

Macroinvertebrates of Flooded Trees in the Man-Made Volta Lake (Ghana) with Special Reference to the Burrowing Mayfly *Povilla adusta* Navas

by

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INTRODUCTION

During the lacustrinization of the Man-made Volta Lake in Ghana, periphyton has steadily increased in importance as a food source for aquatic animals. Flooded trees have provided a suitable substrate for periphyton in the epilimnion of the inshore and off-shore areas, the land not having been cleared before the Lake was formed. The biomass of periphyton has greatly exceeded that of benthos (PETR, 1969a) since even in relatively shallow water a deoxygenated water layer has frequently developed at the bottom and prevented the formation of benthos.

Investigation of the food of the most important commercial fish species of the Volta Lake showed that during 1965 and 1966, i.e. one to two years after the Akosombo dam was closed, periphyton did not form a very significant part of fish diet (LAWSON et al., 1969). The indirect importance of periphyton was however great as it provided food and shelter for aquatic invertebrates. Some of these invertebrates became extremely abundant and their importance as fish food gradually increased.

TERMINOLOGY

The animals considered in the present paper inhabit the surfaces of flooded trees, covered by periphyton, and burrow into the substrate itself.

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Received September 5th, 1969.

The most adequate terms for such organisms seem to be those suggested by ŠRÁMEK-HUŠEK (1946) and SLÁDEČKOVÁ (1962) who describe them as attached and dependent organisms. The attached organisms, the true periphyton, are immobile and adapted to a sessile life, whereas the dependent organisms, the pseudo-periphyton, are free-living, creeping and grazing among the former. Nymphs of *Povilla adusta* NAVAS (Ephemeroptera), the commonest organisms of flooded trees, hide in burrows inside the wood during the day, and crawl on the periphyton and wood surface, or swim in the surrounding water during the night. They could therefore be called pseudoperiphyton. Because of their mode of life during the day the term endobenthon could also be used; this has been proposed by DUSSART (1966) for organisms which inhabit the interior of solid substrates.

In this paper for simplicity the term "periphytic macroinvertebrates" will be used both for dependent organisms of periphyton and for endobenthon.

MATERIAL AND METHODS

The importance of periphyton and especially of periphytic macroinvertebrates in the Volta Lake ecosystem was recognized only after studies on the bottom fauna had been carried on for some time. A full time-table did not allow extensive observations to be made at individual stations. Sampling at different stations (see map) was therefore irregular but has served to provide data upon which to assess the importance of this community and to allow comparison between the benthic and the periphytic faunas.

Bark and wood were collected from submerged parts of trees standing in water or from fallen trees floating at the water surface. In most cases it was no longer possible to identify the trees attacked by *Povilla*. In the south the nymphs were very abundant in *Ceiba* and *Bombax*, common genera of large trees having soft wood. In the northern savanna, the hard wood and fire-resistant *Terminalia* predominated and *Povilla* was found to be less abundant. The flooded gallery forest in the north also, however, provided soft wood species.

A simple method of sampling was used. Bark and wood were broken off the submerged parts of trees near the water surface and transferred to a bucket filled with water. Living organisms, visible to the naked eye were immediately removed. The bark and wood was then broken into small pieces and any animals thus exposed were collected. Finally the wood was left in the sun and the remaining fauna collected as it emerged. All organisms were preserved in 4 % formal-

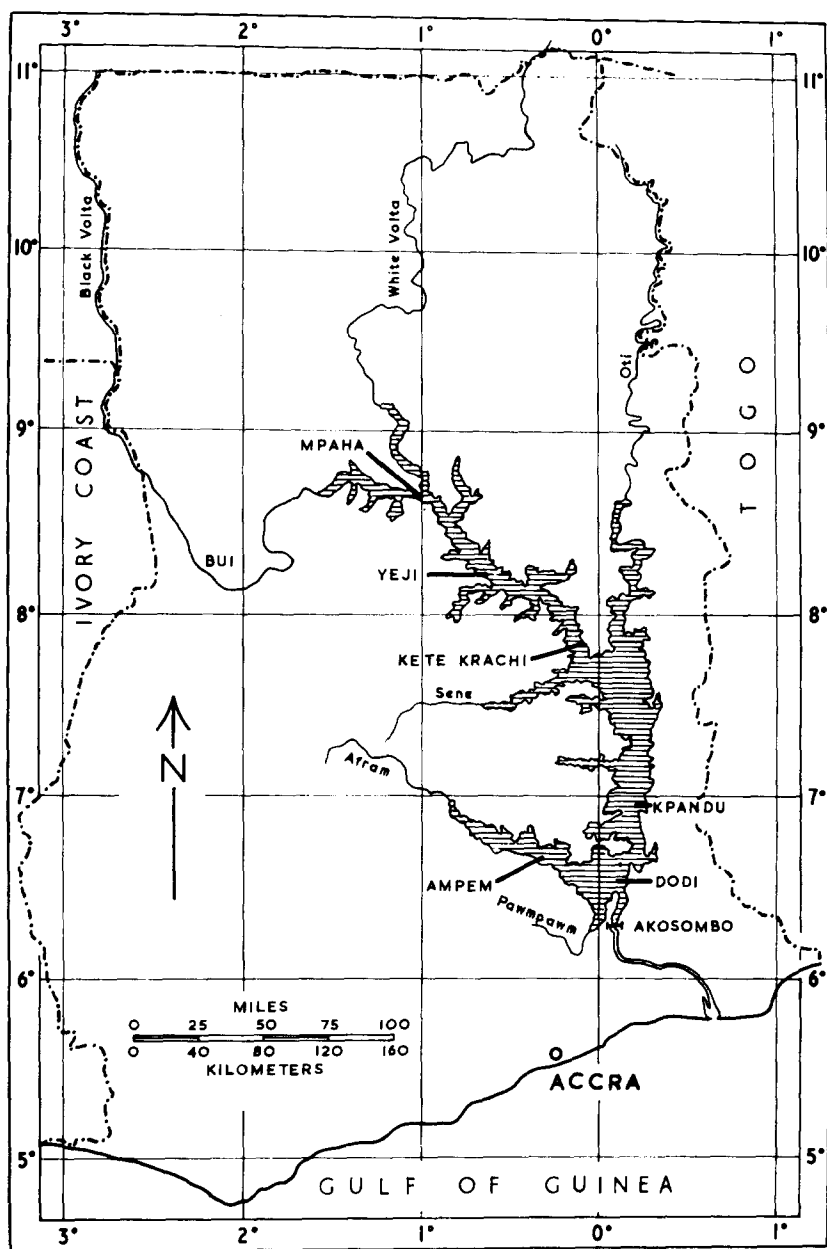


TABLE I
Periphytic macroinvertebrates of flooded trees (Abundance by number of organisms).

Organism	1	2	3	4	5	6	7	8	9	Total	Percentage occurrence	Percentage total organisms collected
Oligochaeta	2	4			6	3		1		16	55.5	0.25
Naididae	2	4			6	3		1		16	55.5	0.25
Hirudinea					3			3		6	22.2	0.10
Crustacea					7				1	8	22.2	0.13
Ostracoda					4				1	5	22.2	0.08
Conchostraca					3					3	11.1	0.05
Cyclotheria hislopi					3					3	11.1	0.05
Hydracarina					1					1	11.1	0.02
Ephemeroptera	75	1592	189	173	485	1313	478	53	114	4472	100.0	74.97
Procloeon					1					1	11.1	0.02
Provilla adusta	75	1592	189	173	484	1313	478	53	114	4471	100.0	74.95
Odonata		1			1					2	22.2	0.03
Zygoptera		1			1					2	22.2	0.03
Trichoptera	5	58	4		16	661	44	9	11	808	88.9	13.55
Orthotrichia					1				1	2	22.2	0.03
Ecnomus	5	58	2		7	164	44	9	10	299	88.9	5.02
Amphipsyche			2		8	497				507	33.3	8.50
Coloptera		1	7		4	16	3		1	32	66.7	0.54
Potamodytes									1	1	11.1	0.02
Hydroptilidae					4					4	11.1	0.07
Coleoptera not ident. l. + im.		1	7			16	3			27	44.4	0.45

Diptera	19	201	41	75	193	53	6	26	614	88.9	10.29
Chironomidae	19	181	41	75	181	16	4	26	543	88.9	9.10
Tanypodinae		1	2					3	6	33.3	0.10
Ablabesmyia nilotica		1	2					3	6	33.3	0.10
Orthocladiinae					20				20	11.1	0.34
Cricotopus					20				20	11.1	0.34
Chironomini	19	180	39	75	161	16	4	23	517	88.9	8.66
Nilodorum	16	158	37	34	4	11	3	22	285	88.9	4.78
Dicortendipes chloronotus				13					13	11.1	0.22
Endochironomus				2					2	11.1	0.03
Chironomus				2					2	11.1	0.03
Polypedilum				15	94	4	1		114	44.4	1.91
Dicortendipes sp. 1		3							3	11.1	0.05
Dicortendipes sp. 2		2			49	1			52	33.3	0.87
Chironomini pupae	3	17	2	9	14			1	46	66.7	0.77
Ceratopogonidae		20			12	37	2		71	44.4	1.19
Mollusca				7					7	11.1	0.12
Gastropoda				7					7	11.1	0.12
Anisus coretus				1					1	11.1	0.02
Bulinus truncatus				6					6	11.1	0.10
Total	101	1857	200	214	605	2186	578	72	153	5966	100.00

No	Station	Date	No	Station	Date	No	Station	Date
1	Ampem	21.6.1968	4	Kpandu	8. 4.1967	7	Kete Krachi	9.5.1969
2	Ampem	13.5.1969	5	Kpandu	19.12.1967	8	Yeji	10.5.1969
3	Dodi	7.5.1969	6	Kpandu	8. 5.1969	9	Mpaha	16.6.1968

dehydrate solution. In some cases the bark and wood were kept and later dried for 24 h at 85°C in an electric oven to obtain a standard dry weight. The surface area of bark was measured before the wood dried.

In the laboratory organisms were separated into species or higher taxa, and counted. To estimate the standing crop, specimens were placed for about five min on blotting paper, to remove excess moisture. The representatives of each taxon were then weighed on a torsion balance to the nearest 0.2 mg.

In some cases the length of *Povilla* nymphs was measured to the nearest 0.1 mm. The length measured was the distance from the distal end of the mandible to the tip of the abdomen, without cerci. Exuviae of *Povilla* nymphs were measured in a similar way. Each size-group of nymphs within a range of 1 mm was weighed, and the mean weight for each range calculated.

The food of some chironomid, trichopteran and *Povilla* larvae was studied by examination of the gut contents.

Eggs of *Povilla* were hatched in aerated water.

Emerging *Povilla*, attracted to the deck lights of the boat were collected shortly after dusk. No quantitative samples were taken; adults were fixed in 70 % alcohol. On some occasions eggs were obtained from living females by dipping their abdomen into water. Each sample was kept separately; the number of eggs was later counted, and their size measured.

RESULTS

Periphytic macroinvertebrates

In the period 1967-1969 periphytic macroinvertebrates were sampled from flooded trees at six stations. The taxa and species are listed in Table I.

Povilla adusta nymphs, collected from all samples have the highest percentage by number. They are followed by larvae of *Amphipsyche* and *Ecnomus* (Trichoptera) and *Nilodorum* (Chironomidae). *Amphipsyche* was common at Kpandu, *Ecnomus* was collected at all localities. *Nilodorum* was not present in Dodi samples, where no chironomids were found in the wood.

Povilla nymphs formed 74.95 % of the total number of organisms collected, followed by *Amphipsyche* with 8.50 %, *Ecnomus* with 5.02 % and *Nilodorum* with 4.78 %. The relatively high percentage proportion of *Amphipsyche* larvae is due to its high frequency in samples collected at Kpandu.

Differences between the species composition at individual sta-

TABLE II
Periphytic macroinvertebrates of flooded trees (Standing crop in mg).

Organism	1	2	3	4	Station			6	7	8	9	Total	% total standing crop
Oligochaeta	0.1	1.2			2.4			93.0		0.1		96.8	0.151
Naididae	0.1	1.2			2.4			93.0		0.1		96.8	0.151
Hirudinea					2.0					33.2		35.2	0.055
Crustacea					3.5						0.4	3.9	0.004
Ostracoda					1.0						0.4	0.5	0.001
Conchostraca					2.5							2.5	0.003
Cyclotheria hislopi					2.5							2.5	0.003
Hydracarina					0.5							0.5	0.001
Ephemeroptera	617.9	17100.0	3800.0	302.1	2545.3			19500.0	9400.0	1600.0	3204.9	58070.2	90.423
Procloeon					1.0							1.0	0.002
Povilla adusta	617.9	17100.0	3800.0	302.1	2544.3			19500.0	9400.0	1600.0	3204.9	58069.2	90.421
Odonata		29.0			23.0							52.0	0.081
Zygoptera		29.0			23.0							52.0	0.081
Trichoptera	10.9	129.7	18.5		132.5			4338.5	89.7	21.5	24.9	4766.2	7.428
Orthotrichia					1.0						0.5	1.5	0.009
Enomus	10.9	129.7	5.0		15.0			386.2	89.7	21.5	24.4	682.4	1.062
Amphipsyche			13.5		116.5			3952.3				4082.3	6.357
Coleoptera		1.5	52.0		5.2			245.5	5.5		14.4	324.1	0.502
Potamodytes											14.4	14.4	0.022
Hydroptilidae					5.2							5.2	0.006
Coleoptera not ident.		1.5	52.0					245.5	5.5			304.5	0.474
Diptera	39.6	313.0		42.6	60.4			343.5	27.0	6.1	26.1	858.3	1.336
Chironomidae	39.6	309.5		42.6	60.4			249.5	20.5	5.9	26.1	754.1	1.174
Chironomidae l.	33.1	273.5		38.3	51.5			151.0	20.5	5.9	24.9	598.7	0.932
Chironomidae p.	6.5	36.0		4.3	8.9			98.5			1.2	155.4	0.242
Ceratopogonidae		3.5						94.0	6.5	0.2		104.2	0.162
Mollusca					11.8							11.8	0.019
Gastropoda					11.8							11.8	0.019
Anisus coretus					1.0							1.0	0.002
Bulinus truncatus					10.8							10.8	0.017
Total	668.5	17574.4	3870.5	344.7	2786.6			24520.5	9522.2	1660.9	3270.7	63219.0	100.000

tions can be best seen from samples obtained in the same month, i.e. in May 1969 (Table I, columns 2, 3, 6, 7, and 8). At this time a complete absence of chironomids for Dodi is apparent. At Ampem, *Nilodorum* predominates amongst the chironomids while the sample from Kpandu is dominated by *Polypedilum*. The tube building larvae of *Nilodorum* are typical algal grazers. Their stomachs contained predominantly filamentous green algae (*Oedogonium*, *Spirogyra* and other unidentified genera), and blue green algae (*Oscillatoria*). *Polypedilum* is a typical detritus feeder, and no filamentous algae were found in its stomach. The other two common larval types at Kpandu, Orthocladiinae (*Cricotopus*) and *Dicrotendipes* sp. 2 were found to be periphyton grazers, but the food of *Dicrotendipes* sp. 2 contained a strong admixture of detritus. The number of *Nilodorum* larvae was low in the sample of periphytic macroinvertebrates collected from the north of the Lake at Yeji.

Among the trichopteran larvae *Amphipsyche* occurred in large numbers at Kpandu. It is a typical grazer of periphytic filamentous algae. *Ecnomus*, the food of which is more variable and consists of filamentous algae, detritus, but also of Oligochaeta and Copepoda, seems to be omnivorous in its feeding habits.

Povilla nymphs are the major component of the standing crop in which they form 90.42 % of the total (Table II). *Amphipsyche* larvae, the second by biomass, amount to 6.36 %. These are followed by chironomid larvae with 1.17 % and *Ecnomus* with 1.06 % of the total standing crop.

A decrease in number and weight of organisms can be observed towards the north of the Lake. In May 1969, when all stations were sampled the greatest abundance both in number and in standing crop was found at Ampem (south), and the lowest at Yeji (north). The standing crop was about 11 times higher at Ampem than at

TABLE III

Periphytic macroinvertebrates of flooded trees (bark), Volta Lake May 1969 (Percentage abundance and standing crop at four stations).

Station	No/m ²	No/1000 g dried bark	mg/m ²	mg/1000 g dried bark
Ampem	6879	2321	65.09	21.97
Kpandu	6246	1853	60.06	20.77
Kete Krachi	1503	472	24.42	7.68
Yeji	267	76	6.16	1.74

Yeji. From one kg of dried bark more than 30 times as many organisms were obtained in the south than at Yeji, while the total biomass was 13 times greater (Table III).

At all stations *Povilla* was the most common organism both by number and weight, and except at Kpandu it formed more than 96 % of the total standing crop. At Kpandu the proportion of *Amphipsyche* larvae (Trichoptera) was high. The percentage abundance of Diptera was very similar at all stations (Table IV), though their standing crop decreased towards the north of the Lake being lowest at Yeji.

TABLE IV
Periphytic macroinvertebrates of flooded trees (bark), Volta Lake May 1969 (Percentage abundance and standing crop at four stations).

Station	Percentage abundance by number			Percentage standing crop by weight		
	Epheme- rotera	Trichop- tera	Diptera	Epheme- rotera	Trichop- tera	Diptera
Ampem	85.73	3.13	10.82	97.30	0.74	1.75
Kpandu	60.06	30.24	8.83	79.54	17.70	0.98
Kete Krachi	81.57	7.51	10.41	98.71	0.94	0.29
Yeji	73.61	12.50	8.34	96.33	1.30	0.36

In an attempt to follow the depth distribution of periphytic organisms six crosses constructed of masonite were fixed at one metre intervals to a rope and submerged. Masonite was found to be most suitable, as it allows not only algae but also animals that burrow into the substrate, such as *Povilla* and some chironomids, to settle. After 32 day exposure above a depth of some 10 m not far off-shore, the masonite crosses were removed from the water and the number of organisms on a 50 cm² area counted. The results are summarized in Table V, giving the absolute number of organisms for each depth.

Most of the organisms decreased in number with depth, only ostracods being more common at depth than in shallow water. The slight difference in number of chironomids suggest that they found all depths within the first six m equally suitable. Turbellaria have not previously been recorded from the Volta Lake and the present species are very small.

TABLE V

Periphytic macroinvertebrates on masonite crosses exposed for 32 days (24.2. 1968—27.3. 1968) at various depths at Pawm-Pawm, Volta Lake (absolute No/50 cm²).

depth (m)	1	2	3	4	5	6
Turbellaria	16	9	12	11	1	6
Oligochaeta	26	15	12	6	9	7
Cladocera						1
Copepoda						2
Ostracoda	2		5	6	6	6
Povilla	18	21	3	9	5	3
Orthotrichia	6	2	7	2		
Chironomidae l.	4	4	4	8	6	4
Chironomidae p.	1					

DISCUSSION

The qualitative and quantitative composition of macroinvertebrates in flooded trees differs in various areas of the Volta Lake. This is best shown in the results of observations carried out in May 1969. The differences seem to be closely related to different exposure of the flooded trees to wave action.

Amphipsyche is a species which was collected from the bark of trees exposed to waves in the Kpandu area. When a piece of bark from a submerged tree is kept in still water in a dish, *Amphipsyche* is the first of the various organisms present to die. It may be that it requires a continuous supply of well oxygenated water, rather than the actual mechanical action of waves.

The chironomids *Polypedilum*, *Dicrotendipes* sp. 1, and Orthocla-diinae (*Cricotopus*) also inhabit the bark of trees in the Kpandu area, but occur in low numbers or are completely absent elsewhere. Larvae of Orthocla-diinae are well represented both in numbers and species in waters of the north temperate zone. According to BRUNDIN (1951) they require an environment rich in oxygen, and the group is particularly abundant in running water and in arctic and alpine lakes. In tropical lakes this subfamily is very rare. However, it has frequently been found in cold streams of the Kenya Highlands and Indonesian mountain streams. MACDONALD (1956) suggested that temperature is the limiting factor for many species of Orthocla-diinae. In the Black Volta River rapids Orthocla-diinae (*Cricotopus*) are common on substrates exposed to a water current of 75 cm/sec where they formed 24 % by number of the total of chironomid larvae collected (PETR, 1970). These findings, together with the present observations

that are confined to trees continuously exposed to wave action, support the idea that the oxygen concentration of the water is of great importance in determining distribution of Orthoclaadiinae in the Volta Lake and the Black Volta River.

Nilodorum is a chironomid typical of quiet bays in which it is the dominant species. The larvae need detritus for the construction of the tubes which they inhabit. Strong wave action would probably result in the destruction of their tubes. This genus would appear to tolerate much lower oxygen concentrations than other chironomids in the Lake as it is most abundant where the water is not always well oxygenated.

TABLE VI

Periphytic macroinvertebrates of flooded trees (bark), Volta Lake May 1969 (Absolute numbers of individual taxa at five stations).

Station	Kpandu	Dodi	Kete Krachi	Yeji	Ampem
Character of the station	1	2	2	2	3
Tanypodinae	0	0	0	0	1
Orthoclaadiinae (Cricotopus)	20	0	0	0	0
Nilodorum	1	0	11	3	158
Dicrotendipes sp. 1	0	0	0	0	3
Dicrotendipes sp. 2	49	0	1	0	2
Polypedilum	94	0	4	1	0
Amphipsyche	497	2	0	0	0
Ecnomus	164	2	44	9	58
Povilla	1313	189	478	53	1592
Other groups	45	7	40	6	43

Differences in the environment of flooded trees have already been stressed by MORDUKHAI-BOLTOVSKOI (1956) who classified flooded trees in man-made lakes in the U.S.S.R. into three types according to their exposure to wave action: (1) forests exposed to full wave action, (2) forests protected from waves by islands, and (3) protected forests in bays. His classification seems to apply equally well to the Volta Lake, and is used in Tables VI, VII, and VIII. Type (2) is used for the Volta Lake in an extended meaning to include localities which are not openly exposed to large waves, but also not too sheltered. Trees there are partly sheltered and protected against waves by other trees or by the configuration of the shoreline, as at Kete Krachi and Yeji.

The burrowing forms represented by *Povilla* and perhaps also by the chironomid *Polypedilum* whose larvae were often removed from the inside of the wood, predominated over the surface forms both in

TABLE VII

Periphytic macroinvertebrates of flooded trees (bark), Volta Lake May 1969 (Abundance of individual taxa by No/m² and by No/1000 g dried bark at four stations).

Station Character of the station	Abundance by No/m ²				Abundance by No/1000 g dried bark			
	Kpandu	Kete K.	Yeji	Ampem	Kpandu	Kete K.	Yeji	Ampem
	1	2	2	3	1	2	2	3
Povilla	3752	1226	197	5896	1113	385	56	1990
Amphipsyche	1420	0	0	0	421	0	0	0
Ecnomus	469	113	133	133	215	36	10	73
Chironomidae	517	61	15	671	154	19	4	226
Other groups	128	103	22	97	26	32	6	32
Total	6246	1503	267	6879	1853	472	76	2321

TABLE VIII

Periphytic macroinvertebrates of flooded trees (bark), Volta Lake May 1969 (Standing crop of individual taxa by g/m² and by mg/1000 g dried bark at four stations).

Station Character of the station	Standing crop g/m ²				Standing crop g/1000 g			
	Kpandu	Kete K.	Yeji	Ampem	Kpandu	Kete K.	Yeji	Ampem
	1	2	2	3	1	2	2	3
Povilla	55.0536	24.1026	5.9259	63.3300	16.5114	7.5800	1.6716	21.3800
Amphipsyche	11.1584	0	0	0	3.3465	0	0	0
Ecnomus	1.0903	0.2300	0.0796	0.4804	0.3270	0.0740	0.0226	0.1612
Chironomidae	0.7044	0.0526	0.0328	1.1463	0.2113	0.0165	0.0062	0.3869
Other groups	0.9585	0.0308	0.1242	0.1304	0.2705	0.0096	0.0353	0.0441
Total	69.2268	24.4160	6.1625	65.0871	20.7454	7.6801	1.7357	21.9731

number and in biomass (Tables VII and VIII). The high or low total abundance and biomass of invertebrates is determined by the high or low abundance or biomass of *Povilla*. In the Volta Lake the number and standing crop under one square metre is considerably higher than that given by LUFEROV (1963) for Rybinsk reservoir on the Volga river in the U.S.S.R. For forests exposed to full wave action (type (1) above), he gives an abundance of 4984 organisms/m², equivalent to a standing crop of 0.703 g/m², for the type (2) trees 639 org./m² (1.596 g/m²), and for the type (3) trees 735 org./m², (5.841 g/m²). The figures for the type (3) trees do not include molluscs. The low biomass in Rybinsk is attributable to the fact that the fauna consists almost exclusively of chironomids. Chironomids formed more than 99 % by number and 93 % by biomass of the total number of organisms in the type (1) trees, 84 % by number and 91 % by biomass in the type (2) trees, and 48 % and 31 % in the type (3)

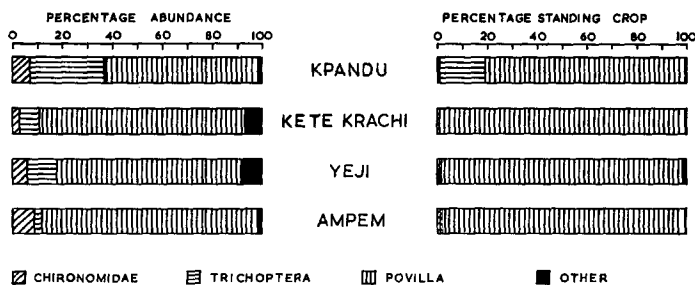


Fig. 1. Periphytic invertebrates of flooded trees in Volta Lake, May 1969.

trees. In the Volta Lake the percentage abundance of chironomids did not exceed 9%, and the percentage standing crop was less than 2% of the total (Fig. 1). The number of chironomids under m^2 was lower in Volta than it was in Rybinsk, except in trees in protected bays (trees type (1)). An average chironomid weight was calculated from LUFEROV's data, and compared with that for the Volta (Table IX). The average weight of Rybinsk chironomids increases with the decreasing exposure of trees to wave action, i.e. from type (1) to type (3). This is evidently due to the high predominance of small larvae, such as *Cricotopus ex gr. silvestris* (Orthoclaadiinae) in his type (1) trees, where these comprised 39% by number of the total. In the type (2) trees they formed only 12% of chironomids, and they were absent from type (3) trees. In the Volta Lake, in type (1) trees the chironomid larvae are on average less heavy than those from the type (3) trees. The sample for type (2) was too small to be significant. Orthoclaadiinae (*Cricotopus*) represent 12% of the total number of chironomids in type (1) trees, but they are absent from types (2) and (3). Chironomids of protected forests have the highest average weight, though this is only one third of that in Rybinsk.

The reason why the biomass and abundance of periphytic organisms were lower in Rybinsk than in the Gorkij reservoir, which was established much later on the same river as the Rybinsk reservoir, can be attributed to the fact that the trees which had been flooded for 20 years, had probably lost most of their bark, which, as observed in the Volta Lake, is much richer in fauna than the wood proper. Another factor may be the gradual decrease in nutrients in the water of new man-made lakes; this is likely to have an effect on the primary and secondary productivity of flooded trees. The abundance and biomass of invertebrates of flooded trees in Gorkij in the third and the fifth year after the dam was closed were two to three times higher than at Rybinsk.

The most apparent difference between Rybinsk, Gorkij and Volta Lake is that in the first two no large forms such as *Povilla* exist in

TABLE IX

Comparison of the abundance, standing crop and average weight of chironomids in flooded trees of the Volta Lake and Rybinsk reservoir.

Type of flooded trees	No. org. /m ²		Standing crop g/m ²		Average weight of chironomid larva (mg)	
	Volta	Rybinsk	Volta	Rybinsk	Volta	Rybinsk
1	517	4968	0.704	0.655	1.3	0.13
2	36	541	0.043	1.424	1.2	2.6
3	671	349	1.146	1.863	1.9	5.3

such large numbers, though in general the number of burrowing organisms in trees is quite substantial, and its biomass, represented by chironomid larvae, is higher than that of the tree surfaces (LUFEROV, 1965). In the Volta Lake the gradual disappearance of the softer parts of trees such as bark and soft wood, will eventually affect burrowing forms such as *Povilla*, whose number may be expected to decrease.

***Povilla adusta* Navas**

INTRODUCTION

Shortly after the trees in the Volta Lake were flooded their bark and wood were attacked by burrowing nymphs of *Povilla adusta* (Ephemeroptera). This species, not common in the original river, rapidly colonized the whole Lake, and in 1967 it was collected from all parts of the Lake (Fig. 2). During the short time of about two years *Povilla* has become the most common organism among the

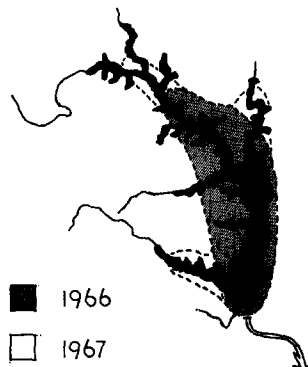


Fig. 2. Establishment of *Povilla* in Volta Lake in 1966 and 1967.

periphytic macroinvertebrates, and after chironomid larvae was also the second most important organism of the bottom fauna (PETR, 1969b). *Povilla* became an important link in the food web being a consumer of planktonic and periphytic algae and being readily utilised by many fish species as their food (PETR, 1969a). The establishment of *Povilla* has greatly contributed to the secondary production of the Volta Lake.

Some aspects of the biology of *Povilla* from natural lakes and East and Central Africa were studied by ARNDT (1938), CORBET (1958a, 1958b) and HARTLAND-ROWE (1953, 1955, 1958). No studies have been carried out in West Africa, and nothing is known on the importance and biology of *Povilla* in other African man-made lakes.

The main aim of this study was to establish the quantitative importance of *Povilla* in relation to other invertebrates in the periphyton. Some biological aspects of *Povilla* were also followed with the aim of giving an account of the biology of this insect from the first tropical African man-made lake where it has become of primary importance.

RESULTS AND DISCUSSION

Observations on eggs, nymphs and adults of *Povilla* from the Volta Lake provide information additional to our knowledge of the biology of this species from Lake Victoria and the Rift Valley Lakes.

The egg

Eggs, released by females of *Povilla* as two egg packets, were collected immediately after being laid. The number of eggs collected ranged from 900 to 2600 per female which is in agreement with the observations of HARTLAND-ROWE (1958) who recorded a range of 900—2500 eggs. A description of the packets of eggs is given by HARTLAND-ROWE. In the Volta Lake, the average length of an egg is 0.29 mm, and width 0.21 mm, based on measurements of 100 eggs.

Packets of eggs were put into aerated lake water in plastic dishes and kept initially at a temperature ranging between 27.2 and 33.1°C. On the fifth day they were transferred to the laboratory and kept in aerated dishes at temperatures between 24.6 and 26.7°C. This was about 2—6°C lower than that of their natural habitat. The first nymphs hatched from the eggs on the seventh day, and the number of eggs hatching increased from day to day. The highest number of new nymphs was observed between the eighteenth and twentieth day from laying of eggs. HARTLAND-ROWE (1958) estimated the

duration of the egg stage in the field at 11 to 12 days. The development of his nymphs, hatched under laboratory conditions in a water tank of 22—24°C, took 12 to 15 days. He found eggs in Lake Victoria only during the two weeks following an emergence of adults. The reason why no egg packets were found after two weeks may be due to the fact that as has been observed in the laboratory, the gelatinous packets of eggs, by absorbing more water, lose their cohesion and disintegrate into small parts. This disintegration of the egg packets seems to be of considerable importance, as the eggs, originally situated in the centre of the packet, become exposed and hence are provided with a better supply of oxygen. Such eggs start to hatch.

The nymph

The average length of first instar *Povilla* nymphs measured without cerci is 0.72 mm. The mandibles of the first instar nymphs are not yet visibly sclerotized. By the twenty-fifth day the nymphs have reached the second instar, have an average body length of 0.82 mm, and the mandibles are sclerotized. An attempt to keep the nymphs of the second instar alive was not successful. The first instar nymphs are positively phototactic. They were found to congregate at the side of the dish where the illumination was strongest. Nymphs were observed to swim towards the surface of the dish; after reaching the water surface they became motionless and would sink passively before starting to swim up again. The reason for this is not known. During the first instar the nymphs most probably do not feed, as they retain the vitelline cells in the mid-gut for several days after leaving the egg, as has also been observed by CORBET (1958a) for nymphs in Lake Victoria.

Larger nymphs were obtained from pieces of bark and wood. The nymphs show a tendency of sudden increases in length at regular intervals up to 6 or 7 mm length. The clusters of length data may correspond to individual instars (Fig. 3). This can be best seen in the Ampem sample, where there are seven or eight clusters between the 3 mm and 6 mm lengths, these corresponding probably to 7 or 8 instars. The nymphs of larger size do not seem to occur in such obvious clusters, and one of the reasons is that from the size of 6 mm the females are differentiated from males and have probably a different rate of growth, with ecdysis occurring at different sizes than in males. The cumulative curve in Fig. 3 does not allow any conclusions to be made on the number of instars during, and after the emergence of males, as the number of nymphs collected was too small. The adult females emerge at sizes from about 14 mm to over 22 mm length. It would be interesting to know whether nymphs of

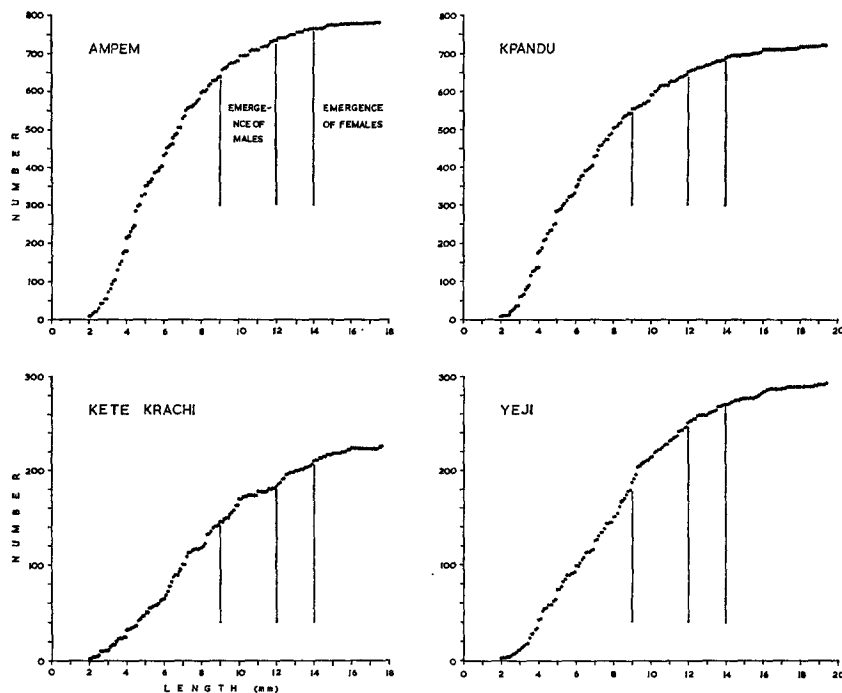


Fig. 3. Cumulative number of *Povilla* nymphs collected from flooded trees at various stations in May 1969.

14 mm length pass through the same number of instars as those 22 mm long, or whether they do not have to proceed through so many instars to be able to emerge. If the latter is true, then if one presumes that the number of instars for mayflies is close to 20 (IMMS, 1965) those nymphs emerging at the nymphal size of about 14 mm must be some five or even more instars younger than those 22 mm long.

As mentioned already, macroscopically the male nymphs can be distinguished from female nymphs from the size of 6.0 mm. Males develop much longer lateral cerci, have narrower heads and more slender bodies. Wing pads are longer and more brownish in colour than those of females of the same size. Males are on average heavier than females, up to the size of 8.0—8.9 mm. After that some females exceed the males in weight (Table X). In samples investigated the largest males were recorded in the size range 10.0—10.9 mm, which well corresponds with the size of the exuviae (Table XI). Eggs are macroscopically visible in female nymphs from the size of 11.0—11.9 mm. Only a minority of female nymphs, however, contain eggs at that time. With increasing size more females contain eggs and in the last instars only females with eggs are present. The

TABLE X

Number and weight of male and female nymphs of Povilla of different sizes, collected from the bark of flooded trees at Yeji and Dodi (Volta Lake) in May 1969.

size in mm	Yeji 15.5.1969			average weight (mg)	
	males	Number females without eggs	females with eggs	males	females without eggs
6.0— 6.9	1	19		9.0	7.1
7.0— 7.9	6	18		12.0	9.1
8.0— 8.9	5	18		15.4	13.3
9.0— 9.9	5	16		17.7	20.9
10.0—10.9	0	13			
11.0—11.9		15	1		
12.0—12.9		7	4		
13.0—13.9		6	4		
14.0—14.9		2	3		
15.0—15.9		0	1		
16.0—16.9		1	1		
17.0—17.9		0	2		
18.0—18.9			1		
19.0—19.9			0		
20.0—20.9			0		
21.0—21.9			0		
22.0—22.9			1		
Dodi 7.5. 1969					
8.0— 8.9	2	11		15.0	13.9
9.0— 9.9	1	4		19.0	20.3
10.0—10.9	1	7		22.0	28.8
11.0—11.9	0	3	0		
12.0—12.9		1	1		
13.0—13.9		1	2		
14.0—14.9		2	2		
15.0—15.9		0	2		
16.0—16.9		0	2		
17.0—17.9		0	1		

TABLE XI

Lengths of nymphal exuviae of Povilla collected from the water surface at Kete Krachi (Volta Lake) on the 22.7.1967.

Length in mm	9.0— 9.9	10.0— 10.9	11.0— 11.9	12.0— 12.9	13.0— 13.9	14.0— 14.9	15.0— 15.9
males	8	9	1				
females						2	1
Length in mm	16.0— 16.9	17.0— 17.9	18.0— 18.9	19.0— 19.9	20.0— 20.9		
males							
females	4	3	5	0	1		

first females emerge at the size of 14 mm length, which corresponds with the size of the nymphal exuviae.

The weights for individual size groups for five samples collected at different localities in May 1969 are plotted in Fig. 4. It is clear that the nymphs collected at Kpandu and Ampem in the south are heavier than those collected from other stations. Both Kpandu and Ampem have a much higher concentration of *Povilla* than the local-

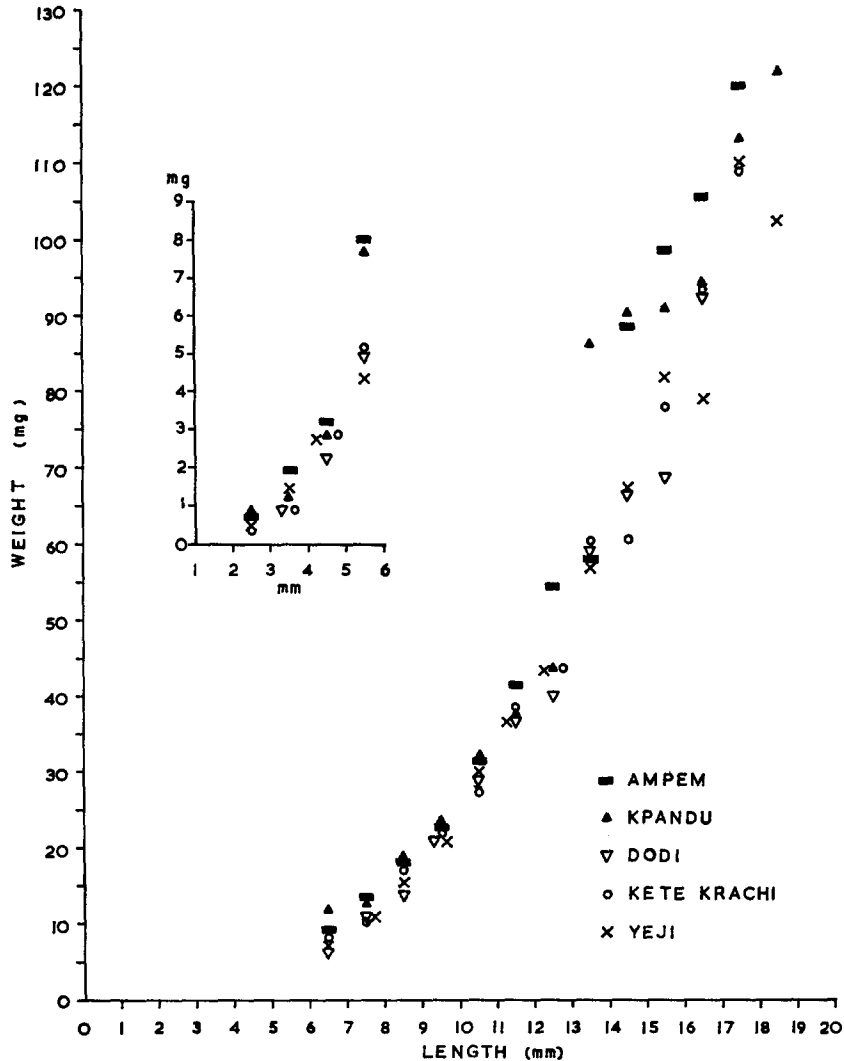


Fig. 4. Length-weight relationship of five populations of *Povilla* nymphs collected from flooded trees at various stations in May 1969.

ities in the north (c.f. Tables VII and VIII). The tree surfaces at both localities have a rich growth of periphytic algae, providing an abundant food and good shelter for the nymphs. One can assume that nymphs which are less well fed will be lighter at the same body length than those with plentiful food. If one further assumes that any one individual can only start oogenesis (or vitellogenesis) when it has reached some particular weight, then the nymphs which are less well nourished will be longer when they become sexually mature. Thus, the difference in the weight of nymphs seems to reflect a metabolic difference between the southern and northern populations of *Povilla*. It seems likely that in the denser population at Ampem, with an abundance under one square metre of bark thirty times larger than that at Yeji (c.f. Table VII), the natural loss in the overcrowded population of *Povilla* nymphs and the loss due to the predation by fish, which are most probably attracted in large numbers by the easily available highly concentrated food, will be much heavier than that of the Yeji population.

The large increase in weight of nymphs from the 12 to 14 mm length can be attributed to the rapid development of eggs in females during this period of growth. The scatter of weight of large nymphs can be attributed to variation in the number of eggs in last instar nymphs. Another probable reason for this is the uneven maturation of females. When the first females start to emerge at 14.0 mm length, some of the nymphs have not yet developed or are only starting to show macroscopically visible eggs, as can be seen from Table X for Yeji and Dodi.

The percentage of males in nymphal instars between the length of 6.0 and 10.0 mm is 25 % for the Volta Lake. At smaller sizes the sexes cannot be distinguished. This suggests that females should predominate in catches at light, as is shown later.

Analysis of the food of *Povilla* from the Volta Lake suggested that plankton is not the sole source of food, as it is in Lake Victoria (CORBET, 1958a, HARTLAND-ROWE, 1953, 1958 and KIMMINS, 1949). HARTLAND-ROWE (1953) has described the feeding mechanism of *Povilla*. A current of water is produced by the action of the six pairs of feathery gills, the water then being filtered through brushes of pinnate setae on the mandibular tusks and forelegs. The observation described below, however, show that *Povilla* is not exclusively a filter-feeder. Detritus, diatoms, green coccal algae, *Scenedesmus* and *Tetraedron* can be considered as the major food for the smaller instars, and these were found in practically all larger nymphs as well. From 4.0 mm upwards filamentous algae are regularly found in the alimentary canal of nymphs. The most common is *Oedogonium* but the blue-green algae (*Oscillatoria*) and conjugates are also fre-

quent. These observations suggest that the periphytic coatings of flooded trees can be intensively exploited as food. Algae and detritus in the diet probably originate chiefly from the periphyton, as indicated by the predominance of non-planktonic forms of diatoms, *Tetraedron* and *Scenedesmus*. Non-attached algae are loosened from the substrate, i.e. from the attached periphytic algae, by the water current produced by its gills and then filtered into the alimentary canal. This current is obviously not strong enough to break off from the substrate the attached filamentous algae. These must be actively grazed by *Povilla*. Pieces of wood, presumably originating from their burrows, are often present in their alimentary canal. It would be interesting to know whether the wood is just an accidental component of its food or whether *Povilla* has the ability to digest woody matter.

Starting from the second instar the nymphs tend to keep to their burrows during the day. At night they have been observed to creep about on the surface of flooded trees and this seems to be the time when they feed.

The adult

The emergence of adults in the Volta Lake takes place shortly after dusk. As the Volta Lake is situated from 6°15' N to 9°N there is only about half-an-hour difference in day length throughout the year. Adults start to emerge between 18.30 and 19.00 h, and the emergence extends over a period of about one h. Emergence of the males precedes that of the females by about five to ten min. The emergence of adults was directly observed on the lake surface in the vicinity of flooded trees. Nymphs ascend to the water surface using their gills for swimming. Within a few seconds of a nymph's approach to the surface, the dorsal cuticle splits and the subimago immediately flies up into the air. Many of the nymphs are eaten by fish during their ascent to the water surface; many also fail to fly straight out into the air and fall back onto the water surface. Once wet, they usually do not succeed in getting into the air again.

The emerging adults of *Povilla* were collected from the vicinity of boat lights to which they were attracted. The boat was anchored between, or close to submerged trees, i.e. in the environment from which *Povilla* emerges. The distance from the place of emergence to lights on the boat was in most instances only a few metres. Therefore one could expect the two sexes to be caught in proportion to their frequency of occurrence in spite of the probability that the two sexes are not attracted equally to light. It was found that females always outnumbered males.

TJØNNELAND (1960) found for Lake Victoria at Jinja that 76 % of

adults attracted to light are males. He used a mercury vapour light trap situated about one metre above the ground, and some 150 m from the nearest part of the lake shore. He suggested that as the eyes of the males of *Povilla* differ considerably from those of the females (NEEDHAM, TRAVER & HSU, 1935) the two sexes are not attracted equally to the light. This may be true when trapping at a light source situated a considerable distance from the actual place of emergence. In May 1968, during a short visit to Jinja nymphs of *Povilla* were collected from submerged trees and from dead parts of papyrus stems. From the 36 nymphs of 6 mm or larger, which were collected, only two were males. The ratio between the males and females was thus 1 : 17. Corresponding figures for the Volta Lake are 1 : 11 at Dodi ($n=43$), and 1 : 8 at Yeji ($n = 150$). Since adult males predominated in light catches at Jinja, but the female nymphs are more numerous in flooded trees and papyrus, one can conclude that the light trap catches on land were selective for males. This was proved to be true also for the Volta. At Kpandu on one occasion a hurricane lamp was hung in front of a white canvas attached to the wall of a fisherman's hut, about 50 m from the shore line. Males comprised more than 90 % of this catch. This experiment was not repeated, but it suggests that in the Volta, as on Lake Victoria, a light source situated on land at some distance from the shore, will have a selective effect and attract more male than female *Povilla*.

Adults usually live less than one hour. During three years of observations only very few living adults were found after 20.00 hrs.

The pattern of emergence of *Povilla* for three years of irregular observations suggests that *Povilla* emerges from the Volta Lake throughout the year at all stations without any particular periodicity. All records of *Povilla* emergence relative to the moon phase have been plotted for individual stations and in total (Fig. 5). The absence of a lunar emergence rhythm is in contrast with a lunar rhythm of emergence shown in Lake Victoria (CORBET, 1958b, HARTLAND-ROWE, 1955, 1958 and TJØNNELAND, 1960). Available information from other water bodies of Eastern and Central Africa summarized by HARTLAND-ROWE (1958) however suggests that in Lake Albert, Edward, Tanganyika, Kivu, and in other localities the emergence of *Povilla* is not associated with a lunar cycle.

Several factors greatly interfered with the sampling of emerging adults. The research vessel to the lights of which the insects were attracted, was not always anchored at the same place. Sometimes the offshore distance was quite considerable so that the emerging adults had to fly long distance to get from the place of emergence to the light. Strong winds blowing during the emergence also interfered with catches.

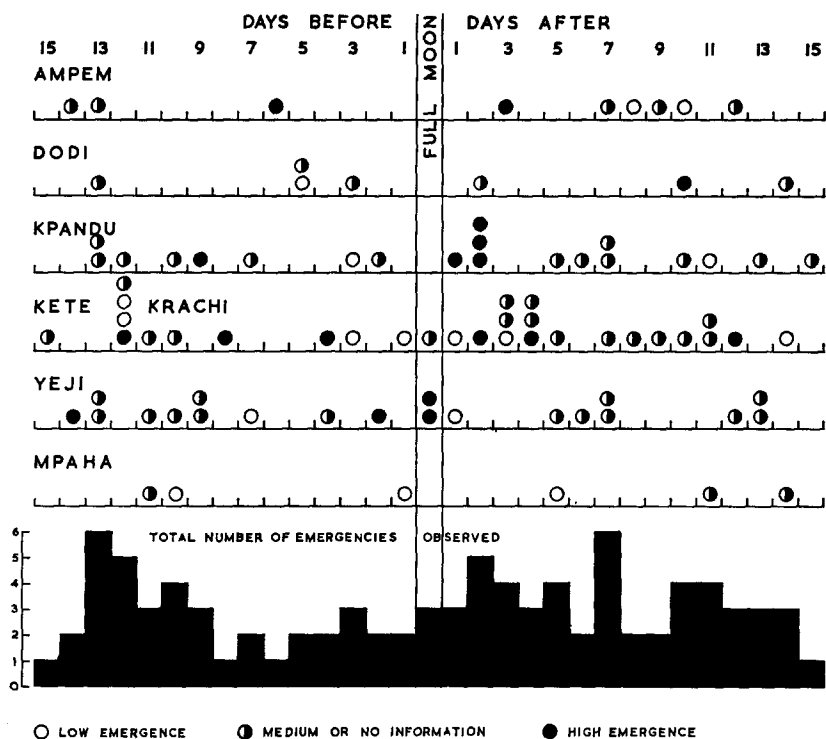


Fig. 5. Emergence of *Povilla* for individual stations, and for the total Volta Lake, 1966—1968.

During one cruise when the meteorological conditions could be considered as favoring *Povilla* emergence, the following differences in emergence at different stations on the Lake were observed: on 14.i.1967, i.e. 12 days before the full moon, a weak emergence of *Povilla* was recorded at Kete Krachi. The boat was anchored at the ferry with only a few flooded trees in the immediate vicinity. Three days later, i.e. 9 days before the full moon the boat was anchored at the other bank, where trees were abundant. At that place the *Povilla* emergence was high. Strong emergences were recorded on the 12 and 18.i.1967, at Kpandu and on 16.i.1967 at Yeji. Thus, at all stations mentioned a strong emergence was recorded between the eighth and fourteenth day before the full moon. In the following month at Kpandu and Kete Krachi on the eighth and ninth day before the full moon there were strong emergences; at Yeji, however, on the seventh day before the full moon the emergence was very low, though the meteorological conditions were favourable. On 18.i.1968 three days after full moon, a very strong emergence of *Povilla* was

observed at Kpandu, just as had occurred two and one day previously at Kete Krachi and Yeji.

From what has been said above and from Fig. 5 it can be concluded that the emergence of *Povilla* in the Volta Lake has a continuous pattern which is independent of the moon phase. A strong emergence is probably determined by the density of flooded trees, i.e. by the availability of a suitable habitat for burrowing nymphs in the near vicinity of the anchoring place.

SUMMARY

The species composition of periphytic macroinvertebrates on and in flooded trees differs at different localities on the Volta Lake. The main differences concern chironomid and trichopteran larvae. The reasons for this lie in the different exposure of trees to wave action, in the availability of soft wood and bark as a substrate, and in the distance of trees off-shore. All these factors determine the intensity of growth of the periphytic algae. The growth of the periphytic fauna will also be influenced by the density of phytoplankton on which it feeds. Other factors, such as oxygen concentration and the turbidity of the water, are also likely to affect the productivity of the whole community.

The abundance of *Povilla* nymphs, the most common organism in trees, seems to depend on the type of the substrate. The bark of trees is exploited more than the wood, and trees with harder wood are less attacked than those with soft wood. Macroscopically, the male nymphs can be distinguished from female nymphs from a length of 6.0 mm, and they start to emerge when 9.0 mm long. Females emerge from 14.0 mm length. Nymphs tend to be heavier in dense populations. The difference in the weight of nymphs may be due to differences in availability of food.

Nymphs of *Povilla* were found to feed both on solitary and attached periphytic algae, together with detritus and planktonic algae. Because of the great abundance of *Povilla* the nymphs of this species are of great importance in the conversion of algae into animal protein, being themselves heavily exploited by fish.

No lunar periodicity, such as occurs on Lake Victoria, was found, and *Povilla* in the Volta Lake seems to emerge continuously.

ACKNOWLEDGEMENTS

I wish to express my thanks to Professor D. W. EWER and Dr. M. EDMUNDS for valuable criticism of the manuscript. For much help in

the field and in the laboratory I offer my thanks to Mr. H. O. ANKRAH and Mr. OSEI-FRIMPONG. Part of this work has been carried out when the Volta Basin Research Project became a member organization of the Volta Lake Research Project.

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