvae at Dodi only in 1967 may be somehow connected with the spread of this species in the lake, rather than with its preference for a particular type of substratum or oxygen saturation of water.

*Tanytarsus group lauterborni* sp. II (Fig. 18).

A description of this larva is given by CHRISPEELS (1959) who collec-



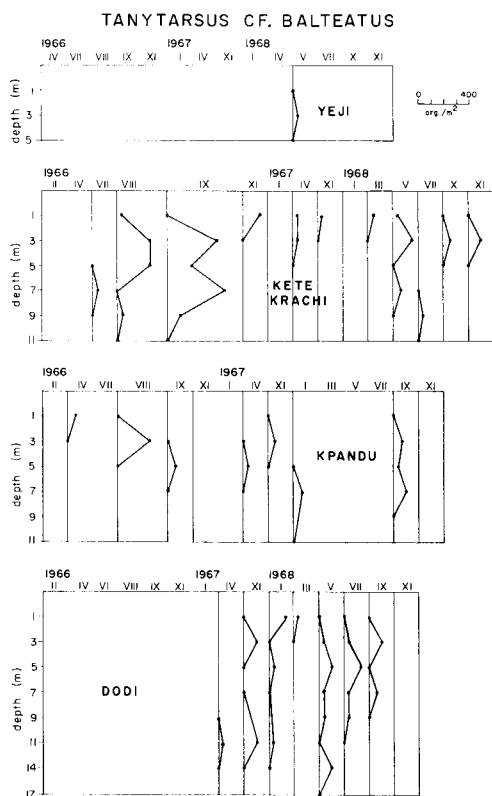


Fig. 17. Abundance and depth distribution of *Tanytarsus cf. balteatus* larvae.

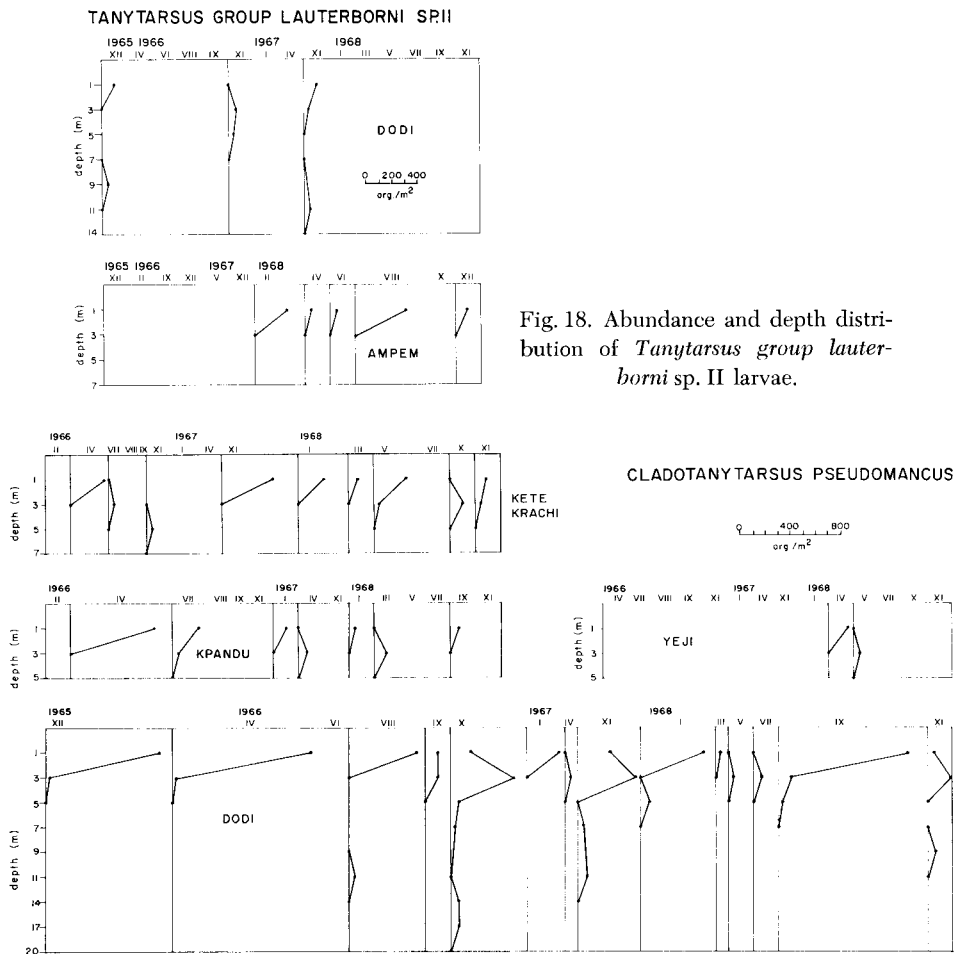
ted it from Lake Edward from the stomach of the fish *Clarias lazera* VAL. The species appears to have a preference for high oxygen concentrations, as suggested by its distribution at Ampem, where it appeared only in well oxygenated water at 1 m depth, and at Dodi, where it was found only at the end of floods when the water was best oxygenated. It has apparently no particular preference for substratum since at Dodi it was found on sandy bottoms and at Ampem it was collected from mud. It is not known why this species was limited in distribution to the south and southwest of the lake.

*Cladotanytarsus pseudomancus* GOETCHEBUER (Fig. 19).

The larva was identified by KUGLER (personal communication) who collected this species in the littoral of Lake Tiberias (KUGLER 1966). McLACHLAN (1969 a) described this larva which he found present in large numbers in shallow water in Lake Kariba as *Cladotanytarsus cf. pseudomancus*. The adults were collected from all stations on the Volta Lake (PETR 1970 c).

The red coloured larvae build tubes from sand in the shape of the letter C. The larvae were most abundant at Dodi, where the substrate is

composed predominantly of sand. Muddy bottoms, as at Ampem, were avoided. But it seems possible that it is the need of these larvae for high oxygen concentrations which determines their distribution rather than a preference for a particular type of substratum. At most localities the larvae



occupied the well oxygenated shallows. Only at Dodi, the locality with the best contact with open lake water, and therefore, with a permanently high oxygen saturation reaching deep, were the larvae found deeper. This suggests that as the oxygenation of the bottom layers of water improves these larvae may come to occupy deeper zones in other areas with sandy bottoms. This species seems to have become well established in the maturing Volta Lake.

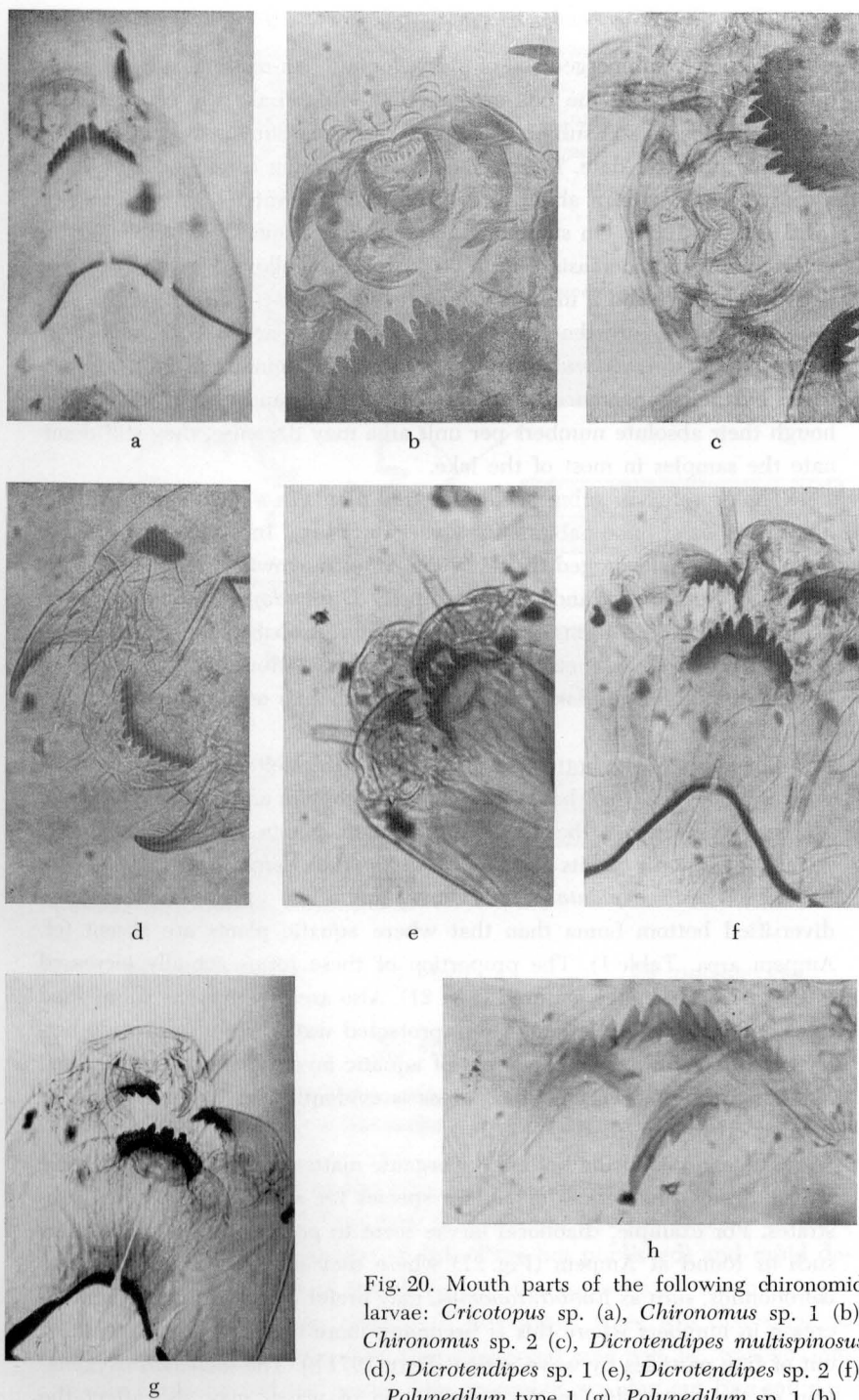


Fig. 20. Mouth parts of the following chironomid larvae: *Cricotopus* sp. (a), *Chironomus* sp. 1 (b), *Chironomus* sp. 2 (c), *Dicrotendipes multispinosus* (d), *Dicrotendipes* sp. 1 (e), *Dicrotendipes* sp. 2 (f), *Polypedilum* type 1 (g), *Polypedilum* sp. 1 (h).

### Discussion

The newly submerged soil of a developing man-made lake is relatively quickly colonized by the bottom fauna. In Volta Lake the concentration of chironomids on soil submerged for 25 days was similar to that recorded any time after this date. In Lake Kariba the bottom chironomids assumed a characteristic pattern about a month after high water level was reached (McLACHLAN 1965). On submerged sticks in the same lake the biomass of invertebrates was increasing up to 30 days, to be followed by a slight drop between 30 days and 2 months (McLACHLAN 1970).

Chironomids are the first to occupy the new areas. *Chironomus formosipennis* and *Nilodorum fractilobus* are the dominant species, as indicated by their appearance as adults (PETR 1970c) and also as larvae. Although their absolute numbers per unit area may decrease, they still dominate the samples in most of the lake.

The presence of submerged terrestrial plants in a new lake provides a great number of microhabitats for a variety of taxa. In Volta Lake the presence of wood encouraged the development of burrowing forms such as the mayfly *Povilla adusta*, and of the caddisfly *Dipseudopsis njalana* living inside the wood. Both forms appeared only later, probably due to their originally very low abundance in the riverine system. However, the spread of *Povilla* throughout the lake was explosive, although not long lasting (PETR 1970a).

The study of the bottom invertebrates of the Volta Lake indicates that the abundance of Oligochatea, Crustacea, Zygoptera and to a certain extent Mollusca is related to the presence of aquatic plants. Bottom in the close vicinity of aquatic plants such as *Ceratophyllum demersum* L., *Pistia stratiotes* L., *Vossia cuspidata* (ROXB.) GRIFF. and some others, harbour more diversified bottom fauna than that where aquatic plants are absent (cf. Ampem area, Table 1). The proportion of these forms actually increased in this area as the lake matured (Fig. 21). Also areas with many submerged trees and thus with relatively calm, protected waters seem to provide better conditions for a greater variety of aquatic invertebrates. The increased number of Hydracarina in some areas is evidently due to the abundance of their crustacean food (Table 2).

The analysis of the bottom for organic matter content and for particle size indicates preferences of certain species for a particular type of substrates. For example, chaoborid larvae seem to prefer the finest substrates such as found at Ampem (Fig. 21) where they are most common. Some chironomids, such as *Endochironomus*, may prefer coarser substrate, and increase in numbers where this is becoming more available by the washing out of fine particles by wave action (PETR 1971b). The increased oxygenation of the water due to the same action of waves may also affect the

abundance of this chironomid. The burrowing larva of *Povilla* will appear only in a substrate into which it can burrow i.e. where grass or woods is present on the bottom. In Volta Lake the molluscs, especially the gastropod *Bulinus truncatus*, seem to be associated predominantly with aquatic plants (PETR 1968b), where they feed on periphytic algae.

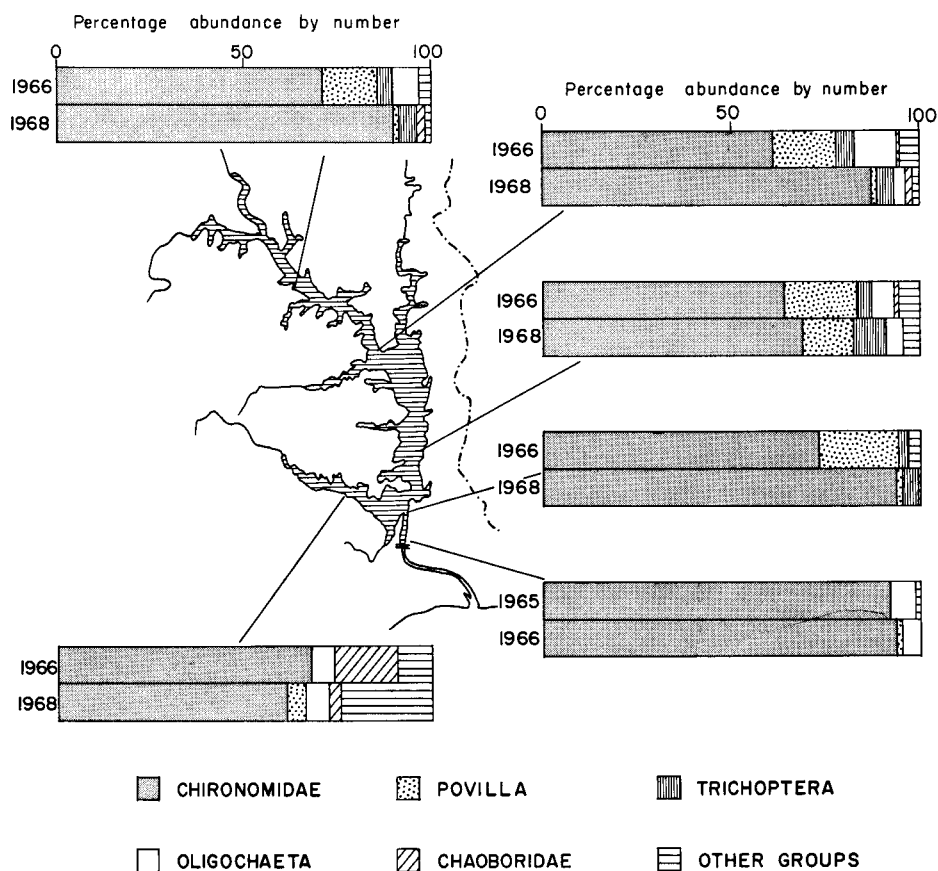


Fig. 21. Percentage abundance by number of the major groups of the bottom fauna in 1966 and 1968 (except at Akosombo, where the data are for 1965 and 1966).

In the littoral belt of the lake, with a more or less stabilized water level, the soft terrestrial flora such as grass and tree leaves soon becomes destroyed by grazing activities of fish (PETR not published) and rapid decomposition. The slope of the shore and the exposure of the bottom to waves, together with the density of submerged trees will determine to what extent and at what rate the submerged soil will be washed into greater depth by agitated water. The process of washing out fine soil par-

ticles is fairly rapid in certain areas, such as islands exposed to intensive wave action. So the species composition of the bottom fauna is changing rapidly, with taxa such as Cladocera, Copepoda, Ostracoda, Conchostraca, Hydracarina, *Micronecta*, Zygoptera decreasing in numbers or completely disappearing from this area (Table 1). Generally speaking, the number of taxa present in such habitats will decrease as the lake matures.

On the other hand, the number of chironomid species remains fairly constant (Table 4), although the species composition changes. A profound change was recorded in the quantitative distribution of the dominant chironomids. The abundant *Nilodorum*, *Chironomus* and *Dicrotendipes* larvae, typical of well protected undisturbed bottoms, greatly decreased in number (Dodi, Fig. 10) and were replaced by *Endochironomus* (PETR 1971 b). Species such as *Tanytarsus balteatus* and *Polypedilum* type 1 which seem to prefer better oxygenated water, increased in abundance. As the larvae of the first group are generally larger than those of the second, there was a decrease in the biomass of chironomids in these areas as the lake matured.

Protected areas with gently sloping bottom are more likely to develop aquatic plants, both rooted and floating. Their establishment may be considered as one of the important factors responsible for an increase in number of taxa present in the bottom (Ampem, Table 1, Table 4). The reason for this may be the provision of additional niches and a large supply of food. In Lake Kariba the presence of plants such as *Potamogeton pusillus* A. BENN, *Ludwigia stolonifera* GUILL & PERR, and *Ceratophyllum demersum* L. resulted in the appearance of several new species (McLACHLAN 1969 c) not previously recorded in mud.

*Nilodorum* and *Chironomus*, the two genera dominating the biomass of the Volta chironomids (PETR 1971 b), have a broad oxygen tolerance. Their abundance seems to be determined by two factors: the presence of fine mud particles for construction of tubes, which they inhabit, and quiet, nonagitated water. Their numbers are low in areas with permanently disturbed water, where only heavy sand particles remain in the substrate. On the other hand, the majority of other chironomids in the new lake seem to have a constant high oxygen requirement (Table 4). In Volta the appearance in the protected area of the new chironomid species *Dicrotendipes multispinosus*, *Cryptochironomus* cf. *dewulfianus*, *Tanytarsus nigrocinctus*, *T. group lauterborni* sp. II may be associated with an improved oxygenation of water as the lake matured.

While the *Chironomus*, *Nilodorum*, *Dicrotendipes chloronotus* and *Dicrotendipes* sp. 2 prefer a muddy bottom, the substrate preference of other species is much less clear. Often the sandy bottoms are those which are well oxygenated, and *Endochironomus*, for example, may prefer this type of environment solely for its high oxygen content. The types of substrate in

the Volta which harbour populations of *Tanytarsus* cf. *balteatus* and *Stictochironomus cafferarius*, are different from those in Lake Kariba (McLACHLAN 1969 b) and Lake Tiberias (KUGLER 1966) for the same species. This may be because Volta Lake has no established sediments, and there are patches of various types of substrate within a small area. In addition the soil was overgrown at the time of flooding by a great variety of terrestrial vegetation, now submerged. It has been suggested (PERR 1971 b) that a soil analysis of the bottom during the first years of a man-made lake may be misleading in many cases since the distribution of the bottom fauna will probably be as patchy as the distribution of various types of soil and submerged vegetation. In most parts of the lake the percentage abundance by number of chironomids increases, as the lake matures (Fig. 21).

The occurrence of the freshwater medusa *Limnognathia* in a bottom sampler must be considered a peculiarity, as this planktonic organism was most probably brought down to the bottom by the descending sampler. Some other organisms, such as *Ceriodaphnia*, Copepoda, *Cloeon* and perhaps to a certain extent the Ostracoda and *Cyclotheria* were collected in a similar way. It is however, a matter of interest, that the only specimen of *Limnognathia* recorded from the Volta Lake was obtained in this way.

### Summary

During the early stages of the formation of the Volta Lake, only the most marginal areas of the bottom could be colonized by aquatic fauna. This was due to the fact that oxygen was only found in the surface water layers. Chironomid larvae, as the most important organisms of the bottom, were the first to colonize the submerged land. Altogether 21 larval types of chironomids were distinguished in routine examination, although 45 species could be identified among the adults. The pattern of distribution of individual chironomid larvae shows their preferences for different types of habitat. The most common large tubiculous larvae of *Nilodorum*, *Chironomus* and *Dicortendipes* show preference for quiet undisturbed water and seem to occur most commonly in areas with fine soil particles. They also tolerate considerable changes in oxygen concentration of water.

The bottom fauna has been subject to two major types of changes — seasonal changes determined by the alteration of dry and wet seasons, and long term changes occurring as a result of the gradual filling of the lake, including changes in the character of the substratum. During 1966—1968 the composition of chironomids changed particularly in areas open to wave action, where *Endochironomus* became the dominant genus. The maturation of the lake, with better oxygenation of the deeper waters, resulted in the bottom fauna becoming more abundant in the profundal. Most of the profundal organisms were chironomids.

In protected shallows the diversity of aquatic invertebrates increased with the establishment of aquatic macrophytes in the littoral zone.

Among the invertebrates other than chironomids the nymphs of *Povilla adusta* were very common in bottom where there were remains of grass and wood. Fine particles of mud harboured considerable numbers of chaoborid larvae. On seve-

ral occasions both taxa dominated the total biomass of the bottom fauna. However, in 1968, with changes in the substrate, the numbers of both invertebrates were very low, compared to 1966.

### Zusammenfassung

Während der Füllung des Voltastausees in Ghana konnte zunächst nur der seichtere Teil des Litorals von Bodenfauna besiedelt werden. Als Hauptgrund hierfür muß der Sauerstoffmangel in den tieferen Zonen gelten. Chironomidenlarven waren die ersten Organismen, die sich in den neu überschwemmten Gebieten ansiedelten, um dort eine relativ hohe Bevölkerungsdichte zu erreichen. Im ganzen konnten 21 Typen von Chironomidenlarven im Voltasee bestimmt werden, während sich die Zahl der Arten im Imaginalstadium auf 45 belief (PETR 1970 c). Man konnte feststellen, daß gewisse Chironomidenlarventypen bestimmten Substraten den Vorzug geben, z. B. finden sich die sehr zahlreichen Larven von *Nilodorum*, *Chironomus* und *Dicrotendipes* vor allem in stillen, ungestörten Gewässern u. zw. sind sie am zahlreichsten an den Stellen, welche feine Schlammpartikel aufzuweisen haben. Diese Larven zeichnen sich auch durch eine verhältnismäßig hohe Toleranz gegen Sauerstoffkonzentrationsschwankungen des Wassers aus.

Die Bodenfauna des Voltastausees wird in erster Linie durch zwei Faktoren bestimmt, u. zw. einerseits durch den regelmäßigen Wechsel von Trocken- und Regenzeiten, und andererseits durch die allmähliche Füllung des Stausees, die sich über mehrere Jahre erstreckte und der ein wichtiger Einfluß auf die Zusammensetzung des überschwemmten Substrats beizumessen ist. In den Jahren von 1966—1968 hat sich die Zusammensetzung der vorhandenen Chironomidenlarven von Grund auf verändert, insbesondere in den Gebieten, wo die Litoralzonen mit dem tieferen Wasser, das durch Wellenbewegungen ausgezeichnet ist, zusammenstoßen. An solchen Stellen sind die Gehäuse bauenden Larven, wie *Chironomus*, *Nilodorum* und *Dicrotendipes*, bald verschwunden, um ihren Platz in der Bodenfauna den *Endochironomus*-Larven zu räumen. Im Laufe der Jahre stieg der Sauerstoffgehalt der tieferen Teile des Sees an, und nun konnte auch der Boden dieser Gebiete besiedelt werden. Dennoch wurden benthische Organismen nur ausnahmsweise in einer Tiefe von mehr als 20 m festgestellt.

Sobald das seichte Litoral von Makrophyten besiedelt wurde, erhöhte sich auch die Zahl der dort vorkommenden Arten.

Die überschwemmten Gebiete, deren Boden mit Gras und Holz bedeckt war, zeichneten sich häufig durch eine große Konzentration von Larven der Eintagsfliege *Povilla adusta* aus. Feiner Schlamm wurde von einer relativ großen Anzahl von *Chaoborus*-Larven bevorzugt. Zu einigen Zeitpunkten herrschten diese beiden Organismen sogar in der Bodenfauna vor. Auffällig war der Rückgang dieser beiden Arten seit 1968, also vier Jahre nach Abschluß des Staudamms; von diesem Zeitpunkt an herrschten Chironomidenlarven in der Bodenfauna aller Gebiete des Voltasees vor.

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