Journal of Animal Ecology (1985) **55**, 93–110

FIELD EXPERIMENTS ON THE RELATIONSHIP BETWEEN DRIFT AND BENTHIC DENSITIES OF AQUATIC INSECTS IN TROPICAL STREAMS (IVORY COAST). II. *CHEUMATOPSYCHE FALCIFERA* (TRICHOPTERA: HYDROPSYCHIDAE)

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SUMMARY

(1) Gutters containing natural substrata colonized by benthic macroinvertebrates were exposed in streams in the Ivory Coast (West Africa) and drifting organisms were captured in 790 samples over a period of more than 600 h.

(2) Drift was related to density and to abiotic factors for instars of the hydropsychid caddis *Cheumatopsyche falcifera* (Ulmer), of which about 55 000 were caught.

(3) Drift of larvae peaked at different times at night. Emerging adults and pupal exuviae appeared briefly after sunset. Exuviae of larval instars I–IV were present throughout 24 h.

(4) The relationship of drift (y: drift out of $0{\cdot}1\ \mathrm{m}^2$ per unit time or individuals per $1\ \mathrm{m}^3$) of a larval instar to its own benthic density (x) differed in its significance at various times and between larval instars.

(5) No consistent relationship was found in instar I. In later instars it was best described by $y = a + b_1x - b_2x^4$ (instar II); $y = ax^b$ (instar III); $y = ae^{bx}$ (instars IV and V). Since instars IV and V predominated in our trials, an exponential relationship was also found for total larvae of the species.

(6) Self-regulation of an upper benthic density by emigration through drift was statistically not evident.

(7) Models based on benthic densities explained up to 99% of the variation in the drift; the drift of a larval instar was often defined more precisely by the benthic density of another instar than its own.

(8) We conclude that a net of behavioural interactions in the benthic population had a large effect on the loss of individuals through drift.

(9) Drift increased with increasing water temperature and velocity in the gutter; moonlight had no depressant effect on the drift.

(10) Minor manipulations of the gutter, less drastic than in laboratory experiments, resulted in artifacts in the drift.

(11) The average percentage decrease of density through drift over 24 h was 5·6, 9·9, 17·0, 14·3. 5·1, and 9·2 in instars I, II, III, IV, V, and total larvae.

(12) Moulting rates, estimated from larval exuvial drift, indicated that the development period for the instars I–IV took more than a month.

(13) Drift was reduced in some cases in streams previously treated with insecticides. Drift as determined in the West African Onchocerciasis Control Programme to monitor

the effects of the insecticides on the non-target organisms will hardly indicate insecticide-related harmful effects on a species with the characteristics of *C. falcifera.*

INTRODUCTION

Benthic macroinvertebrates which are dislodged from the stream bottom become part of the drift. A recent review (Statzner, Dejoux & Elouard 1985) shows that drift is a relatively complex phenomenon. Natural drift is normally related to the abiotic factors daylight, discharge, velocity, substratum, water temperature, turbidity, and moonlight. Abundance of food, predators, and especially its own benthic density are regarded as the most important biotic factors affecting the drift of a taxon.

These biological details have nearly always been studied using somewhat artificial systems, e.g. laboratory stream tanks. The construction of '*in situ*' trough (gutter) systems (Dejoux 1975) gave us the opportunity to study the above topics in the field under quasi-natural conditions. The relationships of four drift parameters to factors assumed to influence drift (see Table 1) were studied from 1977 to 1981 in the Ivory Coast (West Africa). Most of the streams in that area are regularly sprayed with insecticides against larvae of the *Simulium damnosum* complex in the Onchocerciasis Control Programme (OCP) (Davies *et al.* 1978). Since OCP tries to monitor effects of the treatments on the non-target fauna through drift net samples, we shall also review our results in relation to this topic.

Our studies will appear in a series of papers. The introductory (Statzner, Dejoux & Elouard 1985) and the concluding publications will appear in the *Revue d'Hydrobiologie tropicale.* This paper deals exclusively with *Cheumatopsyche falcifera* (Ulmer), a hydropsychid caddis-fly.

This species belongs to an interesting subfamily: benthic larvae live in aggregations (Resh 1979) and occupy territories which they defend against other larvae (Sattler 1958; Glass & Bovbjerg 1969; Schuhmacher 1970; Mogel, Rieder & Statzner 1985). During these aggressive encounters larvae communicate via stridulation (Johnstone 1964; Jansson & Vuoristo 1979; Silver 1980). Seasonal growth patterns can be related to benthic densities (Tanida 1980) and cannibalism occurs (Hynes & Williams 1962; Kaiser 1965; Schröder 1976). This behaviour, together with the fact that space for immatures becomes scarce on stream riffles in the study area during periods of low discharge (Statzner 1982), makes *C. falcifera* an ideal test subject for the above topics.

Since immatures could be identified to the instar, we can demonstrate how drift data may be of low significance if identification stops at the species level and does not go on to classify the instars.

MATERIALS AND METHODS

A detailed description of the methods is published elsewhere (Statzner, Dejoux & Elouard 1985) and we will deal only with essentials here. We placed natural substrate colonized by benthic animals into a gutter exposed in a stream in such a way that part of the discharge flowed through the system. After a period of adjustment a net was fixed to the front of the gutter to prevent the entrance of drifting insects. At the other end another net sampled animals drifting out of the system. After drift samples had been collected the abundance of the insects remaining in the gutter was evaluated. Thereby four drift parameters could be determined (see Table 1). Since drift exhibits diurnal cycles we considered morning drift (MD), day drift (DD), afternoon drift (AD), night drift (ND), and peak drift (PD).

Mean mesh size used in the experimental procedures ranged from 0·20 to 0·28 mm. We worked with four differently shaped gutters. Drift transport per unit area and drift density per unit area were related to a theoretically mean benthic standard area within the gutter (0·1 m^2). The gutters were stocked with natural stream substrata (stones, gravel, sand, wood, leaves) several hours (eight tests) or 5–14 days (sixteen tests) before the start of the trials. Discharge through the gutter, velocity in the gutter, turbidity, and water temperature were recorded as means over the whole experimental periods (usually about 24 or 48 h). In two parallel trials at full moon over two nights one gutter was covered to exclude moonlight on the first, and the other on the second night. Eleven tests were run in stream reaches not treated with insecticides in the OCP either immediately before or for a long time (at least 6 months), while thirteen were carried out in places previously treated with larvicides against the *Simulium damnosum* complex. The period between the last insecticide application and the beginning of a trial was 5–6 days in these cases.

Cheumatopsyche falcifera was studied at six localities on four different streams. About 55 000 specimens were caught; 87% of these were identified to instars using a key now published by Statzner (1984). Most trials were carried out at relatively low and stable discharge conditions in the stream, when populations of *C. falcifera* were dominated by older instars. The initial population density (benthic density) in a trial was calculated from the sum of specimens which drifted during the test plus those removed from a gutter at the end of a trial. Hence the population structure was considered as static during a trial, although moults and thus changes of an individual from one instar to the next certainly occurred and an unknown loss due to predation was very probable.

The statistics applied were based on Elliott (1977), Riedwyl (1980), and Sokal & Rohlf (1981). Since zero counts occurred, all drift parameters (except exuvial drift and mean drift rate) were transformed to $n + 1$. Data were fitted to polynomials only if this made sense. Single terms of the polynomial which did not significantly contribute to the model were ignored. Before multivariate analyses were started we transformed all dependent variables to *ln*. Drift rate models were also established for untransformed data.

Since intercorrelations between the variables were frequently indicated by product moment correlation coefficients, forward stepwise multiple linear regressions were computed by adding one variable to the model at each step. No critical F-value was used to remove variables from the calculations in early steps, since these variables may (and did) contribute significantly to the model later.

The number of drift samples in our study amounts to 790, covering an experimental period of more than 600 h. In order to reduce time for computation and space for the graphs, means of longer periods (e.g. ND and DD, calculated after *ln* transformations of the original data) will be treated in later sections. Due to the large number of samples we will rarely indicate *n*s.

RESULTS

Diurnal drift patterns

Two samples were chosen to demonstrate that larvae usually drifted more intensely at night than during the day (Fig. 1). The distinct peak in the day drift at Yaoukro was

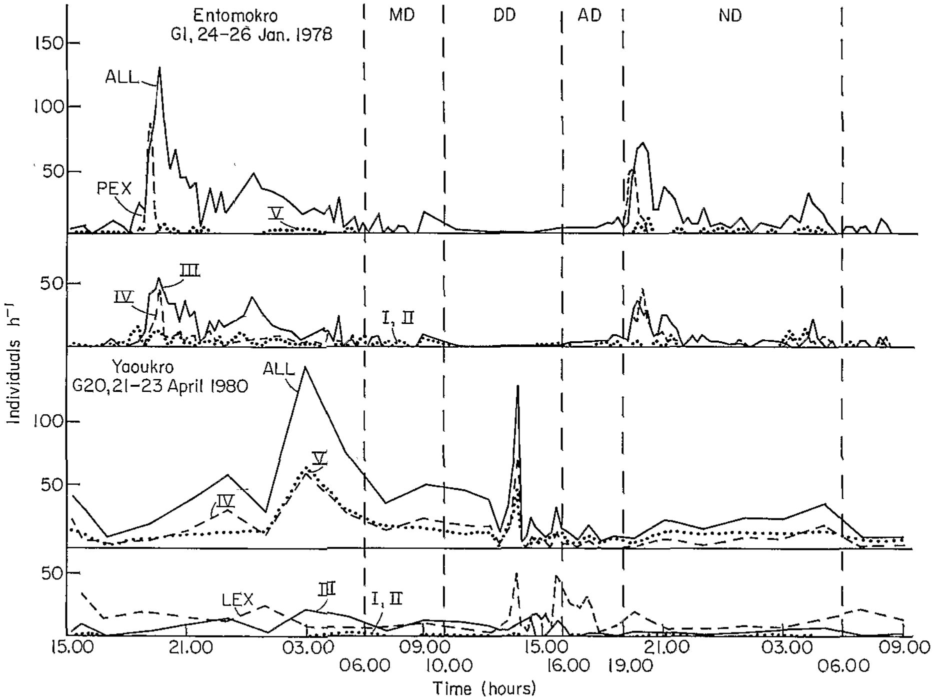

FIG 1. Diurnal drift pattern of all larvae together (ALL), larval instars I–V, pupal exuviae (PEX), and exuviae of larvae I–IV (LEX). The periods of morning drift (MD), day drift (DD), afternoon drift (AD) and night drift (ND) will be treated as units in further considerations.

probably an artifact due to experimental manipulations on neighbouring gutters at this time (see Elouard 1983). In both trials the drift was higher on the first than on the second night. Larval drift peaked early in the night in Entomokro and later in Yaoukro.

Pupal exuviae occurred only briefly after 19.00 hours, together with adults captured during their emergence. This indicated that pupal exuviae were collected immediately after the ecdysis. In larvae, which inhabited tubes frequently situated in the interstices of the substratum, there might have been some delay between ecdysis and capture of exuviae. Since larvae V moult to pupae in a pupal chamber all whole larval exuviae captured by us must have been that of larvae I to IV. They did not show up in a distinct periodicity.

Drift v. *benthic density*

Drift of a specific larval group and its own benthic density are considered in this section. Patterns of the relationship between benthic density of larvae and their drift transport per unit area (Fig. 2) differed between larval instars. The confidence limits became narrower from young to older larvae. However, even in the latter a linear relationship fitted only slightly worse than the exponential one. In such a situation further analysis is required to decide whether the model is density dependent or not. According to Chang & Sell (1984) the polynomial regressions indicate density dependence of drift. For larvae I (only DD), III, IV, V, and all larvae together we tried to confirm the density dependence of the models shown in Fig. 2 by relating drift rates to benthic densities (these drift rate models should have a slope significantly different from zero if they are density dependent).

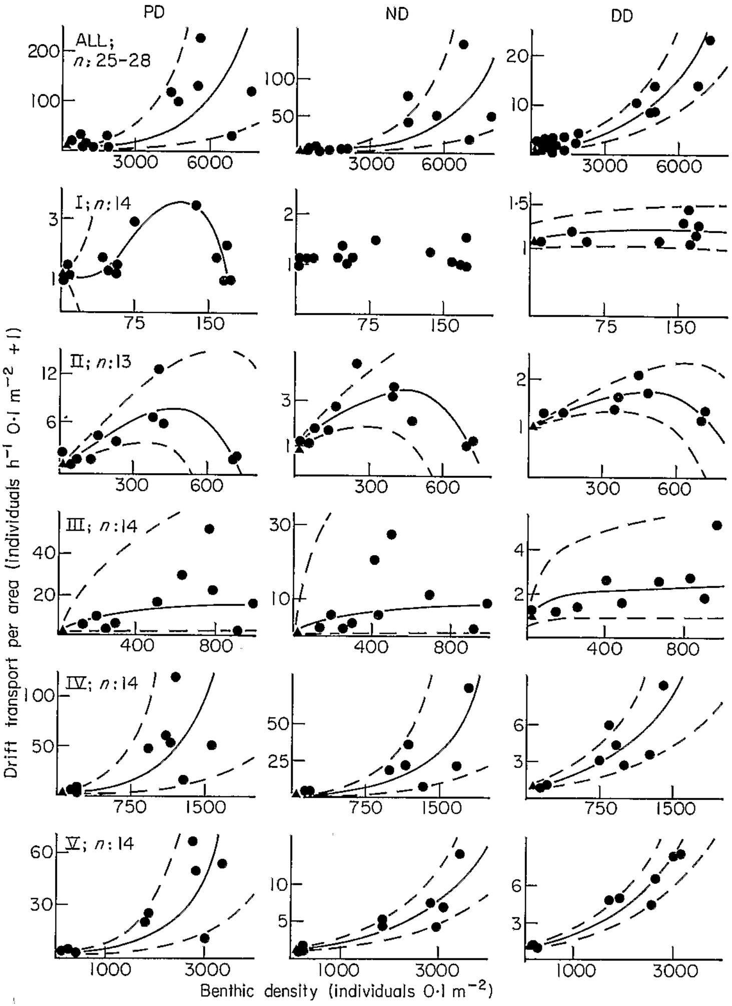

FIG. 2. The relationship between benthic density (individuals 0·1 m^{-2}) and the drift transport per unit area (individuals h^{-1} from each 0·1 m^2 + 1) for all larvae together and larval instars I–V shown for peak drift (PD), night drift (ND) and day drift (DD). (▲), More than one data point. Broken lines indicate the 95% confidence limits of the equations. See Fig. 3 for further statistics.

This attempt failed. Thus, we have no statistical proof that benthic density was self-regulated by emigration through drift.

The relationships between benthic density of larvae and their drift density, as well as their drift density per unit area, followed patterns which were similar to those of drift transport per unit area.

The maximal benthic densities increased from larvae I to V as did the maximal numbers in the drift (Fig. 2)—it was this dominance of larvae IV and V in our trials which was reflected in the patterns of all the larvae together.

In general, the 95% confidence limits of the factor *b* became narrower and the coefficient of determination increased from younger to older instars (Fig. 3). Significances

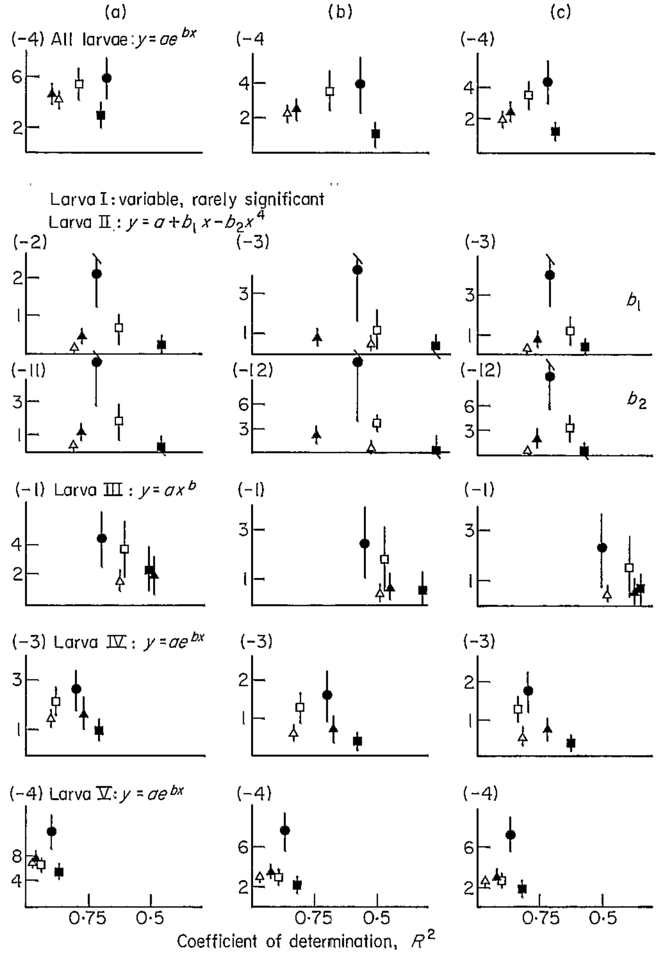

FIG. 3. Significance of regressions of drift (y) *v.* benthic density (x) of all larvae together and the single larval instars. (a), Drift transport per unit area; (b), drift density; (c), drift density per unit area. The equation given for each group of immatures is the best fitting in all or the majority of cases. From these equations, b ($\pm$ 95% confidence limits; y-axes) is plotted against the coefficient of determination R^2 (x-axes) for morning drift (▲), day drift (△), afternoon drift (■), night drift (□), and peak drift (●). Numbers in parentheses above the y-axes are the power of ten with which b has to be multiplied.

of drift density models were usually lower than those of drift transport per unit area or drift density per unit area. Frequently day drift and morning drift were more closely related to benthic density than was drift during the other periods. A considerable overlap of the 95% confidence limits of the factors b occurred, and b was rarely significantly different between e.g. night drift and day drift.

Multivariate drift models

The method of multiple linear regression can be applied only if the number of observations (see *n*s in Fig. 2) is higher than the number of independent variables (Table 1). Thus, most models were calculated for two subgroups of independent variables: one composed

TABLE 1. Variables tested in the drift models

Dependent variables
(for a larval instar or all larvae)

Drift transport per unit area (ln (drift h^{-1} 0·1 m^{-2} + 1)): Y_1
Drift rate (ln (drift h^{-1}:benthic density + 1)): Y_2
Drift density* (ln [(drift:discharge) h^{-1} + 1]): Y_3
Drift density* per unit area (ln [(drift 0·1 m^{-2}: discharge) h^{-1} + 1]): Y_4

Independent variables

Benthic density of that larval group treated in Y_n (individuals 0·1 m^{-2}): *OWN*
Benthic density of larval instars I–V and pupae (individuals 0·1 m^{-2}): I, II, . . . V, P
Mean discharge through the gutter (m^3 h^{-1}): *DIS*
Mean current velocity in the gutter (cm s^{-1}): *VEL*
Mean water temperature (°C): *TMP*
Turbidity (Secchi-transparency: cm): *TRB*†
Moon (1 = new, . . ., 5 = full, . . ., 1 = new): *MON*
Previously treated with insecticide (1 = no, 2 = yes): *PTI*
Month of trial (1–12): *MTH*
Exposure of gutter prior to trial (days): *EXP*
First (1) or second (2) 24-h period of trial: 1/2
Type of gutter‡: *TYP*
Location‡: *LOC*

* Drift density is used as a synonym to drift concentration here.
† Transparency larger than depth of water: 110.
‡ Since a positive or negative relationship of these items to the dependent variable make no sense, § will indicate a significant influence in the below drift models.

of those factors commonly used for the explanation of stream drift (*OWN*, *DIS*, *VEL*, *TMP*, *TRB*, *MON*) and one composed of density parameters of the different instars.

Models describing drift transport and drift density of all the larvae together and using a large number of independent variables (Table 2) showed some similarities: it was almost always *OWN* which explained most of the variation, and this to a higher degree during morning and day drift than at other periods. Thus, non-*OWN* variables became more important during the night (PD and ND). Drift rate (Y_2) was not significantly related to *OWN*, and these models were either less significant than the Y_1, Y_3, and Y_4 models or reached significance, if at all, only after a considerable number of independent variables had been introduced. Note, especially in Y_2 models, the importance of factors which related to the experimental design (*TYP*, *EXP*, 1/2), and that drift had negative significant relationships to previous insecticide treatments (*PTI*). Models with raw (not *ln*-transformed) drift rates fitted less well.

If the independent variables were reduced to the common ones used for the interpretation of stream drift, the models taking all larvae into account became less significant (Table 3). With one exception, Y_2 models did not reach significance, and drift rate was no longer considered here and in the single instar models. The latter exhibited large differences in the significances reached between larval instars. In cases of significance the dependent variables were always positively related to water temperature, velocity in the gutter and, less frequently (once even in the afternoon), to moon-phase. No clear tendency was found for turbidity and discharge. Models on drift transport per unit area and drift density per unit area were usually more accurate than those on drift density. Some models introduced so far described the drift with a precision which is rare in field studies. This precision could even be increased by relating the drift to benthic densities of the different instars (Appendix 1). The striking feature of Appendix 1 is that the drift of a specific larval instar was frequently more closely related to benthic densities of other instars than to its own.

TABLE 2. All larvae together. Cumulative percentage of variation explained in drift models after the stepwise introduction of independent variables (chosen according to the highest F') in forward stepwise multiple linear regression, considering only the first five out of twelve and all twelve variables. Abbreviation of variables as in Table 1. Statistics refer to the moment a variable is introduced into the model

	Y_1	Y_2	Y_3	Y_4
PD	+‡*OWN*:70***	§†*TYP*:38**	+‡*OWN*:57***	+‡*OWN*:72***
	+†*EXP*:81***	−†*EXP*:53***	+†*EXP*:68***	*EXP*:75***
	+†1/2:85***	−‡*PTI*:79***	−†*TRB*:76***	+†1/2:81***
	TRB:87***	−‡*TRB*:90***	−†1/2:81***	*DIS*:83***
	TMP:89***	§†*LOC*:94***	*DIS*:82***	*LOC*:86***
	All:92***	All:99***	All:90***	All:90***
ND	+‡*OWN*:79***	+†*DIS*:29**	+‡*OWN*:69***	+‡*OWN*:80***
	+†*EXP*:86***	−†*EXP*:43**	+†*EXP*:76***	1/2:82***
	§†*LOC*:89***	−†*PTI*:53***	§†*LOC*:80***	*MON*:84***
	−†*DIS*:91***	−†*VEL*:63***	−†*DIS*:85***	*EXP*:85***
	1/2:93***	*MTH*:67**	−†1/2:88***	*LOC*:87***
	All:96***	All:70 N.S.	All:93***	All:93***
MD	+‡*OWN*:89***	*TYP*:10 N.S.	+‡*OWN*:84***	+‡*OWN*:87***
	TMP:90***	*LOC*:18 N.S.	1/2:85***	1/2:89***
	1/2:91***	*OWN*:28 N.S.	*EXP*:86***	*DIS*:89***
	EXP:91***	*TRB*:34 N.S.	*TRB*:87***	*LOC*:89***
	TRB:92***	*VEL*:42 N.S.	*LOC*:88***	*EXP*:90***
	All:94***	All:64 N.S.	All:91***	All:91***
DD	+‡*OWN*:88***	*PTI*: 9 N.S.	+‡*OWN*:85***	+‡*OWN*:89***
	§†*TYP*:90***	*EXP*:16 N.S.	*DIS*:87***	*TYP*:90***
	1/2:91***	+†*TRB*:29 N.S.	1/2:87***	1/2:91***
	LOC:92***	*LOC*:31 N.S.	*TYP*:88***	*TRB*:92***
	TRB:92***	*VEL*:40 N.S.	*TRB*:89***	*LOC*:92***
	All:93***	All:86***	All:92***	All:93***
AD	+‡*OWN*:70***	−†*TRB*:33**	§‡*LOC*:54***	§‡*LOC*:74***
	EXP:76***	−†*PTI*:59***	+†*EXP*:70***	*TYP*:77***
	§†*LOC*:84***	*EXP*:66***	*DIS*:74***	−†*PTI*:82***
	TYP:87***	*TMP*:72***	*TMP*:78***	*VEL*:83***
	TRB:89***	*OWN*:76***	*PTI*:80***	*DIS*:85***
	All:91***	All:85***	All:86**	All:91***

+† or −† ($P < 0{\cdot}05$), +‡ or −‡ ($P < 0{\cdot}001$) = significance of the positive or negative relationship of Y_n to an independent variable; N.S. ($P > 0{\cdot}05$), * ($P < 0{\cdot}05$), ** ($P < 0{\cdot}01$), and *** ($P < 0{\cdot}001$) = significance (ANOVA) of the whole model. PD: peak drift; ND: night drift; MD: morning drift; DD: day drift; AD: afternoon drift.

Exuvial drift

We restrict this section to the relation of the exuvial drift to the benthic densities of pupae and larvae in order to give a rough indication of field moulting rates in this tropical caddis-fly. Since the larval exuviae (pool of larvae I–IV) might have been captured long after moulting, we indicate in Table 4 only means per hour for longer periods or totals for the whole day without statistical treatments. On average about 15% of larvae I–IV moulted in 24 h.

Drift rates of larvae

We have already stated that larval drift rates were not significantly related to benthic density of larvae. Plots of larval versus exuvial drift rates also exhibited no significant relationship.

TABLE 3. All larvae together and larval instars I–V. Cumulative percentage of variation explained in drift models restricted to the independent variables *OWN*, *DIS*, *VEL*, *TMP*, *TRB* and *MON*. Detailed information is only given for significant models until the last independent variable with a significant relationship is introduced. See Table 2 for further details

	All larvae			Larvae I		
	Y_1	Y_3	Y_4	Y_1	Y_3	Y_4
PD	+‡*OWN*:70*** All:77***	+‡*OWN*:57*** All:70***	+‡*OWN*:72*** All:77***	N.S.	N.S.	N.S.
ND	+‡*OWN*:79*** +†*MON*:83*** All:84***	+‡*OWN*:69*** +†*MON*:74*** All:77***	+‡*OWN*:80*** All:83***	N.S.	N.S.	N.S.
MD	+‡*OWN*:89*** All:91***	+‡*OWN*:84*** All:86***	+‡*OWN*:87*** All:88***	N.S.	N.S.	N.S.
DD	+‡*OWN*:88*** All:91***	+‡*OWN*:85*** All:88***	+‡*OWN*:89*** All:91***	+†*OWN*:42* All:52 N.S.	+†*OWN*:31* All:47 N.S.	+†*OWN*:43* All:50 N.S.
AD	+‡*OWN*:70*** All:78***	+‡*OWN*:52*** All:63*	+‡*OWN*:69*** All:74***	N.S.	*VEL*:21 N.S. +†*MON*:50* All:52 N.S.	N.S.

	Larvae II			Larvae III		
	Y_1	Y_3	Y_4	Y_1	Y_3	Y_4
PD	+†*VEL*:52** All:68 N.S.	N.S.	+†*VEL*:50** All:64 N.S.	+‡*TMP*:77*** All:84*	+†*TMP*:60** All:75 N.S.	+‡*TMP*:69*** All:77 N.S.
ND	+†*TMP*:42* −†*OWN*:71** +†*VEL*:84*** All:90**	+†*TRB*:31* *OWN*:37 N.S. +†*VEL*:77** All:80*	+†*TMP*:44* −†*OWN*:72** +‡*VEL*:93*** All:94**	+‡*TMP*:73*** All:84*	+†*TMP*:52** All:75 N.S.	+‡*TMP*:61*** All:78*
MD	+†*VEL*:33* −†*OWN*:71** All:74 N.S.	*TMP*:22 N.S. −†*OWN*:50* All:64 N.S.	+†*VEL*:35* −†*OWN*:66** All:70 N.S.	+‡*VEL*:71*** All:73 N.S.	+‡*TMP*:59*** All:62 N.S.	+‡*VEL*:62*** All:64 N.S.
DD	+‡*TMP*:68*** All:78 N.S.	+†*TRB*:55** All:75 N.S.	+†*TMP*:62** All:73 N.S.	+‡*OWN*:79*** All:80*	+‡*OWN*:64*** All:66 N.S.	+‡*OWN*:70*** All:72 N.S.
AD	+†*OWN*:42* All:49 N.S.	N.S.	+†*OWN*:54** All:59 N.S.	+†*TMP*:63** −†*OWN*:83*** +†*VEL*:90*** All:92**	+†*TMP*:39* −‡*OWN*:84*** All:91**	+†*TMP*:55** *OWN*:70** −†*TRB*:91*** All:95**

	Larvae IV			Larvae V		
	Y_1	Y_3	Y_4	Y_1	Y_3	Y_4
PD	+‡*TMP*:91*** All:94***	+‡*TMP*:80*** All:88**	+‡*TMP*:81*** −†*TRB*:87*** All:90**	+‡*VEL*:91*** All:95***	+‡*OWN*:87*** All:90**	+‡*OWN*:87*** All:90**
ND	+‡*OWN*:89*** All:92**	+‡*OWN*:82*** All:84*	+‡*OWN*:84*** All:85*	+‡*OWN*:95*** All:96***	+‡*OWN*:89*** All:90**	+‡*OWN*:90*** All:90**
MD	+‡*OWN*:78*** All:83*	+‡*OWN*:68*** All:72 N.S.	+‡*OWN*:72*** All:73 N.S.	+‡*OWN*:95*** All:97***	+‡*OWN*:92*** All:93**	+‡*OWN*:92*** All:92**
DD	+‡*OWN*:89*** All:91**	+‡*OWN*:82*** All:83*	+‡*OWN*:82*** All:83*	+‡*OWN*:97*** +†*VEL*:98*** All:99***	+‡*OWN*:97*** All:97***	+‡*OWN*:97*** All:97***
AD	+‡*OWN*:71*** All:72 N.S.	+†*OWN*:58** All:65 N.S.	+†*OWN*:63** All:63 N.S.	+‡*OWN*:87*** All:90*	+‡*OWN*:82*** All:92*	+‡*OWN*:82*** All:83*

TABLE 4. Exuviae in the drift expressed as percentage of the benthic density (moulting rate) of larvae I–IV and pupae on an hourly (AD, ND, MD, DD) or daily (24 h) basis

	AD	ND	MD	DD	24 h
Larvae I–IV					
G20*	0·31	0·34	0·21	0·33	7·63
G20†	0·43	0·24	0·48	0·27	7·46
G21*	1·98	0·49	0·39	1·50	22·51
G21†	—	—	—	0·68	—
G22	1·13	1·87	0·62	0·45	32·49
G23	1·01	0·35	0·15	0·50	11·31
G24	0·63	0·22	0·20	0·23	6·78

Pupae (24 h^{-1})
G1*:23·0 G1†:30·9 G2*:20·0 G2†:36·7

(*), First and (†), second 24-h period of the trial.

Nocturnal drift rates were higher than those during the day (Appendix 2). In general, rates were low in larvae I, increased in the next instars, and decreased again to low rates in larvae V. This pattern was more pronounced in the night drift than in the day drift. On two clear nights with a full moon, drift rates were not higher in the gutters covered to exclude moonlight. Various tendencies in drift rates were related to experimental design and insecticide treatment. Rates for trials in which there had been a long exposure before the trial began, for trials from the second 24-h period, and for trials from untreated streams, which we assume to be data with the least possibilities of artifacts, did not significantly differ from the results obtained when all data were pooled. The 24-h results sometimes reached maximal values between 33% and 50%, i.e. a third to a half of the population of a specific instar was lost through drift in 24 h.

Relevance of drift data for monitoring the effects of insecticides

In the OCP monitoring programme (Lévêque, Odei & Pugh Thomas 1977; Dejoux 1983; Elouard 1983) drift net samples are taken from the stream for 30 min about 1·5 h before (OCP day drift) and for 3 min about 1·5 h after (OCP night drift) sunset, and expressed as drift density. Animals are usually counted at family level. Generally, several hydropsychid species occur together in field drift samples; however, we consider only one species here. Another difference between OCP drift data and ours is that we sampled the total water column above the bottom, whereas OCP drift was sampled close to the water surface, close to the bottom, or close to both, depending on the hydrological season, and thus the water depth, at a sampling place.

OCP night and day drift and the ratio of night drift to day drift are expected to reflect long-term effects of insecticide applications on the benthic community, if they exist, i.e. drift densities are used as an indicator of the condition of the benthos. Therefore, we defined drift density (individuals m^{-3}) as the independent variable (x) and benthic density (individuals 0·1 m^{-2}) as the dependent (y) variable in the following. We chose those data from our samples which corresponded most closely to the point of time of OCP drift sampling for these analyses.

ANCOVA resulted in no significant differences between OCP day drift from treated and untreated stations. Both groups pooled led to $y = 292\ (\pm 813) + 3072\ (\pm 833) \log x$ ($n = 21$; $r = 0{\cdot}87$; 95% confidence limits in parentheses). For OCP night drift, highly significant differences of the slopes occurred ($F_{1,21} = 9{\cdot}83$; $P < 0{\cdot}01$) between treated

($y = 664$ (± 1261) + 1937 (± 747) log x ($n = 15$; $r = 0{\cdot}84$)) and untreated ($y = 62$ (± 301) + 315 (± 225) log x ($n = 10$; $r = 0{\cdot}75$)) stations as we found for data on drift rates (see Appendix 2). If the ratio of OCP night drift to OCP day drift were taken as the independent variable, regressions were not significant.

DISCUSSION

The nocturnal drift peak of *Cheumatopsyche falcifera* larvae and the distinct peak of emergence is in agreement with results on related species from other geographical areas (e.g. Elliott 1969; Cloud & Stewart 1974; Dudgeon 1983; Mogel, Rieder & Statzner 1985). The whole set of drift patterns (see Fig. 1 for two examples) gave no evidence that insecticide treatments or changes in the night-length induced the shift of maximum larval drift from early night (Entomokro) to late night (Yaoukro). The annual variation in night-length is only about 45 min in the study area, thus this shift is unlikely to be related to this factor as it is in higher latitudes (Müller 1970). Whether properties of the 'gutter community' or parts of it or traditional fishing techniques using poison (Elouard, Dejoux & Troubat 1982) further upstream induced this shift in larval drift is unclear.

While the diurnal drift curves of the single larval instars were similar, the other parameters treated on the instar level lacked uniform patterns throughout all instars. This restricts our discussion to some extent, since most papers on Hydropsychidae related to our study do not extend beyond the species level.

Even in larvae IV and V, the two instars which reached high abundances in our trials, no self-regulation of benthic density through drift was evident. A population whose members live in very restricted territories (Glass & Bovbjerg 1969; Schuhmacher 1970; Jansson & Vuoristo 1979) should not exhibit such a density-dependent drift before a specific level of benthic density is surpassed, and this density level may be variable under the influence of other biotic and abiotic factors. We believe this has led to different conclusions on the density dependence of drift in Hydropsychidae (Schuhmacher 1970; Reisen & Prins 1972; Hildebrand 1974). Thus, we must evaluate how closely the benthic densities in our trials resembled those reported on natural rapids. On natural gravel/pebble substrata, benthic densities of *C. falcifera* vary with discharge and are highest when the populations are relatively old (Statzner 1982). Highest abundances reported (including hyporheic individuals) were about 20 000 individuals m^{-2} of all larvae. Our trials always included several tests for all larvae and for the single instars where these maximal densities known from comparable natural substrata were reached and surpassed. It is important to note that all our trials with higher benthic densities were carried out in gutters which were exposed for more than 5 days before the test started: in contrast to laboratory experimental devices, we thereby gave an overcrowded gutter population the chance to regulate itself according to the carrying capacity in the gutter.

Surprisingly, the exponential pattern in drift curves of larvae IV and V was not so distinct in the peak drift, when benthic interactions are assumed to be highest, as in the day drift. Larvae V of Hydropsychinae usually construct a new tube to live in prior to pupation (Haller 1948; Sattler 1958; Schuhmacher 1970; Mogel, Rieder & Statzner 1985), but not all species do so (Fremling 1960; Rhame & Stewart 1976). Species which construct a new pupal building also do so during the day, and real battles between the larvae for building material have been reported (Mogel, Rieder & Statzner 1985). It seems that this behaviour was also true of *C. falcifera*: benthic density of pupae, which may well be an indicator of building activities and the thereby induced aggressive encounters of larvae V, defined the day drift of larvae V better in two cases than the density of larvae V itself. This could explain the more distinct exponential pattern of drift curves of larvae V during the daytime and also the same phenomenon in larvae IV: an increased level of aggressive encounters between larvae V may well lead to an increase of such interactions between larvae V and the frequently inferior larvae IV (Schuhmacher 1970; Jansson & Vuoristo 1979), which would therefore also exhibit a higher drift.

These are only a few examples of the possible nature of the biological relationships which led to the results in Appendix 1. This appendix was added in its entirety to facilitate precise future experiments on these details. We assume that the biological interactions between immatures were more complicated during the period of peak drift and night drift than during the day; this would explain the reduction in the variability of drift data from night to day. The properties of the whole benthic community may have further bearing on the drift behaviour of *C. falcifera*—a possibility that will be evaluated in future papers.

Compared with the characteristics of the immature population, the factors usually considered as important influences on the phenomenon of drift played a less significant role in the models. A positive relationship between drift and water temperature was already reported by Müller (1963) who discussed the activity of benthic invertebrates and its effects on the drift in relation to temperature dependent physiological processes. The positive relationship between drift and velocity could be the result of an increase in erodibility of larvae at higher velocities (Kovalak 1979) and an increase in the drift distances travelled (Elliott 1971). The lack of a depressant effect of moonlight on the drift of *C. falcifera* is no surprise, since literature reports are very diverse on this question (Statzner, Dejoux & Elouard 1985). The lack of a clear relationship between drift and (i) discharge as well as (ii) turbidity in this study we put down to the facts that (i) a relatively feeble discharge passed through our gutters which was completely sampled and (ii) turbidity did not vary much between the trials if compared with the annual variations occurring in these streams (Iltis & Lévêque 1982).

The drift models shown in Table 2 indicated that the experimental design affected the drift of *C. falcifera*. Therefore, drift rate was also checked in relation to these factors. Data on larvae IV and V in Appendix 2, which exhibited high benthic densities in one group of the pairs (small and treated gutters) but not in the other group, should be interpreted with caution, due to the tendency of these instars to increased drift rates at higher abundances. The trials which were run after a short exposure period all took place at relatively low benthic densities of *C. falcifera*. Due to the lower number of tests in this group, we assume that these rates were only accidentally lower than those of the long exposure trials. In other studies in which gutters were only briefly exposed (unpublished reports), we realized relatively early that drift rates on the first night could be distinctly higher than on the second night. We interpreted this as an artifact due to activities of the benthos leaving unsuitable microhabitats in the first night after being disturbed (see Brooker & Hemsworth 1978). But even in gutters exposed for more than 5 days before the test started we usually observed a higher drift rate during the first (i.e. the night following the mounting of the nets) than during the second night (1/2 in Appendix 2), and brushing of the front net of the gutters sometimes also slightly increased the drift. Thus, artifacts occurred even at the almost natural conditions of our tests. This should be carefully considered when evaluating the results of laboratory stream experiments, which frequently expose the test specimens to much more manipulation than we did.

However, since the differences of the drift rates between the data from the second

24-h period of trials with a long exposure time in untreated streams and the data pooled for all tests were insignificant, we concluded that the general tendencies discovered in this study were not caused by artifacts.

The very high drift rates of single instars of *C. falcifera* in some trials occurred in the progressing dry season. Due to the morphology of the streams, drifting riffle fauna will reach a long, deep pool with standing water very soon during these periods. There the velocities are usually much lower than those reported by Vinikour (1981) and we expect the probabilities of drift through the whole pool to be distinctly lower in our study area. Thus, a considerable number of drifters will die (Dendy 1944), although a few are probably able to survive in such pools (Statzner 1982). The high emigration rates from riffles were not compensated by faster reproduction cycles. Cycles of *C. falcifera* were found to be relatively long (Statzner 1982), and if we take the mean 15% day^{-1} as an average moulting rate of the group of larvae I–IV, this points arithmetically to about one moult per larvae week^{-1}. Since the duration of larval instars generally increases from instar I to V in caddis, the average length of the reproduction cycle of *C. falcifera* is assumed to be similar to that known for Hydropsychidae from relatively temperate regions during the summer (e.g. Mackay 1984).

It is unclear whether or not the reduction in the drift rates observed in previously treated populations reflects the start of an insecticide resistance in *C. falcifera*—as was developed by the *S. damnosum* complex (Guillet *et al.* 1981). A selection of larvae with a specific behaviour as a result of the insecticide application, e.g. a preference for lower microcurrents and thus lower possibility for erosion, would have led to such a reduction in drift rates.

Our results have shown that conclusions on benthic densities can hardly be drawn from drift data on younger instars, a group which occurs most frequently in the drift samples of the OCP monitoring. This point (i), the observed changes in the drift peak and a fixed time of sampling of the OCP drift (ii), the changes in the sampling distance from the bottom in OCP sampling (iii), and the fact that Hydropsychidae are treated on the family level in OCP monitoring (iv) led us to predict that the OCP drift programme can only by chance forecast an ecological effect of the insecticides for *C. falcifera* or a species with its ecological characteristics. OCP expects that a comparison of field drift data from one place and the same hydrological season over a long time will indicate changes in the benthos due to insecticide treatments, if their use has any effects at all. Probably such changes will become clear only when insecticides are applied which have stronger side effects on the non-target fauna than Abate, which was used in nearly all our treated streams. But, to be certain, we suggest changing the OCP monitoring drift programme. In *C. falcifera* a 6-h sample taken from 10.00 to 16.00 hours with a very coarse mesh will capture larvae IV and V only: these are easily identified and will give the most precise indication of the situation of the benthic population of these instars, if this is considered by the drift method. Short period samples with fine meshes as used up till now could be additionally applied to evaluate the presence of first instar larvae and thus oviposition and hatching.

ACKNOWLEDGMENTS

We wish to thank Mr J.-J. Troubat, Mr G. Nankodaba, Mr M. Bihoum, and Mr K. Kouame for technical assistance in the Ivory Coast as well as Mrs E. Lunk (Karlsruhe) for preparing the ink drawings and Mrs L. Mole (Weinheim) for linguistic advice. Parts of this study were financed by the World Health Organization through a consultantship to B. S. and a convention with the Hydrobiological Laboratory of the O.R.S.T.O.M. in Bouake.

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(*Received 3 December 1984*)

APPENDIX 1

All larvae together and larval instars I–V. Cumulative percentage variation explained in drift models restricted to the independent variables benthic density of larvae I–V and pupae. Detailed information is only given for significant models until the last independent variable with a significant relationship to Y_n is introduced. See Table 2 for further details.

	All larvae			Larvae I		
	Y_1	Y_3	Y_4	Y_1	Y_3	Y_4
PD	+‡I:62*** II:71** +†III:84*** All:92**	+†I:40* −†II:60* All:82*	+‡I:67*** −†II:77*** +†III:90*** All:94***	IV:11 N.S. −‡II:65** All:80*	II: 6 N.S. +‡IV:65** All:80*	IV:19 N.S. −‡II:77*** P:83*** III:84** −†V:90*** All:91**
ND	+‡IV:84*** V:87*** −†I:94*** −†II:97*** All:99***	+‡IV:79*** II:85*** −†I:92*** +‡III:99*** All:99***	+‡IV:88*** −†II:94*** −†I:97*** +†III:98*** All:99***	N.S.	N.S.	P:16 N.S. −†III:42** −†*OWN*:72** All:81*
MD	+‡V:90*** I:91*** P:93*** II:95*** −†III:97*** All:97***	+‡V:86*** All:94***	+‡V:88*** All:92***	*OWN*: 4 N.S. −†V:56* P:62* III:62* IV:69 N.S. +†II:87*	P: 3 N.S. *OWN*:17 N.S. −†V:55* All:68 N.S.	*OWN*: 7 N.S. −†V:50* P:56* IV:57 N.S. III:67 N.S. +†II:86*
DD	+‡I:96*** +†V:98*** All:98***	+‡P:95*** All:97***	+‡P:96*** All:98***	+‡III:62*** −‡V:89*** II:93*** +†P:96*** All:96***	+†III:50** −†V:80*** All:86**	+‡III:61*** −†II:86*** IV:89*** +†P:95*** +†*OWN*:97*** All:97***
AD	+‡IV:75*** All:93**	+†IV:60** III:66** I:75** −†V:88*** +†P:94*** All:94**	+‡IV:76*** III:82*** I:88*** V:91*** +†P:98*** All:98***	N.S.	N.S.	N.S.

	Larvae II			Larvae III		
	Y_1	Y_3	Y_4	Y_1	Y_3	Y_4
PD	+†I:38* All:68 N.S.	N.S.	+†V:40* *OWN*:58* P:67* −†III:83** All:86*	+‡IV:61*** II:72*** −†I:84*** +‡*OWN*:94*** −†P:97*** All:98***	+†IV:43* −†II:61** −†P:77** −†*OWN*:86*** −†I:92*** All:92**	+‡IV:63*** −†II:82*** −†P:92*** −†*OWN*:97*** −†I:99*** −†V:99***
ND	N.S.	N.S.	+‡IV:37** −†*OWN*:72** All:92**	+‡IV:64*** −†V:80*** −†I:90*** −†II:96*** −†*OWN*:98*** All:98***	+†IV:46** −†V:71** I:80*** −†II:92*** −†*OWN*:96*** All:97***	+‡IV:65*** −†V:85*** −†II:90*** −†I:96*** All:97***
MD	I:20 N.S. −†*OWN*:72** All:85*	I:15 N.S. −‡*OWN*:81*** All:89**	I:25 N.S. −†II:74*** +†V:87*** All:90**	+‡IV:65*** All:81*	+‡I:59*** All:78*	+‡IV:63*** All:74 N.S.

APPENDIX 1—*continued*

	Larvae II			Larvae III		
	Y_1	Y_3	Y_4	Y_1	Y_3	Y_4
DD	+‡I:63*** −‡V:89*** −†*OWN*:93*** All:94***	+†I:38* −‡P:81*** All:88**	+†I:61** −†IV:86*** All:94***	+‡IV:79*** All:86**	+‡IV:64*** All:75 N.S.	+‡IV:72*** All:81*
AD	+†*OWN*:42* P:53* −†III:81** All:88*	I: 8 N.S. −†V:44 N.S. −†IV:67* All:87*	+†I:39* II:56* −†V:75* All:85*	+†I:45* *OWN*:50* IV:60* −†V:82** All:94**	I:25 N.S. *OWN*:44 N.S. IV:53 N.S. −†V:83* All:96**	+†I:46* *OWN*:54* +†IV:73* V:85** +†P:94** All:95**

	Larvae IV			Larvae V		
	Y_1	Y_3	Y_4	Y_1	Y_3	Y_4
PD	+‡*OWN*:80*** II:85*** −†I:95*** +†III:97*** All:98***	+‡*OWN*:69*** −†II:79*** −†I:90*** All:94***	+‡*OWN*:81*** −†II:90*** −†I:96*** −†P:98*** III:98*** −†V:99***	+‡IV:91*** II:94*** −†I:97*** −†P:99*** All:99***	+‡*OWN*:87*** −†II:93*** +†III:95*** −†P:98*** All:99***	+‡*OWN*:87*** −†II:93*** +†III:95*** −†P:97*** All:98***
ND	+‡*OWN*:87*** −†II:94*** −†I:97*** −†V:98*** +†P:99*** All:99***	+‡*OWN*:82*** −‡II:94*** −†I:97*** −†V:99*** All:99***	+‡*OWN*:84*** −‡II:96*** All:99***	+‡*OWN*:95*** P:96*** +†I:97*** All:98***	+‡*OWN*:89*** All:95***	+‡*OWN*:90*** All:95***
MD	+‡V:80*** All:92**	+‡V:71*** All:89**	+‡V:75*** All:86*	+‡*OWN*:95*** +†P:96*** All:97***	+‡IV:94*** All:95***	+‡IV:93*** All:95***
DD	+‡V:95*** All:95***	+‡V:86*** All:91**	+‡V:83*** All:92**	+‡*OWN*:97*** +†I:98*** All:99***	+‡P:99*** +†I:99*** +†II:99*** All:99***	+‡P:99*** +†*OWN*:99*** I:99*** +†II:99*** All:99***
AD	+‡*OWN*:71*** −†III:87*** All:94**	+†*OWN*:58** −†III:84*** All:93**	+†*OWN*:63** −†III:88*** All:96**	+‡*OWN*:87*** All:98***	+‡*OWN*:82*** All:97***	+‡*OWN*:82*** −†III:88*** All:97***

APPENDIX 2

Drift rate of all larvae and the larval instars I–V (%). We indicate the mean and the 95% confidence limits of the mean (all calculated after arcsine transformations of the square root of *P*) for night drift, day drift, and 'all' data of the 24 h group. The non-'all' data of the 24 h group are arithmetic means and ranges (; between the minimum and the maximum). Data for 24 h are based on sums of the original drift counts. A few 24-h periods were not totally sampled. These were completed by filling the gaps (a few hours of daydrift) by replicating data of the appropriate period: thereby twelve 24-h periods were available for larval instars and twenty-one for all larvae. Day drift and night drift calculations are based on periods longer than 30 h, except those mentioned with a prime (′) (between 20 and 30 h) or double prime (″) (10–20 hours)

	Type of gutter (*TYP*)		Previous exposure time (*EXP*)		OCP-insecticiding (*PTI*)	
	Large	Small	>5 days	<5 h	Treated	Untreated
Night drift (rate h^{-1})						
All	0·61 (0·34–0·96)	0·56 (0·38–0·78)	0·57 (0·44–0·71)	0·64 (0·12–1·56)	0·40 (0·25–0·58)	0·81 (0·49–1·20)
I	0·17 (0·05–0·36)	0·07 (0·01–0·19)	0·14 (0·06–0·24)	0·13 (0·01–0·69)	0·07 (0·01–0·20)	0·19 (0·05–0·43)
II	0·50 (0·30–0·76)	0·43 (0·19–0·76)	0·64 (0·46–0·86)	0·05 (0·01–0·33)	0·32 (0·13–0·61)	0·63 (0·41–0·91)
III	0·84 (0·48–1·30)	1·76 (1·12–2·55)	1·63 (1·01–2·40)	0·10 (0·02–0·61)	1·01 (0·55–1·61)	1·15 (0·68–1·74)
IV	0·55 (0·25–0·97)	2·42 (1·70–3·26)	1·32 (0·97–1·72)	0·25 (0·02–1·27)	1·24 (0·68–1·96)	0·81 (0·38–1·39)
V	0·07 (0·03–0·13)	0·73 (0·55–0·93)	0·27 (0·18–0·37)	0·05 (0·00–0·12)	0·48 (0·30–0·71)	0·07 (0·03–0·18)
Day drift (rate h^{-1})						
All	0·10 (0·01–0·28)	0·17 (0·12–0·23)	0·13 (0·09–0·18)	0·15 (0·01–0·50)	0·12 (0·08–0·17)	0·16 (0·04–0·37)
I	0·05 (0·00–0·26)	0·06 (0·01–0·16)	0·06 (0·01–0·13)	0·09 (0·02–0·21)′	0·04 (0·01–0·11)	0·07 (0·01–0·37)
II	0·05 (0·01–0·12)	0·08 (0·03–0·16)	0·13 (0·07–0·22)	0·00 (0·00–0·01)′	0·05 (0·02–0·11)	0·07 (0·02–0·17)
III	0·11 (0·01–0·34)	0·21 (0·11–0·34)	0·17 (0·11–0·26)	0·11 (0·00–0·51)′	0·14 (0·06–0·24)	0·16 (0·01–0·48)
IV	0·02 (0·00–0·11)	0·30 (0·17–0·45)	0·15 (0·08–0·24)	0·02 (0·00–0·09)′	0·19 (0·09–0·32)	0·03 (0·01–0·15)
V	0·01 (0·00–0·02)	0·17 (0·11–0·24)	0·09 (0·05–0·15)	0·00 (0·00–0·01)′	0·11 (0·06–0·18)	0·01 (0·00–0·03)
24 h (rate day^{-1})						
All	7·4 (0 ;13·8)	12·1 (2·5;29·5)	11·0 (0 ;29·5)	6·0 (5·2; 6·9)	9·5 (2·5;29·5)	13·1 (6·6;22·1)
I	7·7 (2·0;13·6)	4·8 (1·0;12·5)	5·8 (1·0;13·6)	8·3 (8·3; 8·3)	5·7 (1·0;12·5)	7·4 (2·0;13·6)
II	12·7 (2·5;20·4)	9·9 (0·9;22·9)	12·0 (0·9;22·9)	8·1 (2·5;13·6)	9·4 (0·9;22·9)	15·1 (10·6;20·4)
III	14·6 (0·5;36·2)	24·9 (3·1;43·8)	23·4 (3·1;43·8)	1·6 (0·5; 2·8)	19·1 (0·5;43·8)	21·1 (10·3;36·2)
IV	6·4 (0 ;13·2)	30·0 (8·2;53·5)	21·9 (6·4;53·5)	0 (0 ; 0)	22·5 (0 ;53·5)	9·7 (6·4;13·2)
V	1·5 (0·4; 3·1)	11·2 (6·3;17·4)	7·5 (1·6;17·4)	0·5 (0·4; 0·5)	8·5 (0·4;17·4)	2·1 (1·6; 3·1)

	First or second 24-h period (1/2)		Full moon		Long EXP, 2nd 24 h, untreated	All data
	First	Second	Exposed	Protected		
Night drift (rate h^{-1})						
All	0·66 (0·46–0·90)	0·39 (0·28–0·51)	0·75 (0·52–1·04)′	0·66 (0·47–0·88)′	0·50 (0·34–0·69)′	0·58 (0·41–0·78)
I	0·24 (0·09–0·47)	0·05 (0·00–0·16)	0·13 (0·02–0·33)′	0·28 (0·09–0·57)′	0·08 (0·01–0·24)′	0·13 (0·05–0·26)
II	0·93 (0·59–1·35)	0·33 (0·14–0·61)	0·84 (0·50–1·27)′	0·79 (0·43–1·26)′	0·44 (0·19–0·80)′	0·48 (0·32–0·67)
III	1·89 (1·29–2·60)	0·82 (0·50–1·21)	1·77 (1·06–2·67)′	1·33 (0·89–1·86)′	1·03 (0·64–1·51)′	1·09 (0·64–1·65)
IV	1·02 (0·61–1·53)	0·58 (0·34–0·88)	0·75 (0·50–1·05)′	0·76 (0·31–1·41)′	0·59 (0·30–0·97)′	0·98 (0·63–1·41)
V	0·12 (0·04–0·24)	0·13 (0·07–0·20)	0·05 (0·01–0·12)′	0·13 (0·07–0·21)′	0·10 (0·05–0·18)′	0·20 (0·13–0·28)
Day drift (rate h^{-1})						
All	0·19 (0·10–0·31)	0·11 (0·06–0·19)′	—	—	—	0·14 (0·08–0·22)
I	0·10 (0·00–0·37)	0·05 (0·00–0·22)″	—	—	—	0·05 (0·00–0·17)
II	0·06 (0·01–0·15)	0·07 (0·00–0·26)″	—	—	—	0·06 (0·03–0·11)
III	0·24 (0·09–0·46)	0·11 (0·02–0·28)″	—	—	—	0·15 (0·05–0·29)
IV	0·50 (0·12–1·13)	0·15 (0·03–0·36)″	—	—	—	0·09 (0·03–0·18)
V	0·19 (0·10–0·33)	0·14 (0·03–0·35)″	—	—	—	0·04 (0·02–0·08)
24 h (rate day^{-1})						
All	10·5 (5·7;13·8)	5·8 (3·5; 8·3)	10·2 (6·6;13·8)	9·6 (8·3;11·0)	7·4 (6·6; 8·3)	9·2 (6·0–13·0)
I	7·2 (1·0;13·6)	3·4 (1·0; 7·1)	7·0 (6·9; 7·1)	7·8 (2·0;13·6)	4·5 (2·0; 7·1)	5·6 (3·2– 8·5)
II	13·4 (1·2;20·4)	10·1 (8·8;10·8)	15·6 (10·8;20·4)	14·5 (10·6;18·4)	10·7 (10·6;10·8)	9·9 (5·4–15·6)
III	22·9 (15·8;36·2)	11·6 (3·1;21·3)	23·3 (10·3;36·2)	19·0 (16·7;21·3)	15·8 (10·3;16·7)	17·0 (8·2–28·2)
IV	13·6 (7·0;20·7)	8·9 (6·4;12·1)	9·8 (6·4;13·2)	9·6 (7·0;12·1)	9·2 (6·4;12·1)	14·3 (5·1–27·0)
V	5·1 (1·6;10·6)	3·3 (1·7; 6·3)	1·6 (1·6; 1·7)	2·5 (2·0; 3·1)	1·8 (1·7; 2·0)	5·1 (2·2– 9·1)

Fiche descriptive

(à joindre à tout envoi de document)

B. STATZNER, J.-M. ELOUARD* AND C. DEJOUX

Auteur(s): FIELD EXPERIMENTS ON THE RELATIONSHIP BETWEEN DRIFT AND BENTHIC DENSITIES OF AQUATIC INSECTS IN TROPICAL STREAMS (IVORY COAST).

Titre original II. *CHEUMATOPSYCHE FALCIFERA* (TRICHOPTERA: HYDROPSYCHIDAE)

Titre en français : (si le document est en langue étrangère)

Mots-clés matières : (10 au plus)

Français

Anglais

Résumé en français :

Résumé en Anglais :

SUMMARY

(1) Gutters containing natural substrata colonized by benthic macroinvertebrates were exposed in streams in the Ivory Coast (West Africa) and drifting organisms were captured in 790 samples over a period of more than 600 h.

(2) Drift was related to density and to abiotic factors for instars of the hydropsychid caddis *Cheumatopsyche falcifera* (Ulmer), of which about 55 000 were caught.

(3) Drift of larvae peaked at different times at night. Emerging adults and pupal exuviae appeared briefly after sunset. Exuviae of larval instars I–IV were present throughout 24 h.

(4) The relationship of drift (y: drift out of $0 \cdot 1$ m^2 per unit time or individuals per 1 m^3) of a larval instar to its own benthic density (x) differed in its significance at various times and between larval instars.

(5) No consistent relationship was found in instar I. In later instars it was best described by $y = a + b_1x - b_2x^4$ (instar II); $y = ax^b$ (instar III); $y = ae^{bx}$ (instars IV and V). Since instars IV and V predominated in our trials. an exponential relationship was also found for total larvae of the species.

(6) Self-regulation of an upper benthic density by emigration through drift was statistically not evident.

(7) Models based on benthic densities explained up to 99% of the variation in the drift; the drift of a larval instar was often defined more precisely by the benthic density of another instar than its own.

(8) We conclude that a net of behavioural interactions in the benthic population had a large effect on the loss of individuals through drift.

(9) Drift increased with increasing water temperature and velocity in the gutter; moonlight had no depressant effect on the drift.

(10) Minor manipulations of the gutter, less drastic than in laboratory experiments, resulted in artifacts in the drift.

(11) The average percentage decrease of density through drift over 24 h was 5·6, 9·9, 17·0, 14·3. 5·1, and 9·2 in instars I, II, III, IV, V, and total larvae.

(12) Moulting rates, estimated from larval exuvial drift, indicated that the development period for the instars I–IV took more than a month.

(13) Drift was reduced in some cases in streams previously treated with insecticides. Drift as determined in the West African Onchocerciasis Control Programme to monitor the effects of the insecticides on the non-target organisms will hardly indicate insecticide-related harmful effects on a species with the characteristics of *C. falcifera*.

Résumé Français

1. Des gouttières contenant des substrats naturels colonisés par des macroinvertébrés benthiques ont été immergées dans des rivières de Côte d'Ivoire (Afrique de l'Ouest) et les organismes dérivant capturés dans 790 prélèvements sur une période de plus de 600 h.

2. La dérive est rapportée au densités et aux facteurs abiotiques en ce qui concerne les larves de *Cheumatopsyche falcifera* (Ulmer)(Trichoptera : Hydropsychidae) pour lequel 55 000 individus ont été capturés.

3. La dérive des larves culmine à différentes heures de la nuit. Les adultes émergent et les exuvies sont récoltées peu après le coucher du soleil. Les exuvies des larves de stades I à IV sont présentes tout au long du nycthémère.

4. La relation entre la dérive d'un stade larvaire (y = dérive pour 0,1 m^2 par unité de temps ou individuellé par m^3) par rapport à sa densité benthique propre (x) diffère dans sa signification aux différentes heures et selon les stades larvaires.

5. Aucune relation forte n'a été observée pour le stade I. Pour les autres stades elle est le mieux décrite par les relations $y=a+b_1x-b_2x^4$ (stade II), $y= ax^b$ (stade III), $y=ae^{bx}$ (stade IV & V). Du fait que les stades IV et V dominent dans nos expériences, une relation exponentielle a également été trouvée pour l'effectif total de l'espèce.

6. L'autorégulation des grandes densités benthiques par émigration au moyen de la dérive n'est pas prouvée.

7. Les modèles basés sur les densités benthiques expliquent 99 % des variations dans la dérive; toutefois, la dérive d'un stade donné est souvent mieux décrite par les densités benthiques d'un autre stade que par la sienne.

8. Nous concluons qu'un réseau d'interactions comportementales dans les populations benthiques agit de façon importante sur la perte d'individus dans la dérive.

9. La dérive s'accroit avec la température et la vitesse du courant dans les gouttières; le clair de lune n'a pas d'effet dépressif sur la dérive.

10. Des manipulations mineures des gouttières, moins fortes que dans les expériences de laboratoire, engendrent une dérive artéfactuelle.

11. Les diminutions des pourcentages moyens des densités dans la dérive sur 24 heures sont 5,6 , 9,9 ,17,0 , 14,3 , 5,1 et 9,2 pour les stades I, II, III, IV, V et le total des larves.

12. Le taux de mues, estimé a partir de la dérive exuviale des larves, indique que la durée de développement des larves I-IV prend plus d'un mois.

13. La dérive est réduite dans les rivières précédemment traitées aux insecticides. La dérive telle qu'elle est mesurée dans le Programme de Lutte contre l'Onchocercose pour surveiller l'impact éventuel des insecticides sur les organismes non-cibles devrait fortement indiquer les effets nuisibles sur des espèces ayant les charactéristiques de *C. falcifera*

Reprinted from

THE JOURNAL OF ANIMAL ECOLOGY
VOL. 55

BLACKWELL SCIENTIFIC PUBLICATIONS
OXFORD LONDON EDINBURGH
BOSTON MELBOURNE