SOME FACTORS LIMITING THE DISTRIBUTION OF *POVILLA ADUSTA* NAVAS (EPHEMEROPTERA, POLYMITARCIDAE) IN AFRICAN LAKES

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INTRODUCTION

With the establishment of the Volta Lake in Ghana, there occurred a massive development of the burrowing mayfly nymph *Povilla adusta*. The presence of *Povilla* has also been reported from the man-made lakes Kariba (McLACHLAN, 1970) and Kainji (LELEK, personal communication). The nymphs serve as an important source of food for some fishes (REYNOLDS, 1970) and they play an important role in the destruction of the bark and wood of the flooded forests, which form one of the habitats for *Povilla* (PETR, 1970). *Povilla*, as an algal feeder, is an important link in the food chain connecting the primary producers with the tertiary consumers. This paper discusses some of the factors determining the rapid development and maintenance of *Povilla* in artificial and natural water bodies, and the economic importance of its aquatic larval stage.

THE HISTORY OF THE ESTABLISHMENT OF *Povilla* IN THE VOLTA MAN-MADE LAKE

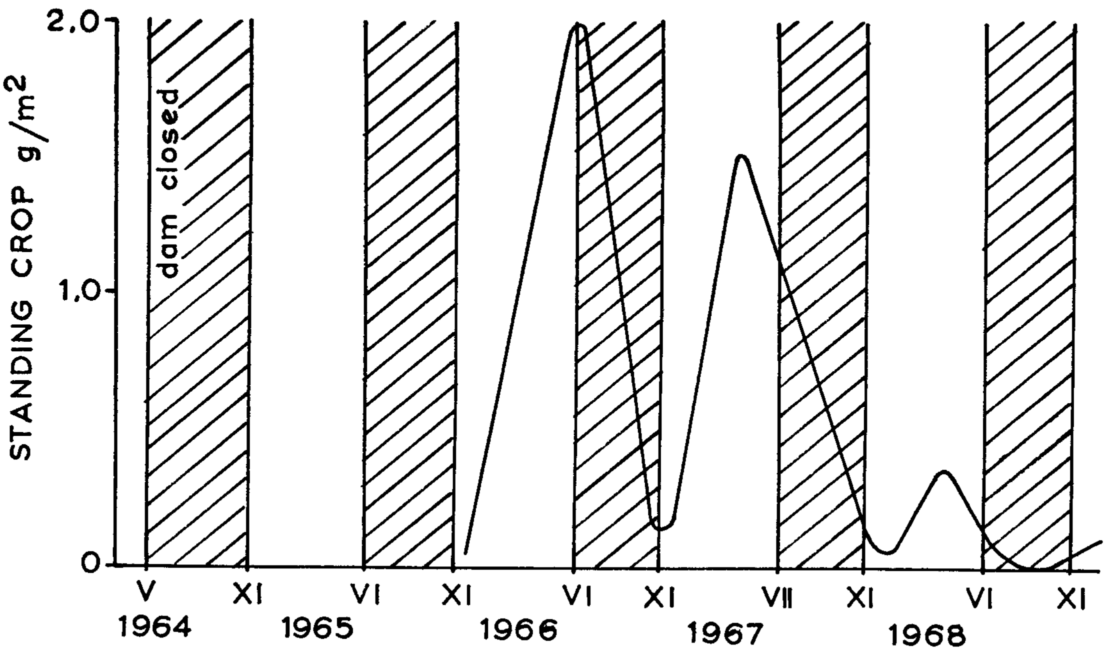

FIGURE 1. The development of *Povilla* in the bottom of the Volta Lake. Shaded areas indicate the seasons with rising lake water level.

In December, 1965, i.e. some one and a half years after the dam was closed, adults were first observed around lights, and nymphs were collected from the bottom. This was a few months after the first nymphs were seen in fish stomachs (REYNOLDS, 1967). During 1966 and 1967, the nymphs were especially abundant, chiefly in flooded grass and pieces of wood, sometimes dominating the total biomass of bottom fauna. In 1968, they became much less common (Fig. 1), probably as a result of the decomposition of the small wood particles and submerged grass, and their decrease in abundance was partly responsible for the decrease in the total biomass of the bottom fauna (PETR, 1969a). In the 1966-1968 period the average percentage abundance (by number) of *Povilla* in the bottom represented 7 % of all the invertebrates present there.

The bark of flooded trees soon became the preferred substratum. In May, 1969, *Povilla* in the bark and wood represented 75 per cent (by number) of all invertebrates present, this corresponding to an average standing crop of 93 per cent (by wet formalin weight).

OCCURRENCE OF *Povilla* IN SOME NATURAL AFRICAN LAKES

In the Central and East African natural lakes *Povilla* nymphs are found mainly in the dead stems and rhizomes of *Cyperus papyrus* fringing these lakes. In Lake George, for example, the *Povilla* nymphs have been found in the papyrus at a distance of approximately 1.5 m from the outer edge (Fig. 2A). In Lake Victoria large numbers of adults were attracted to lights at Jinja (TJONNELAND, 1960), these mainly originating from the nymphs inhabiting the papyrus zone. In Lake Chad, although mainly inhabiting papyrus, the nymphs are also found in roots of *Pistia stratiotes* (DEJOUX, 1969). The presence of dead trees in natural lakes is usually the result of exceptional circumstances, such as, for example, the rise in the water level of Lake Victoria in 1961, resulting in flooding of the shore-line vegetation. In this habitat *Povilla* is also present. The geographical distribution of *Povilla* in Africa has been revised by HARTLAND-ROWE (1958). He also gives some data on its biology and suggests that the nymphs may be found in almost any material of suitable consistency.

FACTORS LIMITING THE DISTRIBUTION OF *Povilla* IN AFRICAN LAKES

The investigation of some aspects of the biology of *Povilla* in the Volta Lake (PETR, 1970), Lake Victoria (HARTLAND-ROWE, 1958) and my recent observations on Lake George in Uganda suggest that the *Povilla* nymphs have three basic requirements for their successful establishment. Firstly, they need a suitable substratum into which they can burrow; secondly, this substratum must allow the nymphs to obtain their planktonic algal food from the outside, whilst remaining inside, and also provide surfaces suitable for the development of the attached algae which form a food source for the larger nymphs; and finally, the nymphs seem to require fairly well oxygenated water.

Substratum and food

When burrowing into the submerged parts of plants the nymphs prefer firm to very soft plant tissue (PETR, 1969b). Spongy wood, heavily soaked with water, seems to be avoided. Hardwood tree species are less densely inhabited than others. In Lake George and Lake Victoria, *Povilla* is present in firm dead parts of papyrus, yet absent from those in an advanced stage of decomposition. On the other hand, the hard stems of *Phragmites* sp. harbour only small populations. In the Volta Lake in 1969, the nymphs were commonly found inside the living hollow stems of *Polygonum senegalense* and probably, with the gradual disappearance of submerged standing trees, this plant will become one of the few habitats in which the nymphs can reside. *Povilla* therefore does not avoid living plants if these can provide a suitable substratum. The low incidence of the nymphs in *Pistia* in the Volta Lake seems to support this suggestion, as *Pistia* does not provide very suitable protection for the nymphs.

The burrowing activity appears to have the major result of protecting the soft bodied nymphs from predators. The nymphs do not feed on the plant material through which they burrow; this is indicated by the fact that the pieces of wood found in the alimentary tracts of the nymphs were not digested. Once in its burrow, the nymph maintains contact with the external environment through respiratory currents, produced by gill movements. These currents provide phytoplankton and well oxygenated water. During the day the nymphs avoid light by staying in their burrows. During the night they are more active, and in the Volta Lake they have been observed crawling on the submerged tree surfaces and feeding on the periphytic attached algae, such as *Oedogonium.* Periphyton seems to form a regular food item for nymphs of 6 mm and larger.

Whilst feeding on the periphytic algae, the nymphs, though partly hidden in the dense algal coatings, are still vulnerable to predators. In Lake Victoria the nocturnal mormyrid fishes feed to a large extent on *Povilla* removing all instars from the substratum. In Lake Volta, the nymphs are the major food item of dusk- and night-feeding pelagic fishes such as the clupeid *Pellonula afzeliusi,* and several species of *Alestes* (Reynolds, 1970). In this case, it is the last instar which is consumed whilst ascending to the water surface for emergence.

The vertical distribution of the food organisms, i.e. the planktonic and periphytic algae, seems to be one of the major factors determining the vertical distribution of the nymphs. This distribution is not obvious in floating papyrus plants, as their rhizomes do not reach deeper than 0.5 m. In flooded trees, the nymphs are found deeper, due to the presence of a suitable substratum. It is assumed that they are regularly present in trees down to a depth of 7-8 m, which is the usual maximum depth at which the nymphs are found on the bottom during stratification periods.

The high concentration of *Povilla* in the bark and wood of trees close to the water surface seems to be due to the presence of adequate numbers of phytoplankton and periphytic algae. The development of the attached algae is dependent on the light intensity and, with more light being available at the surface, denser periphytic algal growths develop, thus providing not only better feeding, but also better protection for the nymphs. In papyrus, the limit of the horizontal distribution of the *Povilla* nymphs can also be correlated with the gradual disappearance of the planktonic and periphytic algal sources, as a result of the lower light intensities inside the papyrus mat.

Oxygen concentration

In Volta Lake there are seasonal periods of stratification and mixing. During statification the oxygen ranges from ca. 90 per cent saturation at the surface to less than 10 per cent at the bottom. The vertical distribution and abundance of *Povilla* shows a seasonal pattern but this does not seem to be directly correlated with oxygen concentrations. During the stratified periods when the water is clear and there is a well developed periphytic algal growth, *Povilla*

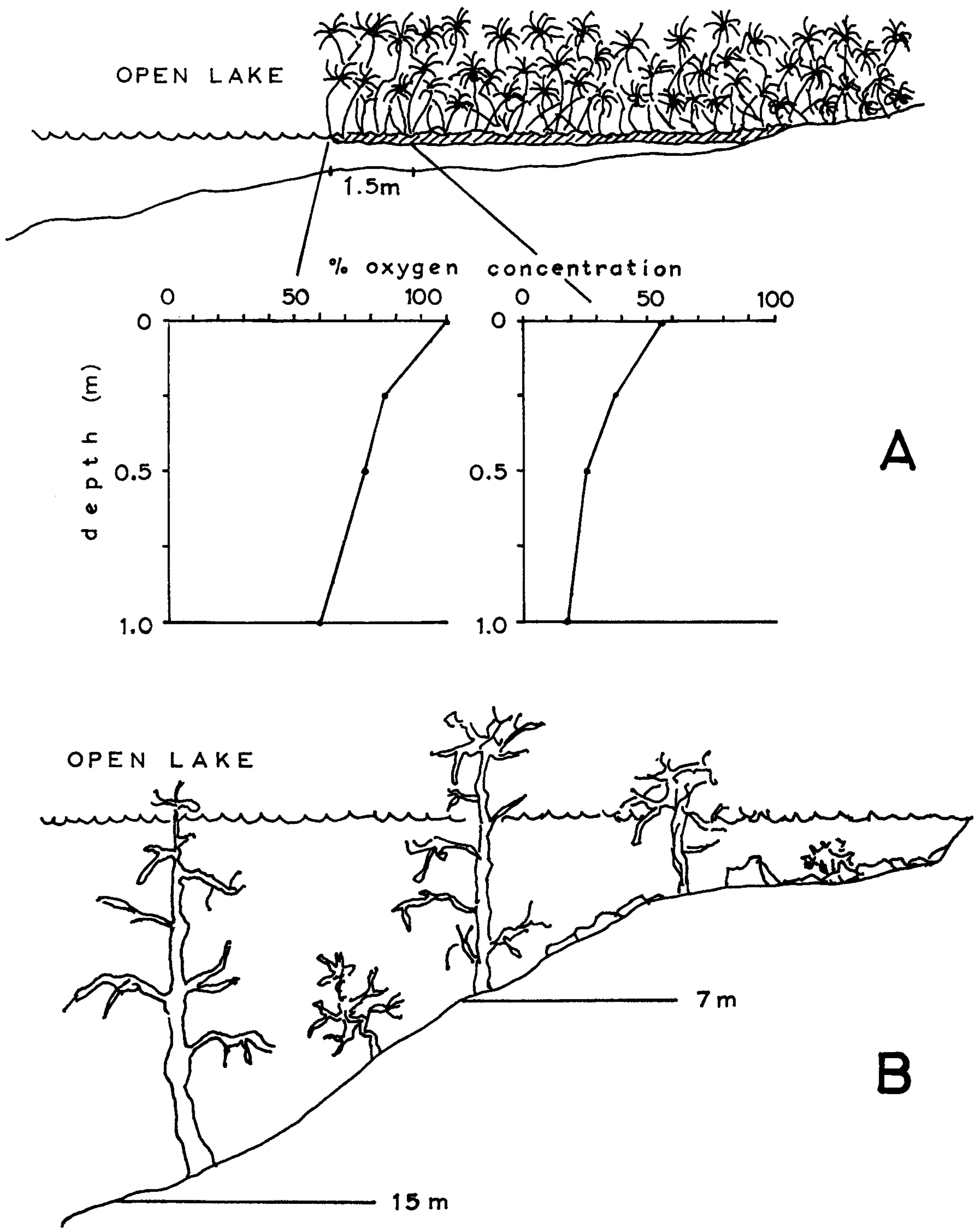

FIGURE 2. Habitats occupied by *Povilla* in Lake George, Uganda (A), and in the Volta Lake (B). A : Horizontal distribution of *Povilla* in the papyrus of Lake George, in relation to the oxygen concentration in water. B : Lake Volta (1966-1968). The average maximum depth of *Povilla* occurrence during stratification is 7m, with an average minimum oxygen concentration of 70 per cent saturation. The maximum depth of *Povilla* occurrence during mixing is 15 m, with an average minimum oxygen concentration of 40 per cent saturation.

tends to be restricted to the top 7 m, usually with the maximum abundance at about 4 m. Here the oxygen saturation is from ca. 70 to 90 per cent. The maximum range of distribution of *Povilla* was recorded during periods of water mixing, when it was collected from the 15 m depth (Fig. 2B). During mixing the oxygen is evenly distributed throughout the total water column, although the oxygen concentration is not as high as that found in the epilimnion during periods of stratification. At these times, although the organisms may be distributed deeper, their total number may be low. This probably reflects an intolerance to water of low oxygen concentration, although one nymph was found in water only 18 per cent saturated. Certainly the survival of *Povilla* nymphs in the laboratory was found to be markedly affected by oxygen concentration.

Povilla was found in the papyrus fringe of Lake George but it was restricted to the strip extending 1.5 m from the open water (Fig. 2A). Inland of this strip the oxygen concentration was less than 50 per cent of the value at the papyrus/open-water interface. The low oxygen concentration inside the papyrus mat may be the primary limiting factor, but the almost complete absence of both the planktonic and periphytic algae here may also limit the distribution of *Povilla* (see above). Also, the pH value of the environment may be of some importance. In Lake George *Povilla* nymphs have been collected from papyrus stems of pH 6.5 to 7.6, which are surrounded by water of pH 9.0. The nymphs were absent, however, in papyrus of pH value of 6.3 and less, these plants being in an advanced stage of decay. Whether the absence of *Povilla* in the papyrus is due to the low pH value, the soft spongy structure of the plant, or low oxygen content inside the decaying plant, is not known. Perhaps all three factors combine to control the horizontal distribution of the nymphs in the outer fringe of the papyrus.

Economic Importance of *Povilla*

In newly formed tropical man-made lakes no information is available on the speed with which flooded trees decay. Fish feeding on higher plants and detritus soon graze away flooded grass and the leaves of the submerged trees (personal communication, several sources). The wood and bark of trees above the water surface are attacked by wood-boring beetles, whilst those under water are burrowed by the *Povilla* nymphs. If the lake fills over several years, as in the Volta, the trees are gradually submerged and *Povilla* takes over the destruction of the wood and bark as the water level rises. The burrowing activity of *Povilla* is in part responsible for the quick disappearance of those trees with soft and moderately soft wood standing in the shallow waters. The trees become riddled and thus fragile through the activities of the nymphs, and are then more easily broken by wave action. In deeper waters the trees tend to remain intact.

As mentioned above, many fish feed directly on the nymphs of *Povilla*. In a newly formed man-made lake the fish population is recruited from the original riverine fauna, with a predominance of unspecialised feeders. These fishes easily adjust themselves in the lake to the new food sources unknown to them in their old habitats. The pelagic clupeid *Pellonula*, which exploits the nymphs as its main food source (Reynolds, 1970), developed into a large population in the lake, although it was never common in the river. Also other insectivorous and some omnivorous riverine fishes have started to exploit the new feed source. Altogether 14 fish species have been found to feed on *Povilla* in the Volta Lake (Reynolds, 1970).

In Lake Victoria the mormyrids are the main fish family feeding on *Povilla*, but in Lake

Volta this fish group has failed to establish itself. Although many insectivorous and omnivorous species of fish, originally in quantity in Lake Volta have failed to establish themselves permanently, this is apparently not due to the lack of a suitable food supply (PETR, 1968).

Early in the history of a man-made lake the fish production is high but the trees and other vegetation present prevent the use of efficient fishing methods for commercial exploitation. To overcome this problem, the authorities attempt to clear the trees from the major prospective fishing areas before flooding, and in the Volta this was done in two areas. But when the lake was established, the fishermen preferred to fish among the remaining trees. Analyses of the fish catches provide the answer to this seemingly illogical practice. The fish population in the new lake soon became dominated by tilapias, mainly *Tilapia galilaea* and *T. nilotica* (PETR, 1967). These fish congregate around the flooded trees, from which they graze away the attached algae. The fishermen soon discovered that nets set between and around trees catch more fishes than nets set in the cleared areas. Where partially submerged trees are present, tilapia fisheries have developed.

Povilla has one characteristic which has given it a central position in the productive ecology of the Volta Lake : the nymph is mobile. NEEL (1953) has emphasised that it is those aquatic insects which have mobile juvenile stages and can also make long lights for mating and oviposition, that are especially well adapted to conditions where there are seasonal changes in water level. During its maximum abundance in the Volta Lake *Povilla* lacked any marked seasonal emergence pattern, such as was observed in Lake Victoria (TJONNELAND, 1960); this continuous emergence allowed it to spread rapidly over the lake. Since it was the final instar nymphs which were much exploited as fish food, this pattern of continuous emergence also provided a steady supply of food. Organisms with a limited emergence period may be present in greater abundance, but are less valuable for fish production as they provide only an intermittent food supply.

The presence of flooded trees was responsible for a fairly high level of fish production for several years. The clearing of trees from large areas of Lake Kariba, whilst certainly resulting in good conditions for the use of fishing equipment, nevertheless leads to poor yields.

RÉSUMÉ

Facteurs limitant la distribution de *Povilla adusta* NAVAS (Éphéméroptères, Polymitarcidae) dans les lacs africains

1. Les larves de *Povilla adusta* NAVAS sont largement distribuées dans les eaux d'Afrique tropicale. Elles ont colonisé rapidement les grands lacs artificiels, l'exemple le plus spectaculaire se rencontrant dans le lac Volta, au Ghana.

2. Dans les lacs artificiels récents les larves s'enfouissent dans le bois et l'écorce des arbres debout et submergés où elles dominent la faune invertébrée. Les parties mortes du papyrus forment leur habitat dans les lacs naturels, bien qu'elles aient été trouvées dans d'autres types de substratum ayant une consistance plus ferme.

3. La distribution verticale et horizontale des nymphes semble être gouvernée par trois facteurs : la présence d'un substratum d'une consistance adéquate, une concentration suffisante en aliment, exemple : plancton, algues périphytiques, et une concentration en oxygène favorable. Dans le papyrus, un pH faible pourrait être la cause de l'absence de larve.

4. Dans le lac Volta les larves de *Povilla* contribuent grandement à la productivité totale du lac, en établissant un lien entre le producteur primaire et le consommateur tertiaire, et en étant largement consommées par les poissons insectivores. Leur activité fouisseuse augmente la vitesse de destruction des arbres submergés dans les nouveaux lacs artificiels et aussi celle des papyrus en décomposition sur le bord des lacs tropicaux naturels d'Afrique.

Zusammenfassung

Einige Faktoren, welche die Verbreitung von *Povilla adusta* Navas (Ephemeroptera, Polymitarcidae) in afrikanischen tropischen Seen bestimmen.

1. Die Nymphen von *Povilla adusta* Navas bewohnen mehrere afrikanische tropische Süssgewässer und haben schnell die grossen tropischen Stauseen wie Kariba und Volta, besiedelt.
2. In den neuen Stauseen bohren sich die Nymphen von *Povilla* in die Rinde und das Holz überschwemmter Bäume. Hier dominieren sie über andere Wirbellose wie Larven von Chironomiden und Köcherfliegen und stellen mehr als 90 % der Biomasse. In den natürlichen Seen wie zum Beispiel Viktoria und George-See findet man die Nymphen von *Povilla* in toten Teilen der Papyruspflanze, aber auch in anderen Wasserpflanzen.
3. Die vertikale und horizontale Verteilung der Nymphen auf einem Wasserboden scheint von drei Faktoren abhängig zu sein : von einem günstigen Substrat, von einer ausreichenden Nahrung wie Plankton- und Aufwuchsalgen und von einer ausreichenden Sauerstoffkonzentration des Wassers. Im Lake George (Uganda) vermeiden die Nymphen faulende Papyruspflanzen, in welchen pH-Werte von 6,3 und weniger gemessen wurden.
4. Die Nymphen von *Povilla* haben viel zu der Produktivität des Voltastausees beigetragen, wobei sie in der Nahrungskette, welche sie zwischen den Primärproduzenten, d.h. Planktonalgen und Aufwuchsalgen, welche sie konsumieren, und den Insektenfressenden Fischen, welchen sie als Nahrung dienen, stehen.

Discussion

L. Berner : I was very pleased to see the pictures of the Volta River, because I had not seen it in 20 years. When I last saw the lake area, it was a gorge with an extremely rapid portion of river and at that time I saw no *Povilla* at all.

G. Edmunds : Yes, Dr. Berner did the original preimpoundment survey on this river.

C. Fremling : I thought it interesting that fish only feed on the last instar nymphs. In American waters where we have burrowing mayflies, fish feed on all instars. Apparently they do this by biting into the bottom and taking a mouthful of mud. Fish get *Hexagenia* when the nymph is in the burrow, and also when it leaves its burrow because of low oxygen levels or intraspecific strife. But in Ghana, apparently, fish cannot bite into the trees to get nymphs, so they only feed on the last instar of *Povilla*.

G. Edmunds : Does *Hexagenia* drift only in times of stress ?

C. Fremling : I think the main cause is intraspecific strife. They also leave their burrows in lakes if the oxygen level in the hypolimnion is decreased. This explains why there sometimes are peaks of *Hexagenia* nymphs in certain species of fish, like walleye. In the Mississippi River we find *Hexagenia* nymphs of all instars will drift down the river by the tons. There are other factors, but I only know of two for sure.

G. EDMUNDS : They drift more at night than during the day?

C. FREMLING : Yes, at night.

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