

DURATION OF THE AQUATIC STAGES OF *POVILLA ADUSTA* NAVÁS  
(EPHEMEROPTERA: POLYMITARCIDAE).

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The mayfly, *Povilla adusta* Navás, is widespread in Africa. The tubicolous larva (fig. 1) lives over a wide variety of substrata in rivers, lakes and ponds, and is a filter-feeder (Hartland-Rowe, 1953); its food consists of microscopic algae (Kimmins, 1949; Hartland-Rowe, personal communication, 1956). This insect is well known to boat-builders in East Africa because the wood-boring

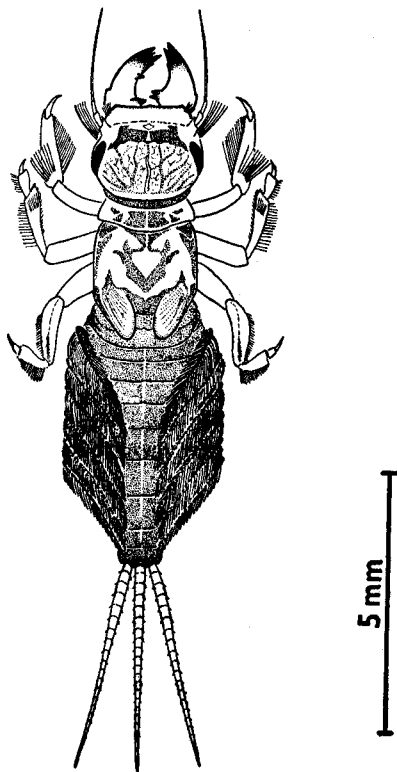


Fig. 1.—*Povilla adusta* Navás. Half-grown larva, about 6 weeks after hatching from the egg.

activities of its larvae can cause serious damage to structures beneath the water-line. In Lake Victoria, and doubtless elsewhere, both larvae and adults provide an important element in the food of several species of fish.

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A remarkable feature of the life-history is the swarming of adults which occurs every month shortly after full moon (Hartland-Rowe, 1955). It seems that most of the adults each month appear on a single night, smaller numbers emerging on two, or sometimes three, other nights just before or just after the main swarm. The regular appearance of the main swarm at Jinja ( $33^{\circ}12\frac{1}{2}'E.$ ,  $0^{\circ}25\frac{1}{2}'N.$ ) is shown in fig. 2. On the night of a swarm, adults emerge shortly after dusk. They

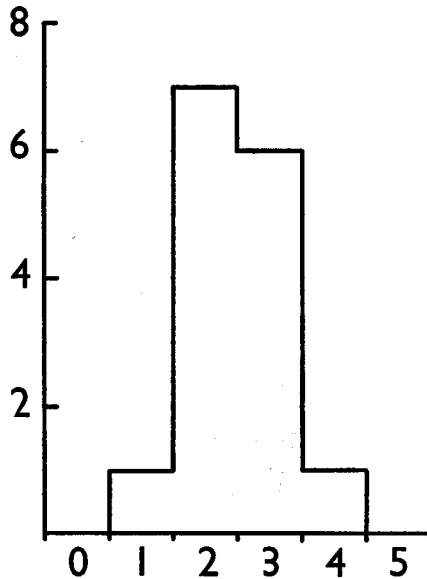


Fig. 2.—Times of main adult swarms at Jinja, in relation to full moon, from July 1954 to September 1955.

*Abscissa:* Days after full moon.

*Ordinate:* Frequency.

are rarely encountered at light before 1930 hr. (Local Mean Time) or after 2130 hr., and they only live for about an hour (Hartland-Rowe, 1955). The periodicity of emergence makes it possible to estimate growth-rate by the analysis of larval samples.

#### Methods.

Since larvae frequently inhabit holes in rock and wood, it is very difficult to collect them by conventional methods. It was therefore thought that satisfactory samples might be obtained from the stomachs of the fish, *Mormyrus kannume*

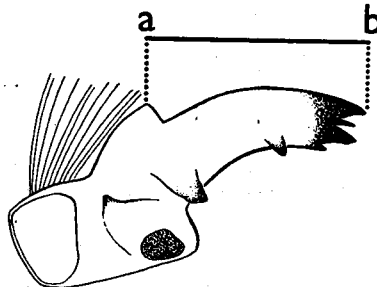


Fig. 3.—Left larval mandible in dorsal view, showing distance measured (*ab*).

Forsk., which feeds heavily on *P. adusta* larvae in certain habitats. Accordingly, larval samples were examined from the stomachs of fishes caught at regular intervals over appropriate feeding-grounds. A similar technique was used by Macdonald (1956) to determine the life-histories of certain CHIRONOMIDAE and CULICIDAE in Lake Victoria.

It would be unreasonable to claim that samples derived in this manner are representative of the whole larval population. *A priori*, there are two circumstances which may be expected to reduce the chances of fishes eating either particularly small or particularly large larvae. In the first place, fishes do not eat *P. adusta* larvae of below a certain size (ca. 3 mm. length). We may therefore expect the "availability" of larvae to show a progressive increase above this size. On the other hand, mortality during larval life will have the opposite effect, making large larvae less available than small ones. The resultant of these conflicting factors should be that fishes will tend to feed mainly on larvae of an intermediate size. This tendency for fishes to feed on medium-sized larvae was found to be a frequent feature of larval samples. Therefore, for purposes of analysis, especial attention has been given to length-frequency modes amongst smaller larvae, since these seem to result from excessive abundance of a particular age-group, rather than from selective feeding on the part of the fishes.

The fishes were caught in gill-nets, set in the evening and lifted in the morning, and situated about 50 yards from the shore of Lake Victoria, near Jinja, Uganda. The nets were set over a bottom of gravel, rock and sand, on which grew submerged plants; the depth was about 20 feet. In this habitat, *P. adusta* larvae provided the second most important item in the food of *M. kannume*, occurring

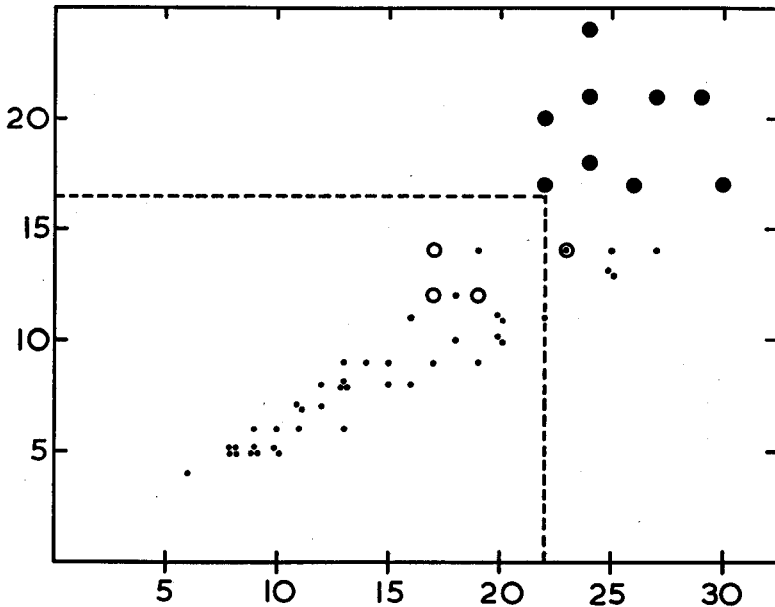


Fig. 4.—Relationship between mandible size and body length. Small dots: unsexed larvae. Empty circles: male larvae undergoing metamorphosis. Full circles: female larvae undergoing metamorphosis. The dotted line indicates the average size at which metamorphosis takes place in male and female larvae.

*Abscissa*: Mandible size, in eye-piece units.  
*Ordinate*: Body length, in mm.

in 49.6 per cent. of all fishes that contained food, and occupying more than half the volume of food in 15 per cent.

After the total length of a fish had been measured, its stomach contents were examined and all head-capsules of *P. adusta* larvae removed. These were placed flat on a microscope slide and the left mandibles were measured from a dorsal aspect, using a micrometer eye-piece scale. Only mandibles attached to heads were recorded. The distance measured is shown in fig. 3, the eye-piece units being such that  $17\frac{1}{2}$  were equivalent to 1 mm. The relationship between mandible size and body length (excluding the anal cerci) is shown in fig. 4.

There were indications that the size of larvae eaten depended to some extent on the size of fish (see fig. 5) and therefore measurements of *P. adusta* for each fish were recorded separately.

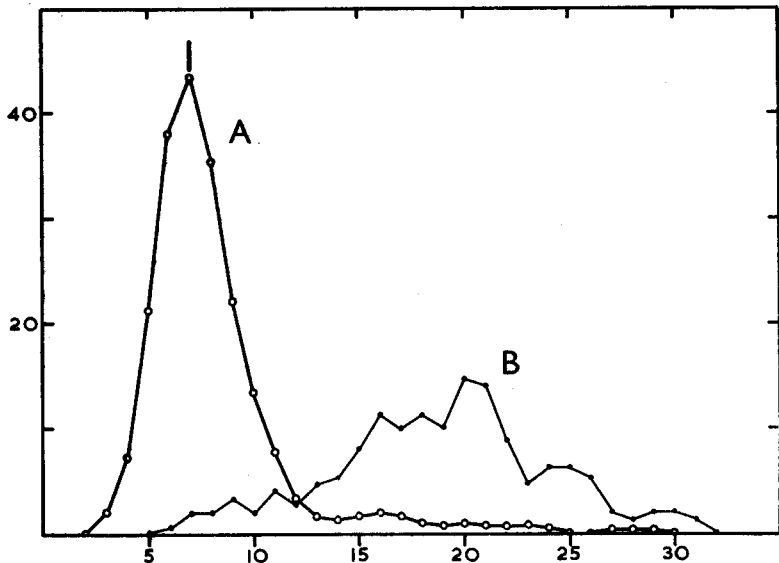


Fig. 5.—Length-frequency distributions of larvae eaten on 13th September 1954 by two fishes, 20 cm. (A) and 31 cm. (B) total length. This date was 27 days after the last swarm. A thick vertical line indicates the mode of sample A.

*Abscissa*: Mandible size, in eye-piece units.

*Ordinate*: Frequency, smoothed by a moving average of 3.

The onset of metamorphosis is usually associated with changes in the pigmentation of the wing-sheaths (Hartland-Rowe, personal communication, 1956), and this fact was used to estimate the average size at which larvae can metamorphose. It was found that males metamorphose at a smaller size (average mandible size: 19 units) than females (25.3 units). In the present study, where most of the material consisted of detached heads, it was not possible to distinguish the sexes. It has therefore been assumed that they were represented approximately equally in samples, and the mean of the male and female average mandible sizes (ca. 22 units) has been used to determine when a larval population could begin to metamorphose.

### Results.

Between 21st July and 21st October 1954, 4,403 larvae from 44 fishes were measured. The total size-range of these fishes was 19–43 cm., and was determined by the mesh of the gill-nets used for capture. In the majority of

cases, however, the length-frequency modes amongst smaller larvae were not sufficiently well-defined to be useful. In general, this was due either to the sample being too small, or else to the fish having fed mainly on large larvae; the latter circumstance was common in the case of fishes more than 30 cm. long. Accordingly eight samples, comprising a total of 993 larvae, were selected for consideration. These samples stood apart from the rest in having well-defined

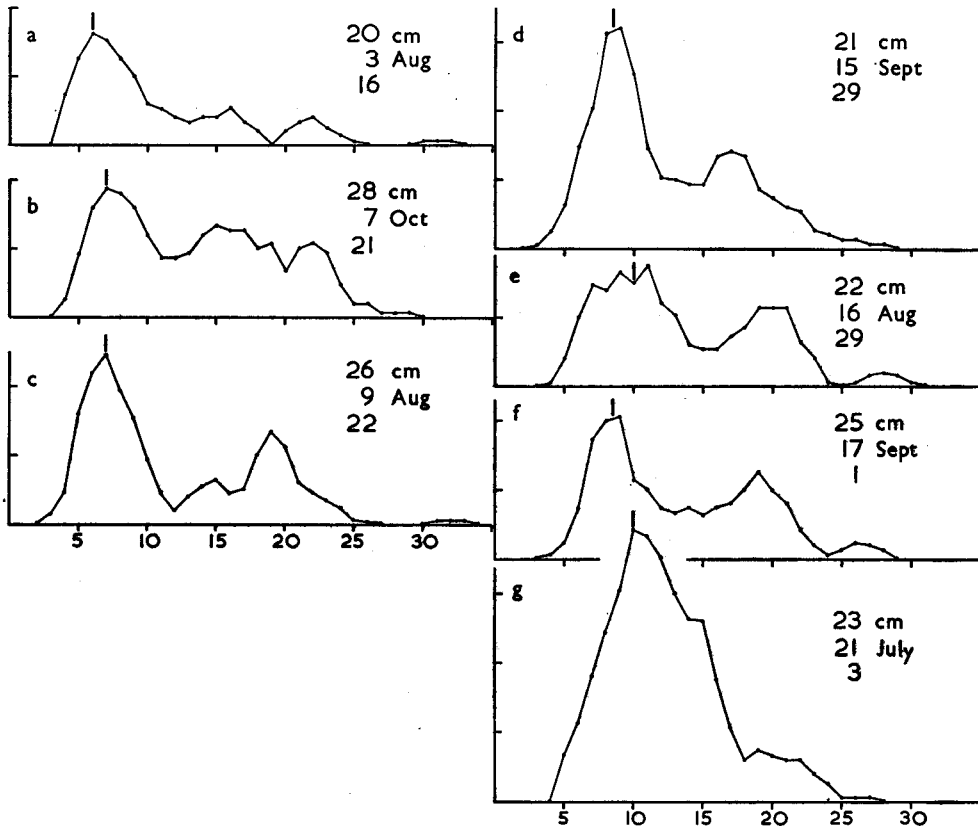


Fig. 6.—Length-frequency distributions of larval samples from fish stomachs. Thick vertical lines indicate the modes used in fig. 7 to estimate larval growth-rate. For each sample is given the total length of the fish, the date upon which it fed, and the number of days that had elapsed since the last swarm.

*Abscissa*: Mandible size, in eye-piece units.

*Ordinate*: Frequency, in units of 5, smoothed by a moving average of 3.

modes and in coming from fishes between 20 and 28 cm. long. The length-frequency distributions of these samples form the subject of figs. 5 and 6; in fig. 7 their smaller modes are shown in the context of the life-history.

The periodicity of adult swarms makes it clear that the duration of the aquatic stages must be a whole number of lunar months. But before the length of larval life can be inferred from larval samples, it is necessary to know how long the eggs take to hatch.

Duration of the egg stage was determined by keeping egg-masses in the laboratory. The times elapsing before hatching occurred are given in Table I. Egg-masses were obtained from gill-nets, in which they sometimes became

entangled, or from adult females that had been attracted to light. Only in the latter case was it known exactly when eggs were laid; the date of laying of eggs found on gill-nets was deduced from the time of the previous main swarm.

The results in Table I refer to eggs kept in lake water, since it was found that hatching was delayed in tap water. The temperature at which eggs were kept

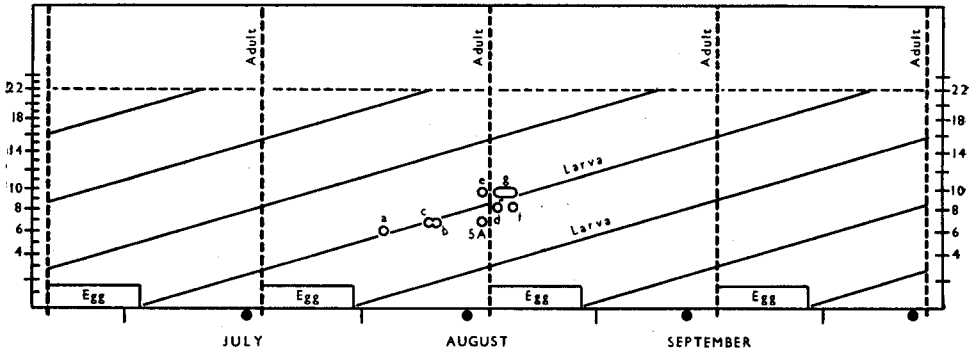


Fig. 7.—Diagram of life-history. Dates of the main swarms in July, August and September 1954 are indicated by thick vertical broken lines, and the times of full moon in figs. 5 and 6 have been inserted. The egg stage and the modes of larval samples shown have been placed in the appropriate positions for August only. This has been done by assuming that all the larvae measured came from eggs laid in the June swarm. Thus, maximum and minimum values are indicated for the July mode (g), since the date of the May swarm (when the eggs of this age-group would supposedly have been laid) is unknown. The upper horizontal broken line shows the average size at which metamorphosis occurs. The lines representing larval growth-rate have been fitted by eye. It can be seen that a generation is completed in 4 or 5 lunar months.

*Abscissa:* Months in 1954.

*Ordinate:* Mandible size of larvae (log. scale).

(ca. 20°C.) was slightly below that which they would experience on the bottom of Lake Victoria, either in deep or shallow water. (Bottom temperatures at 19 metres, near Buvuma Island, over the period 1951–53 varied between 23.8 and 26.7°C. (Fish, personal communication, 1954).) Thus, if egg development has a

TABLE I.

Duration of egg development.

Date of main swarm	Date of collection	Date of first hatching	Maximum duration (days)
1954 17 Aug.	19 Aug.	6 Sept.	18
16 Sept.	17 Sept.	4 Oct.*	17
1955 8 Apr.	8 Apr.†	26 Apr.*	18
9 May	11 May	25 May*	16
9 May	20 May	21 May	12
7 June	11 June	22 June	15

\* On or before date given.

† Exact date of laying; oviposition observed.

positive temperature coefficient, its duration in nature will be somewhat shorter than it is in the laboratory. In support of this, we may note the rapid hatching of eggs obtained on 20th May 1954 (Table I). These were presumed to have been laid on the night of the main swarm, and to have hatched after only 12 days, 11 of which would have been spent in the lake. Another batch of eggs, laid in July 1955 and allowed to remain in the lake throughout the incubation period, began hatching after only 11 days (Hartland-Rowe, personal communication, 1956). It is reasonable to assume that about 12 days is the usual duration for egg development in nature at this latitude.

Returning to fig. 7 with this in mind, we can see that the best fit (by inspection) for growth-rate involves most of an age-group reaching the average size for metamorphosis about eight days before a swarm.\* It is not known whether this period is sufficient to allow all larvae to metamorphose, although it is probable that some are able to do so, since ripe eggs have not been discerned in female larvae earlier than three days before a swarm. There can be little doubt, however, that those unable to complete metamorphosis in this time would emerge the following month. Thus, a single generation must be completed in either four or five lunar months, a finding which necessitates a revision of Kimmins' earlier opinion (1949) that more than one year is required for larval development. Further work is needed to determine whether male larvae (on account of their smaller size) reach maturity more quickly than female.

The possibility that larvae could reach a modal size of six units in two days (thus reducing the estimated duration by one month) has been shown to be unreasonable by rearing larvae in the laboratory. Lack of suitable food could not have been responsible for the difference observed, since larvae retain the vitelline cells in the mid-gut for several days after leaving the egg, and at least until the 2nd instar (Hartland-Rowe, personal communication, 1956).

Some recent observations (Hartland-Rowe, personal communication, 1956) lend support to this interpretation of the life-history. Larvae from a single egg-mass, kept in a cage on the lake bottom, reached a modal mandible size of 11.8 units 51 days after hatching, whereas the comparable value derived from fig. 7 is 59 days.

### Discussion.

These findings indicate that, as a rule, three generations are completed in 12 to 15 months, and that four or five age-groups usually co-exist in a population. For slightly less than half of the time (*i.e.*, during the first 12 days of each lunar month) one of these age-groups is present as eggs; for the rest of the time, all age-groups exist as larvae.

This periodic change in the composition of the population affects the feeding habits of several species of fish. *M. kannume*, the principal predator of larval *P. adusta* in certain habitats, feeds on a greater volume of larvae at full moon than at other times. Also, the number of larvae found in stomachs shows an abrupt decrease shortly after a swarm has taken place. Probably other species of MORMYRIDAE are affected similarly. Despite these fluctuations, however, the existence of four temporally-separated age-groups means that larvae of a wide size-range will always be available as food for fishes.

The lunar rhythm of *P. adusta* has a still greater effect on surface-feeders or generalised predators. Thus, at the time of a swarm, it is common for such

\* Only the smallest size-mode of each sample has been included in fig. 7. As mentioned above, the larger modes are thought to be less reliable, due to selective feeding on the part of the fishes. If, however, the larger modes are plotted in fig. 7, they fall very close to the growth-lines of the older age-groups, and thus lend support to the interpretation based on the smaller modes. Actually, values for the second largest modes fall slightly above the fitted growth-line, implying that larvae may in fact reach the average size for metamorphosis rather sooner than eight days before a swarm.

fishes as *Alestes nurse* Rupp., *Barbus altianalis* Blgr., *Bagrus docmac* Forsk., and *Clarias mossambicus* Peters to feed exclusively on emerging individuals.

*P. adusta* provides an extreme example of an insect in which a short adult life is associated with efficient synchronisation of emergence. The biological significance of this synchronisation may not be connected entirely with the short life of the adult. Some relatively short-lived insects seem to show a more or less continuous emergence near the equator (see Corbet & Tjønneland, 1956). It may be that *P. adusta* exists at too low a density for continuous emergence to be practicable from a reproductive point of view. Although dense masses of adults are encountered around lights on swarm nights, the nightly numbers would be small were these adults to be distributed evenly throughout a month.

In temperate regions, the seasonal change in temperature is thought to play an important part in determining the need for synchronised reproduction. In a tropical environment, where conditions may often be suitable all the year, it may well be that low density is closely associated with the need for synchronisation of the reproductive stage. Thus, we might expect that only exceptionally abundant species would breed continuously throughout the year.

### Summary.

The duration of the aquatic stages of the mayfly, *Povilla adusta* Navás, in Lake Victoria, Uganda, has been determined by analysing larval samples from the stomachs of an insectivorous fish, *Mormyrus kannume* Forsk., and by culturing eggs *in vitro*. Emergence shows a well-defined lunar rhythm and, since adults live for only about one hour, duration of the aquatic stages must be an integral number of lunar months. Results indicate that a generation is usually completed in four or five months. Approximately the first two weeks of this period are spent in the egg.

The periodicity of reproduction imposes a feeding rhythm on certain species of fish in Lake Victoria. Some biological implications of the need for synchronisation are briefly discussed.

### Acknowledgements.

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