

Population dynamics of Hydropsychidae (Insecta ; Trichoptera) in the N'Zi River (Ivory Coast), a temporary stream partly treated with the insecticide Chlorphoxim⁽¹⁾

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Abstract

In the temporary river N'Zi —an affluent of the Bandama (Ivory Coast)—the population dynamics of four species of hydropsychid caddis flies, Cheumatopsyche spp., and Aethaloptera dispar, were followed from January 1977 until March 1978. From June 1977 until December 1977 parts of the N'Zi were treated with the insecticide Chlorphoxim (organophosphate compound) in order to evaluate the effects of such treatment on Simulium damnosum—the vector of human onchocerciasis in West Africa—and on the non-target fauna.

The hydropsychid larvae and pupae were obtained by using a Surber sampler, a core sampler, and from qualitative samples, yielding a total of about 17,000 specimens. These were identified to the instar level.

Densities at the surface of the substratum as well as in the hyporheic habitat appear to be influenced by the discharge pattern. Decreasing discharge and consequently a reduction of areas with sufficient current produce increasing larval and pupal densities per surface unit. It is suggested that zones with sufficient current, which are controlled by the morphology of the rapid in relation to a certain discharge and to some extent by the density of larval tubes of A. dispar, determine the level of intra- and interspecific aggression between the Cheumatopsyche spp. and thereby leads to changes in relative abundances of the species and probably their instars.

While A. dispar is not able to survive the periods without flow in its aquatic stage, Cheumatopsyche spp. can, probably in the remaining stagnant pools. The instar distribution as well as the changes in the mean weight of the Cheumatopsyche spp. suggest that a period of increased reproduction occurs after resuming flow and at the end of the spate of the main rainy season. Undoubtedly the larval life of the species studied here lasts longer than is generally assumed for insects of tropical rivers, and probably only two or three generations per year occur.

The results are discussed in relation to the secondary productivity of African streams.

Since all four species are seriously affected by the chlorphoxim treatment, their disappearance is briefly discussed in relation to the consequences for the ecosystem, and especially to the decrease in the predator pressure on Simulium damnosum.

KEY WORDS : Africa - Running Water - Benthos - Ecology - Development - Pesticides - Ivory Coast.

Résumé

Dynamique des populations d'Hydropsychidae (Insecta; Trichoptera) dans le N'Zi (Côte d'Ivoire), rivière temporaire partiellement traitée à l'insecticide Chlorphoxim

La dynamique des populations de quatre Hydropsychidae (Trichoptera), trois Cheumatopsyche spp. et Aethaloptera dispar, a été étudiée de janvier 1977 à mars 1978 sur le N'Zi, affluent du Bandama (Côte d'Ivoire), cours d'eau temporaire. De juin 1977 à décembre 1978 certaines parties du N'Zi furent traitées avec un inseclicide

⁽¹⁾ The field studies and parts of the laboratory studies were carried out during a period of World Health Organization consultantship in the Onchocerciasis Control Programme (O.C.P.).

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(Chlorphoxim, composé organophosphoré) dans le but d'étudier les effets sur la faune cible et non cible, de tels épandages destinés à détruire Simulium damnosum, vecteur de l'onchocercose humaine en Afrique de l'Ouest.

Dic-sept mille spécimens d'Hydropsychidae, déterminés au niveau du stade larvaire furent récoltés par prospections qualitatives et quantilatives à l'échantillonneur de Surber et au carottier.

Les densités tant hyporhéiques qu'à la surface du substrat varient en fonction du débit. Un débit décroissant lié à une diminution des zones présentant un courant suffisant augmente les densités larvaires et nymphales par unité de surface. Il est vraisemblable que le niveau d'agression inter- et intraspécifique entre les Cheumatopsyche spp. modifie les abondances relatives des espèces et probablement des stades larvaires. Il est déterminé par l'existence de zones présentant un courant suffisant, ces zones étant elles-mêmes, sur chaque rapide, fonction de la morphologie du cours d'eau, du débit et de la densité des tubes larvaires d'A. dispar.

Contrairement à A. dispar, les Cheumatopsyche sont capables de survivre à l'état larvaire pendant la période d'étiage, probablement dans les mares stagnantes qui subsistent. Les répartitions par stades et les changements de poids moyen suggèrent qu'une période de reproduction accrue survient après le retour de l'écoulement ainsi qu'à la fin de la période de crue de la principale saison des pluies. La durée du développement larvaire des espèces étudiées ici est plus longue que celle généralement avancée pour les insectes des rivières tropicales et il n'y a probablement que deux ou trois générations par an. Ce résultat est discuté dans le cadre de la production secondaire des fleuves africains.

Les quatre espèces étudiées ici étant sérieusement affectées par les traitements au chlorphoxim, leur disparition est brièvement discutée dans l'optique de ses conséquences sur l'écosystème et en particulier de la diminution de pression prédatrice sur Simulium damnosum.

Mots-clés : Afrique — Eaux Courantes — Benthos — Écologie — Développement — Pesticides — Côte d'Ivoire.

1. INTRODUCTION

Seasonal tropics or constant tropics? Considering benthic invertebrates of permanent streams near the equator in Africa, their populations are obviously fluctuating (Böttger, 1975; CRIDLAND, 1958; Ko-PELKE, 1981; LEHMANN, 1979; MALAISSE and RIPERT, unpubl., cit. ex MALAISSE, 1974; RAMANAN-KASINA, 1973; STATZNER, 1976; ZWICK, 1976).

Such fluctuations in the benthic invertebrate fauna have been suggested and confined also for temporary or nearly temporary streams in African savannah areas (CRISP, 1956; HARRISON, 1966; J. D. HYNES, 1975a, b; LE BERRE, 1966; PETR, 1970). However, probably due to taxonomic difficulties of such studies, detailed investigations on the population dynamics of single species are few, and, in these African areas, to the best of my knowledge, restricted to the *Simulium damnosum* complex (LE BERRE, 1966), the vector of human onchocerciasis in West Africa.

The temporary river N'Zi (Ivory Coast) was chosen for a large-scale field investigation into the effects on the aquatic target and non-target fauna of regular applications of the insecticide chlorphoxim, directed against *Simulium damnosum*.

It was hoped that observations on the recovery of the fauna after larviciding as compared with data from the untreated control section of the N'Zi would give indications about the life cycles of the four abundant hydropsychid species studied in this paper as well as their contribution to secondary production. The use of insecticides in such kinds of studies was introduced by H. B. N. HYNES and WILLIAMS (1962).

This paper also considers the effect of the insecticide on the four hydropsychid species it deals with. Other invertebrate species from different streams in the Ivory Coast will be studied in papers shortly to be published by the hydrobiological team of the O.R.S.T.O.M. in Bouaké (Ivory Coast), with which I was associated during a period as consultant of the W.H.O.

2. METHODS

Five sampling places were visited once a month between January 1977 and March 1978. At low and medium discharges qualitative samples were taken from all substrata colonized by the four hydropsychid species. This was carried out according to the approximate relative abundance of the hydraulic conditions (combination of the factors: velocity, substrate type, water depth) on a rapid, a method which is thought to be necessary in studies on life cycles of running water species (STATZNER, 1981a). Three additional samples (June 1977) came from gutter experiments, a method described in detail by DEJOUX (1975) and TROUBAT (1981). The samples were brushed into a bucket, the content of the bucket then was sieved through a $200 \,\mu m$ mesh.

At one rapid (Ouokoukro, see 3.) Surber samples were taken from a gravel and pebble substratum. The sampler used (see fig. 3 in Lévêque et al., 1977) was almost square sampling an area of 16×17 cm, with the mean mesh size of $320 \times 200 \ \mu\text{m}$. Since the net was made from curtain material, variations in the meshes reached up to $600 \times 280 \ \mu\text{m}$.

At the same rapid where Surber samples were taken, the colonization of the hyporheic habitat (gravel/pebble substratum) was investigated through one year; at other rapids this aspect was studied only occasionally. This was done by using a core sampler (for details see STATZNER, 1979). During the dry season in 1978, a hole was dug in the dry part of the rapid until the subterranean water appeared. The water was then sieved through a 200 μ m mesh.

In the field the material was conserved by using ca. 80 % alcohol, and lateron sorted out in the laboratory with the aid of stereomicroscopes. Instar separation and dry weight determination were carried out as described in STATZNER (1979).

3. AREA STUDIED - THE N'ZI RIVER

3.1. General description, chlorphoxim application, geomorphology

The N'Zi River in the Ivory Coast is a tributary of the Bandama River (fig. 1). Similarly to most of the large rivers in that country, the N'Zi flows from the north to the south. In the rainy season the N'Zi originates south of Ferkéssédougou. It enters the Bandama north of Tiassalé, thus extending between 6° and 10° North.

Among the numerous rapids, five rapids accessible by car were chosen for a regular survey. Since the effect of a regular insecticide application on the nontarget fauna of that river was the primary aim of the investigation, out of five stations, three were situated in the treated area: Tinbé, Kolomikro, and Bocanda (fig. 1).

Tinbé was the only station situated in the operational area of the Onchocerciasis Control Programme (O.C.P.) at that time, thus it was treated before with Temephos (Abate), the operational larvicide used during the first phase of the area treatment since 1974. Abate applications stopped on the 1st December, 1976.

The application of Chlorphoxim, the larvicide tested during the period of this investigation, started on 14th of June 1977 at Tinbé and on 28th of June 1977 at Kolomikro and Bocanda.



FIG. 1. — The area studied with the monthly sampled rapids of the N'Zi River (indicated by a black triangle) considered in this study. Dashed: area of larvicide application

The N'Zi and, occasionally, some affluents of the N'Zi were treated with Chlorphoxim sprayed from a helicopter once a week. During the dry season each rapid was treated separately, during the rainy season (when the insecticide carries better) the insecticide was applied in general every 20 km. Normally 0.025 ppm per 10 minutes of Chlorphoxim was applied, but sometime overdosage occurred, especially in the north during low discharge conditions. The last Chlorphoxim application was on the 14th December, 1977.

The middle section of the studied stretch of the N'Zi was chosen as control and it was not treated with larvicide. Here two sampling stations were established at Fetekro and Ouokoukro (fig. 1). Fetekro was treated previously with Abate (from Oct. 1976 until 1st Dec. 1976). At Ouokoukro, an unknown poison was probably applied between Nov. and Dec. 1977 (local fishermen use this method sometimes for fishing). The investigated stretch of the N'Zi exhibits only a weak slope (DE MERONA, 1981). The five rapids' characteristics are:

Tinbé: a natural rapid; mostly smooth rocks and stones.

Fetekro: an artificial rapid, remains of an old bridge; mostly large stones with a smooth surface.

Ouokoukro: a natural rapid; mostly gravel/pebble, few rocks with a smooth surface.

Kolomikro: a natural rapid; mostly rocks and large stones with an uneven surface.

Bocanda: a natural rapid; mostly rocks, large stones with an uneven surface; gravel/pebble.

The main difference between these five rapids was in the cross-section (fig. 2), which, in periods of diminishing discharge resulted in a different speed of the decrease of the area of habitats with current. For example in Kolomikro the surface area and the number of habitats in the current decreased more rapidly with a reduced discharge, than in Bocanda, where a small decrease in discharge resulted in a more gradual reduction of such habitats, until the whole rapid dried out except a small v-shaped channel.

The part of the N'Zi investigated flows through savannah. The banks of the N'Zi, covered by a gallery forest, were mostly undisturbed, except for small areas of cultivation. There were only two regions in which large plantations were situated, viz. around M'Bahiakro (rice) and around Kolomikro (cotton).

3.2. Physical and chemical properties

Data on the hydrology of the N'Zi came from different sources. The hydrological team of O.R.S.-T.O.M. monitored four water gauges in the experimental area of the N'Zi on a more or less regular basis. Where necessary, the records of O.R.S.T.O.M. were complemented with data from ILTIS (pers. communication) and O.C.P. (measurements by helicopter pilots). Where data were available, with the curves from CAMUS (1971) and preliminary curves for Tinbé the discharge was calculated for four points (fig. 3). It should be noted that the Bocanda gauge was situated about 10 km downstream from the principal sampling place.

The discharge pattern was similar at all stations. At the beginning of 1977 discharge decreased to zero first in the north and later also in the south. The river started flowing again in the last week of April, reaching a peak in June, and dropping afterwards. At the end of August the main rainy season started. The annual maximum of discharge was recorded in September and October. With the beginning of the dry season at the end of October discharge decreased



FIG. 2. — Scheme of the cross section of the five monthly sampled rapids

again and in the northern station reached zero in February 1978.

The 16 years' discharge data for the N'Zi (CAMUS, 1971) demonstrate a high variation. The monthly means of these 16 years (fig. 3) differ as a lot of the single years from the pattern of the study period by the lack of the decrease in discharge from June to August. Considering these means, discharge steadily increased from March until the rainy season. Cessation of flow was not observed during CAMUS' investigations in Fetekro, M'Bahiakro, and Bocanda. Sometimes the discharge decreased to a few litres/sec, the minimum reported was 1 litre/sec in February 1957 in Bocanda. From the hydrological data one can conclude that the N'Zi was running over the whole stretch only in the rainy season. As the discharge decreased the river became a series of interconnected pools divided by rapids. These rapids can be characterized as short lake outflows and inflows. After the river stopped flowing the pools remained. This had an effect on water temperature and transparency (fig. 3).

Water temperature showed a relatively large range at the beginning of the year (low discharge) as compared to the narrow range in the rainy season (maximum discharge).

Transparency (measured by a Secchi disc) increased with decreasing discharge and vice versa. At Bocanda, where the transparency was measured most frequently, it was significantly related to the discharge by : transparency (cm)=45.7-14.4 log discharge (m³/sec) (n=11; r=-0.65).

Although relationships between discharge and the transport of particulate matter are complex (MAN-GELSDORF and SCHEURMANN, 1980), the above formula implies that transparency was mainly influenced by soil wash-in and sedimentation.



Fig. 3. - Discharge, transparency, and water temperarure of the N'Zi River

Planktonic primary production, which in the pools is expected to be highest at lowest discharge, did hardly affect the transparency. Benthic primary production was related to transparency, since aquatic macrophytes covered large stones and rocks only in periods of high transparency.

pH-values, obtained by ILTIS (pers. communication) are available for Tinbé and Fetekro over one year and range between 7.0 and 7.5.

Chemical analyses of the N'Zi at Tinbé were presented by the hydrobiological team of O.R.S.-T.O.M. in O.R.S.T.O.M.-O.M.S. (1976). The annual

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values measured for samples collected from running water only, are ranging as follows:

Conductivity: 37-51 µmhos/cm.

The N'Zi is essentially a typical white water river, due to the character of soil, vegetation and rainfall (SIOLI 1965, 1975). Its chemistry lies within the range of many other West African rivers such a listed by VISSER and VILLENEUVE (1975).

TABLE I

Head capsule width (µm; in brackets: standard deviation) and dry weight (mg; cf. text for determination) of instars of the species studied

Instar		Larva l	Larva 2	Larva 3	Larva 4	Larva 5	Pupa
Cheumalopsyche digilata Cheumalopsyche sp. 111 Cheumalopsyche sp. V11	{ μm mg μm μm μm (μm	$\begin{array}{cccc} 185 & (7) \\ 0.0017 \\ 152 & (5)^* \\ 0.0025 \\ 152 & (11)^* \\ 238 & (16) \end{array}$	$\begin{array}{cccc} 278 & (8) \\ 0.0079 \\ 220 & (11) \\ 0.0094 \\ 231 & (8) \\ 342 & (19) \end{array}$	$\begin{array}{c} 425 & (16) \\ 0.0379 \\ 283 & (10) \\ 0.0233 \\ 344 & (10) \\ 448 & (20) \end{array}$	660 (24) 0.193 403 (14) 0.0835 553 (12) 769 (36)	$\begin{array}{c} 1005 & (40) \\ 0.917 \\ 590 & (17) \\ 0.329 \\ 803 & (23) \\ 1253 & (60) \end{array}$	1.261 0.522
Aethaloptera alspar	(mg	0.0053	0.0182	0.0456	0.287	1.507	2.594

* The quotient headcapsule length: width of the larva one is 1.03 in Cheumatopsyche sp. III and 1.13 in Cheumatopsyche sp. VII.

4. SPECIES STUDIED

Hydropsychid larvae are usually regarded as a difficult group to identify, concerning especially tropical material and individual instars. The characteristics useful for the determination of species are briefly described by STATZNER (1981b).

One of the four species investigated is Aethaloptera dispar Brauer. This species has the code number T32 in an O.R.S.T.O.M.-calatogue on aquatic invertebrates from the Ivory Coast (under publication). The other three species, which are briefly described in STATZNER (1981b), are placed in the genus Cheumatopsyche Wallengren (sensu KIMMINS 1963). One is C. digitata (Mosely) (O.R.S.T.O.M.-catalogue: T10). The second one, Cheumatopsyche sp. VII, is expected to be a new species (near C. copiosa Kimmins) (O.R.S.T.O.M.-catalogue: T5) and the third, Cheumatopsyche sp. III (O.R.S.T.O.M.-catalogue: T1) probably is *C. falcifera* (Ulmer). A definite determination of Cheumatopsyche sp. III and VII cannot yet be given, since the knowledge about these and several other hydropsychid species obtained from the Ivory Coast indicates, that correlations between 33, 22, and larvae given in the literature are often incorrect. For the width of the head capsule see Tab. I. The dry weight of each instar was calculated from formulae obtained by regression analyses. The formulae are (x=headcapsule width in mm):

C. digitata :	$mg = 0.9x^{3\cdot7}$ (n = 3; r = 0.986).
Cheumatopsyche sp. III :	$mg = 2.2x^{3.6}$ (n = 3; r = 0.999).
A. dispar :	$mg = 0.7 x^{3 \cdot 4}$ (n = 2).

Pupal weights are from direct determinations.

5. BENTHIC AND HYPORHEIC ABUNDANCES

The abundance of the benthic fauna per area of the substrate increased in periods with decreasing

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discharge and vice versa. This was best demonstrated by the results from Surber samples at Ouokoukro (fig. 4). This trend was shown by the benthic fauna as a whole as well as by Chironomidae and Trichoptera. The Ephemeroptera, nearly all Caenidae and Baetidae, did not follow the same pattern at the beginning of 1977 nor 1978, when abundance decreased.

This decrease is assumed to be related to the very high abundance of *Cheumatopsyche* spp. in the same periods (fig. 4). Cheumatopsyche is a known predator of Ephemeroptera (H. B. N. HYNES and WILLIAMS, 1962) and it is the most common predator of the N'Zi in untreated rapids. It is not yet clear what caused the low abundance of Cheumatopsyche in August 1977 in spite of a very low discharge at that time. It was probably the absence of A. dispar, which was missing after the period in which this rapid was dry. Larvae of A. dispar construct a tube similar to that of Macronema (SATTLER, 1963, 1968), with the inflow opening protruding into the current. Between these tubes Cheumatopsyche spp. construct their living tubes and their nets (fig. 5), often several larval chambers on top of one another. It is thought that the tubes of A. dispar ameliorate the habitat for Cheumatopsyche by altering the microcurrents above the substratum as well as the substratum itself.

The abundance of hydropsychids in the hyporheic habitat, which was checked at Ouokoukro from February 1977 until January 1978, showed variations similar to the abundances at the surface. They were highest in February 1977, when many larvae were found in the core sample. Less hyporheic larvae were found in August 1977 and January 1978, when the surface densities were also higher. In the other months no Hydropsychidae were found in the core samples. Tab. II demonstrates that the hyporheic abundances reached the level of the surface abun-



FIG. 4. — Densities of benthic invertebrates on a gravel/pebble substratum at the rapid at Ouokoukro. Above : — : total; ---: Chironomidae;: Ephemeroptera; -.-.: Trichoptera. Below : — : Cheumatopsyche sp. III; ----: Cheumatopsyche sp. VII;: C. digitata; — : A. dispar.

TABLE II

Comparison of the abundances at the surface of the substratum (Surber samples, 0 to about 5 cm deep) and in the hyporheic habitat (core samples, deeper than 5 cm), considering gravel/pebble substrata (abundance in 10³ individuals/m²)

	surber	cores					
	Ouokoukro Febr. 77	Ouokoukro Febr. 77	Bocanda March 77				
Cheumatopsyche digitata	22.3	13.4	38.2				
Cheumatopsyche sp. III	9.9	11.8	1.4				
Cheumatopsyche sp. VII	2.2	1.1					
Aethaloptera dispar	2.0	6.1	0.3				





FIG. 5. - Surface of the substratum in the Ouokoukro rapid, February 1977, showing tubes of A. dispar (e.g. \longrightarrow) and between them nets of *Cheumatopsyche* spp. (e.g. \Longrightarrow). The nets of *Cheumatopsyche* are clogged. The number of *Cheumatopsyche* nets visible on the area photographed was about 40 or 50, while the density of larvae exceeded this number by a factor of approximately 15, i.e. barely 10 % of the larvae constructed visible nets

dances. In the core most larvae were found in the upper 5-15 cm section, few were found in the section 15-25 cm and they rarely occurred in deeper layers.

Core samples from the dry rapid as well as the filtration of a large volume of hyporheic water obtained from a hole yielded no hydropsychid larvae. A single *Cheumalopsyche* larva was captured in a core sample from sand in a stagnant pool by Tinbé in a period without flow.

The relative abundance of the various species was approximately equal in surface and core samples (Tab. II). The relative abundances in surface samples are shown in fig. 6 for all five rapids. This figure demonstrates, that *A. dispar* was not able to survive the period without flow and therefore was probably restricted to the southern part of the N'Zi,

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FIG. 6. — Relative abundances of the four Hydropsychidae on the five rapids studied (Fetekro and Ouokoukro: control stations). The numbers above the columns indicate the number of specimens identified. Dry indicates, that there was no flow on the rapid, n.s. indicates, that no samples could be taken, due to the spate

where an interruption of flow is assumed to be much less frequent than in the north. During Chlorphoxim treatment it was not able to recolonize the southern part of the N'Zi, but it did occur at Ouokoukro after the flood from September and October. This would infer that females are able to fly a distance of about 80 km, probably from the N'Zi south of Bocanda or





FIG. 7. — Cheumatopsyche digitata. Percentage instar-distribution at the five rapids. Application of Chlorphoxim is indicated by the black horizontal bar for each treated rapid. Date and number of specimens identified are given for each sample. Black portion of the pupae-column indicates prepupae. If samples contained only few specimens, they are represented directly by points. Dotted parts of the columns at Tinbé (Febr. 1978) indicate the proportion of specimens, which were dead (sample from stagnant water)

from the Comoe, which is the nearest permanent river to that place. After the end of the treatment this species appeared again at Bocanda and therefore the failure to recolonize the southern part might be expected to have been the result of larvicide application.

To a certain extent the n-values in fig. 6 reflect the difficulty in finding enough larvae during periods of medium discharge, when the material was yielded by plunging. Furthermore they indicate, that the three Cheumatopsyche spp. were very abundant on all rapids before the start of Chlorphoxim treatment. They were doubtless the most important invertebrate group in respect of biomass. Cessation of flow seemed to have only minor influence on this genus. After the beginning of larvicide application no serious reduction was observed at Tinbé. At Kolomikro and Bocanda this genus was reduced heavily, only a few specimens surviving the treatment. This situation lasted in Kolomikro until August, but in Bocanda an earlier recovery from July to August was

observed. After the flood, in November and December, Cheumatopsyche was affected so seriously that it was either completely absent in the samples or only a few early instars were found. On the control rapids *Cheumatopsyche* occurred at all times in "normal" abundance with one exception: In December 1977 Cheumatopsyche were reduced to some extent at Ouokoukro. This as well as the condition of the whole benthic fauna clearly indicated the application of an unknown poison to this rapid.

From January to March 1978, Cheumatopsyche were well represented in the samples from all rapids. The change in relative abundance of these four species is relevant to what is discussed above. Evidently A. dispar had an important position at all three southern stations of the N'Zi, in January and February 1977. In the period from November 1977 to February 1978 it reached a similar position again only at Ouokoukro, the control station.

The change of relative abundance of the single Cheumatopsyche species, which showed an increase of C. digitata at all stations with decreasing discharge after the flood during September and October and a decrease in the period from the start of flow up to the flood cannot be due to chlorphoxim treatment. Only the higher relative abundance of C. digitata at the treated rapids compared to the control rapids in the beginning of 1978 can probably be explained by the previous larviciding.

The reasons which led to these changes in the relative abundances of *Cheumatopsyche* will be discussed in connection with the life cycle data below.

6. POPULATION STRUCTURE

This chapter deals with the dynamics of the population structure of the four species, with respect to the instar distribution and the mean weight. Data from two core samples, which yielded a considerable number of hydropsychids, are included. Based on these results the nature and the causes of the life cycles of the four hydropsychids are discussed at the end of this chapter.

6.1. Instar distribution for surface samples

When the monthly sample was not too fragmentary, the instar distribution of any one species of all five rapids was compared by χ^2 -tests (mxn-tables). These tests always indicate highly significant differences in the group of the five rapids. For reasons for this see later.

6.1.1. Cheumatopsyche digitata

C. digitata (fig. 7) became older as the rapids were drying up. Except at Fetekro, pupae were most numerous immediately after the river started flowing in May, there was a distinct increase of younger instars at the other four stations until the beginning of June. At Fetekro this increase of juveniles did not take place until July. At the two control stations, older instars increased from July to August. After decrease in the discharge in November C. digitata was rare. In December a few specimens were found at Fetekro but only two were captured at Ouokoukro. The very low numbers at Ouokoukro were probably the result of poisoning of this rapid as mentioned already above. At Fetekro, older instars dominated until March and the instar composition equalled that of the previous year at the same hydrological period. At Ouokoukro, the situation was different from the year before and the young and especially first instar larvae were frequent even in March. At the treated rapids things developed differently. In Tinbé the first Chlorphoxim application did not change the general dominance pattern.

However, in July older stages were missing and youngers grew only slowly up to August. September data are not comparable with the rest as they were obtained near the bank in shallow water. In November and December, only young larvae, almost all first instar, were present. However, in January the instar quantities were similar to those of the control stations. In February, all specimens were sampled from a very small stagnant pool remaining on the rapid and in which several specimens were alive and reacted "normally". In this sample, fifth instar formed almost 75 % of the population.

In Kolomikro and Bocanda, the application of Chlorphoxim immediately drastically reduced the population, leading to the presence of only old instars. In Bocanda, all instars were again present in August whilst no recolonization occurred at Kolomikro. Up to the end of the application the species remained rare but, from January to March, the population reached a level similar to the year before.

6.1.2. Cheumatopsyche sp. 111

This species (fig. 8) appeared in the samples as well as \hat{C} . digitata with few of the youngest instars at the beginning of the investigation. At Tinbé, Fetekro, and Bocanda only few or no specimens of *Cheumatopsyche sp. III* were found in May. Until June, the number of young instars increased except at Fetekro where this occurred until July. Older instars increased up to August and then decreased again up to November. At Fetekro, older instars increased again up to February.

After the suspected poisoning in December at Ouokoukro, in January young instars were more numerous than older ones. In contrast to *C. digilala* younger instar numbers decreased until March.

At Tinbé the start of the application seemed to have the same effect on this species as on C. digitata. However, Cheumalopsyche sp. III was rare in August. In November, nearly all specimens were first instar larvae, and in December the species was almost eradicated. In January and February, the situation was as in C. digitata with the difference that no live specimens were found in the still water.

At Kolomikro and Bocanda, the treatment had nearly the same effect as on C. digitata with the difference that several older specimens were captured at Kolomikro in July. At both sampling stations the numbers of specimens collected in samples after the application remained low.

6.1.3. Cheumatopsyche sp. VII

Cheumalopsyche sp. VII (fig. 9) seemed to be most seriously affected by the stop of flow. Only a few



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specimens were found in May, all older than second instar. In June the population still seemed to be old and then the percentage of young instars increased until July at Tinbé, Fetekro, and Ouokoukro.

At the control stations development up to the end of the period studied was similar to that of *Cheumatopsyche sp. 111.* Only the recovery at Ouokoukro after December seemed less pronounced in *Cheumatopsyche sp. VII.* At Tinbé, the situation seemed equivalent to that of *Cheumatopsyche sp. 111,* although only a few specimens were caught during the period of larvicide application. After larviciding was stopped, *Cheumatopsyche sp. VII* was captured only in March at Kolomikro and Bocanda.



FIG. 10. — Aethaloptera dispar, at the southern rapids of the N'Zi. Cf. fig. 7 for further details.

6.1.4. Aethaloptera dispar

The fourth sepcies under study, A. dispar, was frequent at the beginning of the investigation at the southern sampling places. As already mentioned in section 5., this species was not able to survive the period without flow and needed up to November to recolonize the rapid at Ouokoukro. Fig. 10 demonstrates that in this species the numbers of old instars also increased with decreasing discharge. In December at Ouokoukro, the population was not as much affected by the expected poisoning as those of *Cheumatopsyche*. However, after that poisoning in A. dispar the quantities of younger instars were also higher than in the previous year.

6.2. Mean weights at the substrate surface

The dynamics of the populations studied here are probably most readily illustrated by the mean weight changes (fig. 11). Excluding the period of larviciding and those data with only few specimens the following general pattern occurred: The specific mean weight was high at the beginning of 1977 and increased, remained constant, or decreased only slightly over the period without flow in the species present after



FIG. 11. — Mean dry weight of C. digitala, Cheumatopsyche sp. 111, Cheumatopsyche sp. VII and A. dispar at the five rapids. Open symbols: n < 10; solid symbols: n≥10; large open symbols: mean weights in the hyporheic habitat (n > 10)

this period. Then the mean weight decreased until June/July, increasing again until August. After the flood mean weights were lower than before the flood and increased again until the end of the study period.

6.3. Instar distribution and mean weight in the hyporheic habitat

When the material in the core samples was sufficient for analysis, the mean weight of the hyporheic specimens was calculated (fig. 11). Mean weight of the surface and hyporheic specimens were in a comparable range. Differences in the instar distribution were significant in three cases, but not extreme (Tab. III). Evidently the hyporheic fauna is not

TABLE III

Percentage distribution of instars at the surface of the substratum (surf.) and in the hyporheic habitat (hypo.; considering the 5-15 cm part of the core sample, which was the only one with higher abundances of hydropsychids). χ^{2} -analyses (mxn-tables) are based on the original data

		1	2	3	4	5	pupa	
Ouokoukro, Febr. 1977								
Observed and the state	surf	2	14	25	23	24	11	1 0.05
Cheumatopsyche digitata	hypo	2	10	17	24	34	12	$\chi^{*} = 3.35$
~	surf	1	12	28	29	25	6	10.0
Cheumatopsyche sp. 111	hypo	0	3	15	38	44	0	$\chi^* = 13.8$
Aelhaloptera dispar	surf	0	0	2	27	19	52	
	hypo	0	0	5	19	52	24	$\chi^2 = 12.2$
Bocanda, March 1977								
Cheumatopsyche digitata	surf	6	9	11	21	23	29	
	hypo	1	29	26	19	20	6	$X_{*} = 81.0$

restricted to smallest larvae, a result similar to that reported from a tropical stream in Malaysia (Візнор, 1973). The restricted space (see below) at the period of low flow probably led to an immigration of large specimens into the hyporheic interstitial. In temperate zones specimens may immigrate into this habitat frequently in streams with an unstable bottom (SCHWOERBEL, 1967).

6.4. Nature and causes of life cycles

It is assumed that the species considered here are not able to develop from the egg to the pupa within a period of about one or two weeks-to the best of my knowledge such a rapid growth is known for African stream insects only from Simuliidae (LE BERRE, 1966). Then, the three Cheumatopsyche spp. must have survived the period without flow in the aquatic stage, at least in some of the rapids studied. This is indicated by the old populations found after the resumption of flow. These findings are contrary to those of other studies on Cheumatopsyche in intermittent African streams, where recolonization was assumed to be due to egg-laying. Without checking the population structure, HARRISON (1966) proposed this for a Rhodesian and J. D. HYNES (1975a) for a Ghanaian stream. Whether this difference between the N'Zi and the other studies was caused by differences in the species under study, the methods used or the actual climate is not clear. The stream studied by HARRISON usually dried up for longer periods than the N'Zi, and most of his pools dried up completely.

In the stream studied by J. D. HYNES, the flow regime was similar to that of the N'Zzi, and stagnant pools remained permanently. However, no larvae of Cheumatopsuche were found there within the first period (6 to 8 weeks) of steady flow after the dry period in the beginning of the year, until a mat of moss and algae become established. According to HYNES, Cheumatopsyche larvae require a substrate of moss to use as a base for sewing their nets, and therefore larvae occur only when moss is present. As it can be seen on fig. 5, in the present study hardly any Cheumatopsyche built a net, a fact well known for other Hydropsychidae from other studies (FEY and Schuhmacher, 1978; Schröder, 1976; Schuh-MACHER, 1970). Therefore the presence or absence of these animals cannot be explained by the presence or absence of suitable net-sewing-places. Moreover HYNES, results are mainly based on Surber samples from flat horizontal sandstones. In the N'Zi, such habitat, when stones were not covered by macrophytes, was rarely colonized by Cheumatopsyche. However, Cheumatopsyche could be found in microhabitats other than on the top of the stones in periods with and without moss on these stones. Thus, in my opinion, the lack of *Cheumatopsyche* larvae in the Ghanaian stream immediately after the resumption of flow could be due to insufficient sampling.

In the case of the N'Zi, the questions remain as to where the specimens survived. The possibility of survival deep in the substratum as mentioned for example by BOUVET (1978), IMHOF and HARRISON (1981), WILLIAMS and H. B. N. HYNES (1977) was checked by coring and digging, but not animals were obtained. The other possibility, the survival in the pools is difficult to prove considering the difference in the area of a rapid (some dozens of squaremeters) and that of a pool (several hectares). Assuming that dispersion is random, one has to sample a large area to find few specimens in the pools. Although not intensively investigated, this possibility seemed the most probable one, for *Cheumatopsyche* larvae were twice found alive in stagnant water: once in a rapid and once in the psammal of a pool.

Usually *Cheumalopsyche* die in still water and this was also observed for the three species of the N'Zi. Physiological changes may enable some specimens to survive without current in the dry season, a mechanism which has been described for caddis larvae in temporary running waters (BOUVET, 1978). The observed changes in weight over the period without flow could be due to differential mortality of different instars. Then, the presence of specimens on the rapid after flow started could be influenced as much by the survival rate as by the time needed for re-immigration from the pools to the rapids, thereby affecting the larval abundances.

These abundances should be further influenced by emergence and reproduction. In untreated rapids which had not dried up, pupae were present in almost all samples. Therefore, here, the presence of imagines can be expected at all times of the year. Emergence data on Trichoptera from the Red Volta River and the Nasia River, which were based mainly on Chimarra spp., indicate that imagines left water in increasing numbers during decreasing discharge (CRISP, 1956). Whether this was the result of a real increase in the emergence rate within the population or whether this was mainly caused by a concentration of specimens below the emergence trap due to a decrease of areas with suitable current remains uncertain. Therefore that method as well as others usually applied in studying such questions give no indication as to when the imaginal population reached its maximal abundance nor do they indicate the period of maximal successful oviposition, both of which are due to the extremely high dynamic of the environment.

Moreover, the high abundance of first instar larvae could be due to retarded hatching (ILLIES, 1959) and low abundances of first instar larvae could be due to high loss through drift immediately after hatching (STATZNER, 1978a). Hence the decrease of mean weight in the period June/July and the shift in the population structure, interpreted as a peak in reproduction at first glance, probably are caused by other phenomena. However, since a mass reproduction in that period seems to be most probable in the moment, June and July are assumed to be the one major period of reproduction. A lower level of reproduction or better larval hatching is indicated by the lower relative abundance of youngest instars throughout the other periods of the year.

It is expected, that the successful oviposition depends to a high degree on the discharge regime and the reactions of females to it, since Hydropsychidae enter into the water to fix the eggs to the substratum (BADCOCK, 1953). Due to examples of how the larval abundance of caddis flies is influenced by imaginal behaviour (STATZNER, 1978b, Tozer et al., 1981), one could speculate that a lower oviposition activity occurred at low discharge and at high discharge, whilst the period of medium discharge seems to favour oviposition. It might be, also, that the period of highest discharge was that of maximal oviposition activity and that eggs dried up during discharge fluctuations and therefore led to a new founding of the larval populations at the end of the spate, when the data suggest a second peak of reproduction.

At Ouokoukro, *Cheumatopsyche digitata* and *Cheumatopsyche sp. III* seemed to have reproduced after the suspected poisoning of the rapid in December, but not in the previous year at this rapid nor at Fetekro at the same time. This indicates, that oviposition, hatching, or loss of larvae by drift was controlled by the abundance and the age structure of the larval populations on the rapid.

It is well known for Hydropsyche (SATTLER, 1958; SCHUHMACHER, 1970) and Cheumatopsyche (GLASS and BOVBJERG, 1969) that their larvae show a distinct intra- and interspecific aggression. The significance of the larval stridulation (JOHNSTONE, 1964) for this aggressive behaviour was studied by JANSSON and VOUORISTO (1979) who demonstrated that stridulation in connection with size plays an important role in the competition of larvae for space.

The stridulation ridges of the *Cheumatopsyche* spp. of the N'Zi exhibit distinct specific differences (STATZNER, 1981b). Whether this led to different specific successes in competition or not is unknown, but it suggests, that stridulation and size may determine the specific hierarchy in competition between larvae. Such competitions can be expected to occur frequently during periods of decreasing discharge, i.e. decreasing areas with sufficient current, when the larvae are expected to move from the place they settled (EDINGTON, 1968). This factor was probably responsible for the change in the relative abundance of the species as well as in the instar distribution at Ouokoukro in 1978 after the expected poisoning. One could expect that the "competitive pressure" on recently hatched young instars would be different at a densely populated rapid than in a rapid, where the population was previously eradicated.

Finally, since the ovipositing females must come close to the places inhabited by stridulating larvae, perception of larval signals cannot be excluded, and an influence on the oviposition also cannot be ruled out.

Competition for space, as discussed above, could be much more important for the coexistence of this species in the N'Zi than the frequently mentioned food-sharing of filter-feeding caddis larvae due to different mesh-sizes of the nets of coexisting species (WALLACE and MERRITT, 1980). Apart from the fact that nets were built only by a small percentage of larvae, the existing nets were also heavily clogged (fig. 5), i.e. the original meshes decreased to an unknown size. The nets were not steadily cleaned by the larvae, as was reported in field observations on *Hydropsyche* (SCHUHMACHER, 1970). This was probably due to the considerable seston load in the N'Zi.

There a no data on the annual cycle of the primary benthic production and on the organic particle load of the water flow. It can be assumed that benthic primary production was highest at the end of periods with decreasing discharge and a high transparency, while organic matter in the drift was most plentiful at the end of periods of decreasing discharge and especially at the beginning of spates, when pool plankton was transported downstream (MILLS, 1976; STATZNER, unpublished data). Whether this affected the larval growth via availability of food or not remains uncertain.

The differences in *Cheumalopsyche* between Chlorphoxim untreated and treated stations in the period of November and December and in July were certainly abnormal and can only be the result of the treatments. At Tinbé, the aquatic population of *Cheumalopsyche* in the rapid was totally destroyed in November and only newly hatched larvae survived up to the next application. In the southern treated part, only the older instars of *C. digitala* and *Cheumalopsyche* sp. *III* survived the first period of treatment. The retarded growth of *Cheumalopsyche* at Tinbé in July and August (fig. 11) could be due to a direct influence of the larvicide on the organisms themselves or to changes in food or feeding.

In August dense populations of C. digitata and Cheumatopsyche sp. III were observed at Bocanda, indicating a recovery. From this as well as from the population structure change until January at the four stations where larviciding or poisoning was carried out in December, it is concluded that a small percentage of specimens requires a period of only about 4-5 weeks from hatching from the egg to the pupal stage. However, during that recovery period, discharge decreased greatly and a few older specimens which could have been missed before, due to their low density in the benthos or due to their survival of the treatments in places not situated directly on the rapid, were captured then due to their higher concentration.

For A. dispar reasons discussed in relation to the dynamic of the population structure of Cheumatopsyche might also apply in this case. However, A. dispar was eradicated in the southern section of the N'Zi by the Chlorphoxim treatments, it did not survive the period without flow, and thereby did not recolonize the rapid at Ouokoukro rapidly. Therefore data about this species are more fragmentary. Probably the periods of increased reproduction are greatly similar with those of Cheumatopsyche, and the main difference between Cheumatopsyche and A. dispar was, that the latter had to recolonize a stream after the period without flow by means of eggs laid by flying females migrating from rapids with continous flow.



FIG. 12. — Pattern of the discharge, the abundance changes, and the dominant pattern of the development on an untreated rapid of the N'Zi during a flow regime as found in this study. The pattern shown here is valid for *Cheumatopsyche* spp. A. dispar recolonized the rapid after the resumption of flow by means of eggs. Ovi. indicates the main periods of oviposition or hatching, \uparrow indicates pupation and emergence (see text for further details)

7. DISCUSSION AND CONCLUSION

The data allow the reconstruction of general patterns of the population dynamics of the species studied here in untreated sections as they occurred in the N'Zi River. These patterns (fig. 12) are based on the combination of the data from five rapids, excluding the periods of insecticide application.

The overall influence of the discharge pattern is well documented by the corresponding densities of larvae per m^2 . The cross-section of a rapid and the resulting surface area with current during periods of decreasing discharge influences the density per unit of area.

The current investigations indicate that *Cheuma*topsyche spp. survived the period without flow in their aquatic stage. Since the larvae probably reached an age of about three months before the flow stopped, the individuals surviving the drought of the rapids probably reached 5-6 months or more and then emerged. From June/July until the start of the spate, a generation with a shorter life span was produced. What happened during the high water is unknown. When discharge decreased populations started getting older again. This was observed until the end of this study.

It must be stressed here, that the pattern shown in fig. 12 is probably typical of most specimens in the population. There is no doubt that some of the specimens behaved differently, as indicated by broken lines.

A similar pattern to that given in fig. 12 probably would have occurred in *A. dispar* if the southern part of the N'Zi had remained untreated. However, this species had to recolonize a dry rapid after the resumption of flow by means of eggs.

In their larval stage, aquatic caddis flies survive periods without any open water only exceptional (BOUVET, 1978; HARRISON, 1966; IMHOF and HAR-RISON, 1981). Often species in temporary waters exhibit a relatively long adult life compared to the length of the larval life (BOUVET, 1978, WIGGINS, 1973). This can also be assumed for three of the species studied here, since the adult Cheumatopsyche were also captured at the end of the period without flow, during which emergence is assumed to be zero. Whether these specimens contribute to the reproduction in June-July or not remains uncertain. For the geographical area under study such a long life of adults as compared with that of the larvae is well documented for Simulium damnosum (LE BERRE, 1966).

Considering the long larval and imaginal life of specimens, probably only two or three generations per year can be completed. Thus the life of the species under the environmental conditions studied here lasted longer than is generally assumed for African insects living in relatively warm water streams near the equator.

The term generation is used above in the sense of the total length of the period which was needed by the average individuals hatched from eggs at identical times until oviposition of females respectively the death of imagines. It was also used in this sense in a former paper on the Trichoptera of the Kalengo River (Zaïre) (STATZNER, 1976; p. 122), i.e.

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several generations can exist at the same time in the population (SCHWERDTFEGER 1979, p. 77). Both LEHMANN (1979) and KOPELKE (1981) discussed the term generation from the study on the Kalengo Trichoptera much more in the sense of single generations present at one time, as is frequently the case in temperate zones. Such distinct generations (cohorts) are difficult to define in stream invertebrates of the tropics.

Nevertheless some dominant patterns of development, caused by a seasonality in the running waters, can be recognized in the tropics. The rhythmic fluctuations in the emergence of the Kalengo Trichoptera (STATZNER, 1976) as well as the changing instar distribution demonstrated in this study suggest that such dominant patterns of development exist.

In the N'Zi, it is the changing flow regime which seems to determine the dominant pattern of the development in the Hydropsychidae. Due to the poor knowledge of fluctuating factors, such as the flow regime in the N'Zi, in the case of the Kalengo, the light parameter was put into this category. LEHMANN (1979) criticized the latter approach, argueing that day length is so constant near the equator that the light parameter must also be constant. Considering brooks in a dense forest, this is probably correct as suggested by data from DIRMHIRN (1961). However, considering brooks in more open areas, in which the Kalengo was situated, insolation is affected periodically by factors not related to day length in the African tropics as can be seen from GRIFFITHS (1972), MALAISSE (1974) and PAGES et al. (1981).

Reports on the development of Chironomidae and Ephemeroptera (DEJOUX, 1971; CORBET *et al.*, 1974) suggest that both groups have probably shorter life cycles in African waters than most Trichoptera. Therefore such dominant patterns of the development are presumably more difficult to recognize in the Chironomidae (studied by LEHMANN, 1979) and the Ephemeroptera (studied by KOPELKE, 1981) than in the Trichoptera.

The approach of the dominant pattern of development enables the rough estimation of the productivity of African stream invertebrates, which is otherwise very difficult to calculate in the tropics (BEADLE, 1974; BISHOP, 1973).

The maximal biomass (in dry weight) of the hydropsychid larvae and pupae of the N'Zi (tab. IV) exceeded the wet weight values reported by PETR (1970) from the Black Volta River. However, in PETR's study samples were collected only once, at the end of the dry season. The annual mean in the N'Zi exceeded the total caddis fly biomass of the Tshinganda-Luhoho, a river system in the Zaïre (STATZNER, 1975). However, the rapids in the N'Zi represented only a relatively small area of the total

TABLE	IV
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Monthly biomass, annual mean biomass, and estimation of annual production (cf. text for mode of calculation) per m² on the rapid at Ouokoukro (all items in mg dry weight)

	1977 J		M/A	м	JJ						1978			Biomass Pr	Production
		\mathbf{F}				J A	Α	A S/O	Ν	D	J	F	М	1977	1977
Cheumatopsyche digitata	158	9397	0	14	0	4	364	n e	1	0	97	1877	9333	828	9846
Cheumatopsyche sp. III	98	1391	0	1	0	6	442	a r	3	0	26	542	1854	162	1937
Cheumatopsyche sp. VII*	34	195	0	0	0	0	16	l v	0	6	0	18	56	21	208
Aethaloptera dispar	1982	3510	0	0	0	0	0	0?	0	238	203	406	275	477	8872
Sum	2272	14493	0	15	0	10	822	0 ?	4	244	326	2843	11518	1488	20863

* Weights and growth rate based on the instar weights of Cheumatopsyche sp. III

river, i.e. the hydropsychid biomass of an average m² of a whole section of the N'Zi can be expected to be very low.

Due to the fact, that larval densities per m^2 were highest during the periods when the populations reached maximal mean weights, productivity cannot be calculated according to most of the frequently applied methods (EDMONDSON and WINBERG, 1971; WATERS, 1977). Thus annual production (P) was roughly estimated by applying the instantaneous growth rate method over an entire life cycle of the specimens, a method described and discussed in detail by WATERS (1969), using the formula

$$P=\ln \frac{\text{weight of pupa}}{\text{weight of larva l}} \times \text{mean biomass.}$$

It was assumed that one generation was completed in the period November until May/June (Cheumatopsyche) respectively November until February (A. dispar) and another one from June until August (Cheumatopsyche), the period of the spate was completely neglected.

The annual production yielded by this estimation (Tab. IV) seemed to be quite high on the first view, especially if the figures are doubled due to the hyporheic abundance of specimens. However, as mentioned above (section 3), the rapids of the N'Zi represented lake outflows during long periods of the year. In these lake outflow communities the hydropsychids were the most dominant benthic group (biomass), especially if one considers solely that group of benthic invertebrates, which are able to feed by filtration. When comparing the production estimations of the hydropsychids at Ouokoukro with studies evaluating the production of filter feeders s.l. in temperate lake outflows (STATZNER, 1978c, 1979; ULFSTRAND, 1968), the figures of the N'Zi are quite low.

This underlines data obtained from stagnant African waters (DEJOUX et al., 1969; HART, 1980; HART and ALLANSON, in press; Lévêque et al., 1972), all suggesting, that the generally assumed high productivity of tropical macroinvertebrates in African waters has not yet been proved conclusively.

Considering the eradication of all four species studied here, which will almost certainly occur if Chlorphoxim is applied as an operational insecticide in the O.C.P.-area, the following is concluded:

(1) the relatively low productivity of these species on a rapid as well as the small area of a rapid in comparison to the large area of a pool indicate, that their eradication seems to be of minor importance concerning the relationships between productivity of invertebrates and edibles fishes;

(2) it has been established that Cheumatopsyche spp. are predators of Simulium damnosum (BURTON and Mc. RAE, 1972; SERVICE and ELOUARD, 1980). The possibility of Cheumatopsyche eradication and the generally occurring effects of target species' predator eradication by man should be seriously considered before Chlorphoxim is applied against S. damnosum.

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APPENDIX

While the manuscript was in print I was able to identify the two unnamed *Cheumatopysche* spp. with the help of material kindly send to me by Dr. P. C. BARNARD (Brit. Mus.). *Cheumatopsyche sp. III* is *C. falcifera* (ULMER) and *Cheumatopsyche sp. VII* is *C. copiosa* KIMMINS.