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Substrate Relations of the African Wood-burrowing Mayfly *Povilla adusta* Navás (Ephemeroptera, Polymitarcyidae)

by

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Colonization of an artificial substrate (polyurethane foam) by nymphs of the wood-burrowing mayfly *Povilla adusta* was studied in a natural West-African lake (Opi Lake). Nymphs readily colonized the substrate in densities up to 11,000 m^{-2} (early instars) and at depths $\leq$ 1.5 m. Blocks with rough surfaces and those in close proximity to oviposition sites near-shore, had larger densities of nymphs than did those with smooth surfaces or those placed off-shore. The upper surfaces of submerged blocks had smaller numbers of larger nymphs than did lower surfaces. Differences in the abundance of periphyton on the various surfaces may account for some of these patterns. The generation time of *P. adusta* is estimated to be three months in Opi Lake.

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INTRODUCTION

The African wood-burrowing mayfly *Povilla adusta* Navás 1912 may be of considerable economic importance, both through its abundance in the diets of commercial fish species (P. Corbet, 1957; Reynolds, 1970; Petr, 1973) and for the damage it causes to wooden structures such as boats (P. Corbet, 1957; Hartland-Rowe, 1958). Nymphs of *P. adusta* burrow in a variety of firm substrates including submerged trees (Petr, 1970; McLachlan, 1970), aquatic plants (Hartland-Rowe, 1958; Dejoux, 1969) and sandy-clay sediments hardened by previous exposure to air (this study). Nymphs appear to ingest little of the substrate in which they burrow (although wood may be found in the gut; Petr, 1970), but use their silk-lined tunnels as a refuge from predators and a site in which to filter-feed (Hartland-Rowe, 1953). Nymphs play an important role in the breakdown of submerged trees in recently flooded reservoirs and the transfer of energy from primary producers to predators in these systems. Several Oriental species of the genus are likely to have similar habits (Hubbard, 1984).

The occurrence of *P. adusta* nymphs in the hard, irregular surface of woody substrates makes difficult the accurate estimation of population densities. Fur-

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thermore, the co-occurrence of several cohorts (Hartland-Rowe, 1958; S. Corbet, Sellick & Willoughby, 1974) makes difficult the determination of generation time. In order to overcome these difficulties, an artificial substrate from which all nymphs could be easily removed was used in this study. Variations with time, depth and surface roughness were measured. Furthermore, assuming that colonization was effected largely by early instar nymphs, the development of a single cohort could be followed and thus the generation time estimated. The use of an artificial substrate in the natural environment should yield better estimates of population paramaters than those obtained from laboratory studies. However, as with any artificial substrate, results may differ somewhat from those obtained on natural substrates.

STUDY AREA

Opi Lake A (hereafter referred to as Opi Lake) is one of a series of small lakes located near the boundary of the guinea savanna and lowland moist forest regions in southeastern Nigeria (6°45′0″N, 7°29′30″ E; Hare & Carter, 1984). Opi Lake possesses no permanent surface water source and thus undergoes substantial seasonal fluctuations in water depth (Zmax 2.5-4.0 m) and surface area (1.3-2.0 ha). Its waters are very dilute (conductivity 15-24 μS cm^{-1} at 25°C), acidic (pH 6.0-6.5) and of low transparency (Secchi depth 0.6-1.7 m). Lake climate is markedly seasonal in character, alternating between distinct rainy (May-October) and dry (November-April) periods. Lake bottom water temperature is at its minimum (24°C) during the early dry season and reaches its maximum (29°C) in the late dry season, the period of minimum water depth and maximum phytoplankton abundance. Lake waters follow a diel cycle of thermal stratification and destratification except in the late rainy season when low wind speeds lead to permanent stratification and anoxia of the bottom waters. Complete circulation is restored at the onset of the northerly "Harmattan" winds in November or December (Hare & Carter, 1984).

Seventy-five species of phytoplankton are known from the lake. Members of the Chlorophyta (42 spp.), especially the Desmidiales (21 spp.), predominate throughout the year (Biswas, 1984). Most abundant among the zooplankton are several species of Rotifera, the cladoceran *Moina micrura* Kurz and the cyclopoid copepod *Thermocyclops consimilis* (Kiefer) (Hare & Carter, 1987a). The mid-lake benthic fauna is dominated by a few species of *Chaoborus, Chironomus, Procladius* and *Tanypus* (Hare & Carter, 1986), while in near-shore areas many species of Chironomidae (Hare & Carter, 1987b), Ephemeroptera, Odonata, Hydracarina and Oligochaeta are present (Hare, 1986).

METHODS

Experimental designs

Colonization with time
A large number of rigid polyurethane foam (Styrofoam) blocks (17x20 cm in size), were tied individually to an anchor so as to float freely at the water surface, with only the lower side wetted. One such group was placed at a near-shore site adjacent to over-hanging and partially submerged branches of lakeside trees (mid-west side of lake; Hare & Carter, 1984), while a second group was placed over deeper water, 10 m off-shore from the first site. All blocks were placed on 13 October 1979 (time 0). Three blocks were collected from each of the near-shore and off-shore groups on each sampling date between 20 October 1979 (week 1) and 10 February 1980 (week 17).

Colonization and surface texture
The surfaces of Styrofoam blocks (17x20 cm in size) were roughened, either with a metal file or a scalpel (scored with parallel grooves 1.5 cm apart), or left smooth (5 blocks of each treatment). All blocks were attached to an anchor and placed floating at the lake surface, at the near-shore site, for a period of two months (24 November 1979-20 January 1980).

Colonization with depth
Styrofoam blocks (15x13x3 cm in size) were placed on lengths of steel pipe (2.5 cm diameter) through holes cut in their centres. Blocks were tied at 0.25 m depth intervals by holes drilled in the piping. Pipes were pushed into lake-bottom sediments so that their uppermost blocks were 0.25 m below the water surface and the lowermost blocks were at a depth of 1 m (near-shore) or 2.25 m (off-shore). Pipes were pushed further into the sediment on a weekly basis so as to compensate for the gradual decline in water level during the study period. Three lengths of pipe were placed at each of the near-shore and off-shore sites for a period of three months (20 October 1979-12 January 1980).

Laboratory procedures

Blocks were placed individually in plastic bags for transport to the laboratory where nymphs were removed with forceps, counted, preserved in 10% formalin and their total wet preserved weight measured. Nymphs having a head-capsule width $\geq 960\,\mu m$ were sexed by the presence of developing external genitalia on the penultimate sternite of males or their absence on females. Head capsule width was measured as the distance between the tips of the anterior-most tubercles, a pair of which lies at either side of the base of each antenna.

RESULTS

Colonization with time

Blocks were not colonized during the first week of the study (Fig. 1). Mean numbers of nymphs were low prior to week 3, increased somewhat between weeks 3 & 4 and 8 & 11 (Fig. 1A), then changed little or declined until week 14 (off-shore) or 15 (near-shore), after which time large increases occurred (Fig. 1A). Nymphs tended to be more abundant but smaller (prior to week 14) on near-shore than on off-shore blocks (Fig. 1).

Mean nymph weight increased during the first 11 to 13 weeks of the study, then declined (Fig. 1B). This reflected the gradual growth of nymphs up until weeks 11 to 13 and their subsequent emergence (Fig. 2) as indicated by the

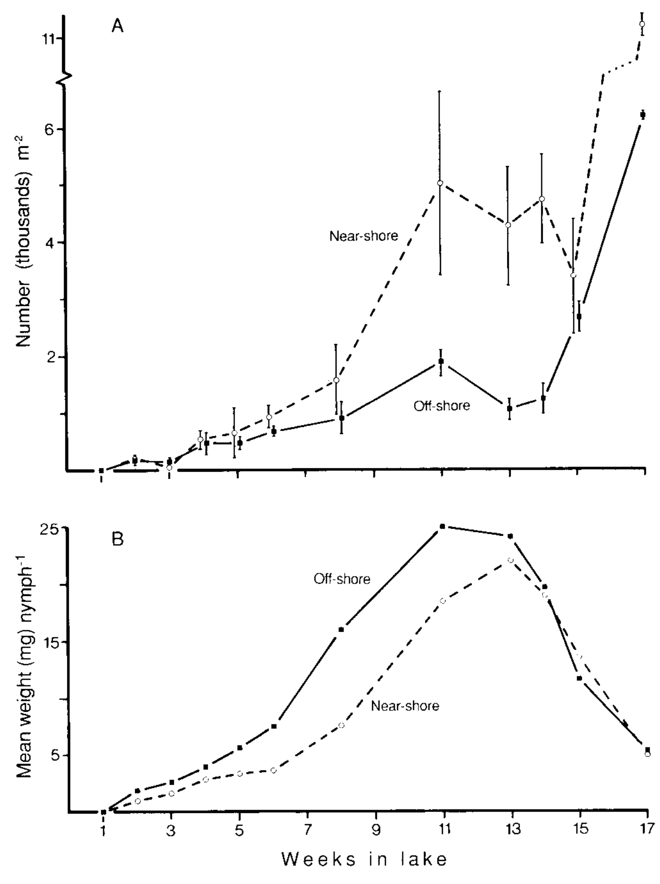

Fig. 1. A) Abundances ($\overline{X} \pm$ S.E., n = 3), and B) mean individual wet weights (n=3), of *Povilla adusta* nymphs on floating Styrofoam blocks placed for various lengths of time at a near-shore or an off-shore site.

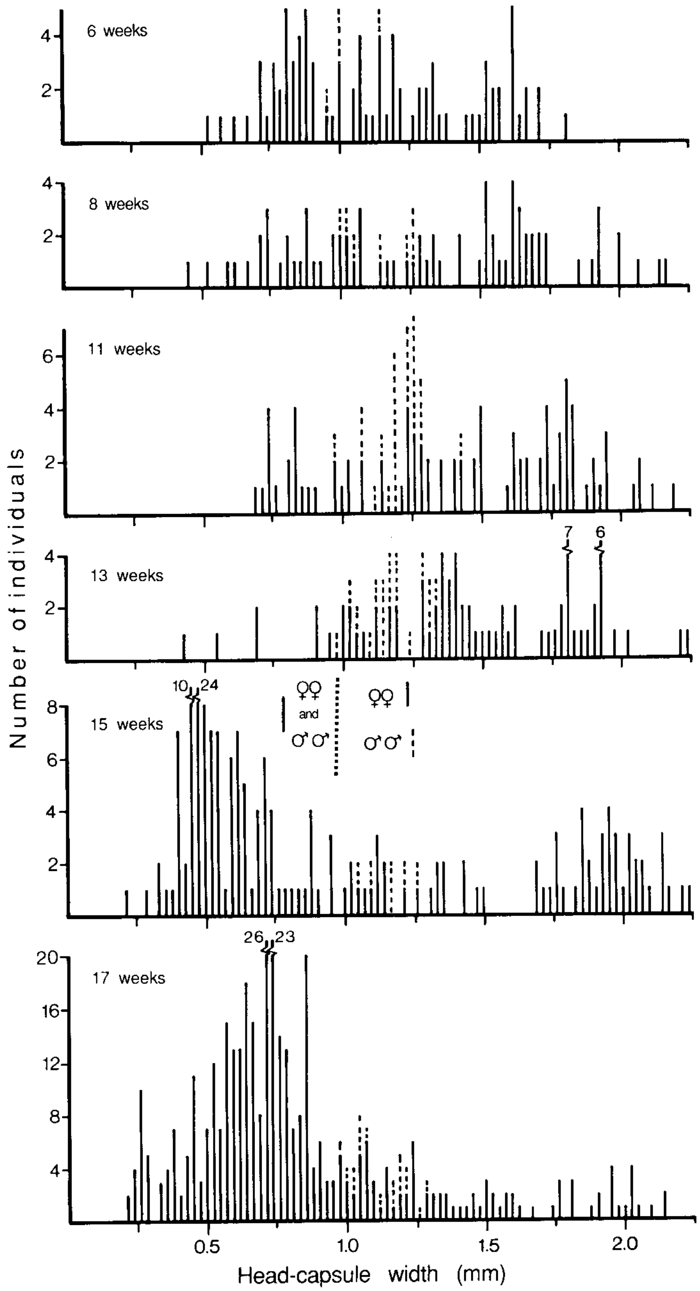

Fig. 2. Size distributions (as measured by head-capsule widths) of *Povilla adusta* nymphs on floating Styrofoam blocks placed for various lengths of time at an off-shore site. Nymphs were sexed at head-capsule widths ≥ 0.960 mm (above this size: females ——; males - - - -).

presence of large empty burrows. The size of male nymphs at emergence was much less than that of females (Fig. 2). A second and larger cohort of early instar nymphs colonized the blocks after week 13 (Fig. 2).

Colonization with depth

Nymphs were not found on blocks at depths beyond 1.5 m (Fig. 3). Abundances varied little above this depth. On the lower surfaces of blocks, nymphs were more numerous (Figs. 3 & 4A) but had a lower mean weight (Fig. 4B) than those on the upper surfaces. Nymphs were more numerous on near-shore than on off-shore blocks (Figs. 3 & 4A).

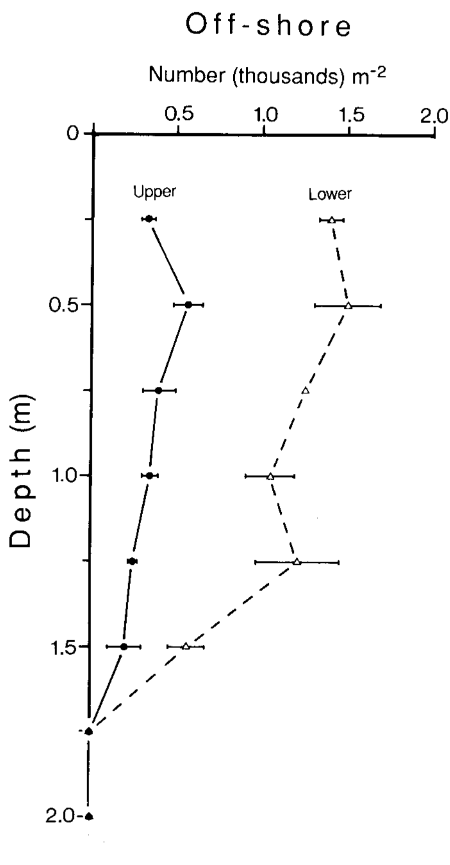

Fig. 3. Abundances ($\bar{X} \pm$ S.E., n = 3) of *Povilla adusta* nymphs on the upper and lower surfaces of Styrofoam blocks placed for three months, at various depths in the water column, at an off-shore site.

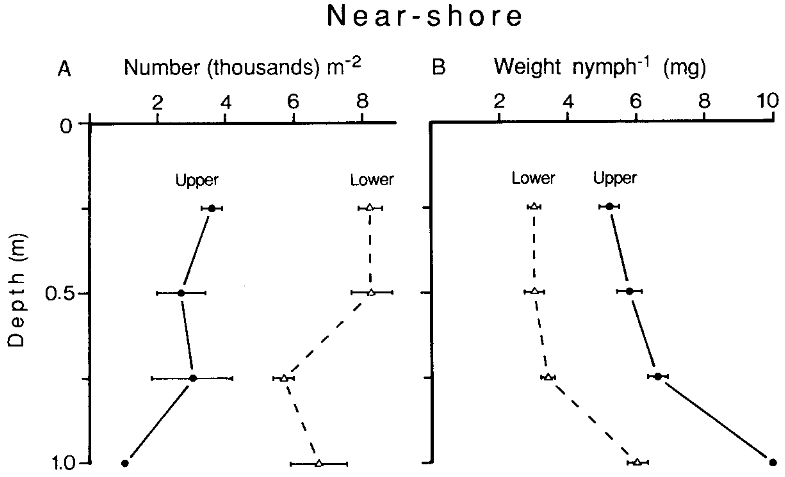

Fig. 4. A) Abundances, and B) mean individual wet weights (all $\bar{X} \pm$ S.E., n = 3), of *Povilla adusta* nymphs on the upper and lower surfaces of Styrofoam blocks placed for three months, at various depths in the water column, at a near-shore site.

Colonization and surface texture

All submerged blocks supported larger densities of nymphs on their edges than on their upper or lower surfaces (data not shown). This result was probably an artefact of the greater roughness of the edges, they being the surfaces along which the blocks were cut from larger sheets. This supposition was supported by results from blocks whose surfaces had been roughned prior to placement. Smooth-surfaced blocks had 525 ± 95 nymphs m^{-2}, while surfaces roughened with as metal file supported 2,615 ± 685 nymphs m^{-2} and those roughened with a scalpel had 3,590 ± 1,000 nymphs m^{-2} (all $\bar{X} \pm$ S.E., n = 5). Mean weights of nymphs on the three types of surfaces differed little (24,23 and 22 mg $nymph^{-1}$, respectively).

DISCUSSION

Colonization with time

Blocks were not colonized during the first week of exposure, either because they required a conditioning period in the lake water, or because potential colonizers were not present at that time. The availability of early instars for substrate colonization may be discontinuous in many systems, a consequence of the periodic mass emergence of adults (Hartland-Rowe, 1958; S. Corbet et al., 1974). Colonization occurred mainly by the influx of early instar nymphs, as large individuals were uncommon during the first weeks of the study. Thus, although large individuals may leave their burrows at night to graze on periphyton (Petr, 1970; Bidwell, 1979), they do not appear to travel far.

After the emergence period, blocks were recolonized to greater abundance levels than those of previous weeks. The increased roughness of the surface due to the presence of old burrows may have increased the surface area available for burrowing by colonizing nymphs. Blocks roughened prior to their placement in the water supported larger numbers of nymphs than those which had not.

The generation time of *P. adusta* is usually difficult to determine since several cohorts will be present simultaneously in natural populations (S. Corbet et al., 1974; Bidwell, 1979). By following a single cohort through its development on a newly-placed substrate, as in this study, a direct estimate of the generation time is possible. Assuming that the duration of the egg stage is two weeks (P. Corbet, 1957; Hartland-Rowe, 1958) and development to the third instar (the first burrowing stage; Hartland-Rowe, 1958) takes one week (Petr, 1970), nymphs colonizing blocks in the second week of the experiment would have been about three weeks of age. As emergence was first observed at the eleventh week, this would indicate a maximum generation time of 12 weeks. Longer generation times (4-5 months) have been proposed for *P. adusta* populations in Lakes Kainji (Bidwell, 1979) and Victoria (P. Corbet, 1957), while a generation time similar to that in Opi Lake (3 months) was proposed for nymphs in the crater lake Barombi Mbo (S. Corbet et al., 1974). Water temperatures in Barombi Mbo and Opi Lake were generally higher than those in the former two lakes, which may explain the shorter development times of *P. adusta* in these systems (S. Corbet et al., 1974; Bidwell, 1979).

Colonization with depth

Nymphs of *P. adusta* have been collected in some lakes at depths as great as 15 m (Petr, 1973). Their limitation to shallow depths in Opi Lake (≤ 1.5 m) was probably not a function of water temperature since depth differences in temperature were slight (< 1.5°C between 1.5 & 2.0 m at any one time).

Late-instar nymphs are known to feed largely on periphyton (Bidwell, 1979), the depth distribution of which may have been light-limited in Opi Lake due to the low transparency of the water (0.6-1.5 m Secchi depth during the study period). At the end of the experiment, blocks at depths ≤ 1.5 m were covered with a distinct green film of periphyton, those at 1.75 m had only a thin film and those below this depth were bare. On the other hand, early instar nymphs, which filter-feed on phytoplankton (Hartland-Rowe, 1953), should have been able to colonize greater depths since phytoplankton was usually abundant below 1.5 m (Biswas, 1984).

Bidwell (1979) has suggested that oxygen levels below 60% saturation may be limiting to *P. adusta*. Lower oxygen concentrations were recorded in Opi Lake early in the study period (minima of 35% & 20% saturation at 1.5 & 2.0 m, respectively during October-November 1979). Later in the study, oxygen levels remained ≥ 60% saturation at depths ≤ 1.5 m but fell to 50% saturation at 2.0 m. Lower levels may have occurred between these weekly measurements. Thus both periphyton and oxygen may act to limit the depth distribution of *P. adusta* nymphs in Opi Lake.

The occurrence of fewer nymphs of larger size on the upper than the lower surfaces of blocks may be a consequence of the presumably greater periphyton abundance on the upper surfaces. Body size of nymphs has been reported to show a direct relationship with periphyton abundance (Bidwell, 1979). Large nymphs, which prefer a periphyton-covered surface for feeding (Bidwell, 1979), may exclude smaller ones from colonizing surfaces on which they are abundant.

Distance from shore

Nymphs were more abundant on near-shore than off-shore blocks, both at the surface and at greater depths, probably a consequence of the proximity of near-shore blocks to oviposition sites (egg masses were collected from the submerged leaves and branches of trees near the blocks). In order to reach off-shore blocks, nymphs would either have had to swim some distance (10 m) or be carried by water currents (which may be weak in this small, sheltered lake). The lower number of nymphs on off-shore blocks would have provided a greater mean feeding area for each nymph, which may explain the more rapid increase in nymph body size observed on these blocks. An alternate possibility, that periphyton abundance was less on near-shore blocks (perhaps a consequence of their shading by trees in the late afternoon) cannot be excluded.

RÉSUMÉ

Povilla adusta Navás (Ephemeroptera, Polymitarcyidae), une espèce répandue en Afrique, a une importance économique due à son habitude de creuser dans le bois submergé (bateaux) et à son abondance dans les diètes de plusieures espèces de poisson. La colonisation par cette espèce d'un substrat artificiel (polyuréthane rigide) était étudiée dans un lac de l'Afrique de l'Ouest (Lac Opi). Les nymphes ont colonisé le substrat en grand nombre (jusqu'à 11,000 m^{-2}) allant jusqu'à une profondeur de 1.5 m. Les blocs de substrat situés plus proches des sites d'oviposition et avec les surfaces plus rugueuses étaient colonisés d'avantage. Sur les surfaces supérieures des blocs immergés, les nymphes étaient moins nombreuses mais plus grosses. L'abondance du périphyton sur les blocs a joué probablement un rôle dans la distribution des nymphes. La durée d'une génération de *P. adusta* est estimée à trois mois dans le Lac Opi.

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