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OBSERVATIONS ON THE BIOLOGY OF NYMPHS OF POVILLA ADUSTA NAVAS (EPHEMEROPTERA: POLYMITARCHIDAE) IN LAKE KAINJI, NIGERIA

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Abstract

Observations on *Povilla adusta* Navas nymphs in Lake Kainji revealed that seasonal fluctuations in abundance were due to a shortage of food during the period of rising lake level rather than a depletion of oxygen in the water column; this shortage was caused by the increased turbidity of the flood waters restricting the growth of both planktonic and periphytic algae. Planktonic algae apparently formed the diet of nymphs $<$ 4-6 mm and also of larger nymphs if their preferred diet of periphytic algae was in short supply. Both depth distribution and individual size of the nymphs were closely related to the distribution of periphytic algae. Depth distribution patterns of the nymphs revealed a peak between 2-4 m below the surface.

The dimensions of the nymphs and the duration of the aquatic stages (3-4 months) in Lake Kainji correspond closely with results obtained elsewhere as does the mean percentage of males in the population (28% ± 10%). Seasonal fluctuations in the sex ratio were apparently caused by variations in the intensity of predation.

Introduction

Nymphs of *Povilla adusta* Navas have been shown to form an important part of the benthic or periphytic biomass of several African lakes (Corbet, 1957; Corbet *et al.*, 1973 and 1974; Dejoux *et al.*, 1969, 1971 and 1972; Hartland-Rowe, 1958; McLachlan, 1970a and 1974; Petr, 1969, 1970 and 1973) and to form an important item in the diets of certain benthic-feeding fish (Ajayi, 1972; Blake, 1977a and 1977b; Corbet *et al.*, 1973; Imevbore & Bakare, 1970; Okedi, 1971; Olatunde, 1977; Willoughby, 1974). Considering their role in the diets of such fish in Lake Kainji and their contribution to the benthic biomass of the lake (Bidwell, 1977) detailed studies of their biology were considered necessary.

The biology of these nymphs in other lakes has been studied previously (Corbet, 1957; Hartland-Rowe, 1958; Petr, 1970) and consequently their basic life-history is well known. However, there is still uncertainty regarding their rates of growth, diet and patterns of emergence.

The substrate into which the nymphs burrow is normally the stems of aquatic plants, wooden boats and amongst shell fragments and gravel (Hartland-Rowe, 1958) but in man-made lakes an additional habitat is provided by submerged woodland (McLachlan, 1970a; Petr, 1970). In Lake Kainji, in addition to submerged woodland, *P. adusta* nymphs have been found burrowing into the sandstone rocks which have been exposed by wave action along the western shoreline of the lake. Nevertheless it has been shown that the nymphs exhibit a preference for softer substrates although very soft tissues tend to be avoided (Bidwell, 1977; Petr, 1970).

In Lake Kainji the major habitats of the nymphs (submerged woodland and emergent plants) are exposed and submerged annually by the large vertical drawdown in water level (8 metres) and this is a major factor affecting the abundance of *P. adusta* at certain times of the year. Indeed, it is suspected that such major environmental changes may account for some of the observed biological phenomena evident in the Lake Kainji population but absent elsewhere. More detailed descriptions of Lake Kainji and the influence of the water level fluctuations have been presented elsewhere (Bidwell, 1976 and 1977; Henderson, 1973).

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Dimensions of the nymphs

P. adusta nymphs reach the final instar, which may be about the 20th (Petr, 1970), at various body lengths depending on their sex and geographical location (Table 1). At emergence the males generally range from 9-12 mm whilst the females vary from 12-20 mm. However, the results from Lake Victoria indicate that the nymphs there were slightly larger than this. It should be noted that Corbet *et al.* (1974) state that the Lake Victoria population was about twice the size of most others i.e. 22-30 mm for female nymphs, but they have misinterpreted Fig. 4 in Corbet (1957).

Head width, body length and dry weight relationships have been determined for the Lake Kainji population in a manner similar to that described by Corbet *et al.* (1974). Sexing of the nymphs by examination of the external genitalia has allowed separate determinations to be made for nymphs greater than 5.0 mm in length.

Comparisons of head width: body length relationships for male and female nymphs (Fig. 1) show that for any given head width (up to the male maximum) the males were generally longer than the females but the differences in length became much less as the males approached their maximum size just prior to emergence. Whether male nymphs at this stage were the same age as female nymphs of equivalent size is not known nor whether they were in the same instar. These results are comparable to those for nymphs collected from Lake Barombi Mbo (Corbet *et al.*, 1974) except that in the case of the males from Lake Kainji the slope of the graph appears to be slightly steeper.

Comparisons of body length: dry weight relationships for male and female nymphs from Lake Kainji (Fig. 2) do not reveal similar trends to that obtained for head width and body length. Instead, it was found that at body lengths of less than 8.0 mm male nymphs were usually heavier than females but above this length the reverse was true. Petr (1970) found a similar situation in Lake Volta but the critical point at which the sex of the heavier nymphs changed was determined as occurring at body lengths of 8.0-8.9 mm. Possible reasons for this slight difference may be that in the present study the relationship was based on dry weights whereas Petr's (op. cit.) were, presumably, wet weights. Differences in the population density may also be responsible since Petr (op. cit.) has shown that nymphs from densely populated trees were generally heavier than those from sparsely populated ones.

Table 1. Body lengths of final instar *P. adusta* nymphs from various locations.

Location (Lake)	Body length in mm. Male	 Female	Source of Information
Victoria	15.0-15.5	16.5-24.0	Corbet *et al.*, 1974
Barombi Mbo	12.0	11.0-16.0	Corbet *et al.*, 1974
Volta	10.0-10.9	14.0-22.0	Petr, 1970
Kainji	7.4-11.3	13.0-22.0	Present study
mean	10.0±1.3	17.0±2.0	

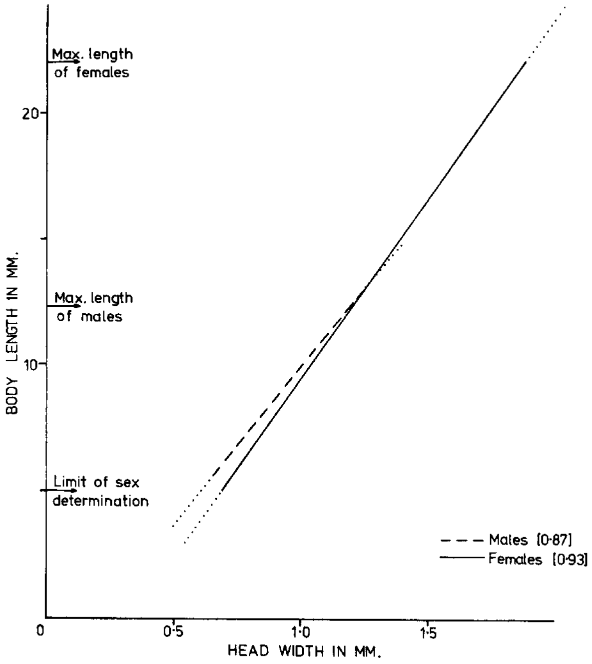

Fig. 1. Head width: body length relationships for nymphs of *P. adusta* (figures in parentheses are correlation coefficients).

Growth rates and duration of nymphal stages

One criterion for obtaining an estimate of the duration of the nymphal stage is that a sufficiently well defined periodicity exists in the deposition of eggs that the nymphs can be segregated into cohorts by measuring certain characters (Corbet, 1956). Lunar periodicity of adult *P. adjusta* at light traps was not as clearly exhibited at Lake Kainji as at Lake Victoria or Barombi Mbo (Bidwell, 1977) but it was suspected that a sufficiently well defined periodicty did exist for cohorts to be distinguished.

Nymphs were collected from submerged trees in a small creek on the western side of the lake at five different

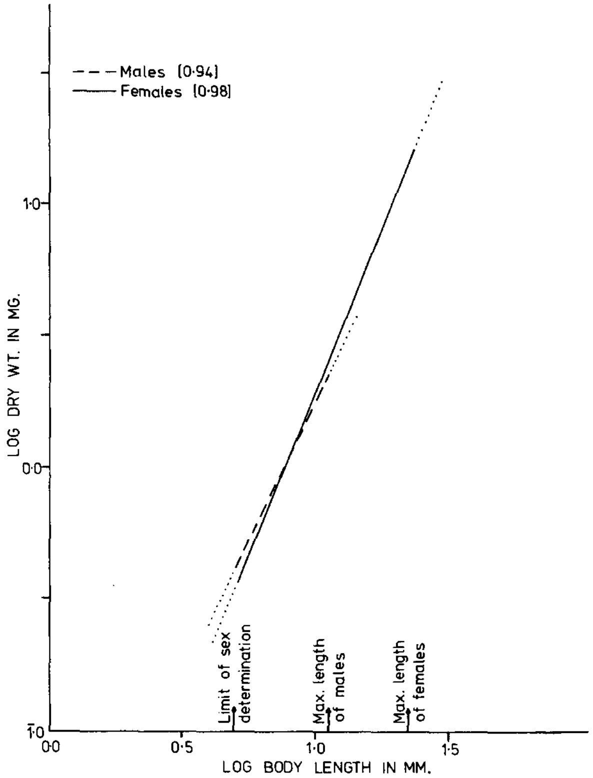

Fig. 2. Body length: dry weight relationships for nymphs of *P. adusta* (figures in parentheses are correlation coefficients).

phases of the lunar cycle. They were sexed and the head-width, as defined by Corbet *et al.* (1974), measured. The data were grouped into size categories, the number in each group expressed as a percentage of the total number of nymphs measured and the results plotted against the phase index. The term 'phase index' refers to the stages of the lumar cycle defined by Bowden & Morris (1975) and is based on the percentage of the moon's surface illuminated by the sun. The scale ranges from 0 (new moon) to 32 with full moon being at phase index 17.

The results are displayed in Figs. 3 and 4; the stippled areas represent the probable pattern of development of the majority of nymphs. Considering firstly the pattern displayed by the female nymphs (Fig. 4) it can be seen that there were four or five fairly distinct cohorts, although the number of individuals intermediate in size was substantial. This probably reflects the lack of a very distinct lunar periodicity of emergence of the adults (Bidwell, 1977). Presuming that the rate of growth is constant throughout the life of the nymph then it can be assumed that the number of cohorts represents the duration time of the immature stages, i.e. the life of the female nymphs was 4-5 lunar months. Referring now to the pattern displayed by the male nymphs (Fig. 3) it can be seen that there appears to be only three cohorts, i.e. a probable duration of 3-4 months. However, there remains considerable doubt as to whether the size intervals were sufficiently small for the male population as the definition of the cohorts was less distinct than in the case of the females, and it may therefore be justifiable to assume that male and female nymphs had a similar generation time.

These figures compare favourably with those determined for other populations, 4-5 months for Lake Victoria (Corbet, 1957) and about 3 months for both male and female nymphs in Lake Barombi Mbo (Corbet *et al.*, 1974). Corbet *et al.* (op. cit.) have suggested that generation time may be dependent on water temperature and the present investigation provides additional evidence for this theory (Table 2).

Food and feeding

The diet of *P. adusta* nymphs appears to have caused some confusion in the literature as they have been described as filter-feeding on planktonic algae (Corbet, 1957 cit. Kimmins, 1949; Hartland-Rowe, 1955) and also as periphytic algal browsers (Petr, 1970).

The nymphs almost certainly do not feed during the first instar as they retain the vitelline cells in the mid-gut for several days after leaving the egg (Corbet, 1957; Petr, 1970) and presumably do not feed before the third instar (Hartland-Rowe, 1953 and 1955) by which time they have become established in a burrow. They clearly have a well developed filter-feeding mechanism which has been described by Hartland-Rowe (op. cit.). The use of this mechanism was evident amongst nymphs collected from Lake Victoria where the gut contents were identified as predominantly planktonic algae (Corbet, 1957) but at Lake Volta periphytic algae, chiefly *Oedogonium* and *Oscillatoria* spp., were of primary importance in the larger nymphs whilst the planktonic algae *Scenedesmus* and *Tetraedron* spp. were the major food source of nymphs less than 4-6 mm long (Petr, 1970).

Examination of the gut contents of nymphs (> 8.0 mm body length) from submerged trees in Lake Kainji revealed that they fed predominantly on the same unidentified species of periphytic algae that colonised the surfaces of the submerged trees. However, when gut analysis

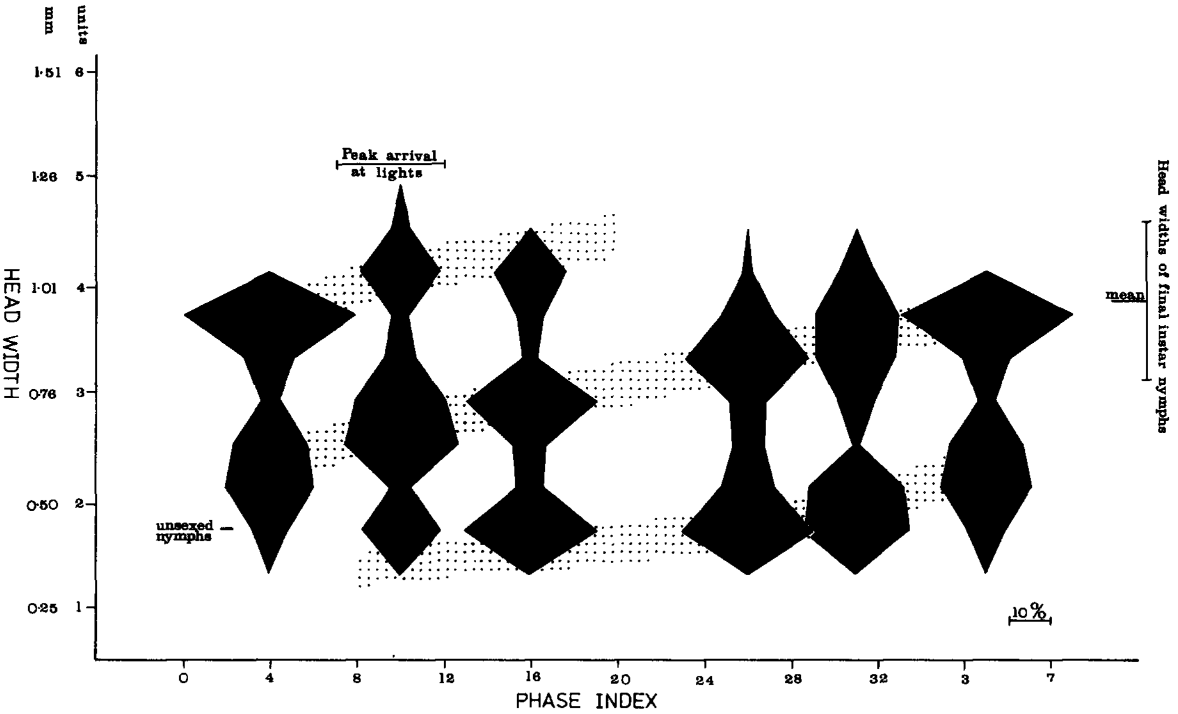

Fig. 3. Growth rates of male *P. adusta* nymphs as revealed by the frequency / size class distribution of the head widths.

was performed on nymphs taken from submerged trees on which there was little or no periphytic algal growth planktonic algae, principally *Microcystis, Anabaena* and *Tetradron* spp., predominated.

It may therefore be concluded that *P. adusta* nymphs of less than 4-6 mm body length are filter-feeders (Petr, 1970) whilst above this size the diet (at least in Lakes Kainji and Volta) consists of periphytic algae, provided that this is in sufficient supply and if it is not the larger nymphs can remain as filter-feeders.

Petr (1970) has stated that the nymphs fed during the night when crawling about on the surface of the substrate and this has also been examined in the present sudy. Twenty nymphs (body length > 8.0 mm) were collected every four hours throughout a two day period from submerged trees in the lake, the guts removed, divided into three equal sections and the number of nymphs with food in each section recorded. The results (Fig. 5) clearly indicated that feeding started just after dusk, i.e. between 19.00-20.00 hours local time, and that the nymphs did not feed during the day; the majority probably stopped feeding sometime after midnight and certainly all ceased feeding before dawn. These conclusions therefore verify Petr's findings (op. cit.).

Depth distribution

Petr (1973) has suggested that the vertical distribution of the food, i.e. planktonic and periphytic algae, may be a major factor in determining the vertical distribution of *P. adjusta* nymphs and this relationship was studied at Lake Kainji.

It was decided that the depth distribution patterns of the nymphs could best be studied on the submerged trees where changes in substrate texture were minimal (unlike the benthic sediments and emergent plants which themselves were directly affected by changes in water depth). However, the submerged trees could not be sampled directly below a depth of 1-2 m and the effects of the frequently changing water level in this man-made lake had to be reduced. Consequently, logs approximately 8 cm in diameter and 50 cm long were cut from previously submerged trees and suspended from a float of rafia poles in such a way that they formed a chain with a log at each of the following depths, 0.5-1.0, 1.5-2.0, 2.5-3.0 and 3.5-4.0 m. The float, which supported a total of six chains, was then anchored amongst submerged trees in a small creek in Lake Kainji and left for 85-100 days to allow colonisation by the nymphs and periphytic algae.

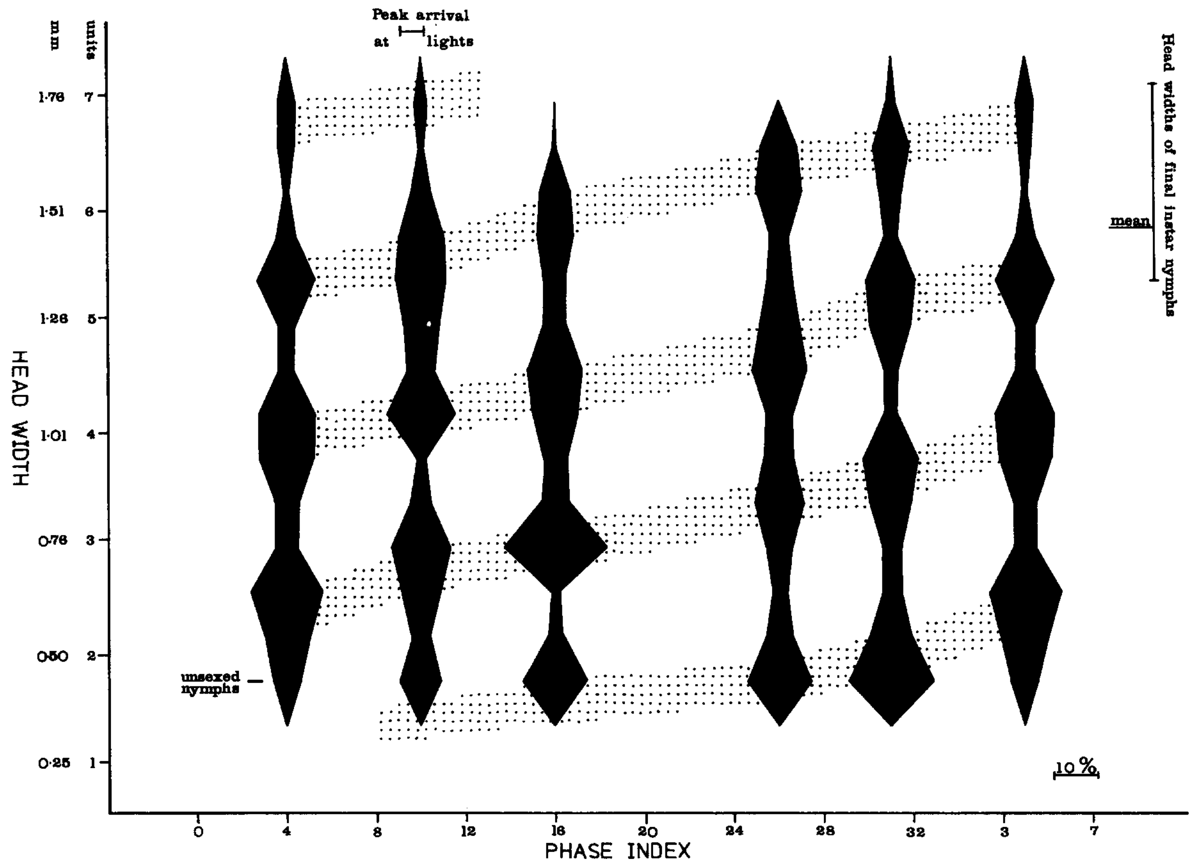

Fig. 4. Growth rates of female *P. adusta* nymphs as revealed by the frequency / size class distribution of the head widths.

At the end of the colonisation period the logs were removed from the lake, suspended over a large tray of water and left to dry in the sun. As the wood dried out so the animals inside emerged from their burrows and fell into the tray of water where they were collected at regular intervals. After approximately 24 hours the log was removed, scrubbed and then resuspended over the tray of water until no further organisms emerged. The material scrubbed from the log was examined against a white background and all organisms removed. The chlorophyll content of the remaining material, mainly periphytic algae, was determined colorimetrically (Golterman, 1969) and finally the approximate surface area of the log measured.

Table 2. Comparison of generation time of *P. adusta* nymphs and water temperature.

Location (Lake)	Temperature in °C at surface	at low.	Generation time in lunar months
Barombi Mbo	30.1	29.4	3
Victoria	23.8-25.8	23.4-25.6	4-5
Kainji	23.6-29.5	22.7-29.0	4-5

There was a significant difference in the number of *P. adjusta* nymphs collected at each depth ($P < 0.05$) with numbers increasing with depth up to 3.0 m after which they declined sharply (Fig. 6). Petr (1973) found that *P. adusta* nymphs in Lake Volta were most abundant at 4 m but normally present up to a depth of 7 m and exceptionally at 15 m. Although the numbers of nymphs at depths greater than 4 m were not examined in the present study it would appear that in both Lakes Volta and Kainji there is a zone from 2-4 m below the surface which is prefered for colonisation. McLachlan (1970a) found that the only depth distribution pattern in Lake Kariba was in response to the establishment of the thermocline at about 15 m. This difference between Kariba and the other two lakes may be due to its greater water trans-

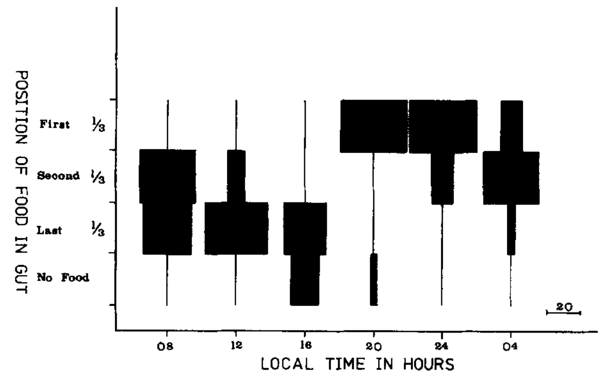

Fig. 5. Times of feeding of *P. adusta* nymphs.

parency; Secchi disc readings 1.0-12.0 m (Coche, 1969) compared with approximately 1.0 m at Lake Volta (Ewer, 1966) and 0.12-1.70 m at Lake Kainji (Clarke, 1977 pers. comm.). The greater light penetration would allow the development at greater depths of the periphytic algae shown to be important in the diet of the nymphs whereas the development of algae in the turbid West African lakes is limited to the top few metres.

The number of *P. adusta* nymphs showed an inverse relationship to the amount of attached algae, i.e. the chlorophyll content of the material scrubbed from the logs (Fig. 6). If the supply of food was the only factor determining the distribution of these nymphs then the results would be slightly anomalous but it has been pointed out by Mundie (1955) that the explanation of any observed distribution should be sought in a combination of factors rather than any one aspect. The log nearest the surface supported the most periphytic algae, due to its proximity to the incident light, but it supported fewer nymphs that the next two logs in the chain. This situation is similar to that found in benthic sediments where fewer animals are normally found at the shallowest depths (McLachlan, 1970b; Mundie, 1955) but the reasons for this are obscure. The number of nymphs increased at depths of 1.5 and 2.5 m whereas the amount of periphytic algae diminished. This may be expected due to the intense grazing pressure on these logs. On the deepest log (3.5 m) the amount of periphytic algae was slightly higher than on the log above yet it supported fewer nymphs and this was probably due to the lower production of algae at depths where the light was least intense.

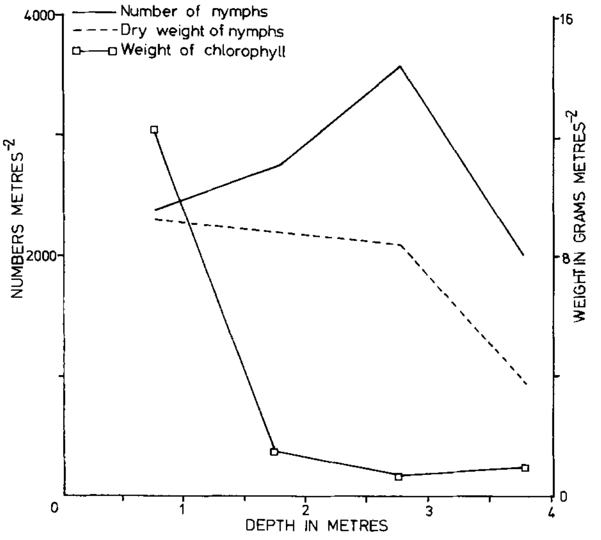

Fig. 6. Relationship between numbers and dry weight of *P. adusta* nymphs and the amount of periphytic algae.

The distribution of total biomass of the nymphs did not follow a similar pattern (Fig. 6); the total biomass supported by each of the top three logs decreased only slightly with depth before falling sharply on the deepest log. This indicates a variation in the mean individual weight of the nymphs from each log, with a higher proportion of large nymphs occurring on the shallower logs. It is therefore apparent that the body weight of the nymphs was not related to their numerical abundance on the logs (as discovered in Lake Volta by Petr, 1970) but was more closely related to the amount of attached algae (as determined by chlorophyll content).

Seasonal fluctuations in abundance

Fluctuations in the abundance of *P. adjusta* nymphs in their prefered habitats in Lake Kainji (submerged trees and emergent plants) appeared to be related to seasonal changes in water level (Fig. 7). The period of minimum density of nymphs was found to correspond to the time of high lake level, especially from October to January, after which numbers increased rapidly, reaching their maximum on the emergent vegetation just prior to the lowest lake levels (which eventually became stranded and therefore temporarily destroyed the habitat) and on the submerged trees (now partially exposed) at even lower lake levels. Clearly many of these fluctuations in population density can be explained with respect to the changes in the amount of habitat available for colonisation but this cannot account for the very rapid and extensive

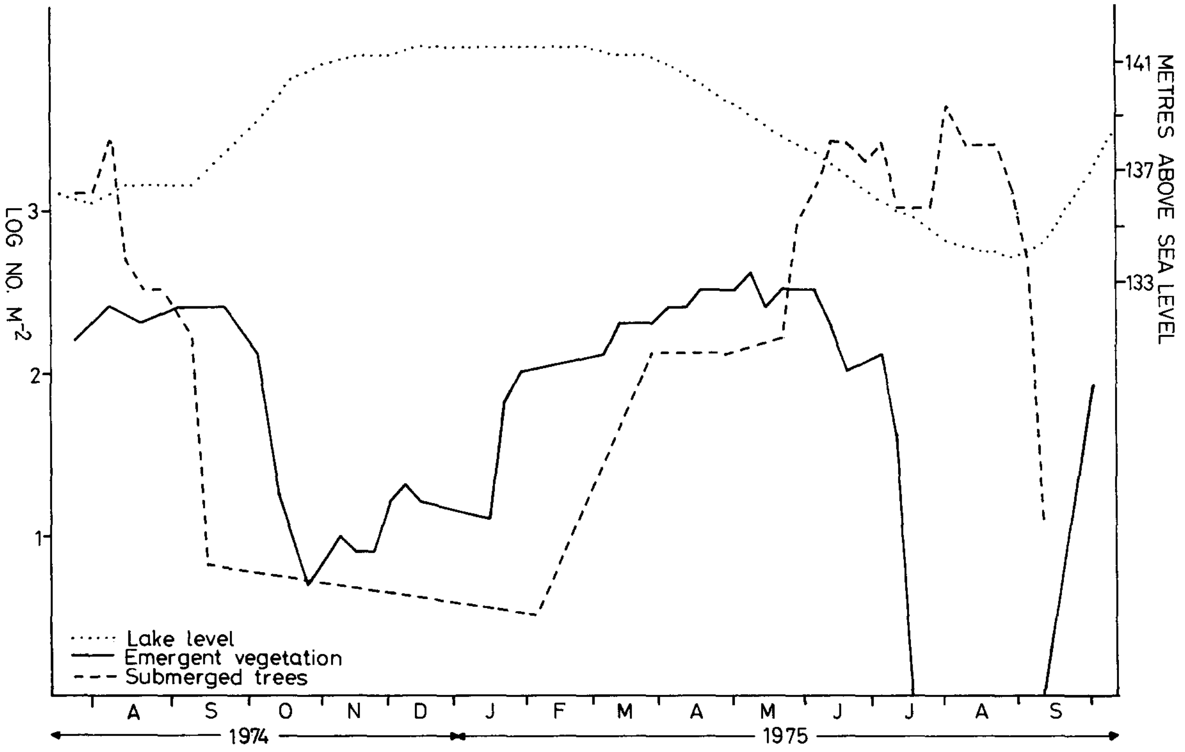

Fig. 7. Seasonal fluctuations in the abundance of *P. adusta* nymphs on submerged trees and emergent plants.

decrease in the overall population during and after the period of rising lake level as revealed by both the density of nymphs in the lake and the numbers of adults attracted to light traps (Bidwell, 1977). Indeed these fluctuations in total numbers can best be revealed by the fact that in both August and September in each year of study almost 11,000 adult *P. adusta* were attracted to light traps whereas a total of only 65 was captured during January 1975.

Petr (1973) has also shown that seasonal periodicity of abundance was displayed by the nymphs in the submerged trees in Lake Volta. He suggested that either changes in the oxygen concentration of the lake water, as flood waters broke down thermal stratification in the lake, or changes in the supply of food created this periodicity. As the timing of this periodicity was identical in the two lakes, with minimum abundance following the inflowing of flood waters and subsequent raising of lake level, it was felt that similar factors were involved in both cases. As a result the oxygen levels of the waters of Lake Kainji were studied and the oxygen demands of the nymphs investigated.

It can be seen from Fig. 8 that there was no large scale decrease in oxygen concentration of the water column during the inflow of flood water, oxygen concentrations in the top 10 metres remaining above 70%. Only during the period of falling lake level, when the numbers of *P. adusta* were actually increasing, did oxygen concentration in this zone become as low as 60-70%.

Many other species of organism colonising submerged trees and emergent vegetation were found to have a corresponding decrease in abundance during this period, including *Nilodorum* spp. (Diptera: Chironomidae) which have haemoglobin in their blood and can presumably withstand fairly low oxygen concentrations. The following experiment was therefore devised to determine the oxygen demands of *P. adusta* nymphs and larvae of *Nilodorum* spp.

Conical flasks of 500 ml and 200 ml capacity were filled to overflowing with varying proportions of cold boiled lake water and oxygenated lake water so that a range of oxygen concentrations (determined by Winkler's method) was created. Control chambers of ordinary lake water were also prepared. Into the 500 ml flasks were placed 10 *P. adusta* nymphs approximately 7-10 mm long (≃ 2-5 mg dry wt. each). These nymphs had been collected and left in a basin of lake water for at least one

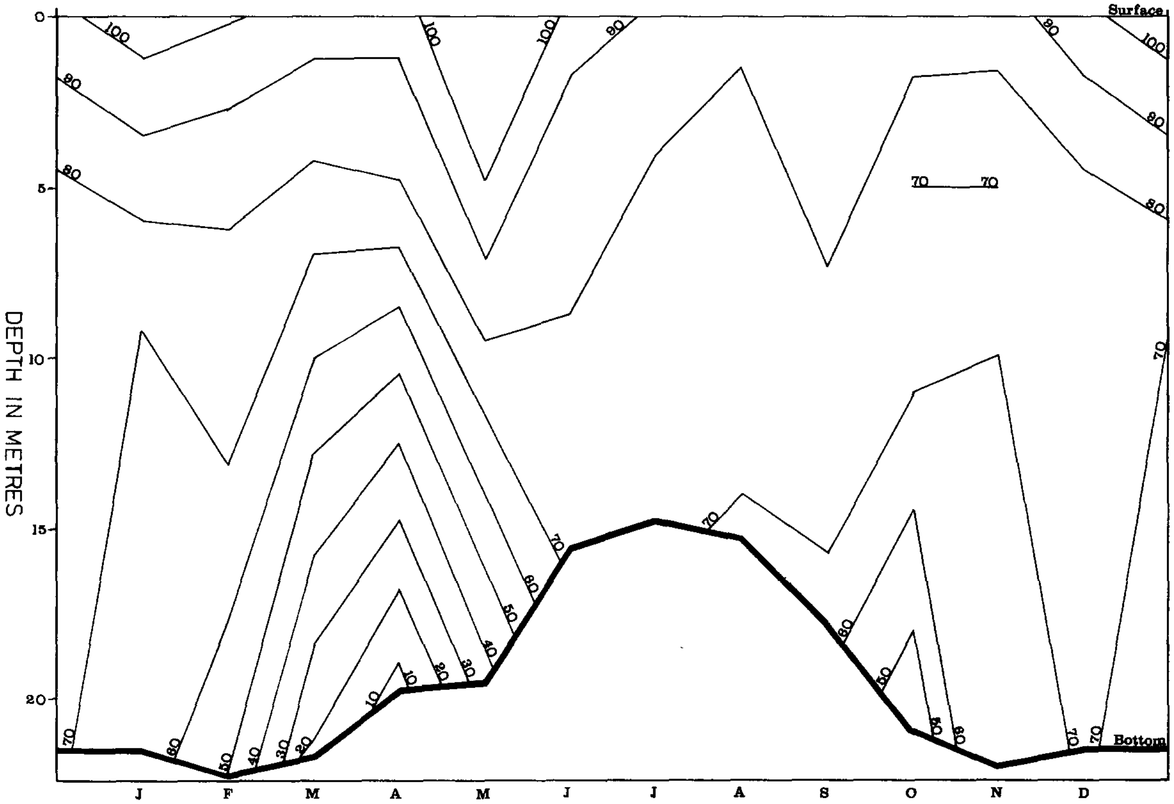

Fig. 8. Oxygen isopleths recorded for Lake Kainji.

hour prior to use in the experiment. To the 200 ml containers were added 50 *Nilodorum* larvae (≃ 0.3 mg dry wt. each) previously left under the same conditions as the *P. adusta* nymphs. The reason for the different numbers and volumes used in the two parts of the experiment was to try to equate the biomasses per 1 ml of water for both nymphs and larvae. The flasks were then sealed with waxed paper and the numbers which had died after various time intervals noted. The times of 50% mortality were determined and the results plotted in Fig. 9.

The results were not conclusive on the critical oxygen tolerances of either *P. adusta* nymphs or larvae of *Nilodorum* spp. This point was masked by the fact that other factors played a significant role in the mortality of organisms after approximately 8.5 hours of experimentation, presumably a stress response to the continual swimming activity of the organisms which itself was due to the removal of the nymphs and larvae from their burrows and cases prior to experimentation, a problem which could not be overcome under the prevailing conditions. However, it is clear from these results (Fig. 9) that oxygen concentrations greater than about 70-75% have only a secondary role in determinations of mortality under these experimental conditions and possibly do not exert any effect at these concentrations (otherwise the slope of the graph at this point would not be horizontal). A second point to note from this experiment was that the larvae of *Nilodorum* spp. live up to twice as long as *P. adusta* nymphs at low oxygen concentrations.

If it is presumed that the critical oxygen concentration for *P. adusta* nymphs in this experiment was 75% then it is probable that under natural conditions and without stress responses the critical value will be considerably lower than this. As the oxygen concentration of the open lake rarely falls below 70% saturation at depths less than 5 metres, where it has been shown that most nymphs live, it would seem doubtful that oxygen concentration plays a part in the destruction of the population of *P. adusta* nymphs during the rising lake level period. Furthermore, the fact that *Nilodorum* spp. larvae undergo a similar decrease yet live for up to twice as long as *P. adusta*

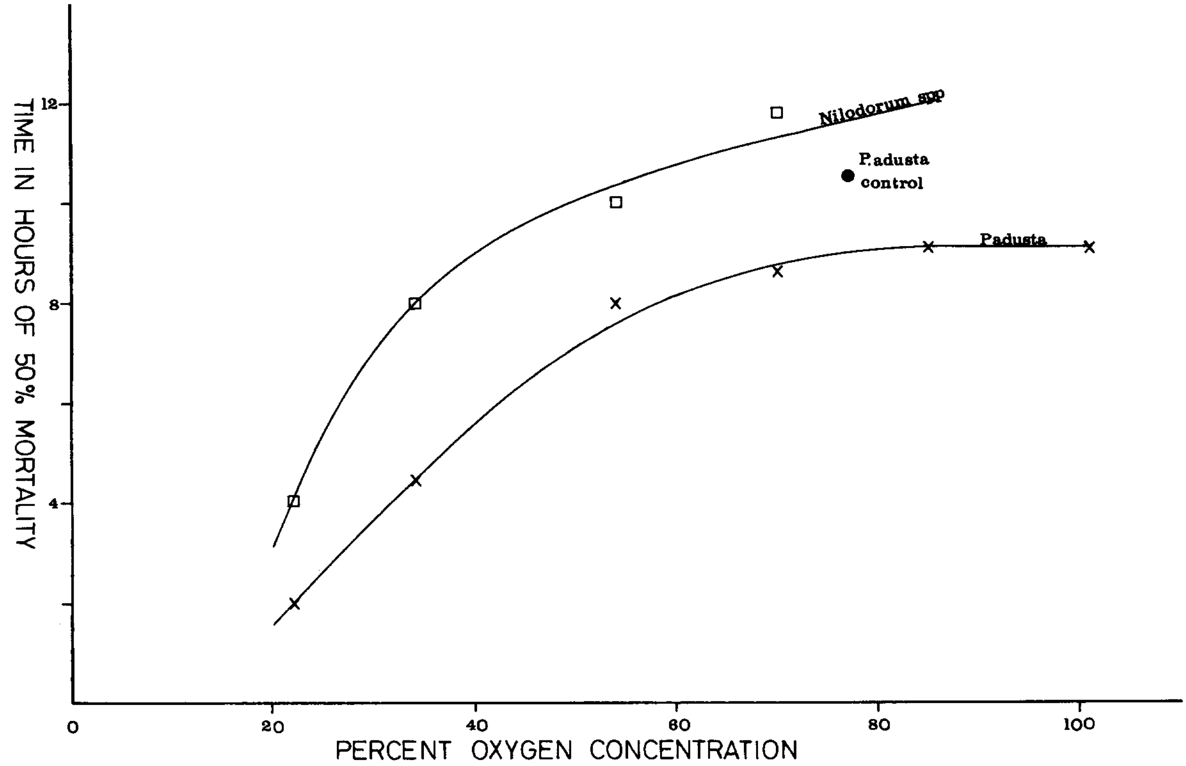

Fig. 9. Effects of oxygen concentration on the time of 50% mortality of *P. adusta* nymphs and *Nilodorum* spp. larvae.

nymphs at the same oxygen concentrations tends to support the view that oxygen was not the most important factor.

Petr (1973) has shown that *P. adusta* nymphs were distributed in the top 7 m of Lake Volta whenever the lake was stratified, corresponding to oxygen concentrations of 70-90%. When mixing occurred and oxygen was distributed evenly throughout the water column, at 40%, nymphs were recorded up to 15 m deep. He has also shown that the horizontal distribution of the nymphs in the papyrus beds of Lake George was limited to 1.5 m at which point oxygen concentration was 50% of the value obtained at the papyrus/open water interface.

The accumulated evidence therefore indicates that at concentrations below 60% oxygen may be a limiting factor in the distribution of nymphs but at the concentrations found in the top 10 m of Lake Kainji even during the time of inflowing flood water, an oxygen deficit was not the main reason for the observed decline in abundance of these organisms. Therefore in both Lakes Volta and Kainji seasonal periodicity of abundance, with minimum numbers occurring after refilling of the lakes, was probably due to a decrease in the amount of periphytic algae caused by the increased turbidity of the lake waters. The nymphs may have attempted to revert to filter feeding of which they have been shown to be capable but, at least in Lake Kainji, this was also a period of low abundance of planktonic organisms (Clarke, 1977 pers. comm.). Consequently with both food sources limited the population of nymphs declined.

Variations in the sex ratio

Light trap catches of adult *P. adusta* (Bidwell, 1977) and examination of nymphs revealed that the sex ratio of this organism was not constant throughout the year. Determination of the sex ratio of adults attracted to lights is not necessarily indicative of the true percentage contribution of the sexes to the population, since Petr (1970) has shown that the percentage of males differs with the distance of the light trap to the shoreline. However, variations in the sex ratio of the nymphs collected directly from their aquatic habitats do represent the true position since this method of collection is not dependent on other factors.

Sex ratios of nymphs greater than 5 mm body length were determined by examination of the external genitalia from collections of insects taken from submerged trees at approximately monthly intervals. Between November-February the number of nymphs collected was so low as to make any sex determination very uncertain and consequently no ratios were derived.

The results are shown in Fig. 10 together with the percentage of males in the adult catches at light. It can be seen that the variation in the percentage of nymphs corresponds closely to that recorded for the adults, and that the variations appear to be related to changes in lake level.

One possible explanation for this behaviour is that *P. adusta* was parthenogenetic or at least is evolving in that direction. The high proportions of males coincided with unfavourable conditions (represented by increased lake level) and the sexually reproduced eggs and nymphs may be more resistant to the unfavourable conditions as occurs in some zooplankton species. However, the evidence for this is rather dubious since the percentage of males was fairly high when compared with other parthenogentic species (Engleman, 1970) and it seems unreasonable to suggest that a greater number of male eggs were produced in response to unfavourable conditions when it would take 4-5 months for that egg to develop into a sexually mature male.

A more plausible explanation would be that the variation in the abundance of males was due to selective predation by insectivorous fish. Corbet (1957) has stated that *Mormyrus kannume* Forsk. in Lake Victoria displayed a tendency to feed on medium sized larvae. Now presuming that:

(a) the generation time of both male and female *P. adusta* was the same in Lake Kainji, 4-5 months

(b) mormyrid fish in the lake displayed a similar preference for medium sized nymphs (say 8-14 mm)

(c) behavioural differences were not displayed by the sexually different nymphs

then, it can be shown that the rate of growth of female nymphs must be quicker than that of males. Therefore male nymphs spend a longer period of time in the 8-14 mm range than do females and consequently the likelihood of predation is increased. The existence of seasonal variation in the abundance of males means that seasonal variation must be displayed by the fish predators-pre-

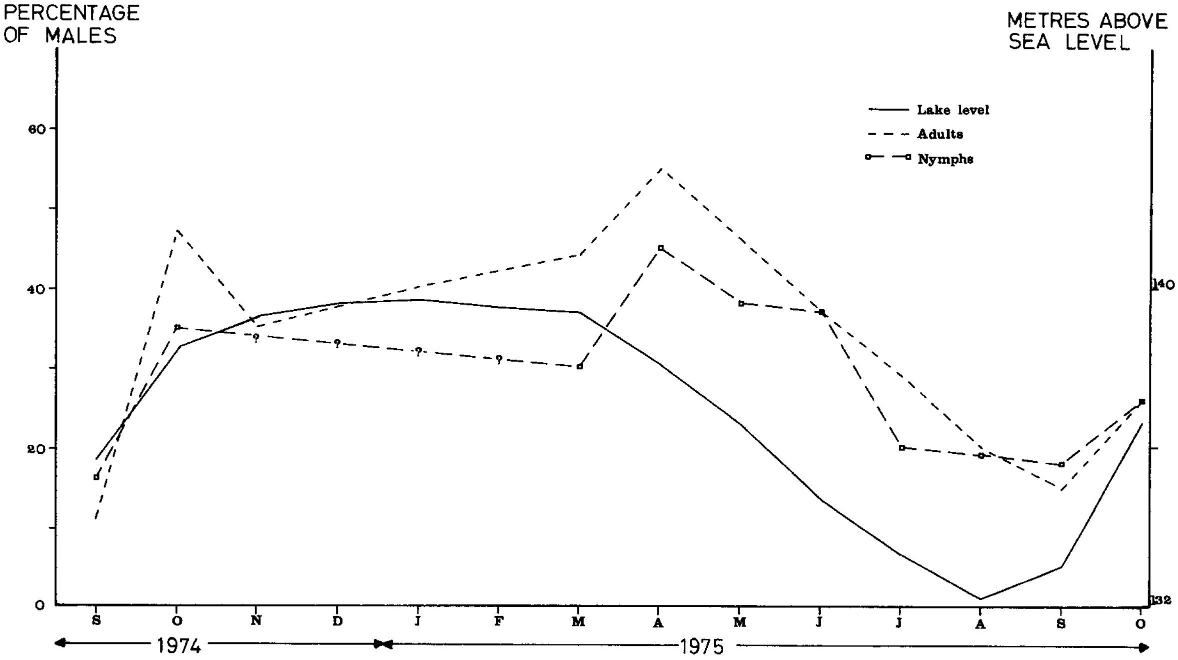

Fig. 10. Percentage contributions of males to the population of *P. adusta* adults at lights and to nymphs colonising submerged trees.

suming that the variation was produced by predation. The mormyrid fish in Lake Kainji do display a variation in the percentage contribution of *P. adusta* nymphs to their stomach contents (Blake, 1977 pers. comm.). The highest predation occurred during periods of maximum abundance of nymphs i.e. June-September and this corresponds to the lowest percentage of males in the population. Conversely, during November-March, when both predation and abundance of *P. adusta* were at their lowest the percentage of males in the population was at its highest.

It would therefore appear that the percentage contribution of males to the population of *P. adusta* was directly governed by the intensity of predation by mormyrid fish. Nevertheless, more information is required to conclusively prove this point especially regarding the size ranges of nymphs preferred by the fish and the sex ratios of nymphs at various body sizes.

The mean sex ratio of male nymphs at Lake Kainji was 28.4% ± 10.0%, a value comparable with the results of other investigations, 23% at Lake Barombi Mbo (Corbet *et al.*, 1974), 38% at Lake Victoria (op. cit.) and 25% at Lake Volta (Petr, 1970).

Summary

P. adusta nymphs occur in large numbers in freshwater lakes in Africa and in the newly created man-made lakes may contribute well over 90% to the biomass of certain habitats (Petr, 1970; Bidwell, 1977). Consequently it is a very important organism in these lakes.

The nymphs appear to have three main requirements for colonisation of any particular habitat:

(a) a suitable substrate for burrowing, which may be submerged trees, emergent plants, gravel or sandstone but a preference is shown for materials that are neither too hard nor too soft.
(b) a good supply of food. Younger instars appear to rely on phytoplankton filtered from the lake water whilst nymphs greater than 4-6 mm apparently prefer periphytic algae browsed from the surface of their selected substrate but are able to survive on a diet of filtered phytoplankton if periphytic algae are unavailable. The time of feeding (on periphytic algae) was determined as occurring between dusk and soon after midnight.
(c) water with a high oxygen concentration. Levels greater than 60-70% do not appear to be limiting on the distribution of nymphs and have been recorded from depths with oxygen concentration as low as 40% (Petr, 1973) although in small numbers.

These requirements were fulfilled at Lake Kainji and consequently a large population of *P. adusta* was present. From measurements taken on specimens from this population it was found that the female nymphs were normally shorter than male nymphs with a similar head width, up to the male maximum. The males were also heavier than the females up to body lengths of approximately 8 mm after which the reverse was true. The time taken for development to the adult stage in Lake Kainji was about 4-5 lunar months by which time the males were 9-12 mm long and the females were 12-20 mm. All these values closely correspond to values obtained elsewhere.

Depth distribution patterns revealed a maximum number of nymphs at 2-4 metres in both Lakes Volta and Kainji but a similar pattern was not evident at Lake Kariba (McLachlan, 1970a). The reason for this difference was attributed to the greater depth distribution of periphytic algae in the clearer waters of Lake Kariba compared with that in the more turbid West African lakes. The mean individual weight of the nymphs in Lake Kainji was apparently more closely related to the abundance of periphytic algae on the substrate than to the total number of nymphs present as discovered by Petr (1970) in Lake Volta.

Seasonal periodicity of abundance was related to changes in water level and the increased turbidity of the inflowing flood waters which resulted in the destruction of periphytic algae and also a decline in the amount of phytoplankton in the lake. The resulting food shortage reduced the standing crop of nymphs on the submerged trees by more than 1000 times.

Finally, variations in the percentage of males in the population have been related to the intensity of fish predation, presuming that the fish selected nymphs of a specific size range. The mean percentage contribution of male nymphs was 28.4 ± 10.0% and this figure is also comparable with values obtained elsewhere.

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