SUBMERGED TREES AS A SUBSTRATE FOR BENTHIC FAUNA IN THE RECENTLY CREATED LAKE KARIBA (CENTRAL AFRICA)*

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INTRODUCTION

The creation of impoundments results in the flooding of large tracts of soil, fauna and flora, and in wooded regions submerged trees often become a conspicuous feature of the lacustrine environment. In the larger reservoirs the cost of clearing the bush tends to be prohibitive except in isolated areas (Ewer 1966), so that dead submerged trees must be regarded as a major feature of this type of lake (Leentvaar 1966). The disadvantages of submerged trees from the fisheries and navigation points of view have been stressed (Federal Government Paper 1960), but their biological implications have been largely overlooked in tropical impoundments.

A 2-year project to study this aspect of submerged trees in Lake Kariba was started in September 1964, when the lake had been in existence for about 6 years. In September 1963, 1 year before the project started and 5 years after the Zambesi River had been dammed, the lake had reached its maximum water level, flooding 5100 km^2 (2000 square miles) of woodland. This marked the end of the 'explosive' phase of the lake's development (Balinsky & James 1960; Harding 1966), and the beginning of a second period when the development of the shore-line, appearance of rooted aquatic vegetation, and the accumulation of sediments were key features (A. J. McLachlan 1968, 1969a, c). All these processes were strongly influenced by an annual fluctuation in lake level resulting from flood-control measures; in addition they occurred against a lowered nutrient background (Harding 1966; A. J. McLachlan 1970). It was during this latter phase that the project was carried out.

DESCRIPTION OF STUDY AREA AND SUBSTRATES

After the rising lake water had reached its maximum level, and a thermocline had become established during the hot season at a depth of 15–20 m (Harding 1966), it was possible to classify the dead submerged woodland as follows:

(1) Periodically immersed woodland, lying between maximum and minimum lake levels (Fig. 1A). This was regarded as the littoral woodland zone, and on gradually shelving areas it was up to 2 km in width.

(2) Permanently immersed woodland, lying between minimum lake level and the thermocline (Fig. 1B). This corresponds to Welch's sublittoral zone (Welch 1952).

(3) Permanently immersed woodland, lying in the hypolimnion (Fig. 1C), which corresponds to the profundal zone of Welch (1952).

When the thermocline was absent during winter (April–August), it was not possible to distinguish between (2) and (3).

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Of the three zones, the littoral woodland zone was the most interesting and was studied in greater detail than the sublittoral and profundal zones. It is important to emphasize that this zone was characteristic of the second phase of the lake's development. During the filling of the lake living trees were being flooded, and there was no period of water recession, so that by definition the littoral zone was absent.

On a submerged tree the substrate normally available to benthic fauna is the bark surface. However, a change in this situation was produced in the littoral woodland by fluctuations in lake level of up to 8 m (Federal Government Paper 1960). During the first period of water recession, which began in late 1963, the exposed, dead, standing woodland was heavily attacked by terrestrial wood borers. The two beetles largely responsible for this attack, *Xyleborus torquatus* Eichh. and *Agelia peteli* Gory, confined their boring activities to the area between the bark and the xylem. When the woodland was resubmerged, there was an additional microhabitat under the bark available to benthic fauna. This development was a particularly important feature of the littoral woodland.

In addition to the two wood-boring species a number of other beetles were found in exposed littoral woodland, notably *Dinoderopsis serriger* Lesne and an unidentified species of Cleridae. Their boring activities in the xylem resulted in mechanical weakening of the

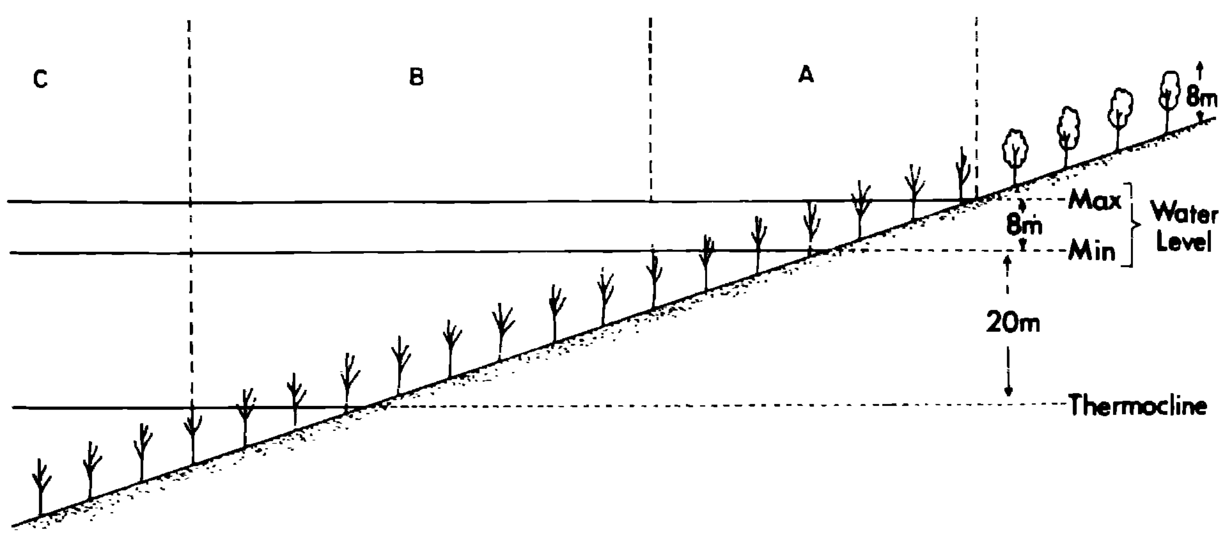

FIG. 1. A classification of the submerged tree habitat based on water levels and position of the thermocline. A, Littoral woodland; B, sublittoral woodland; C, profundal woodland.

trees which then tended to break off at the minimum water-level mark. Thereafter the fallen crowns disappeared, either being destroyed by wave action along the shore-line, or becoming masked by silt. In addition, trees stranded on dry land at low water level were frequently broken down by elephant and/or destroyed by termites (Magadza 1969). A study of sixteen plots, each 225 m^2 in area, showed that 23% of the trees in littoral woodland were destroyed during the period of study. There is, therefore, a tendency towards destruction of the littoral woodland zone.

From the measurements of trees within the plots an estimate was obtained of the ratio of tree-surface area to the area of lake bottom, the value being 2·1 : 1·0. This is an underestimate for two reasons: (i) the roughness of the bark was not taken into account and (ii) branches of less than 0·5 cm in diameter were not considered as they tended to disappear rapidly after the trees were immersed. However, the estimate is of value as it indicates that at least twice as much tree-surface area as lake bottom is available to benthic fauna. The tree substrate must therefore be regarded as a major habitat of the lake.

The area selected for examination, the Mwenda 'Estuary' (Fig. 2), was characteristic of most of the southern shore of the lake. The dominant woodland species was *Colophospermum mopane* Kirk ex Benth. growing on Karroo sandstones and grits. The shore-line types included gradually and steeply shelving exposed coasts, sheltered shore-lines and isolated trees remote from the shore, as well as trees in the littoral and sublittoral zones and in the hypolimnion. The steeply shelving exposed coast (Fig. 2, station 1) tended to erode rapidly, the water being discoloured by silt; sedimentation rates of up to 1763 $g/m^2/day$ were recorded here (A. J. McLachlan 1968). Submerged trees off such coasts therefore became heavily blanketed by silt, and benthic algae were sparse. In

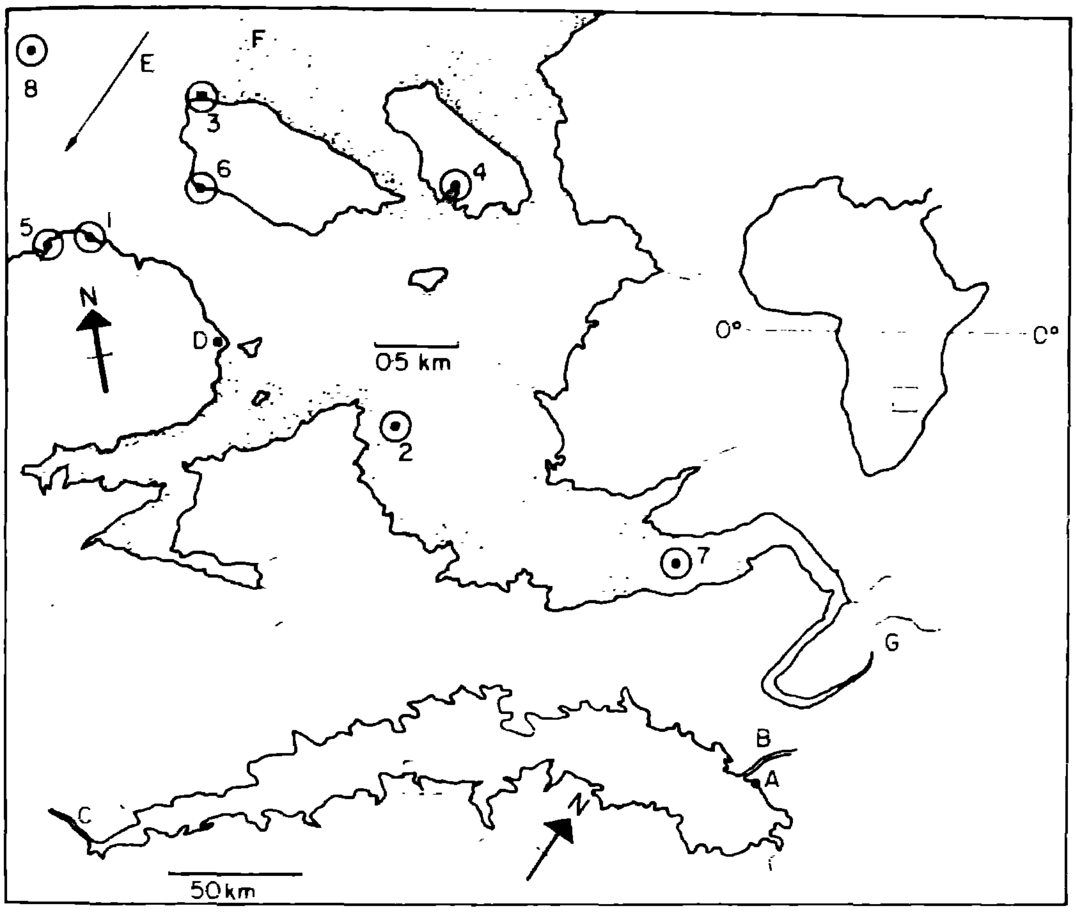

FIG. 2. The Mwenda 'Estuary' with insets showing its location in Lake Kariba, and the position of the Lake in Africa. A, Kariba town at the dam wall. B, Zambesi River outflow. C, Zambesi River inflow. D, Nuffield Lake Kariba Research Station. E, Direction of prevailing north-easterly wind. F, Partially submerged trees in the littoral zone. G, Mwenda River. Filled circles in open circles, sampling stations in the Mwenda 'Estuary'.

contrast, at a beach developed on the gradually shelving exposed coast (Fig. 2, station 3), the bottom deposits were sandy, the water was free from suspended matter and benthic algal masses were conspicuous on the submerged trees. The isolated clump of trees at station 8 resembled station 3 in terms of algal development. At the sheltered habitats, stations 4, 5 and 6, and to a lesser extent station 2, algal development was intermediate possibly owing to the reduction of light by floating mats of the fern *Salvinia auriculata* Aubl.

METHODS OF STUDYING THE SUBMERGED TREE FAUNA

Direct examination of the fauna of submerged trees could not be undertaken; an alternative method was accordingly adopted. Sticks of a convenient size for handling, 50 cm long and about 3 cm in diameter, were cut from the woodland and joined end to end to form a chain. By attaching the top end of the stick-line to a cable supported by trees emerging from the water surface, and anchoring the bottom end with a rock which rested on the mud, a replica of an immersed tree was obtained. Continuous lines of sticks suspended vertically in the water under the desired conditions could later be drawn to the surface and the fauna removed by scrubbing. With one exception the material obtained was washed through a 250 μ gauge sieve and the fauna sorted by eye against a white background. Quantitative results were expressed as numbers and dry weights of fauna/m^2 of tree surface.

The majority of the stick-lines were set at the midpoint of the littoral zone in 4 m of water. A stick-line of eight ½ m sticks was therefore necessary; in practice nine sticks were used in each line, the first protruding partly from the water surface. At the deep water stations (7 and 8) stick-lines consisted of thirty-six and twenty-two sticks respectively.

Sticks were cut from the dominant woodland type, *Colophospermum mopane*. Material from living trees (trees not exposed to wood borer activity) was used to simulate conditions in the sublittoral zone and hypolimnion; these sticks are referred to as 'submerged' sticks. In addition, sticks were cut from the dead woodland, which had been attacked by terrestrial wood borers. Used specifically to replicate conditions in the littoral zone, these sticks are referred to as 'resubmerged' sticks.

Naturally occurring woodland was sampled occasionally as a qualitative check against the stick-lines.

DISCUSSION OF METHODS

The use of lines of sticks from the surrounding woodland in studying the distribution of benthic fauna has obvious advantages over the use of artificial substrates. Kajak (1968a, b) has emphasized the importance of approximating as closely as possible to natural conditions. The method used is believed to provide an accurate imitation of immersed trees except in one respect: the roughness of the bark surface is not independent of stick size, but is directly proportional to stick diameter. Stick-lines were therefore only representative of the 3 cm wide branches of *Colophospermum mopane*. However, branches of about this diameter were estimated to account for nearly 30% of the total tree surface area.

Another draw-back to the method used was the possible loss of fauna when the stick-lines were drawn from the water for scrubbing. No method was devised to estimate this loss, but the efficiency of the scrubbing technique itself was tested by examining thirty sticks under a dissecting microscope after scrubbing. Of the total number of individuals, 97% were found to be removed by scrubbing. The remaining 3% were mainly young instars of chironomid larvae which made little difference to the biomass estimates presented in the results. The sieve mesh normally used (250 μ) and the method of sorting also tended to underestimate the number of first instar chironomid larvae.

PROCEDURE

The following aspects of the benthos of submerged trees were studied.

(1) The rate of colonization of stick-lines. Lines of both submerged and resubmerged sticks were immersed in the littoral zones of stations 1 and 4 for time intervals from 12 h to 4 months at different times of the year.

(2) The effect of wood-borer activity in the littoral zone. Lines of resubmerged sticks

and control sets of submerged sticks were set at littoral stations 1 and 4. The lines were removed at intervals of 2–4 months. When scrubbing resubmerged sticks, care was taken to remove fauna from under the bark. In some cases, fauna from the bark surface and from under the bark were treated separately.

(3) Spatial distribution of benthic fauna. This series of experiments was designed to detect the effect of water depth, type of shore-line and distance of trees from the shore on the benthic fauna. Duplicate lines of sticks were removed bi-annually after 2–4 months immersion from all stations. Resubmerged sticks were used throughout except

Table 1. *Species occurring on submerged and resubmerged stick-lines in the Mwenda Estuary*

Species	A	B
Chironomidae		
Tricladius pretorianus Freeman	×	×
Pentaneura (Ablabesmyia) *appendiculata* Kieffer	×	×
Tanytarsus (Tanytarsus) *balteatus* Freeman	×	–
T. (Tanytarsus) *spadiceonotatus* Freeman	×	×
T. (Tanytarsus) sp. d*	×	×
T. (Cladotanytarsus) *pseudomancus* Goetghebuer	×	×
Chironomus (Nilodorum) *fractilobus* Kieffer	×	×
C. (Nilodorum) *brevibucca* Kieffer	–	×
C. (Dicrotendipes) *sudanicus* Freeman	×	×
C. (Cryptochironomus) sp. 128*	–	×
Stictochironomus caffrarius Kieffer	×	×
Polypedilum (Polypedilum) *bipustulatum* Freeman	–	×
P. (Polypedilum) *deletum* Goetghebuer	×	×
P. (Polypedilum) sp. 10 (i)*	×	×
P. (Pentapedilum) *wittei* Freeman	×	×
Ephemeroptera		
Povilla adusta Agnew	–	×
Cloeon crassi Agnew	×	–
Trichoptera		
Ecnomus oppidanus Brmrd	×	×
E. thomassetti Nosely	×	×
Ecnomus sp. indet	×	×
Amphipsyche senegalensis Brauer	–	×
Oligochaeta		
Aulophorus pectinatus Brinkhurst	×	×
Dero digitata Brinkhurst	×	×
Nais sp. indet.	×	×
Total numbers of species: 24	19	22

* Larval types (A. J. McLachlan 1969b) (n = 978).
A, Submerged stick-lines; B, resubmerged stick-lines; ×, species present; –, species absent.

for the sublittoral and hypolimnion portions of stations 7 and 8 where submerged sticks were used.

Natural variation due to roughness of bark and degrees of wood borer activity necessitated the use of large numbers of samples. The number of sticks per analysis (n) is reported in the results. Results are generally given as the mean and standard error. Significance of populations changes as determined by Student's t test was accepted at the 5% level, and the probability values are included in the results.

Species and types of chironomid larvae cited in the text have been described elsewhere (A. J. McLachlan 1969b).

RESULTS

A list of the benthic species found on stick-lines is shown in Table 1. This agrees well with occasional samples taken from naturally occurring immersed trees. Of the twenty-four species recorded, over half were immature chironomids. Not only did chironomids constitute the bulk of the species present, but they were found on all sticks examined and were numerically the most common. Oligochaetes occurred on 57% of the sticks, while trichopterans and ephemeropterans occurred at frequencies below 30%. The differences between submerged and resubmerged sticks shown in Table 1 will be discussed in a later section (page 259).

Colonization of submerged stick-lines

The time available for colonization of any particular stick in the littoral zone is limited to 4 months because of the prevailing regime of water level fluctuations. The pattern and

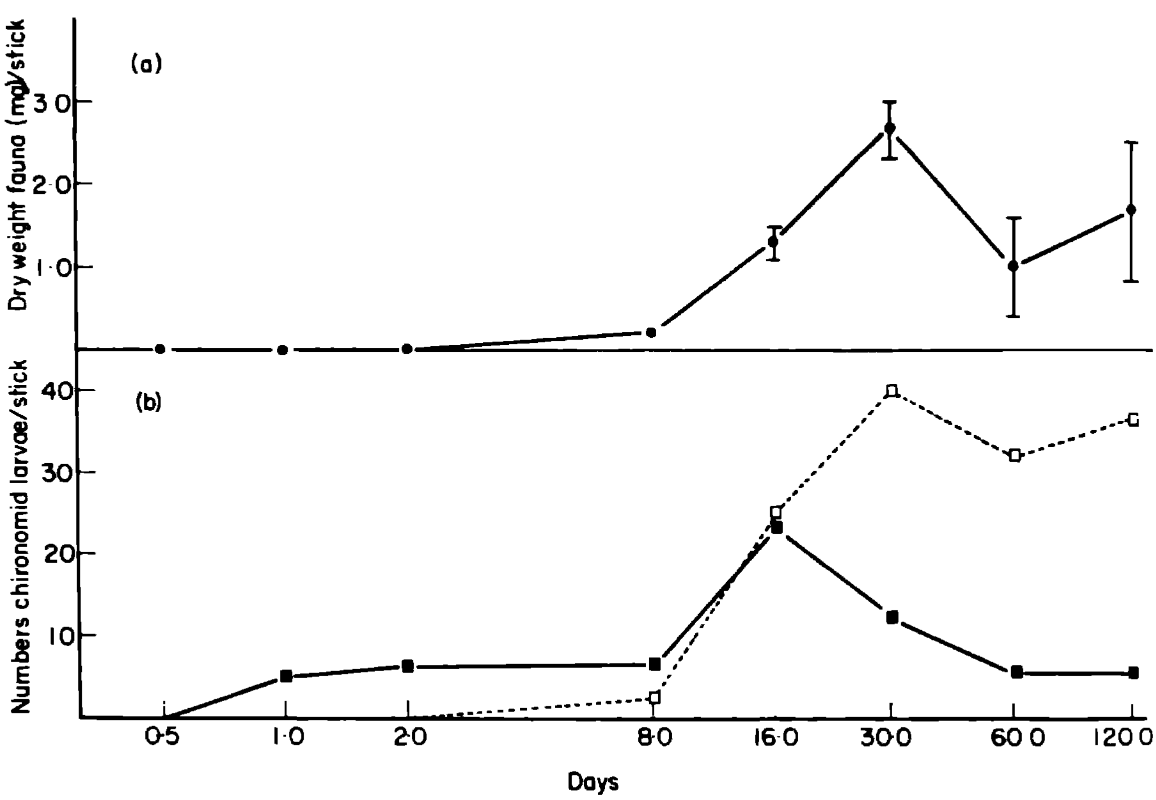

FIG. 3. Colonization of stick-lines over a 4 month period. (a) Total biomass (mg dry weight/stick). Vertical lines, mean and standard error ($n = 500$). (b) Numbers of chironomid larvae/stick. ——, Instar I; – – –, instars II–IV ($n = 90$).

method of colonization were therefore of particular interest. No seasonal differences were detected in the rate of colonization; mean values for samples taken throughout the year will therefore be considered. The data presented in Fig. 3(a) shows that fauna first appeared about 8 days after immersion. Thereafter, there was a period of rapid increase in biomass up to 30 days, followed by a slight drop between 30 days and 2 months. The salient features of the graph are: (i) that once colonization begins it proceeds very rapidly and (ii) that the stick-lines are fully colonized for three quarters of the time for which the habitat is in existence. The standard errors included in the graph indicate an increasing variation with time, and suggest that a large species at low frequency of occurrence was responsible. The significance of this is discussed in the following section.

Colonization by insects could be accomplished in two possible ways: by migration of populations from adjacent submerged woodland, or by migration of first instars following oviposition. In the first instance, a mixture of instars might be expected, while in the second, first instars only would be detected initially. Material from stick-lines drawn at the same time and at the same places as those providing data for Fig. 3(a) was washed through a 125 μ mesh sieve to retain the first instar larvae and the residue was examined under a dissecting microscope. The results of this analysis with respect to chironomid larvae are summarized in Fig. 3(b); the data have been plotted separately for the numbers of first instar larvae and for the remaining instars II–IV. The graph for the older instars followed very much the same pattern as that for the total community biomass. However, the distribution of first instar larvae was quite different. They appeared in considerable numbers as early as 24 h after immersion. First instar larvae were therefore responsible for the initial colonization of sticks. Since chironomid egg masses require as little as 1 day to hatch under tropical conditions, the results of the analysis focus attention on the oviposition behaviour of the adult female. This is considered later. The increase in

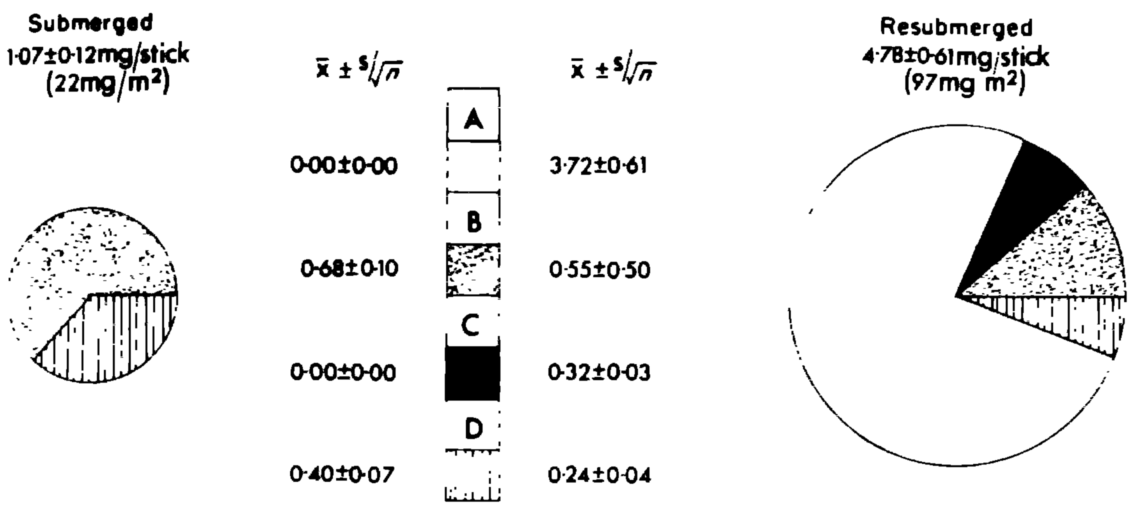

FIG. 4. Comparison of the faunas of submerged and resubmerged sticks. The area of the circles are proportional to faunal dry weight (mg/stick and mg/m²). Contributions by constituent populations are indicated graphically and numerically ($\bar{x} \pm s/\sqrt{n}$: mean ± standard error). A, Ephemeroptera (*Povilla adusta*); B, Chironomidae; C, Trichoptera (*Amphipsyche senegalensis*); D, Oligochaeta ($n = 68$).

numbers of mature instars between 8 and 120 days of immersion was accompanied by a decrease in the first instar populations. It seems probable that the rise in biomass shown in Fig. 3(a) was due to maturation of the first instar populations responsible for colonization.

The effects of terrestrial wood borer activity on the littoral woodland

The species composition of submerged and resubmerged sticks is compared in Table 1. There are some important differences, in particular the appearance on resubmerged sticks of a trichopteran, *Amphipsyche senegalensis* Brauer, and of an ephemeropteran, *Povilla adusta* Agnew. Three new chironomid species also appeared, *Polypedilum bipustulatum* Freeman, *Nilodorum brevibucca* Freeman and *Cryptochironomus* sp. 128 (A. J. McLachlan 1969b). Two of the species present on submerged sticks were absent from resubmerged sticks; however, the total number of species on the latter sticks was slightly higher than that for submerged sticks (twenty-two compared with nineteen).

The mean total weight of fauna supported by submerged and resubmerged sticks as well as the contribution by weight of the major constituent populations is illustrated in Fig. 4. The resubmerged sticks supported a significantly larger population ($P<0{\cdot}001$), the increase being almost entirely due to the presence of *Povilla adusta*. There were also significant changes in the other constituents, the smallest change being in the chironomid population ($0{\cdot}02<P<0{\cdot}05$).

The appearance of *P. adusta* can also be shown to explain the increase in standard errors observed with increasing time of immersion. (Fig. 3a). The biomass values per stick after 4 months of immersion were as follows:

Submerged sticks:	$1{\cdot}07 \pm 0{\cdot}06$ mg/stick
Resubmerged sticks:	$6{\cdot}23 \pm 1{\cdot}69$ mg/stick

The standard error for resubmerged sticks is clearly much greater than that for submerged sticks. This is due to the presence of large individuals of *P. adusta* at a low frequency of occurrence. The increase in standard error is masked in Fig. 4 where mean values for sticks immersed for 1–4 months are considered.

Table 2. *Comparison of the species composition in terms of percentage dry weight of the fauna on the bark of submerged sticks, and fauna on and under the bark of resubmerged sticks*

Species	Submerged On bark	Resubmerged On bark	Resubmerged Under bark
Chironomidae			
Polypedilum bipustulatum	0	0	4
Pentapedilum wittei	1	1	0
Dicrotendipes sudanicus	54	47	1
Tanytarsus balteatus	1	1	0
Cryptochironomus sp. 128*	0	1	0
Nilodorum fractilobus	2	1	3
N. brevibucca	0	0	1
Ablabesmyia appendiculata	4	2	0
Ephemeroptera			
Povilla adusta	0	0	90
Cloeon crassi	1	1	0
Trichoptera			
Ecnomus oppidanus	1	20	0
Amphipsyche senegalensis	0	0	1
Oligochaeta			
Dero digitata	32	23	0
Other species	5	3	0
Total dry weight (mg/m²)	22	21	76
		Σ: 97	

* Larval types (A. J. McLachlan 1969b) ($n = 68$).

By treating the populations on the bark surface in both cases separately from the fauna found under the bark on resubmerged sticks, the microhabitat responsible for the increased weight after wood borer activity was traced. Table 2 shows that the species specific to resubmerged sticks, that is, *Polypedilum bipustulatum*, *Nilodorum brevibucca*, *Povilla adusta* and *Amphipsyche senegalensis*, occurred exclusively under the bark. It was these populations, in particular *Povilla adusta* and *Amphipsyche senegalensis*, that were responsible for the weight increase (Fig. 4). In fact, a comparable biomass was supported by the on-bark habitat in both cases, additional weight being almost entirely due to the under-bark habitat (Table 2). The exposure of littoral woodland to wood borer activity, therefore, resulted in major changes in the benthic populations.

Spatial distribution patterns of the benthic community

We have been largely concerned so far with the dynamic situation in littoral woodland induced by water level fluctuations. This section deals with the influences of water depth, type of shore-line, distance from shore and seasonal variations on the spatial structures of the benthic communities of the submerged woodland as a whole.

The effect of water depth on the benthos of immersed trees was of interest. In Fig. 5 the vertical distribution of fauna along a stick-line is depicted in terms of the mean weights

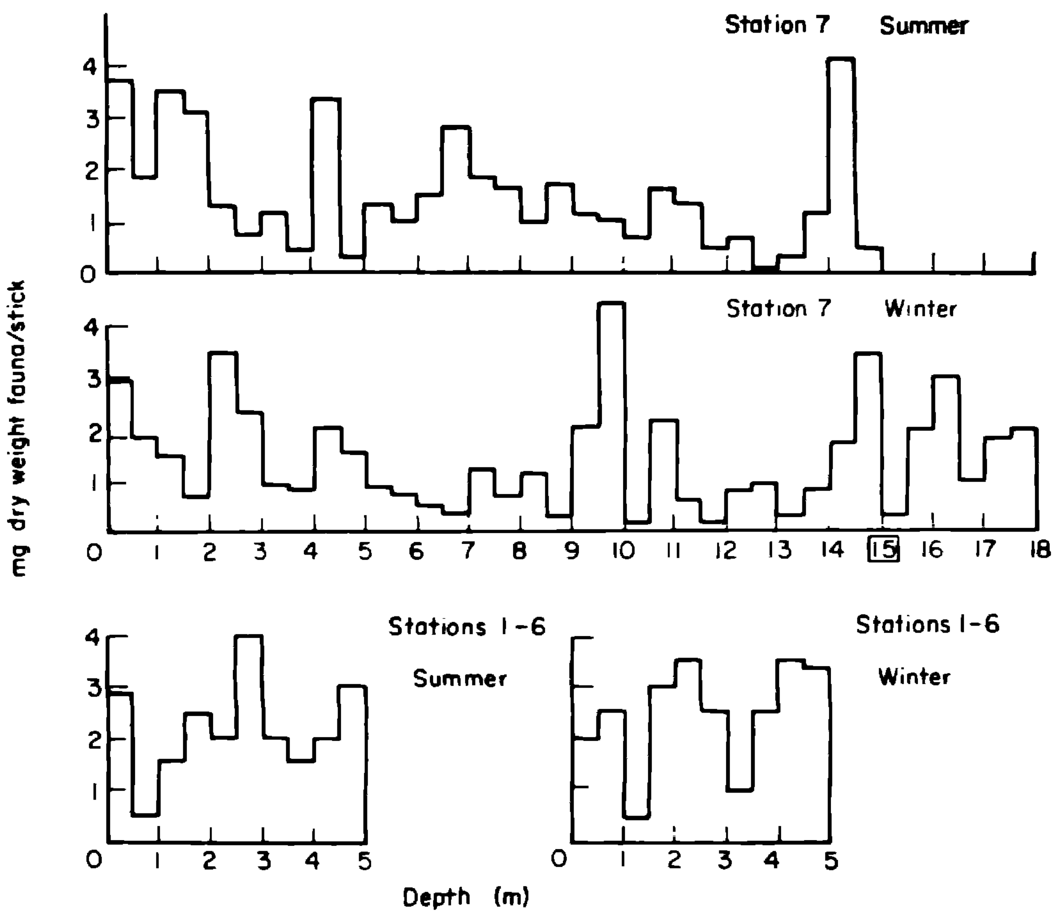

FIG. 5. Depth distribution of fauna on stick-lines in dry weight/stick in summer and winter. Values for station 7 and a mean value for the littoral stations 1–6 are given. The boxed number indicates the depth of the thermocline in metres (n = 978).

for summer and winter for submerged and resubmerged sticks. There was no indication of a preferred depth at the littoral stations 1–6. Nor was any depth distribution pattern detected in winter at station 7. The only response to depth was found in relation to the presence of the thermocline which developed at about 15 m during the hot season; fauna was absent from sticks in the hypolimnion at this time.

The influence of type of shore-line on the fauna of littoral woodland was examined at stations 1, 3 and 4 with respect to biomass and species composition:

(1) A comparison was made of the values for total biomass and biomass of constituent populations for all resubmerged sticks immersed for a period of over a month. At station 3 the values for total biomass and biomass of the *Povilla adusta* populations differed significantly from the corresponding values for stations 1 and 4 (Table 3: P = 0·05 and P<0·001 respectively).

(2) In terms of species present, the chironomid populations at each station appeared to be distinctive (Table 4). Ten species were recorded at station 4, and six and four at stations 1 and 3 respectively. One species, *Tanytarsus spadiceonotatus* Freeman, was distinct to station 1, and three species, *Tricladius pretorianus* Freeman, *Ablabesmyia appendiculata* Kieffer and *Cladotanytarsus pseudomancus* Goetghebuer, were only found at station 4. Only two species, *Polypedilum bipustulatum* Goetghebuer and *Dicrotendipes sudanicus* Freeman, were common to all three stations.

The effect of distance of trees from the shore-line on the tree fauna was investigated by comparing biomass values for Chironomidae at station 8, which was 2000 m from the shore, with the mean biomass values for the remaining stations, none of which was over

Table 3. *Total biomass and biomass of* Povilla adusta *at stations* 1, 3 *and* 4 (*results are expressed as the mean ± standard error*)

Station	Dry weight mg/stick: Total biomass	*P. adusta* biomass	*n*
1	2·4 ± 0·4	0·7 ± 0·1	30
4	2·0 ± 0·3	0·5 ± 0·1	30
3	5·2 ± 1·5	3·5 ± 0·2	60

Table 4. *Chironomid species records from submerged sticks from stations* 1, 3 *and* 4

Species	Station 1	3	4
Nilodorum fractilobus	×	–	×
Cryptochironomus sp. 128*	–	×	×
Dicrotendipes sudanicus	×	×	×
Polypedilum bipustulatum	×	×	×
P. deletum	×	–	×
Pentapedilum wittei	×	–	×
Tricladius pretorianus	–	–	×
Ablabesmyia appendiculata	–	–	×
Tanytarsus spadiceonotatus	×	–	–
Tanytarsus sp. d*	–	×	×
Cladotanytarsus pseudomancus	–	–	×
Total no. of species	6	4	10

* Larval types (McLachlan 1969b).
×, Present; –, absent.

100 m from the shore (Table 5). Station 8 supported a significantly smaller population than any of the other stations ($P < 0{\cdot}001$).

DISCUSSION

The bark surfaces of submerged trees support a fauna in which chironomid larvae are numerically predominant. It has been shown in the case of the latter that colonization is undertaken by first instar larvae. An attempt is made in Fig. 6 to summarize the observed distribution patterns of the tree fauna as a whole, and to relate these patterns to some environmental conditions. The fauna appeared to be influenced by three factors: water depth, type of shore-line and distance of the trees from shore.

The response to water depth was associated with the presence of a thermocline at about 15 m during the summer months (September–March), no fauna being present in the hypolimnion (Fig. 6, station 7), which was known to be anaerobic during this time (S. M. McLachlan 1969). In the epilimnion during summer, however, and in both epilimnion and hypolimnion during winter, there was no indication of a preferred depth zone. This was in sharp contrast to the faunal situation in the mud in the epilimnion where numbers were found to decrease rapidly with increasing depth of water (A. J. McLachlan 1968, 1970). The results are also contrary to those of Luferov (1962) who found a distinct depth zonation of chironomid larvae on submerged trees in 3 m of water.

Table 5. *The influence of distance from shore on the chironomid biomass of resubmerged sticks*

Station	Distance from shore (m)	Chironomidae (dry weight mg/stick)	*n*
1–6	< 100	4·2 ± 0·4	978
8	2000	0·6 ± 0·2	60

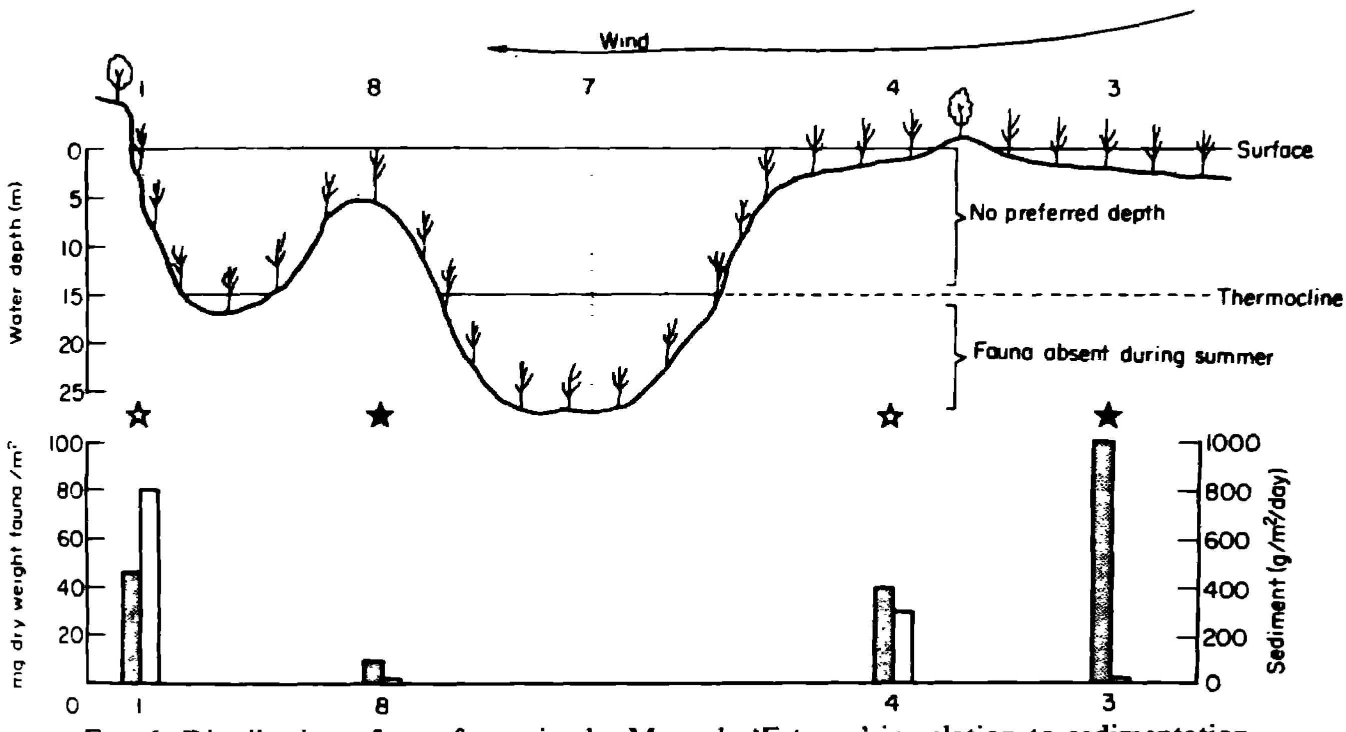

FIG. 6. Distribution of tree fauna in the Mwenda 'Estuary' in relation to sedimentation rate, benthic algal development, water depth and distance from shore. Broken vertical lines represent experimental stick-lines at stations 1, 3, 4, 7, and 8. Open star, poor benthic algal development; closed star, benthic algae well developed; open columns, sedimentation rate ($g/m^2/day$); stippled columns, faunal dry weight/m^2.

The three shore-line types examined, gradually shelving exposed coast, steeply shelving exposed coast, and sheltered coast (Fig. 6, stations 3, 1 and 4 respectively) each supported a characteristic tree fauna both in terms of species and total biomass. The richest faunal standing crops were recorded at station 3, where the sedimentation rates were low and the benthic algae well developed. Both the remaining categories of shore-line experienced heavy sedimentation. It seems likely that the biomass of the tree fauna is proportional to the quantity of benthic algae, and that benthic algal development is inhibited by high sedimentation rates. Associations of benthic faunas with benthic algae have been observed in African waters by Chutter (1968) and Weir (1969). Kirpichenko (1965) and Clafin

(1968), working in Russia and America respectively, found the submerged tree fauna to be related to the presence of benthic algae.

An exception to this rule was the group of trees at station 8, where despite dense accumulations of benthic algae the faunal biomass was poor. This may have been due to the fact that of all the stations, this was the most remote from land. It is generally believed that chironomid oviposition occurs inshore (MacDonald 1956; Berg 1938; A. J. McLachlan 1970), the female chironomids tending to oviposit around objects emerging from the water surface (Fryer 1959). In Kariba, adult chironomids of the species found inhabiting trees were frequently observed ovipositing within the partially submerged tree belt, but never in open water. If this is taken to be the general rule, the paucity of fauna at station 8 may have been a direct result of this station's distance from shore combined with the fact that few branches emerged from the water surface here. In addition to the other factors discussed (i.e. sedimentation rates and algal development), it seems probable that the oviposition behaviour of adult females, in the case of Chironomidae at least, played an important role in determining the spatial distribution of fauna on immersed trees. Macan (1961) has shown that selective oviposition behaviour occurs in a number of aquatic insects. It seems likely, therefore, that the standing crop of fauna on immersed trees may be inversely proportional to the distance from shore.

The widely observed depth distribution of mud fauna in the epilimnion of lakes (Welch 1952; A. J. McLachlan 1970) may be a response to distance from shore rather than water depth. The depth zones on any one immersed tree or stick-line are a constant distance from shore. It is perhaps not surprising, therefore, that there is no response of the fauna to depth except in the presence of the thermocline.

The importance of submerged woodland as a substrate for benthic fauna can be assessed by comparing the standing crop supported by trees with that supported by two other major substrates in Lake Kariba, mud and aquatic macrophytes. Mud in the epilimnion of Lake Kariba supported a mean faunal weight of 206 mg/m^2 (A. J. McLachlan 1968); aquatic vegetation, 1064 mg/m^2 (A. J. McLachlan 1969c); and littoral trees, 60 mg/m^2. There is no doubt that trees formed the poorest of the substrates, but the tree surface area available is considerable. In addition, in areas like the Mwenda Estuary, aquatic macrophytes were relatively scarce, rooted macrophytes being virtually absent until recently (Bowmaker 1968; A. J. McLachlan 1969c). Trees must therefore provide a valuable additional habitat when vegetation is present, and substitute to some extent for vegetation before it appears. They also play an indirect role in stabilizing the distribution of floating mats of macrophytes like *Salvinia auriculata* (Bowmaker 1968), itself an important substrate for benthic fauna (A. J. McLachlan 1969c).

The influence of water level fluctuation on the fauna of immersed trees was considerable. The activity of terrestrial wood borers at low lake level resulted in the development of an additional habitat under the bark of trees, so that resubmerged littoral woodland supported the highest biomass of benthic fauna. This situation provides a good example of an interaction between terrestrial and aquatic faunas as the result of lake level fluctuations. However, the activity of wood borers, combined with the destruction of trees by termites and game, suggest that littoral woodland is being rapidly destroyed during the periods of low water level. It must therefore be regarded as a transient feature in the lake's history.

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SUMMARY

Submerged woodland supports a distinctive fauna of which chironomid larvae form the major part numerically. Newly flooded trees were found to be colonized by first instar chironomid larvae within 24 h; after 4 months faunal biomass estimates of up to 97 mg/m^2 were obtained. Twenty-four benthic species were involved, including ephemeropterans, trichopterans and oligochaetes, in addition to chironomids. Apart from the absence of fauna on immersed trees in the hypolimnion, no correlation was found between benthos and water depth. However, the type of shore-line and distance of the substrate from the shore both influenced distribution patterns. These patterns are thought to be due to the distribution of sediment and benthic algae and to the behaviour of ovipositing chironomid females. The annual fluctuation in lake level resulted in a significant increase in the faunal biomass, correlated with a change in the nature of the submerged littoral woodland. The importance of immersed trees in the early years of the lake's development is discussed in relation to other major substrate types.

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