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Population Changes in Aquatic Invertebrates Living on Two Water Plants in a Tropical Man-made Lake

by

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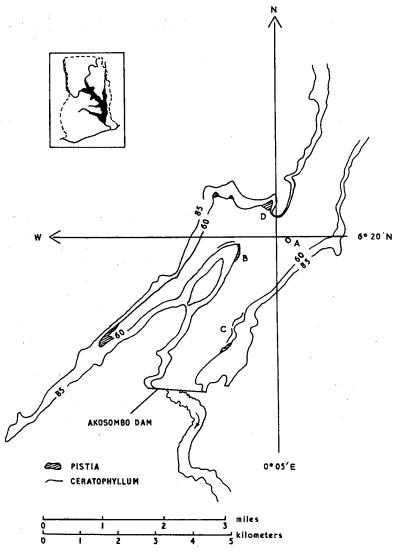
INTRODUCTION

Two aquatic weeds, Pistia stratiotes L. and Ceratophyllum demersum L. have regularly been found for a certain period of each year in various parts of the Volta Lake in Ghana since its formation. Their abundance has never reached a dangerous level as happened some years ago in Lake Kariba in Rhodesia, where the water fern Salvinia auriculata Aubl. showed explosive growth. Both species, the most abundant aquatic plants of the Lake, have become important habitats for many aquatic animals, mainly invertebrates; these serve as an important source of food for fish while some of them are vectors of parasitic and virus diseases.

The present study compares the qualitative and quantitative structure of the invertebrate community of *Pistia* and *Ceratophyllum*, and its changes over a ten months period in 1965 in the Akosombo area (see map). These changes have been studied in relation to the dry and rainy seasons and the rise in water level of the Volta Lake.

DESCRIPTION OF THE LOCALITY AND METHODS

Material was collected monthly at several places in the Gorge region of the Volta Lake (see map) between February and November 1965, i.e. from the tenth to the nineteenth month after the dam was closed. The Akosombo gorge area is characterized by steep sides which drop abruptly to the river bed, and by its relatively great depth which reached a maximum of 55 m in 1965. It has but few shallow bays and thus provides poor conditions for the spread of aquatic weeds. The Gorge region was partly cleared of trees before the Lake was formed so that the number of dead shrubs and trees



Maximal extent of *Ceratophyllum* and *Pistia* in June-August 1965 in the Gorge region of the Volta Lake, A-D, regular sampling stations. Outer contour shows calculated maximal extent of flooded area after filling of Lake is completed. The insert shows the Volta Lake in relation to Ghana.

flooded by the Lake and partially emerging above the surface is relatively small. In 1965 the dead, partly flooded vegetation formed only a narrow strip at the shores, where, together with floating logs, it acted to a certain degree as a breakwater against the action of waves. The small littoral area available was a possible reason why *Pistia* and *Ceratophyllum* did not develop more extensively, as they did in some other areas of the Lake. Patches of several square meters mostly corresponded with partly emerging trees and bush or appeared between floating logs. In one sheltered bay (area D on map) three miles north-west from the dam, *Pistia* formed a dense carpet several acres in surface area during a period of a few months, but this disappeared later with the rise of the water level and with stronger winds and wave action. *Pistia* was collected mostly at B, but at one occasion at C.

During the period of observations it was not possible to keep to the same sampling locality. The wind and waves often shifted *Pistia* from one place to another or simply blew it offshore. Changes in the water level also interfered with sampling. During the rise in water level over the flood season *Ceratophyllum* rooted to the bottom was collected further and further off-shore as the Lake increased in width.

Ceratophyllum was also found freely floating off-shore for a short period of three months (February to April). It was collected from an isolated tree partly emerging in the middle of the Lake (see map, A), where the weed was caught between twigs. Near the shore it typically formed patches of 10 to 20 m²; more rarely, and only during peak growth strips of several hundred meters in length and 5 to 10 m width were formed. Samples were mostly collected at the eastern shore (see map, C).

For sampling Pistia and Ceratophyllum a simple method was used. A plastic bucket was pushed into the water under a mat of Pistia and lifted out with the plants filling the bucket's opening, which was 531 cm². For sampling Ceratophyllum a wire frame of the same size was used; the plants were lifted out of the water framed by this frame and immediately placed into a bucket. Some loss of animals when the plant was lifted could not be avoided. Ceratophyllum rooted to the substrate usually broke when lifted so that on most occasions only upper part was collected. This prevented calculation from the results obtained of the abundance and standing crop (biomass) under 1 m² of the water surface.

The plants were transported into a laboratory on the shore of the Lake and all animals were immediately removed while still alive. The smallest animals collected included the larger Cladocera, Copepoda and Ostracoda.

The plants were then drained on a sieve of 0.4 mm mesh size, and any remaining animals collected. The plants were weighed fresh, and then placed in an electric oven and dried for 24 hours at 85°C, to obtain their dry weight. Animals were fixed in 4% formaldehyde solution.

The collection of animals, which demanded a great deal of time, made it impossible to examine more than one sample at each time. The statistical accuracy of the sampling method could not therefore be checked.

Animals were identified as far as possible and grouped into species, genera or higher taxonomic categories. In each group the number was counted and the weight measured on a torsion balance. The standing crop (biomass) determined from fixed material gives average results a few percent higher than those for living organisms (BORODIČ, 1961). The abundance of animals was expressed as number of animals in 1000 g of the dry weight of the plants and in grams for 1 m² of Pistia. From July the abundance and the standing crop of animals in Pistia was also calculated for the dry weight of 1000 g of Pistia roots, these being the areas actually inhabited by aquatic animals.

No attempt was made to determine the surface area of leaves and roots. Dahl (1948) has stated that the complexities of growth forms in aquatic vegetation make measurements and calculation of 'specific surface' areas of plants so difficult that the errors introduced invalidate the results.

CERATOPHYLLUM DEMERSUM

This plant, which is completely submerged and mainly occurs rooted to the substrate or attached to trees, showed between February and October 1965 distinct vegetational changes, encouraged chiefly by the rise in water level.

In February strong harmattan winds along the North-South axis of the Lake caused large waves, which prevented the enlargement of patches of this weed. Some of the Ceratophyllum plants were even uprooted and driven off-shore, where they were collected during February, March and April. Up to May only a minimal growth of Ceratophyllum was observed: this plant remained restricted to its places of origin and often disappeared from the surface. In May it was found down to 2.5 m depth, and only a few plants reached the water surface. When lifted, they were mostly covered by silt and Aufwuchs. The weight of this might well be one reason why this plant was no longer able to reach the surface. Some of the plants at that time developed flower buds. Bottom sampling experiments in-

dicated that Ceratophyllum formed wide underwater meadows, which were observed at localities B and C. In May and the following months Ceratophyllum was absent from the off-shore areas of the Gorge region.

In the second half of June with the beginning of the rainy season the water level of the Lake rose 60 cm above that for the previous month. The water stratification was disturbed and the water temperature dropped. The inflow of flood water and the subsequent mixing brought up sediments from the depth which resulted in an increase of water turbidity and in a decrease in the transparency, both especially pronounced in July.

Ceratophyllum responded to these changes by vigorous growth and by expanding towards the water surface. Though the water level was rapidly rising Ceratophyllum was able to keep pace with the increase of the water level and reached the water surface in many places. At locality C strips of 50 to 150 m in length and 5 to 10 m wide established themselves at the shore.

In July the growth of Ceratophyllum continued with the weed reaching the surface from a depth of 4 to 5 m. The rise in water level flooding the shores resulted in the separation of Ceratophyllum from the shore by a strip of water from 50 to 200 m wide. July and August showed and optimal growth of the weed and its maximal distribution. In August the strips of this plant became interrupted by patches of free water and at the end of this month Ceratophyllum was found in some places towards the shore, being most probably in many cases uprooted from the bottom further out by waves. Ceratophyllum continued to grow fast throughout this month, as could be seen from the abundant new growth.

In October only small patches of Ceratophyllum were found at the water surface. A bottom sampler brought up the weed from 8 to 10 m depth which corresponds roughly to the initial position in which the weed was found before the Lake started to rise. The Ceratophyllum had evidently ceased its growth and was being increasingly covered by the still rising waters. At a depth of around 10 m it was found silted over, but at the surface new growth was found. On the 23rd November, after the stabilization of the Lake level, no Ceratophyllum was found at the surface. The bottom sampler brought up the weed from 2 m and deeper.

CHANGES IN POPULATION OF AQUATIC INVERTEBRATES LIVING ON INSHORE CERATOPHYLLUM

Fig. 1 shows the quantitative pattern of the total animal population of the inshore *Ceratophyllum* for the whole observation period.

If the method of sampling can be considered reliable, it appears that the quantitative changes in the biomass of animals in *Cerato-phyllum* are closely related to the following periods: resting (February to May), expansive growth (June to August), and again the resting stage (October).

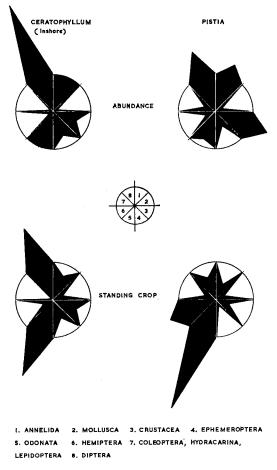


Fig. 1 Abundance and standing crop (biomass) of invertebrates on inshore *Ceratophyllum* and *Pistia* expressed as percentages by number and by weight for the whole observation period. Radius of circles represents 15 per cent of the total animal population.

Before the floods (February to May) the number and weight of animals on the *Ceratophyllum* continuously increased (Fig. 2). The weed, heavily silted and covered by periphyton, provided a stable habitat with an abundance of feeding opportunities for grazing and

filter - feeding animals such as chironomid larvae and oligochaetes, crustaceans (predominantly Conchostraca), and for zygopteran

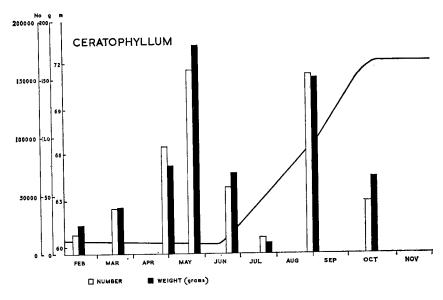


Fig. 2 Changes in population of aquatic invertebrates on the inshore *Ceratophyllum*, expressed as number and weight of animals per 1000 g dry weight of the plants. The curve in this and subsequent figures shows the rise in water level.

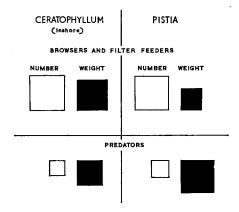


Fig. 3 Structure of invertebrate populations of inshore Ceratophyllum and Pistia according to their feeding habits. Browsers and filter-feeders: Annelida, Mollusca, Crustacea, Ephemeroptera, coleopteran adults (Elminthinae, Hydrophilidae), Hemiptera (Corixidae), Culicinae, Chironomidae, Ceratopogonidae, Stratiomyidae. Predators: Hydracarina, Odonata, Hemiptera (other than Corixidae), coleopteran larvae, coleopteran adults (Dytiscidae).

nymphs (Odonata) preying on other small animals (Fig. 3). It should be stressed here that apart from a single larva of Pyralididae (Lepidoptera), on neither *Ceratophyllum* nor *Pistia* were animals found which fed on the plants themselves.

Table I shows changes in the two most important groups of animals on *Ceratophyllum*, namely chironomid larvae and zygopteran nymphs, both groups being dominated by a single species on this plant.

Table I

Changes in abundance, standing crop (in milligrams) and the mean weight of
Chironomidae and Zygoptera on inshore Ceratophyllum

C	hironomida	.e		Zygoptera	
No.	Wt.	A	No.	Wt.	A
118	80.5	0.68	56	248.5	4.44
665	621.0	0.94	4	29.6	7.37
295	206.4	0.70	366	316.9	0.86
1260	975.0	0.77	146	740.5	5.07
		1.02	60	273.5	4.56
		0.41	8	14.8	1.85
			79	316.0	4.00
251	75 . 5	0.30	433	1089.0	2.52
	No. 118 665 295 1260 858 65 65	No. Wt. 118 80.5 665 621.0 295 206.4 1260 975.0 858 875.0 65 26.5 65 28.2	No. Wt. A 118 80.5 0.68 665 621.0 0.94 295 206.4 0.70 1260 975.0 0.77 858 875.0 1.02 65 26.5 0.41 65 28.2 0.43	No. Wt. A No. 118 80.5 0.68 56 665 621.0 0.94 4 295 206.4 0.70 366 1260 975.0 0.77 146 858 875.0 1.02 60 65 26.5 0.41 8 65 28.2 0.43 79	No. Wt. A No. Wt. 118 80.5 0.68 56 248.5 665 621.0 0.94 4 29.6 295 206.4 0.70 366 316.9 1260 975.0 0.77 146 740.5 858 875.0 1.02 60 273.5 65 26.5 0.41 8 14.8 65 28.2 0.43 79 316.0

The mean weight (A) for each group was calculated for each month.

An increase indicates that larvae of older instars are present, though not always predominant. For the Chironomidae, the higher A for March reflects the appearance of last larval instars. This is confirmed by the presence of a great number of chironomid pupae in the sample. A second peak occurs in June. No sample was obtained for September but the values for August and October suggest that there may have been a third major emergence in the interim. This may indicate that a period of two to three months is necessary for Chironomus to grow from an egg to an adult. Of these more than 90% are Chironomus (Nilodorum) fractilobus KIEFFER.

In the Zygoptera, more than 90% were nymphs of *Pseudagrion* sp., the striking drop between March and April clearly reflects the establishment of a new generation in April. In the following two months older instars predominated, as also in February and March. Another generation clearly starts in July. As with the chironomids there was probably another emergence in September.

Following the onset of rains and the subsequent rise in water

level in June and July, Ceratophyllum responded by the onset of active growth, while the number and the biomass of animals decreased. In these two months the plant surfaces greatly increased and could not immediately be colonized by animals, as can be seen from the low July values. From July young instars of chironomids predominated and also among Zygoptera more young nymphs were present. The predominance of a young population of these two important groups was observed up to the disappearance of the plants in November. This can be followed also from Fig. 2 where the changes in number and weight during the year strongly reflect the sum of the changes of these two groups.

A rapid increase in number and standing crop in August is also seen in other groups of both permanent and temporary fauna: Oligochaeta, Crustacea, Ephemeroptera, and Hemiptera. Oligochaetes found the fresh growth of Ceratophyllum in August extremely suitable as habitats and reached maximum values for the whole period of observation both by number and weight at this time. Crustacea, completely absent in July, appeared again in August, represented mainly by Ostracoda. Conchostraca, most abundant in April and May, were much less common. The greatest expansion of ephemeropteran nymphs occurred in August, with very young nymphs predominating both by number and by weight in the total of animals in this months. In October older instars increased in abundance but the total number sharply decreased.

Changes in population of aquatic invertebrates living on offshore Ceratophyllum

The off-shore Ceratophyllum was observed during a short period of three months, from February to April 1965, after which it disap-

Table II

Comparison of the abundance and standing crop of the inshore and off-shore

Ceratophyllum invertebrates

month		February	March	April
inshore	No.	16502	39020	92156
Ceratophyllum	Wt.	34.07	40.27	75.81
off-shore	No.	12095	6891	6234
Ceratophyllum	Wt.	7.61	5.93	5.16

No. = number, Wt. = weight in grams, in 1000 grams of the dry matter of Ceratophyllum

peared. The number of animals on the off-shore Ceratophyllum never reached even the lowest values of the inshore Ceratophyllum animal population (Table II). While on the inshore plants the fauna increased from February to April both by number and weight, the trend on the off-shore plants was just the opposite.

In April the abundance and the biomass of animals in the inshore weed was about 15 times higher than that of the off-shore plants. When expressed as a percentage for the total of three months, in the off-shore weeds ephemeropteran nymphs, oligochaetes and chironomid larvae were predominant (Fig. 4), while on the inshore weed the most abundant were chironomid larvae, odonatan nymphs and Crustacea, mainly Conchostraca. The trend of changes in each group of animals in both habitats was very similar (Table III). Thus,

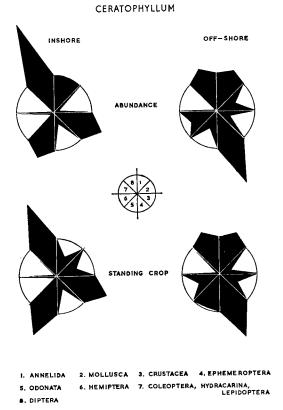


Fig. 4 Abundance and standing crop (biomass) of invertebrates of inshore and off-shore *Ceratophyllum*, expressed as percentages by number and by weight for February, March and April. Radius of circles represents 15 per cent of the three months population.

the increase in Oligochaeta on the inshore Ceratophyllum corresponded to a similar increase on the off-shore weed. Molluscs decreased both off- and inshore. Crustacea, however, with a great predominance of Conchostraca, increased greatly inshore in April, but they disappeared at the same time from the off-shore Ceratophyllum. Zygopteran nymphs and chironomid larvae showed a similar trend in both habitats, with the maximum in March. Among groups of lesser abundance, such as Hydracarina, Hemiptera and Coleoptera, only the Hemiptera seemed to be of greater importance on the off-shore Ceratophyllum, where they formed 11.7% by number in the three months total. The aquatic Hemiptera are good fliers and as such they travel considerable distances. They are not so confined to the substrate as are the other groups.

Table III

Comparison of invertebrates on the off-shore and inshore Ceratophyllum for the period February to April 1965. Numbers and weights showed as percentages of their respective totals

month		Febr	uary	Mai	ch	Ap	ril	Tot	tal
animals		No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
	IN	1.5	0.3	10.4	9,5	18.7	11.3	14.6	8.3
Oligochaeta	OFF	4.3	3.1	18.6	20.6	42.5	37.0	16.7	18.0
Mollusca	IN	13.3	31.5	0.7	0.4	0.7	1.7	2.1	8.1
	OFF	13.4	10.3	0.8	0.3	4.7	1.7	7.8	4.8
	IN	_		2.9	6.2	30.9	39.4	20.0	21.4
Crustacea	OFF	4.4	3.0	13.6	21.8		-	5.8	8.1
	IN		_	_	_	0.2	0.03	0.2	∠0.1
Hydracarina	OFF	_	_				_		
Ephemerop-	IN	10.2	5.3	10.6	14.8	0.6	0.4	4.3	5.5
tera	OFF	59.8	59. 8	5.7	2.8	2.8	6.3	30.9	27.0
	IN	21.2	45.6	0.5	2.9	26.7	28.2	19.2	25.2
Odonata	OFF	1.6	10.3	0.8	0.5	26.4	35.9	7.5	14.3
	IN	6.4	1.3	0.8	1.4			0.9	0.6
Hemiptera	OFF	11.4	8.1	18.6	17.5	4.7	1.4	11.7	9.2
	IN	0.7	0.5	1.0	0.7	0.3	0.3	0.5	0.5
Coleoptera	OFF	0.4	1.6	0.8	0.4	_	_	0.4	0.8
	IN	46.6	15.5	73.1	64.1	21.9	18.7	38.2	30.4
Diptera	OFF	4.7	3.8	41.1	36.1	18.9	17.7	18.3	17.8

The animal population of the off-shore Ceratophyllum was in a much more unstable habitat than that of the inshore weeds. It is not only more exposed to negative influences such as wave action and fish predation, the latter being encouraged by the usually low density

of the off-shore Ceratophyllum, but there is also the fact that the off-shore weed is not rooted and has no contact with the bottom. If an aquatic animal becomes separated in some way from its substrate there exists only a small chance that it will be able to get back again. Emerging adults will also probably search for a suitable substrate for their eggs in an in-shore habitat, where the eggs have much more chance to survive. All these factors contribute to a steady decrease in the animal population of any off-shore water-weed.

PISTIA STRATIOTES

This free floating water plant consists of a rosette of leaves covered with hydrofuge hairs extending above the water surface, and of submerged, finely divided fibrous roots reaching to a depth of 15—20 cm. *Pistia* is not rooted in the substrate and is therefore independent of it. It is often found far off-shore.

Between February and June *Pistia* was restricted to narrow strips extending for 0.5 to 2 m width from the shores at localities B and C. In May *Pistia* retreated as did *Ceratophyllum*, and the plants observed were mostly small with yellowing and drying leaves.

In July *Pistia* carpets started rapidly to increase in size and soon spread out from the original several square meters to cover an area of two to three acres (locality B). At locality D where shelter against waves and wind was provided by a multitude of logs, the *Pistia* cover formed a thick carpet 200 to 300 m long and up to 150 m wide. In several places the carpet was knitted together by *Scirpus cubensis* POEPP. & KUNTH. Both from D, B and other places the wind blew great patches of *Pistia* which were distributed throughout the whole Gorge region.

The increase in the water level in August exposed *Pistia* even more to winds and waves, and patches of it continued to be carried offshore as in the previous month. However, a large area of *Pistia* still occupied part of the bay at locality D where especially those carpets containing *Scirpus* offered resistance to the wind. At the end of August only small patches of *Pistia* were found at B and C with a prevalence of small young fresh green plants, and at D the carpet had retreated considerably.

In November *Pistia* in the Gorge region retreated still further and remained limited to only very small patches, forming strips 50—70 cm wide and 1—2 m long at the shores. The plants present were small and yellowish, with many dry leaves. In December *Pistia* completely disappeared from the Dam region.

Table IV shows the quantitative changes in biomass of *Pistia* per 1 m² during the year.

TABLE IV

The biomass of dried Pistia (g/m²)

month	leaves	roots	tota	
February		_	482.3	
March		-	380.5	
April	_		327.3	
May	_	_	301.3	
June			508.5	
July	357.8	131.8	489.6	
August	135.6	122.4	258.0	
October	103.6	65.9	169.5	
November	160.1	94.1	254.2	
December	0	0	0	

CHANGES IN POPULATION OF AQUATIC INVERTEBRATES LIVING ON PISTIA ROOTS

Fig. 1 shows the quantitative pattern of the total animal population of *Pistia* for the whole observation period.

The first period from February to May is characterized by a very low abundance and standing crop of animals on the *Pistia* (Fig. 5)

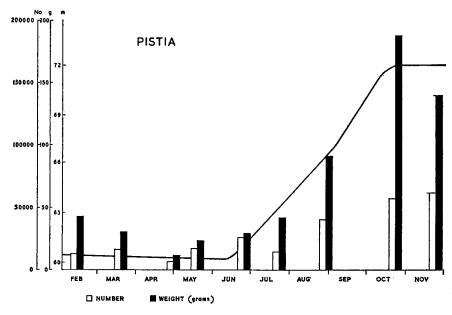


Fig. 5 Changes in population of aquatic invertebrates living on *Pistia*, expressed as number and weight of animals per 1000 g dry weight of the plants.

which maintained over this period a fairly fixed area, without any active growth or spreading.

The two main groups of animals inhabiting *Pistia* roots were dipteran larvae and odonatan nymphs (Fig. 1). In both groups a decrease by number and by weight occurred from February to April as discussed in detail below. Crustacea and Mollusca, the next most abundant groups, increased in March, but in April they were lowest. From May the total standing crop of animals increased, with fluctuating abundance.

The rise of the Lake level in July and the expansion of *Pistia* resulted in the dilution of the animal population. The abundance of animals dropped but the predominance of the heavy older instars, especially of anisopteran nymphs ensured that the standing crop continued to increase. Among the Diptera the larvae of culicids were the most abundant, being the second group by weight that month.

In August a build up in abundance of all groups occurred. Young instars of odonatan nymphs were common, with an increase in abundance to more than eight times that of the previous month, but the presence of many young larvae lowered the standing crop. Chironomid larvae predominated in this month over culicid larvae.

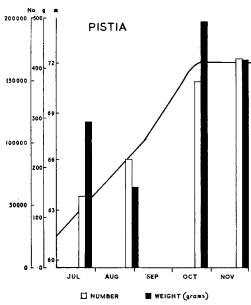


Fig. 6 Changes in population of aquatic invertebrates living on *Pistia*, expressed as number and weight of animals per 1000 g dry weight of the plant's roots.

In October the area of distribution of Pistia was greatly reduced. Bigger plants disappeared and only small plants with a low biomass remained (Table IV). This reduction of Pistia resulted in a high concentration of animals among the roots so that the animal biomass increased significantly (Fig. 6). In October the maximum weight of animals was lower than in November. In October young instars of the odonatan nymphs still predominated, which was reflected in the very low standing crop. The number of dipteran larvae decreased. Ephemeropteran nymphs, represented by Cloeon, reached in October a second peak of abundance. The predatory Hemiptera, represented mainly by the heavy Diplonychus were the leading group by weight. With the presence of younger instars of odonatan nymphs, but also numerous ostracods and oligochaetes Pistia provided a favourable feeding ground for predators. Though low in numbers, they greatly exceeded browsers and filter-feeders in Pistia in biomass not only in October but in total for the whole observation period (Fig. 3).

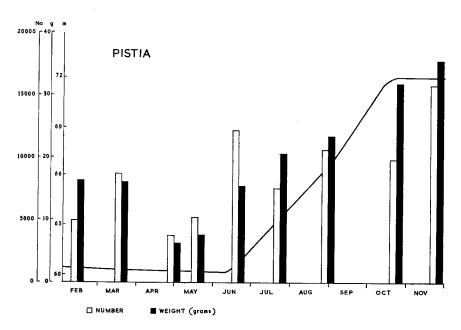


Fig. 7 Changes in population of aquatic invertebrates living on *Pistia*, expressed as number and weight of animals per 1 m².

November, with a further diminution of the *Pistia* mats, showed an increase in animal abundance, but their weight per 1000 g of dry matter showed a decrease (Fig. 5). Figure 7 however indicated that the weight of animals under 1 m² of *Pistia* in fact increased over that

for the previous month. All groups seem to have had favourable living conditions, as indicated by their abundance. Further development of the animal population was however interrupted by a complete disappearance of *Pistia* in December. In general, the animal population in *Pistia* did not seem to be very sensitive to the chemical and physical changes in water during the mixing or to the rise in water level, as will be discussed later.

CHANGES IN TAXONOMIC GROUPS

The total of animals collected from all three habitats was 12718, made up of 7920 from the inshore Ceratophyllum (CI), 484 from the off-shore Ceratophyllum (CO), and 4314 from Pistia (P). Absolute numbers are given in the following paragraphs.

Annelida (CI-1053, CO-79, P-727).

Oligochaeta. Naididae (CI-1029, CO-79, P-724).

All species recorded from both aquatic weeds obtain their food by ingesting the fine periphyton, diatoms and detritus. Naididae, which are the dominant Annelida, occur in the Lake much more frequently on aquatic plants than on the bottom. The physical structure of Naididae, forming zooids in rapid succession which readily break off when sampled, makes their quantitative estimation very difficult. Naididae are more numerous on *Pistia* roots than on *Ceratophyllum*, but by weight the ratio is just the opposite. Table V gives the percentage abundance and standing crop of Naididae for both plants.

TABLE V

Abundance and standing crop of Annelida (Percentage totals for the whole year, by number and weight)

	Ceratophyllum (inshore only)		Pis	tia
	No.	Wt.	No.	Wt.
Naididae	14.49	9.99	19.95	6,39
Enchytreidae	0.00	0.00	0.00	0.43
Hirudinea	0.18	0.33	0.02	0.01
Annelida (total)	14.67	10.32	19.97	6.83

The most common species on Ceratophyllum are Allonais paraguayensis ghanensis Hrabě and Dero digitata (MICHAELSEN). Nais variabilis PIGUET was identified from Ceratophyllum on one occasion. On Pistia Aulophorus ghanensis Hrabě predominates, with Allonais paraguayensis, Dero digitata and Branchiodrillus cleistochaeta I. O. DAHL occurring frequently in samples (HRABĚ, 1966).

The build up in the population of Naididae from February to April can be seen both in the inshore and off-shore Ceratophyllum (Fig. 8, Table III). At the beginning of rain in June Naididae were very low in abundance and biomass on Ceratophyllum and Pistia. With the great expansion of weeds in July and August the number rapidly increased and reached its maximum. The low numbers in October and November may well be brought about by predation of the Naididae by the high numbers of Hemiptera and odonatan nymphs in these months.

Enchytreidae (CI-O, CO-O, P-2).

Only two specimens were found on Pistia in June.

Hirudinea (CI-27, CO-O, P-1).

All leeches were collected before the annual rise of water level in the Lake and seemed to prefer inshore Ceratophyllum; on the offshore Ceratophyllum no leeches were found and only one specimen was found on Pistia. Batracobdella nilotica (Joh.), the most common species, formed 67.9% of the total Hirudinea found, followed by Helobdella conifera (MOORE) (17.8%) and Batracobdella tricarinata (Bl.) (14.3%).

Mollusca. Gastropoda (CI-36, CO-40, P-177).

All three species of molluscs recorded from Pistia and Ceratophyllum belong to the class Gastropoda. The most numerous was Bulinus forskali (Ehrenberg), commonly found also on other substrates from the Volta Lake, such as submerged rocks, trees and other aquatic plants.* Almost all specimens collected from both plants were young. Bulinus feed on unicellular organisms or very small soft organic particles. Older snails also feed on partly decayed vegetable material and its associated fauna.

The other two Gastropoda species found on both plants are *Anisus coretus* (BLAINVILLE) and *Ferrissia* sp. Table VI gives the percentage abundance and standing crop for Gastropoda for both plants.

On Ceratophyllum Gastropoda occurred only before floods, with their greatest abundance and biomass in February (Fig. 8). On Pistia the first maximum fell in March, when Bulinus was very numerous compared with other mollusc species. A second maximum

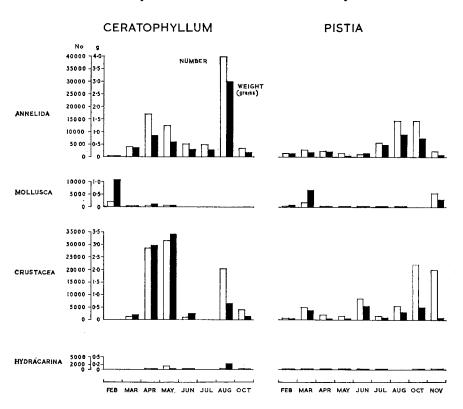
^{*}Bulinus forskali in the Volta Lake later almost disappeared from all sampling stations routinely worked and in the second half of 1966 and in 1967 was replaced by B. truncatus (AUDOUIN).

TABLE VI

Abundance and standing crop of Gastropoda (Percentage totals for the whole year, by number and weight)

	Ceratop (inshor	-	Pis	tia
	No.	Wt.	No.	Wt.
Bulinus forskali	1.40	4.07	0.81	2.69
Anisus coretus	0.37	0.13	2.07	0.76
Ferrissia sp.	0.12	0.05	0.05	0.01
Gastropoda (total)	1.89	4.25	2.93	3.46

occurred in November when Anisus, though low in biomass, was found in considerable numbers being the only gastropod present in that month. It is possible that the increased turbidity of water during the flood season was the factor that lowered the reproductive efficiency of snails so that they were unable to restore the colony. HARRISON &



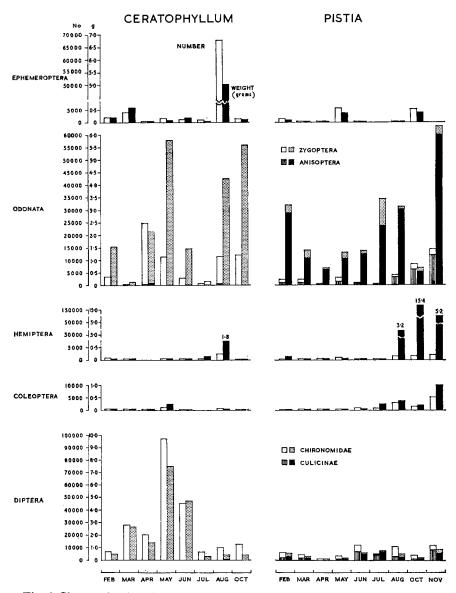


Fig. 8 Changes in abundance and standing crop of individual taxa of aquatic invertebrates on *Pistia* and on inshore *Ceratophyllum*.

FARINA (1965) tested the effects of naturally turbid water on the eggs and egg-laying behaviour of *Bulinus* (*Physopsis*) (MOREL). They found that the egg capsules of this gastropod swelled and the embryos died when laid on glass surfaces in naturally turbid water

containing a mixture of kaolin and illite or sericite or both. Eggs placed on vegetation however developed fairly normally.

Another reason for the disappearance of snails from *Ceratophyllum* during the floods may have been the lack of food. On new plants periphyton has not yet sufficiently developed.

Crustacea (CI-1123, CO-28, P-1032).

The quantitative evaluation of small Crustacea cannot be considered very reliable, as the smallest forms such as Cladocera, Copepoda and small Ostracoda are hardly visible to the naked eye. Table VII gives the percentage abundance and standing crop for Crustacea for both plants.

Table VII

Abundance and standing crop of Crustacea (Percentage totals for the whole year, by number and weight)

		phyllum re only)	Pi	stia
	No.	Wt.	No.	Wt.
Ilyocryptus sordidus	0.01	∠0.01	0.61	∠0.01
Copepoda	0.00	0.00	0.04	∠ 0.01
Ostracoda	2.39	0.37	13.35	1.38
Cyclestheria hislopi	7.39	9.08	8.26	3,99
Crustacea (total)	9.79	9.46	22.26	5.38

Cladocera (CI-1, CO-0, P-46).

Only one species of Cladocera was found, Ilyocryptus sordidus (Liévin) (Macrothricidae) with most of the specimens containing embroys retained in the brood chamber. This littoral species was also common in benthic samples in which it was found to be covered by tiny particles of detritus. Ilyocryptus was collected once from Pistia and once from Ceratophyllum, both findings being from the flood season.

Copepoda (CI-0, CO-0, P-3).

Unidentified copepods were found on *Pistia* once, but they most probably were frequent during the whole period, but as with Cladocera they were not collected due to their small size.

Ostracoda (CI-215, CO-8, P-587).

Eight species were found in the following order of abundance: Cypricercus sp. (comprising 60.9% of the total number collected), Chrissia sp. A (20.3%), Acocypris sp. (7.3%), Strandesia sp. A (5.7%), Strandesia sp. B (3.5%), Stenocypris sp. (1.6%), Chrissia sp. B (0.6%) and Cyprettinid sp. (0.1%). All species were found on both

Ceratophyllum and Pistia except one specimen of an unidentified cyprettinid which was found on Pistia.

Ostracods occurred almost three times as frequently on *Pistia* as on *Ceratophyllum* and were absent from the latter weed in June and July when the inflowing flood waters disturbed the stratification of the Lake causing repeated upwelling of deoxygenated bottom water. The animal community on *Ceratophyllum* was far more affected by these changes than was the invertebrates on *Pistia* roots. Frequently the oxygen content of the bottom layers of water was greatly reduced, even in shallow areas from which *Ceratophyllum* spread towards the surface; the surface water where *Pistia* is found was always better oxygenated (Fig. 9).

76.5% of the individuals collected were females, 13.1% were males and 16.4% juveniles. Females were ovigerous throughout the sampling period (February to November). All males that were found were of the genus *Cypricercus*.

Conchostraca CI—907, CO—20, P—396).

Only one species, Cyclestheria hislopi BAIRD., was found on both plants throughout the whole period of observation. Its food consists of algae, bacteria, Protozoa, rotifers and detritus. Its abundance by number is slightly higher on Pistia than that on Ceratophyllum. On the latter no Cyclestheria was found in July, although the species did occur on Pistia, but was only about one fifth as abundant as during the previous month. The persistance of Cyclestheria on Pistia during the floods, just as that of Gastropoda at a period when both groups were missing on Ceratophyllum, strongly suggests that, as a habitat, Pistia provides greater protection for the animals from environmental changes than does Ceratophyllum. Three or four generations of Cyclestheria were observed in most of the samples. Each month some of the largest specimens contained in their brood chamber eggs or embryos showing that this species reproduces throughout the year. Figure 8 shows the population changes of Crustacea.

Hydracarina (CI-11, CO-0, P-28).

The abundance of Hydracarina on *Pistia* was about three times as great as that on *Ceratophyllum* (Table VIII). Being carnivorous, they found an abundance of food consisting of Entomostraca, small insects and Oligochaeta. They occurred evenly throughout the whole period of observation on both plants (Fig. 8).

Ephemeroptera (CI-736, CO-162, P-208).

With the exception of one Caenis sp. collected from Ceratophyllum all ephemeropteran nymphs taken were Cloeon smaeleni GILLIES, a species feeding on periphytic diatoms. Table IX gives the percentage and standing crop for Ephemeroptera for both plants.

Table VIII

Abundance and standing crop of Hydracarina (Percentage totals for the whole year, by number and weight)

	Ceratophyllum (inshore only)		Pis	tia
	No.	Wt.	No.	Wt.
Hydracarina	0.26	0.10	0.78	0.13

Table IX

Abundance and standing crop of Ephemeroptera (Percentage totals for the whole year, by number and weight)

	Ceratophyllum (inshore only)		Pis	Pistia	
	No.	Wt.	No.	Wt.	
Cloeon smaeleni	10.04	7.50	6.52	2.56	
Caenis sp.	0.05	0.03	0.00	0.00	
Ephemeroptera (total)	10.09	7.5 3	6.52	2.56	

The population of Cloeon shows considerable fluctuations throughout the year (Fig 8). In Pistia the May peak in abundance and in standing crop is followed by extremely low numbers in June, and by the complete absence of Cloeon nymphs in July. In August young nymphs started to appear, and in October a second peak in abundance and standing crop was reached. In November no nymphs were found. This shows that Cloeon emerged from Pistia firstly between May and June, and for the second time between October and November. The quantitative changes of Cloeon in Ceratophyllum did not correspond to those on Pistia. A small peak by number and weight of Cloeon nymphs appeared in March, followed by very low values over the period April-July. The maximum of nymphs observed was in August, two months before the maximum of Cloeon nymphs on Pistia. In October the nymphs occurred again in low numbers. The changes on both plants seem to indicate quite clearly that one generation needs about 5 months to develop from egg to adult. Each of the plants under observation developed its main Cloeon population at different times but the interval between the two peaks of emergence was the same, namely 5 months. On the off-shore Ceratophyllum the peak in

Cloeon abundance was reached in February, followed by a very sharp drop in March (Table III).

Odonata(CI-1169, CO-33, P-609). Anisoptera (CI-17, CO-1, P-418).

A remarkable difference between the animal populations of *Pistia* and of *Ceratophyllum* is seen in the occurrence of a great preponderance of anisopteran nymphs on the first, and zygopteran nymphs on the second (Fig. 8). The preference of zygopteran nymphs for some species of water plants was observed by Rosine (1955) who found that *Lestes* nymphs seem to avoid *Chara* and *Polygonum*, but were common in *Potamogeton* and *Utricularia*. They evidently preferred those plants for oviposition.

All anisopteran nymphs are long – legged sprawlers preying on oligochaets, small crustaceans and larvae of aquatic insects. The following nymphs were identified: Libellulidae: Orthetrum sp., Acisoma sp., Trithemis sp., Thylomis tillarga (FABRICIUS), Brachythemis leucosticta (BURM.), and not identified nymphs of Libellulidae.

Anisopteran nymphs increased on *Pistia* by number and by weight in August in which month also young nymphs first appeared. The great predominance of young instars over the older ones was very noticeable in October, when anisopteran nymphs increased by number, but the biomass remained very low. On *Ceratophyllum* the population of anisopteran nymphs had no pronounced peaks throughout the year.

Zygoptera (CI-1152, CO-32, P-191).

Females of Zygoptera cut holes by means of their ovipositors in the stem of submerged or emergent plants, where they lay eggs. Once hatched, the nymphs keeps in its habitat which supplies it with an abundance of food. Three species were identified, with *Pseudagrion* sp. the most abundant, forming more than 90% of the total of zygopteran nymphs. *Enallagma* sp. an *Ischnura senegalensis* RAMB. were much less common, the last species being found only on *Ceratophyllum*.

The zygopteran nymphs on *Ceratophyllum* showed two pronounced peaks of abundance and of standing crop (Fig. 8). The April peak in abundance of relatively low biomass indicates the occurrence of young nymphs. The peak of standing crop was delayed by one month and appeared in May when the nymphs were large. The second maximum was in October. On *Pistia* no pronounced changes occurred. Nymphs of several instars were present at the same time in all monthly samples but one age group of nymphs usually prevailed.

Table X gives the percentage and standing crop for Odonata for both plants.

TABLE X

Abundance and standing crop of Odonata (Percentage totals for the whole year, by number and weight)

	Ceratophyllum (inshore only)		Pis	stia
	No.	Wt.	No.	Wt.
Anisoptera	0.25	0.61	8.16	42.10
Zygoptera	15.21	32.10	4.41	4.81
Odonata (total)	15.46	32.71	12.57	46.91

Hemiptera (CI-65, CO-57, P-126). Corixidae (CI-23, CO-46, P-11).

Corixidae form the only non-predatory family of Hemiptera. The members of this group obtain their food from the organic cover of the bottom, from periphyton rich in microscopical organisms, and from plant detritus. They can even suck the chlorophyll out of filamentous algae such as Spirogyra (Wesenberg-Lund, 1943). Micronecta is the common hemipteran of shallow littoral regions rich in organic deposits. The following species were found: Micronecta christiniana Lause., Micronecta scutellaris scutellaris (STÅL) and Micronecta sp. Micronecta was found on Ceratophyllum in February and March when this plant was covered by a lot of inorganic and organic detritus. In April this genus disappeared from the inshore Ceratophyllum. Micronecta was the most common hemipteran of the off-shore Ceratophyllum while this lasted. On Pistia it occurred irregularly throughout the year. Its abundance on Pistia was about twice that of Ceratophyllum.

Belostomatidae (CI-5, CO-0, P-49).

Belostomatidae (Diplonychus grassei (Poiss.), Diplonychus gr. nepoides (FABR.) as predatory Hemiptera feed on all kinds of aquatic organisms. Their abundance on Pistia followed the changes in abundance of all the aquatic animals. During the time of stabilized Lake level they formed 0.43 to 1.11% by number of the total animal population but in the flood season, from September to November, they constituted 0.95 to 3.40%. In that period the higher concentration of other invertebrates on Pistia attracted them in great numbers.

In April and May small and medium size larvae of *Diplonychus* were present. In August and October adult females and males, the latter carrying eggs on their backs, were collected. Younger instars were also present in those months when altogether four different instars were simultaneously collected from *Pistia*.

From inshore Ceratophyllum, Diplonychus was recorded only twice,

in July and in August, always in low numbers. On off-shore Ceratophyllum this species was completely absent.

Pleidae (CI-37, CO-11, P-65).

Pleidae (Plea (Paraplea) pullula STÅL) are small Hemiptera which feed mostly on small entomostracans. Their greater abundance on Pistia than on Ceratophyllum may be correlated with the greater abundance of this type of food there. This was shown by their disappearance from the off-shore Ceratophyllum in April, when entomostracans also disappeared from that habitat. No significant seasonal changes in abundance were observed on the inshore Ceratophyllum and on Pistia.

Nepidae (CI-0, CO-0, P-1).

Only one specimen of Ranatra parvipes vicina SIGN. was collected from Pistia in May.

Table XI gives the percentage and standing crop of Hemiptera for both plants. Fig. 8 shows the population changes.

Table XI

Abundance and standing crop of Hemiptera (Percentage totals for the whole year, by number and weight)

	Ceratophyllum (inshore only)		Pis	atia
	No.	Wt.	No.	Wt.
Micronecta spp.	0.81	0.29	1.55	0.31
Diplonychus spp.	0.13	2,83	1.08	17.67
Plea (Paraplea) pullula	0.81	1.10	1.45	0.71
Ranatra parvipes vicina	0.00	0.00	0.00	1.45
Hemiptera (total)	1.74	4.22	4.08	20.14

Coleoptera (CI-42, CO-2, P-205).

Among the larvae (CI—30, CO—0, P—127) dytiscids were predominant. On Ceratophyllum, Laccophilus formed 65% of the total coleopteran larvae, followed by Synchortus (25%) and a species of Hydrophilidae (10%). On Pistia the most common was Synchortus (87%), followed by Hydrovatus (8%), Hydrocanthus (3%), Canthydrus (1%) and Hydrobiinae (1%). Dytiscid larvae are all predaceous, and as such they were able to find an abundance of food on both plants. Hydrophilidae feed on periphytic algae and decaying vegetation (Pennak, 1953). No larvae were found on the off-shore Ceratophyllum.

Among the adults (CI-12, CO-2, P-78) the most common

aquatic beetles were two species of Dytiscidae, followed by the much less common Elminthinae (Dryopidae) and Hydrophilidae.

Table XII gives the percentage and standing crop of Coleoptera for both plants. Figure 8 shows the population changes.

Table XII

Abundance and standing crop of Coleoptera (Percentage totals for the whole year, by number and weight)

	Ceratophyllum (inshore only)		Pis	tia
	No.	Wt.	No.	Wt.
Coleoptera larvae	0.37	0.18	2,56	0.80
Coleoptera adults	0.10	0.27	1.70	2.89
Coleoptera (total)	0.47	0.45	4.26	3.69

Pistia contained more larvae and adults of aquatic beetles than Ceratophyllum throughout the year. An increase in abundance of coleopteran larvae, especially of Synchortus was observed on Pistia from July to November. Several instars of Synchortus larvae were always present. Rosine (1955) found that some beetles showed a preference for particular plants. For example Laccophilus was never found associated with Polygonum, whereas it was common among three other water plants.

Diptera (CI-3682, CO-83, P-1200). Nematocera. Culicinae (CI-4, CO-0, P-707).

Culicinae were almost totally absent from Ceratophyllum (Fig. 8). From Pistia eight species of Culicinae larvae were collected. The most abundant larva was Aedomyia africana N.-L. (49.5% by number) which appeared in all months except August. It was followed by Ficalbia (Mimomyia) splendens Theobald (37.4%) which was collected in all months except April, October and November. The next, in order of abundance, were Mansonia africana Theobald (8.7%), Mansonia uniformis Theobald (2.6%) Ficalbia (Mimomyia) pallida Edwards (0.7%), Culex poicilipes Theobald (0.7%), Anopheles squamosus Theobald (0.2%), Anopheles coustani Lav. (0.2%). From Ceratophyllum three specimens of Aedomyia africana were collected in August, and one Culex poicilipes in March.

The larvae and pupae of *M. africana* breathes by thrusting the specialised tip of its siphon into air cells of *Pistia* roots, a method described in detail for the Indian species by BURTON (1959). The larvae of other species find in *Pistia* both protection and food and it

is said that plant substances play an important part in stimulating the hatching of mosquito eggs in nature (ABDEL-MALEK, 1948). The majority of mosquito larvae ingest any sufficiently small particles, living or dead, floating in the water in which they dwell or lying on the surface of objects in the water. According to HOPKINS (1952) the larvae are not very selective in their food requirements.

The population showed three maxima in abundance during the observation period: the first in February and March, the second, the greatest peak, in June and July, and the third in November (Fig. 8). During the expansion of *Pistia* in June and July a large population of mosquito larvae rapidly colonized the new plants and increased in number. In both months the abundance of anisopteran nymphs on *Pistia* was very low. These nymphs destroy a certain number of mosquito larvae, as HOPKINS (1952) found in Uganda, so that the increase of mosquitoes on *Pistia* may, to some extent, to be related to the decrease in anisopteran larvae.

Aedomyia africana, Ficalbia (M.) splendens, F. (M.) pallida, Mansonia africana, M. uniformis are species which are reported by HORSFALL (1955) as typically associated with Pistia. Mansonia africana is a vector of yellow fever virus, and Anopheles coustani has been found to be naturally infested with plasmodium in the Congo.

Table XIII gives the percentage and standing crop for Culicinae larvae for both plants.

TABLE XIII

Abundance and standing crop of Culicinae (Percentage totals for the whole year, by number and weight)

	Ceratophyllum (inshore only)		Pistia	
	No.	Wt.	No.	Wt.
Culicinae larvae	0.04	0.01	13.87	5.26
Culicinae pupae	0.00	0.00	1.30	2.73
Culicinae (total)	0.04	0.01	15.17	7.99

Chironomidae (CI-3667, CO-83, P-440).

Most of the chironomid larvae on Ceratophyllum and Pistia build tubes of organic detritus and silt, lined with a silky salivary secretion, and these they stick to plant leaves and roots. The commonest larva in the Volta Lake is that of Chironomus (Nilodorum) fractilobus Kieffer, which forms more than 90% of all chironomids by number. The abundance of chironomids in Ceratophyllum is about five times

as high as that on Pistia. The biomass of chironomid larvae on Ceratophyllum is about ten times as great as that found on Pistia (Table XIV); this indicates that Pistia provides a less favourable habitat. Chironomus needs for its tubes a considerable amount of building material such as fine detritus. Pistia roots are sheltered against silting from above by the broad green leaves of this plant, and the periphyton of roots is usually poor. Ceratophyllum, extending from the bottom where the bottom sediments are often disturbed by waves, is covered by sediments and rich periphyton, especially when it is old. Closely connected with this is the supply of food, which Chironomus obtains by filtering off chiefly detritus, microscopic algae, but also Protozoa, Rotifera and occasionally Cladocera and Copepoda into the digestive apparatus (Konstantinov, 1958). The larvae on Pistia roots are also much more exposed to predation by such fish as the cichlids Pelmatochromis and Tilapia. This may partly explain why it was young larvae of chironomids which predominated on Pistia roots.

Chironomid larvae and pupae on Ceratophyllum were the first group by number and the second by weight after odonatan nymphs. The population of chironomids, like that of other temporary fauna responded sharply to changes in their habitat. An increase in number of young larvae was observed on Ceratophyllum in May, and in June just when the Lake started to rise. In August during the great expansion of this weed the total number of larvae diminished considerably (Fig. 8) the abundance by number dropping in this month to 6.3% of total animal population, compared with 46.1% in July and the maximum of 79.7% found in June. This drop corresponded with a decrease in biomass. In October chironomids increased to 29.4% by number.

On Pistia as on Ceratophyllum a decrease in chironomids was observed from February to April. In May and June chironomids increased greatly by number and weight, followed by a decrease in July. The maximum of chironomids was found in August with 17.9% of abundance. In October and November the population of chironomids was low.

The size distribution of larvae in samples throughout the year clearly shows that at least four instars of *Chironomus* (*Nilodorum*) fractilobus are present in most of the months, and that adults emerge all the year around, though not with the same intensity. The limiting factor which appears to decrease the rate is the rapid increase in the Lake level during the rains. Eggs and young larvae are quickly covered by a deep column of water which is often devoid of oxygen and this may have an inhibitory effect on their further development. More observations on this problem are necessary.

TABLE XIV

Abundance and standing crop of Chironomidae (Percentage totals for the whole year, by number and weight)

	Ceratophyllum (inshore only)		Pistia	
	No.	Wt.	No.	Wt.
Chironomidae larvae	43.80	29.10	8.87	2.40
Chironomidae pupae	1.68	1.73	0.59	0.26
Chironomidae (total)	45.48	30.83	9.46	2.66

As the larvae of African chironomids are very little known, identification was made from adults attracted to light. It is necessary to stress here that larvae of species thus obtained inhabit many other environments and are not confined only to Pistia and Ceratophyllum, some having their larval stage most probably completely dissociated from the aquatic weeds. The following identified species therefore must be regarded with caution in this respect: Chironomus (Nilodorum) fractilobus Kieffer, Chironomus imicola Kieffer, Chironomus formosipennis Kieffer, Chironomus calipterus Kieffer, Chironomus transvaalensis Kieffer, Chironomus? pulcher Wied., Chironomus sp. Cryptochironomus diceras Kieffer, Cryptochironomus sp., Dicrotendipes chloronotus Kieffer, Dicrotendipes multispinosus sp. n., Paratendipes sp., Polypedilum sp. nov., Ablabesmyia nilotica Kieffer. Ceratopogonidae (CI—11, CO—0, P—52).

Bezzia pistiae (I. & M.) was the commonest ceratopogonid larva, and prefers Pistia to Ceratophyllum (Table XV). The larval abundance was higher before the floods, with a maximum of 4.41% of total animals present on Pistia in May. In July Bezzia disappeared from both plants, but it was found again in low numbers in August. In the off-shore Ceratophyllum ceratopogonid larvae were not found. One specimen of Palpomyia (?) sp. was found in May on Ceratophyllum.

TABLE XV

Abundance and standing crop of Ceratopogonidae (Percentage totals for the whole year, by number and weight)

	Ceratophyllum (inshore only)		Pistia	
	No.	Wt.	No.	Wt.
Ceratopogonidae larvae	0.04	0.10	1.44	0.23

Brachycera. Stratiomyidae
One stratiomyid larva was found on *Pistia* in April.

Lepidoptera. Pyralididae

One specimen of Nymphula sp. larva without gills was obtained from Pistia in October.

Discussion

The invertebrate fauna of aquatic weeds provides an important source of food for certain fishes, especially for their juveniles, which moreover can utilize also the rich periphyton (Aufwuchs) represented mainly by algae and fine detritus. Thus, for example, young cichlids (Tilapia, Hemichromis, Pelmatochromis) have been observed feeding on periphyton on the roots of Pistia (Petr, 1967). Furthermore both Ceratophyllum and Pistia can harbour vectors of parasites of importance from the viewpoint of public health. With the establishment of Bulinus as a member of the lacustrine fauna of the Volta Lake the danger of bilharzia is increased (Paperna, personal communication). The mosquito Mansonia africana, a species typically associated with Pistia, is a vector of yellow fever virus.

The present study of the fauna of the aquatic weeds in the Gorge Region of the Volta Lake shows two aspects which have to be considered. The one is that the faunas associated with the two types of weed are distinct. The other is that the weeds display an annual cycle and associated with this there are changes in the abundance of the fauna. The conclusions reached can only be provisional as the weed beds being examined died away completely after the end of 1965, preventing further studies in this area, whose physical characteristics are markedly different from that of most of the margins of the Lake.

The fauna of both aquatic plants consists on the one hand of filter feeders and browsers, the dominant group, and on the other of predators. With the exception of an extremely rare pyralidid larva, there are no herbivores feeding on the plants themselves.

The two plants have very different characteristics. Ceratophyllum is typically rooted and may reach to the surface from a depth of several meters so the periphyton with the epifauna will be affected by the conditions in the water to a considerable depth. At the same time the growth form readily allows silt to deposit upon its surfaces; such silt deposits acquire a well marked stability. Furthermore, in conditions when the water is clear, there is active photosynthesis taking place beneath the water surface so that the oxygen concentration in a bed of Ceratophyllum may be higher than that in the surrounding water. Pistia, on the other hand, is feely floating with relatively short roots

so that the fauna will only be exposed to the most superficial layer of the Lake water. The roots moreover do not readily accumulate a silt deposit and it is likely that this will not be stable unless the *Pistia* is immobilised in a dense bed. Finally the oxygen concentration immediately among the roots of *Pistia* is lower than that of the surrounding water.

These two plants therefore offer very different potential habitats and this difference is reflected in their epifauna. Pistia is preferred by the larvae of Anisoptera, Culicinae, the coleopteran Synchortus, the ceratopogonid Bezzia and by the snail Anisus coretus. Ceratophyllum is preferred by the larvae of Zygoptera. Chironomidae and the beetle Laccophilus.

The factors which determine these preferences are poorly understood and probably vary from species to species. One factor is the choice of oviposition sites by the adults. Thus female Zygoptera prefer to lay their eggs in *Ceratophyllum* rather than *Pistia*. The preference of Chironomidae for *Ceratophyllum* may be directly related to the silt load of this plant, as the larvae use this material for the construction of their tubes. Among the Culicinae *Mansonia* is limited to *Pistia* by its respiratory habit of inserting its siphon into the air cell of the roots of the plant. Clearly only detailed investigations can determine the causal factors leading to these differences in distribution.

An examination of Figures 2 and 5 shows that the changes in population density during the course of the year were markedly different on the two plants. While the population density on *Pistia* changed only slightly until about two months after the rise in Lake level, that on *Ceratophyllum* showed a marked increase during April and May followed by a dramatic fall in June and July with a subsequent striking recovery in early September before a final die – away, due to a 'drowning' of the plants by the rising flood waters in late October.

Observations (BISWAS, personal communication) upon the water in the Gorge region show that during the period from March, April and May the transparency of the water steadily increased (Fig. 9) while the oxygen concentration of the surface waters and at 1 m were relatively high. Temperature rose fairly steadily and the concentration of iron in the surface water was low.

These observations suggest that during this period the water conditions in the Gorge region were relatively stable and the *Ceratophyllum*, gathering a steadily increasing load of silt as the water cleared, became an increasingly attractive habitat. In early June conditions altered abruptly. Water temperature fell and the iron content of the surface water rose, reflecting a turn-over of the water in the Gorge region. In July the instability of the water was still

more marked; oxygen concentrations in the surface water was low, turbidity and iron content high. It seems probable that the marked fall in the population of *Ceratophyllum* by late June and the further drastic impoverishment in July are, at least in part, attributable to

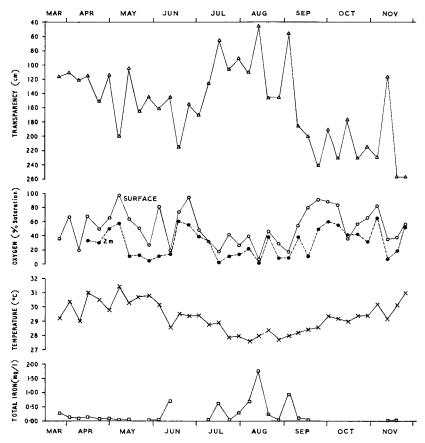


Fig. 9 Variation in transparency, oxygen content, temperature and total iron in the Gorge region of the Volta Lake.

these conditions because the greater part of the fauna would now be exposed to conditions which, especially below the immediate surface of the water, were very unfavourable.

The fauna on *Pistia* would not be markedly affected by these changes. The silting would be relatively slight and the fauna not exposed to the greatly lowered oxygen concentrations which much of the population on *Ceratophyllum* experienced.

Following the overturn in June and with the start of a rising Lake level both plants commenced a vigorous period of growth. At the

same time the water conditions improved slowly. Conditions for a fresh colonisation were established. This occurred rapidly on *Ceratophyllum*, while on *Pistia* the increasing density of plants, often bound together with *Scirpus*, presently offered conditions of greater stability in which a richer sediment could accumulate, allowing the development of a denser population.

While such a description may cover the sequence of events in broad outline and offer some partial explanation of the differences in the fluctuations of the populations on the two weeds, it is clear that other factors must also affect the population density. The first aspect which should be emphasised is the marked lag between the increase in the population of the weeds, which started in late June and that of the fauna which did not become apparent until late August. While some of this may be due to the environmental conditions described above, it is also a reflection of the fact that an increase in population, especially of insect larvae, can only follow a period of oviposition and, with the method adopted in the present survey, by a further period for growth to macroscopically visible larvae. The subsequent development of this newly recruited population will lead to an increase in biomass. This type of event is illustrated when a comparison is made of the population upon Pistia in July and August when both population numbers and standing crop approximately double. The October peak of standing crop, however, reflects a relative increase in the abundance of Diplonychus, the heaviest member of the fauna, which at that time accounted for more than 80% of the total biomass.

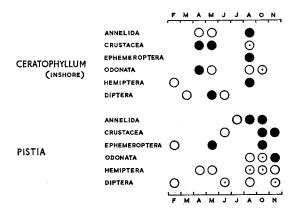


Fig. 10 Peak period of abundance of the most common invertebrate groups on Ceratophyllum and on Pistia, calculated per 1000 g dry plant matter. For each group the total for all months in which observations were made is taken as 100 and the values for individual months expressed as percentages of this total. The peak periods of abundance (30% or more) are indicated by \bigcirc , 29.9–20 by \bigcirc , 19.9–10 by \bigcirc ; less than 10% not shown.

A second aspect which requires mention is a marked difference in composition of the fauna during the two periods of population density on Ceratophyllum (Fig. 10). The abundance for example of Odonata and Annelida broadly reflects the general trend of population throughout the year. However during May Chironomidae were abundant but Ephemeroptera were relatively sparse, while in August the opposite was true: Ephemeroptera were relatively common, Chironomids scarce. It is possible that this reflects differences in the extent of silting on the plants. Early in the year Ceratophyllum carried a moderate and increasing silt load suitable for Chironomids, while later, with new growth following the mid-summer turnover and the rise in Lake level, a lesser silt load was more suitable to Cloeon. It is however important to recognise one further feature here, and that is the effect of dominant groups within the population of Cloeon. Examination of the data for Pistia shows two clear peaks in numbers

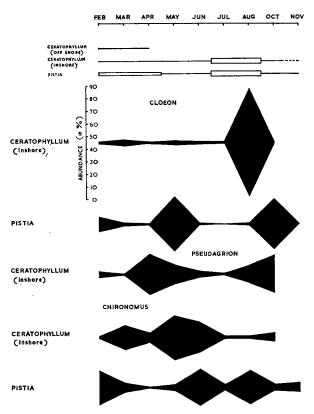


Fig. 11 Variation in abundance of Cloeon, Pseudagrion and Chironomus on inshore Ceratophyllum and Pistia.

both followed by an abrupt fall (Fig. 11). It seems reasonable to conclude that this reflects the growth and mass emergence of a dominant group within the population.

Finally it seems probable that the population density will have been affected both by the suitability and availability of prey and by the activity of the predators, but it is not possible to make any assessment upon their effect in limiting population growth.

The present study is of a preliminary character and was brought to an end by the disappearance of the weeds from the Gorge region of the Lake. Nevertheless, it has brought to light marked differences in the faunistic structure and population changes which may occur in the faunas associated with the two plants studied and indicates some of the major questions which have to be answered if the ecology of the periphyton and the invertebrate populations of these weeds is to be fully understood. Since both species contribute directly and indirectly to the fish productivity of the Volta Lake, such an understanding is essential to a comprehension of the ecosystem of the Lake.

SUMMARY

In the Gorge region of the Man-made Volta Lake in Ghana the submerged weed Ceratophyllum and the floating Pistia were collected with their associated macroscopic invertebrates between February and November 1965. These collections were studied in order to determine the difference in animal population in both plants and their changes over the year during which they experience a tropical climate with one flood season.

During the course of the study 12718 plant-associated water invertebrates were collected, from which 7920 were found on the inshore Ceratophyllum, 484 on the off-shore Ceratophyllum, and 4314 on Pistia.

A sample of each plant was arbitrarily selected from which animals were collected and their abundance and standing crop calculated.

Nearly all animals collected occurred to some extent in both plants, but some groups differed greatly in their densities. Diptera were most abundant on the inshore *Ceratophyllum* while on *Pistia* Diptera and Crustacea were most numerous, followed by Oligochaeta. As regards the standing crop, in *Ceratophyllum* Diptera and Hemiptera were equally important, but in *Pistia* Odonata were predominant.

In the off-shore Ceratophyllum Ephemeroptera were the most abundant group, followed by Diptera and Mollusca, compared with Diptera, Crustacea and Odonata for the inshore Ceratophyllum. In standing crop the habitats are dominated by the same groups respectively.

While in numerical abundance microphagous organisms predominate in both *Pistia* and *Ceratophyllum*, by weight predators, represented by large anisopteran nymphs and *Diplonychus* (Hemiptera) formed more than 70% of the total population in *Pistia*, compared to 37% in *Ceratophyllum*.

Ceratophyllum offers more adequate protection and hiding places for animals as well as a better feeding surface especially for microphagous forms than does Pistia. The habitat in both plants is greatly influenced by physical and chemical properties of water during the season of harmattan winds in February and March and during the flood season, the latter resulting in an increase in Lake level. During the floods the animal population responded by a sharp decrease both in number and weight of animals present. The possible reasons for this phenomenon are discussed in relation to other limnological changes at this time.

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