

Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams (Ivory Coast).

III. Trichoptera

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SUMMARY. 1. Based on *in situ* gutter trials we related the drift of caddis flies to their benthic densities and to various abiotic factors in streams in the Ivory Coast (West Africa). Members of the families Hydropsychidae, Philopotamidae, Hydroptilidae and Leptoceridae were considered in detail.

2. The drift of larvae peaked at night in both early and late larval instars.

3. Drift of a larval group (a certain instar, species or higher taxon) was more often related to the benthic density of other larval groups than to its own benthic density.

4. Self-regulation of an upper benthic density of a larval group by emigration through drift was not statistically evident.

5. There was no straightforward relationship between drift and abiotic factors.

6. Drift rates differed between taxa as well as between larval instars (size groups) within a taxon. Newly hatched larvae had very high drift rates, whereas the last larval instar usually had the lowest drift rate.

7. We related these results to the violently fluctuating discharge of the streams in the study area and the consequent variability of space for lotic insects.

8. Drift estimates, made at the same time as a monitoring programme on possible side-effects of insecticides (Onchocerciasis Control Programme), failed to reflect benthic densities except in the night drift of Hydropsychidae.

1. Introduction

Benthic macroinvertebrates dislodged from the stream bottom form part of the organismic drift. The importance of this drift for population

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dynamics in running water has stimulated much work, which we have recently reviewed (Statzner, Dejoux & Elouard, 1985a). Natural drift is often related to such abiotic factors as daylight, moonlight, water temperature, discharge, current velocity, characteristics of the bottom substratum, turbidity; and to the biotic factors of benthic density of the drifting taxon,

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abundance of its food and predators. Past interest has focused on the question of whether or not drift of a taxon reflects its benthic abundance or even production. Drift is 'density dependent' if emigration rates through drift change with changing benthic densities. In the classical sense, density dependence of drift is described by an exponential relationship between benthic density (x) and drift (y), $y = ae^{bx}$, where a and b are constants. This could be the result of an increase in the rate of drift inducing interactions within a taxon with increasing benthic density.

The relationships between drift and some of the above factors are relatively clear. But in many cases there remain many uncertainties (Statzner *et al.*, 1985a). Although field work on this subject is preferable (Townsend & Hildrew, 1976; Goedmakers & Pinkster, 1981), most experimental studies were carried out in rather artificial stream systems, with the attendant risk of behavioural artefacts. We thus tried to relate drift of benthic stream insects to the above factors under quasi-natural conditions in *in situ* trials with trough (gutter) systems, which were used from 1977 to 1981 in the Ivory Coast (West Africa).

In that area, streams exhibit extreme variations in discharge. Therefore two points are of special interest (Statzner, 1982; Lévêque, Dejoux & Ittis, 1983): (i) space for lotic invertebrates becomes a scarce resource in stream riffles at times of low discharge, (ii) individuals drifting off riffles are rapidly exported to very long pools of almost standing water during such periods. Thus, the question is whether the density of riffle populations is self-regulated through density dependent drift or whether other mechanisms affect population densities under these extreme environmental conditions.

Most of the streams in the study area were regularly sprayed with insecticides against larvae of *Simulium damnosum s.l.* in the Onchocerciasis Control Programme (OCP) (Davies *et al.*, 1978). Since the OCP tries to monitor effects of treatments on non-target fauna by means of drift net samples, we will briefly consider how far our results justify that practice.

We intend to publish our drift studies in a series of papers. The introductory one (open questions in stream drift, methods and experimental conditions; Statzner *et al.*, 1985a) and the concluding (synecological aspects) publication of this series did or will appear in the *Revue*

d'Hydrobiologie Tropicale. Another paper (Statzner, Elouard & Dejoux, 1985b) considered *Cheumatopsyche falcifera*, the most numerous caddis fly in our tests. The present paper deals with the remaining Trichoptera as well as with the question of how much the drift of *C. falcifera* was affected by the benthic density of other trichopteran taxa (section 3.3). We will focus our interest on the Hydropsychidae, since this family was often represented by more than one abundant species in our tests and because we were able to identify larvae to species and instar level. Other taxa sufficiently abundant to be considered in detail were members of the Philopotamidae, Hydroptilidae and Leptoceridae.

Our objective was to relate drift of these caddis flies to light regime, application of insecticides in the OCP, various other abiotic factors (Table 1) and, especially, to the properties of the benthic trichopteran community.

2. Methods and Materials

The methods we applied have been described and discussed in detail elsewhere (Statzner *et al.*, 1985a, b).

TABLE 1. Independent variables tested in drift models

Abiotic	
Mean discharge through the gutter ($m^3 h^{-1}$):	DIS
Mean current velocity in the gutter ($cm s^{-1}$):	VEL
Mean water temperature ($^{\circ}C$):	TMP
Turbidity (Secchi-transparency: cm):	TRB*
Moon (1=new, ... 5=full, ... 1=new):	MON
Biotic	
Benthic density of that larval group treated in the dependent variable (ind. $0.1 m^{-2}$):	OWN
Benthic density of other Trichoptera (ind. $0.1 m^{-2}$):	
<i>Aethaloptera dispar</i> :	ADI
<i>Cheumatopsyche copiosa</i> :	CCO
<i>Cheumatopsyche digitata</i> :	CDI
<i>Cheumatopsyche falcifera</i> :	CFA†
<i>Macrostemum alienum</i> :	MAL
Other Hydropsychidae:	OHY
<i>Chimarra petri</i> group:	CPE
<i>Orthotrichia</i> spp.:	OTT

*Transparency larger than depth of water: 110.

†If drift of larval instars of this species was considered, CFA represented the benthic density of all but the instar tested in the dependent variable.

2.1. Experimental stream protocol

Natural substrata (stones, gravel, sand, wood, leaves) colonized by benthic animals and placed in gutters (length 1.5–3 m, width 0.09–0.2 m) were exposed in streams so that part of the discharge passed through the systems. After various periods of adjustment (see below) nets were fixed to the front of the gutters to prevent the entrance of drifting insects. These front nets were shaped in a way that changes of flow characteristics in the gutters were minimized. At the other end of the gutters a second net sampled animals drifting out of the system. After drift samples had been collected (usually about 24 or 48 h) the abundances of the remaining benthic insects were evaluated from the contents of the gutters. The initial population density (benthic density) in a trial was calculated from the sum of specimens which drifted plus those removed from a gutter at the end of a trial.

Our data base consists of 790 drift samples, representing a survey of more than 600 h, obtained from twenty-four experiments.

Important technical details were: (i) Four differently shaped gutters were used (see Fig. 2 in Statzner *et al.*, 1985a). (ii) In the first eight tests substrata from the stream bottom were put into the gutter several hours before the start of the trials. Later we placed the substrata into the gutters 5–14 days before the tests. (iii) Eleven tests were run in stream reaches never treated with insecticides or not for a long time (at least 6 months), while thirteen were carried out in places previously treated with larvicides against *Simulium damnosum s.l.* in the OCP. The period between the last insecticide application and the beginning of a trial was 5–6 days in these cases. (iv) Discharge through the gutter, velocity in the gutter, turbidity (Secchi disk), and water temperature were recorded as means over the whole period of a test. In two parallel trials at full moon over two nights one gutter was covered to exclude moonlight on the first, the other on the second, night. (v) Mean mesh size used in the experimental procedures ranged from 0.20 to 0.28 mm.

(i), (ii) and (iii) had some effects on the drift of *C. falcifera*, but not so striking that valid conclusions were impossible (Statzner *et al.*, 1985b).

2.2. Reasons for the presentation of selected drift data

For *C. falcifera* we have shown that our data

about drift concentration (=density) are redundant because relatively constant discharge passed through our gutters. Thus we will present results in terms of drift contributed per unit area per unit time (drift transport area⁻¹) and drift rate (percentage of the benthic population lost through drift per unit time). Data from early morning and late afternoon differed only slightly from data between 10.00 and 16.00 hours GMT and gave no better insight into drift phenomena of our caddis. Therefore we will concentrate on the following: the period of peak drift (PD; highest drift within a 24 h period), night drift (ND; 19.00–06.00 hours) and day drift (DD; 10.00–16.00 hours).

When we seek to evaluate the relevance of drift data for monitoring effects of insecticides, data have to be gathered using techniques comparable to those of the OCP monitoring programme. Essentials of the drift studies in the OCP monitoring programme are (Lévêque, Odei & Pugh Thomas, 1977; Dejoux, 1983; Elouard, 1983): (i) 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. (ii) Drift nets may be exposed either close to the water surface, close to the bottom, or close to both, depending on the hydrological season. (iii) Drift is expressed as drift concentration (individuals m⁻³). (iv) OCP night and day drift and the ratio of night drift to day drift are expected to reflect long-term effects of the insecticide applications, if they exist, i.e. drift is used as an indicator of the status of the benthos.

Therefore we chose data from our samples which corresponded most closely with the point of time of OCP drift sampling, tried to relate OCP drift parameters to benthic density and compared these relationships from untreated and previously treated places (see Table 4 in Statzner *et al.*, 1985a, for specification of treatment techniques).

2.3. Statistical methods

Drift parameters were transformed to $n+1$ except when hourly or daily drift rates had been calculated. Means of ND and DD values (calculated after ln transformation of the original data) were used in regression analyses. Multivariate models were established for untransformed and ln transformed dependent variables: that model

giving the best fit was chosen for presentation. In these models a stepwise analysis was performed to investigate the relationship between drift (the dependent variable) and three abiotic and four biotic variables (see Table 1 and Appendix 1). In these forward stepwise multiple linear regression analyses, models were computed by adding the variable with the highest F-prime 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.

Since the method of multiple linear regression can be applied only if the number of data is larger than the number of independent variables, we had to reduce the number of the latter. This was done according to the procedure described in Appendix 1.

2.4. Larval identification

Over 69,000 caddis specimens were identified: Hydropsychidae according to Statzner (1984) and Statzner & Gibon (1985), other species according to Marlier (1962), Gibbs (1973) and Dejoux *et al.* (1981). Four hydropsychids were abundant in our material: *Aethaloptera dispar* Brauer, *Macrostemum alienum* (Ulmer), *Cheumatopsyche digitata* (Mosely) and *Cheumatopsyche falcifera* (Ulmer). *Orthotrichia* larvae were not identified to the species level. The larvae of *Chimarra* all resembled those of *C. petri*. However, adults of *C. petri* and *C. sassandrae* occurred together throughout the study area (Gibon & Statzner, 1985). Since we were not able to discriminate between the larvae of these two species, we have treated all *Chimarra* under the name 'petri group'.

Larval instars of hydropsychid species were separated according to morphological characteristics and head width. The *Chimarra petri* group was treated on a size group level (these groups are thus not larval instars!) established from a head width frequency diagram (group a=smallest larvae; group f=largest larvae). All specimens of *Orthotrichia* were in the fifth instar (Nielsen, 1948).

Because animals are usually identified to family in the OCP monitoring programme we

will pool our material to that level when the relevance of drift data to that programme is considered.

3. Results

3.1. Diurnal drift patterns

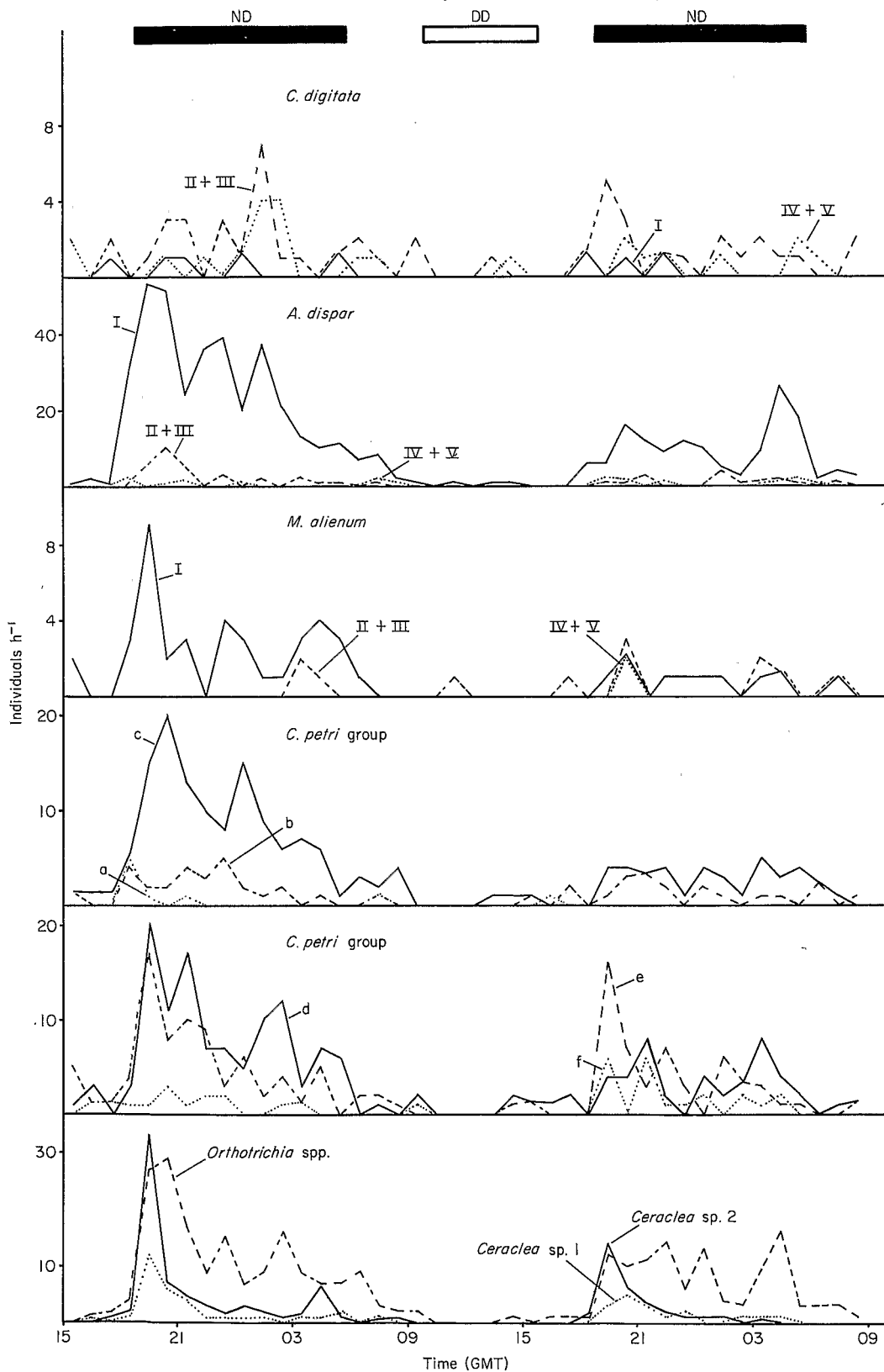
Fig. 1 shows that caddis flies drifted in higher numbers at night than during the day. When very young larvae were abundant, their drift increased slightly earlier in the evening than that of older larvae (*A. dispar*, *C. petri* group, probably *M. alienum*). Almost all larvae I of *A. dispar* and a large proportion of larvae I of *M. alienum* captured in the drift of these two trials had a transparent cuticule, indicating that these specimens had hatched very recently.

3.2. Drift versus benthic density

In this section we will consider drift transport area⁻¹ and drift rate of a larval group in relation to its own benthic density. Only *C. digitata* was abundant enough to evaluate these topics for individual instars: no significant relationships ($P > 0.05$) between benthic density and drift transport area⁻¹ or drift rate were found for any individual instar of *C. digitata*. No significant regression models were obtained by treating *C. digitata* at the species level in day drift, but significant exponential ones could be drawn from night and peak drift (Fig. 2). The same pattern was observed in *A. dispar*, while the *C. petri* group and *Orthotrichia* spp. followed linear, exponential, power and polynomial models (Fig. 2).

Linearity of such relationships shows that drift was not density dependent (i.e. drift rates were constant). Even in the non-linear models of Fig. 2 a straight line was only a slightly worse fit in most cases. Thus further analysis is required to decide whether the model is density dependent or not (Chang & Sell, 1984). According to these authors, polynomial models point to density dependence of the drift, but due to the wide 95% confidence limits this cannot be decided with certainty. In order to test the density dependence of the exponential and power models of

FIG. 1. Example of diurnal drift patterns of the most abundant caddis flies (totals from two experiments) in the Maraoué River, Entomokro, 24–26 January 1978. ND and DD represent the periods of night respectively day drift in the further analyses. Data are given for instars (I–V, sometimes pooled), size groups (a–f) or all larvae of a taxon.



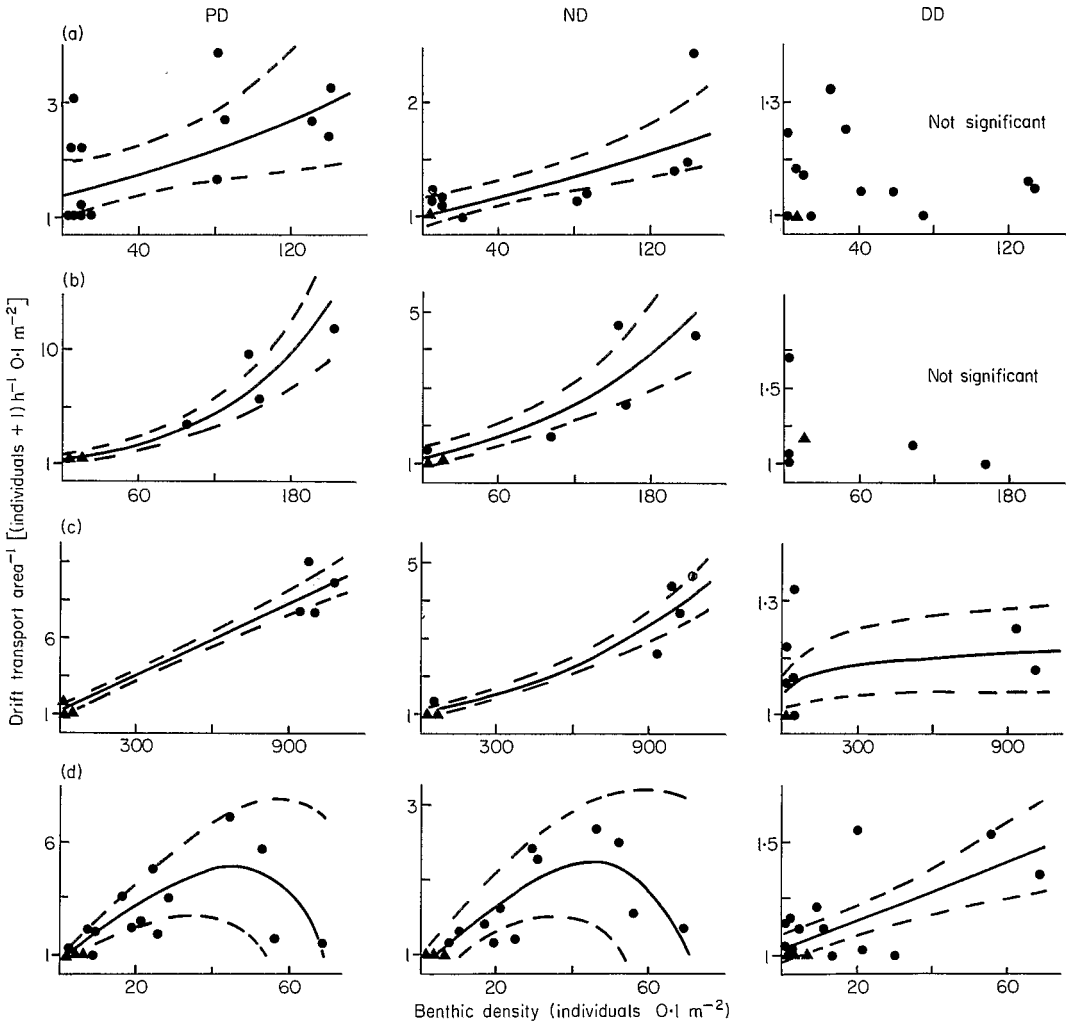


FIG. 2. (a) *Cheumatopsyche digitata*, (b) *Aethaloptera dispar*, (c) *Chimarra petri* group, (d) *Orthotrichia* spp.: Significant relationships ($P < 0.05$) between benthic density and drift transport area⁻¹ shown for peak drift (PD), night drift (ND) and day drift (DD). Triangles: more than one point (see Appendix 1 for full n). Broken lines indicate the 95% confidence limits of the equations which fitted best to the data (see below). The numbers in parentheses in these equations indicate the percentage to be added and subtracted from the slope factor to calculate its 95% confidence limits; r is the coefficient of correlation. Linear models: *C. petri* group; PD: $y = 1.2 + 0.0078(12)x$, $r = 0.98$. *Orthotrichia* spp.; DD: $y = 1.0 + 0.0060(52)x$, $r = 0.64$. Exponential models: *C. digitata*; PD: $y = 1.4 e^{0.0054(84)x}$, $r = 0.60$; ND: $y = 1.0 e^{0.0033(51)x}$, $r = 0.78$. *A. dispar*; PD: $y = 1.3 e^{0.0112(25)x}$, $r = 0.97$; ND: $y = 1.2 e^{0.0068(35)x}$, $r = 0.94$. *C. petri* group; ND: $y = 1.1 e^{0.0013(11)x}$, $r = 0.98$. Power models: *C. petri* group; DD: $y = 1.0 x^{0.0226(85)}$, $r = 0.56$. Polynomial models: *Orthotrichia* spp.; PD: $y = 0.9 + 0.1(34)x - 4.9 \times 10^{-9}(47)x^2$, $r = 0.79$; ND: $y = 0.9 + 0.04(20)x - 1.1 \times 10^{-7}(44)x^4$, $r = 0.86$.

Fig. 2 we checked the drift rates (% benthic population drifting h^{-1}) versus benthic densities. If these models (in the linearized form) have a slope significantly different from zero, drift was concluded to be a density dependent event (Statzner *et al.*, 1985b). This was not the case except in the peak drift of *A. dispar* and the night drift of *C. petri* group. However, even these two

models lost significance if few data from tests with a very low benthic density (less than 1 individual $0.1 m^{-2}$) were removed from the data set. Thus we have no or only weak statistical evidence that drift of the taxa in Fig. 2 was density dependent, and no self-regulation of an upper benthic density by emigration through drift was indicated.

3.3. Multivariate drift models

Drift transport area⁻¹ of a larval group (Appendix 2) frequently was more closely related to benthic densities of other caddis flies than to its own benthic densities. Benthic densities of caddis flies (selected according to the procedure described in Appendix 1) contributed, in thirty-one cases, significantly to the models. In thirteen cases drift of a larval group was related to its own benthic densities (often positively) but in eighteen cases it was related to benthic densities of other groups (positively as

well as negatively). Biotic variables contributed significantly to the models more often than did abiotic ones. Of the latter, only water temperature and velocity in the gutter appeared regularly. Drift was usually positively related to the both.

Models on drift rate (Appendix 3) were not as significant as those on drift transport, and often a considerable number of independent variables had to be introduced until significance was reached. Note that in these models the independent variable OWN benthic densities never played a significant role, but benthic densities of

TABLE 2. Hourly night drift rates (%). We indicated the mean and the 95% confidence limits of the mean (calculated after arcsine transformations of the square root of P). Calculations were based on periods longer than 30 h, except those marked with a prime ('') (between 20 and 30 h) or double prime ('') (between 10 and 20 h). Trials with less than ten specimens of the considered taxon in the gutter excluded. I to V or a to f: instars respectively size groups, all: all larvae of a taxon together.

	Exposure to light of full moon		First or second nights of trials	
	Yes	No	First	Second
<i>Cheumatopsyche digitata</i>				
I	0.04(0.00-0.18)'	0.04(0.00-0.16)'	0.05(0.00-0.19)	0.02(0.00-0.12)'
II	0.10(0.01-0.29)'	0.06(0.00-0.20)'	0.19(0.04-0.43)	0.07(0.00-0.23)'
III	0.03(0.00-0.10)'	0.09(0.01-0.23)'	0.14(0.04-0.30)	0.05(0.01-0.15)'
IV	0.01(0.00-0.04)'	0.02(0.00-0.08)'	0.02(0.00-0.05)	0.02(0.00-0.08)'
V	0.01(0.00-0.03)'	0.00(0.00-0.01)'	0.04(0.01-0.11)	0.00(0.00-0.01)'
All	0.09(0.04-0.18)'	0.11(0.04-0.20)'	0.18(0.09-0.31)	0.09(0.03-0.17)'
<i>Aethaloptera dispar</i>				
I	4.99(3.54-6.66)'	5.55(3.99-7.25)'	5.61(4.34-7.04)'	4.88(3.26-6.81)'
II	0.82(0.17-1.94)'	0.41(0.03-1.24)'	1.23(0.35-2.66)'	0.19(0.00-0.74)'
III	0.31(0.03-0.90)'	0.15(0.00-0.52)'	0.24(0.01-0.77)'	0.20(0.01-0.63)'
IV	0'	0.10(0.01-0.30)'	0.00(0.00-0.02)'	0.07(0.00-0.23)'
V	0'	0.01(0.00-0.05)'	0.00(0.00-0.02)'	0.00(0.00-0.02)'
All	1.72(1.23-2.29)'	1.94(1.45-2.49)'	2.02(1.48-2.64)	1.34(0.95-1.80)'
<i>Macrostemum alienum</i>				
I	0.58(0.17-1.25)'	0.42(0.10-0.94)'	1.03(0.40-1.94)'	0.15(0.02-0.42)'
II	0.00(0.00-0.01)'	0.01(0.00-0.06)'	0.00(0.00-0.01)'	0.01(0.00-0.07)'
III	0.01(0.00-0.05)'	0.01(0.00-0.03)'	0.00(0.00-0.02)'	0.01(0.00-0.07)'
IV	0'	0'	0'	0'
V	0'	0'	0'	0'
All	0.16(0.06-0.33)'	0.12(0.03-0.27)'	0.25(0.10-0.46)'	0.06(0.01-0.17)'
<i>Chimarra petri</i> group				
a	0.00(0.00-0.02)'	0.00(0.00-0.01)'	0.01(0.00-0.04)'	0'
b	0.05(0.02-0.11)'	0.02(0.01-0.06)'	0.05(0.02-0.10)'	0.03(0.00-0.06)'
c	0.20(0.12-0.32)'	0.29(0.18-0.43)'	0.47(0.33-0.64)'	0.09(0.05-0.16)'
d	0.24(0.13-0.38)'	0.23(0.13-0.35)'	0.44(0.30-0.62)'	0.09(0.04-0.16)'
e	0.10(0.05-0.18)'	0.13(0.07-0.20)'	0.15(0.08-0.23)'	0.09(0.04-0.15)'
f	0.04(0.01-0.09)'	0.04(0.00-0.12)'	0.02(0.00-0.07)'	0.06(0.01-0.15)'
all	0.25(0.18-0.33)'	0.29(0.23-0.36)'	0.27(0.15-0.43)	0.18(0.14-0.24)'
<i>Ceraclea</i> sp. 1				
All	1.00(0.38-1.89)'	0.43(0.13-0.90)'	0.96(0.38-1.81)'	0.45(0.13-0.97)'
<i>Ceraclea</i> sp. 2				
All	1.39(0.54-2.63)'	1.69(0.80-2.90)'	2.19(1.09-3.66)'	0.99(0.34-1.97)'
<i>Orthotrichia</i> spp.				
V	2.27(1.28-3.52)'	5.44(3.57-7.68)'	2.27(1.55-3.13)	4.05(2.40-6.10)

other larvae did. Drift rate was always negatively related to significant abiotic variables.

3.4. Drift rates of larvae

The data were sufficient to test the effect of moonlight on drift rates. We also asked whether rates in the first night were different from those in the second night (probable artefacts due to manipulation of the gutter at the beginning of an experiment) (Table 2).

Larvae not exposed to full moonlight did not show higher drift rates than exposed ones. In

many larval groups the drift rate tended to be higher during the first nights of experiments than during the second nights.

Drift rates per 24 h and hourly night and day drift rates often differed between species and between instars of the same species (Table 3). In species which hatched from eggs during the trials, drift rates of young larvae were distinctly higher than those of older ones (*A. dispar*, *M. alienum*). Medium sized larvae of *C. digitata* and *C. petri* group had higher drift rates than smaller and larger ones.

Mean drift rates (per 24 h) of three less abun-

TABLE 3. Drift rates (%). We show the mean and the 95% confidence limits (calculated as described in Table 2). 24 h data were based on sums of the appropriate 24 h period. A few of these periods were not totally sampled. These were completed by filling the gaps by replicating samples of the appropriate period: thus the available number of 24 h periods is added in the last bracket of a line. See Table 2 for further details.

	Day drift (rate h ⁻¹)	Night drift (rate h ⁻¹)	24 h period (rate day ⁻¹)	(n)
<i>Cheumatopsyche digitata</i>				
I	0.03(0.01-0.20)	0.04(0.00-0.11)	7.3(3.3-12.7)	(6)
II	0.03(0.00-0.11)	0.13(0.04-0.26)	13.0(9.1-17.5)	(6)
III	0.09(0.00-0.34)	0.09(0.03-0.18)	8.1(4.2-13.1)	(6)
IV	0.04(0.00-0.18)'	0.02(0.00-0.05)	3.5(0.3-15.9)	(5)
V	0.00(0.00-0.02)'	0.02(0.00-0.04)	3.5(0.1-11.5)	(5)
All	0.10(0.03-0.21)	0.14(0.08-0.21)	7.8(2.9-14.6)	(10)
<i>Aethaloptera dispar</i>				
I	0.18(0.00-0.67)''	5.24(4.18-6.42)	60.6(53.7-67.3)	(4)
II	0''	0.60(0.19-1.24)	34.1(6.9-69.2)	(4)
III	0''	0.22(0.05-0.53)	16.8(1.2-44.8)	(4)
IV	0''	0.02(0.00-0.08)	4.1(0.3-19.8)	(4)
V	0''	0.00(0.00-0.01)	1.6(0.3-4.0)	(4)
All	0.08(0.01-0.22)	1.70(1.36-2.09)	25.8(11.1-43.9)	(7)
<i>Macrostemum alienum</i>				
I	0''	0.49(0.22-0.89)	23.0(6.4-45.8)	(4)
II	0.00(0.00-0.03)''	0.00(0.00-0.02)	1.4(0.2-7.7)	(4)
III	0''	0.01(0.00-0.03)	1.9(0.2-8.1)	(4)
IV	0''	0	0	(4)
V	0''	0	0	(4)
All	0.00(0.00-0.02)''	0.06(0.01-0.14)	6.4(2.2-12.4)	(4)
<i>Chimarra petri</i> group				
a	0''	0.00(0.00-0.01)	2.0(0.0-15.9)	(4)
b	0.01(0.00-0.05)''	0.04(0.02-0.07)	2.4(0.0-11.5)	(4)
c	0.03(0.00-0.10)''	0.25(0.17-0.33)	5.5(1.8-11.0)	(4)
d	0.02(0.00-0.12)''	0.23(0.16-0.32)	5.3(2.3-9.5)	(4)
e	0.00(0.00-0.01)''	0.11(0.07-0.17)	2.9(1.0-5.8)	(4)
f	0.07(0.02-0.44)'	0.04(0.01-0.08)	2.5(0.0-9.6)	(4)
All	0.03(0.00-0.09)	0.24(0.16-0.33)	6.8(2.2-13.6)	(10)
<i>Ceraclea</i> sp. 1				
All	0''	0.68(0.34-1.13)	21.5(11.8-33.3)	(4)
<i>Ceraclea</i> sp. 2				
All	0''	1.53(0.88-2.36)	34.9(25.0-45.4)	(4)
<i>Orthotrichia</i> spp.				
V	0.12(0.01-0.33)	2.93(2.25-3.69)	44.0(23.4-65.7)	(12)

dant taxa were 1.7% in *Polymorphanus* sp. I, 22.9% in *Amphipsyche* spp. and 4.6% in *Tinodes* spp.

3.5. Relevance of drift data for monitoring the effects of insecticides

Three families were sufficiently numerous for analysis: Hydropsychidae, Philopotamidae and Hydroptilidae. We found a significant relationship ($P < 0.05$) between drift concentration (x) and benthic density (y), either in treated or untreated places, in only one case; the night drift of Hydropsychidae. Power models ($y = ax^b$) gave the best fit: from untreated places (95% confidence limits of a and b in parentheses), $y = 39$ (10–154) $x^{1.17(\pm 0.79)}$ ($n = 11$, $r = 0.75$, $P < 0.001$) and from treated places, $y = 343$ (123–961) $x^{1.01(\pm 0.61)}$ ($n = 15$, $r = 0.71$, $P < 0.001$).

While the value of b was not significantly different between the two groups ($F = 0.1$, $P > 0.05$), that of a was ($F = 15.5$, $P < 0.001$). Therefore, the same drift concentration indicated a higher benthic density at treated than at untreated places in the night drift of the Hydropsychidae.

4. Discussion

The diurnal drift patterns (low intensities during the day, higher ones at night) of abundant caddis flies from our tests were similar to those reported by many other authors from other tropical and more temperate areas (see review section in Statzner *et al.*, 1985a). The slightly earlier increase of the drift of very young larvae in some taxa in the evening may be related to a possible tendency for positive phototaxis in that group (Coutant, 1982). These results, however, do not support the hypothesis that drift behaviour of insects has evolved under predation pressure by fish so that tiny, nearly invisible larvae may drift at any time whilst larger ones suppress day drift (Allan, 1984). We found that tiny, young larvae had the same general drift patterns (nocturnal peak) as did larger larvae. This may be due to the fact that predation pressure on day drifting tiny specimens is not negligible in our study area. Thus Dejoux (personal communication) found that if he gently wiped the surfaces of stones with his hand small fishes of the genera *Alestes*, *Micralestes* or *Barbus* started to attack and prey on tiny Baetidae and Tanytarsini, invisible to the naked human eye.

Studies on the density dependence of stream drift must evaluate how closely the densities of animals in tests resemble the maximum density reported in nature; because self-regulation probably will not occur until a specific benthic density (in relation to resource availability) is surpassed (Statzner *et al.*, 1985b). Of the natural gravel/pebble substrata so far studied, which most resemble those in our trials, maximal densities of about 22,000 m^{-2} (*C. digitata*), about 2000 m^{-2} (*A. dispar*), and about 2000 m^{-2} (*Chimarra*) were reported from the upper 5 cm layer of the substratum in a 15-month study (Statzner, 1982; and unpublished). In our trials these densities were surpassed by *C. petri* group, but not reached by *C. digitata*. The maximal densities of *A. dispar* in our test were about equivalent to the figure reported from the natural rapid. However, in our tests with a high density of this species young instars were dominant, while older ones predominated in the field at that time. Comparable field data are not available for *Orthotrichia* spp.

The lack of a distinct self-regulation of an upper benthic density through drift in any of the caddis fly taxa tested surprised us, because we initially expected the extreme concentration of lotic insects on the rapids during periods of low discharge to result in such a self-regulation. Hydropsychinae and Macronematini in the Ivory Coast possess species-characteristic stridulation ridges in the larvae II–V (Statzner, 1984; Statzner & Gibon, 1985). Such structures are used in aggressive encounters (Jansson & Vuoristo, 1979; Boon, 1984), which have been observed in field and laboratory studies (Sattler, 1958; Glass & Bovbjerg, 1969; Schuhmacher, 1970; Pierrot, 1984; Mogel, Rieder & Statzner, 1985). Cannibalism also has been reported in some species (Hynes & Williams, 1962; Kaiser, 1965; Schröder, 1976). Larvae of one hydroptilid species (Hart, 1983) also exhibit aggressive behaviour towards conspecifics. All this led us to expect a density dependent aggressive behaviour (=drift inducing interaction) in the larvae and thus a density dependent drift in our trials.

The fact that the benthic density of other larval groups influenced the multivariate drift models more frequently than their own benthic density, indicated that biological interactions between groups were more important than those within groups (see Statzner *et al.*, 1985b, for a discussion of possible mechanisms).

This tendency may be related to the special

situation in our study area. Specimens drifting out of a rapid during periods of low discharge usually reach a very long pool where flow had practically ceased. Predation by fish (see above) or other mechanisms (see Statzner *et al.*, 1985b) may cause much higher mortalities of drifters in our study area than in, for instance, temperate, permanent streams.

High drift rates of newly hatched hydro-psyche larvae were observed on only one occasion and they usually do not hatch in periods of low discharge in our study area (see Statzner, 1982). Therefore newly hatched larvae usually will not reach a long pool with standing water, but will be dispersed widely within a flowing stream, as found by O'Hop & Wallace (1983) for the North American hydro-psyche *Parapsyche cardis* Ross and *Diplectrona modesta* Banks.

The tendency of higher drift rates in the first night of an experiment compared to those in the second night may indicate possible artefacts in drift due to the experimental procedures (cf. Statzner *et al.*, 1985b). However, differences in drift rates between consecutive nights were never large. Thus, artefacts should only have had a minor influence on our results. Exclusion of drifting food materials caused by the net in front of our gutter systems may have led to further artefacts in species which are considered to be filter feeders. How critical this was is unknown, but these filter feeders do not always construct nets (Statzner, 1982) and most of the planktonic algal drift was small enough (Iltis, 1982) to pass through the meshes of the gutters' front nets.

If we compare the drift rates of caddis larvae from our study with those known from the literature (see Table III in Statzner *et al.*, 1985a), no outstanding differences are evident. However, no data from other geographical regions determined for (i) instars and (ii) under conditions as natural as ours are yet available.

All our data on caddis flies were obtained from tests not under the direct effect of insecticide treatments. Drift samples taken at the same time as in the monitoring programme of OCP failed to reflect benthic densities of caddis families in most cases. Therefore our results hardly supported the approach that drift sampled 1.5 h before and after sunset can be used as an indicator of the status of the benthos.

How drift models of caddis flies behave if other insect groups are also considered will be shown in the last paper of this series. We assume

that our results were caused by a complicated net of biological intra- and interspecific interactions in the benthos, which cannot be clearly understood without further experimental work. The information compiled in the Appendices 1, 2 and 3 can serve as a base for such precise future experiments. Because the physical environment in our gutters was relatively benign it is likely that biological interactions were favoured in our tests (cf. Peckarsky, 1983). Under harsher physical conditions (our gutters could not be used during floods) parameters like velocity or turbidity might have been more important in the types of models described in the Appendices.

Therefore, and because of the instar differences within single species, generalizations about the regulation of benthic populations through drift are hardly possible.

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References

- Allan J.D. (1984) The size composition of invertebrate drift in a Rocky Mountain stream. *Oikos*, **43**, 68-76.
- Boon P.J. (1984) Habitat exploitation by larvae of *Amphipsyche meridiana* (Trichoptera: Hydro-psycheidae) in a Javanese lake outlet. *Freshwater Biology*, **14**, 1-12.
- Chang W.Y.B. & Sell D.W. (1984) Determining the density dependence of immigration and emigration of benthic stream invertebrates: theoretical considerations. *Hydrobiologia*, **108**, 49-55.
- Coutant C.C. (1982) Positive phototaxis in first instar *Hydropsyche cockerelli* Banks (Trichoptera). *Aquatic Insects*, **4**, 55-59.
- Davies J.B., Le Berre R., Walsh J.F. & Cliff B. (1978) Onchocerciasis and *Simulium* control in the Volta River Basin. *Mosquito News*, **38**, 466-472.
- Dejoux C. (1983) Utilisation du téméphos en campagne de lutte contre *Simulium damnosum* en Afrique de l'Ouest. Impact des premiers cycles de traitement sur le milieu aquatique. *Revue d'Hydrobiologie Tropicale*, **16**, 165-179.

- Dejoux C., Elouard J.-M., Forge P. & Maslin J.L. (1981) Catalogue iconographique des insectes aquatiques de Côte d'Ivoire. Rapport de l'Office de la Recherche Scientifique et Technique Outre-Mer, Bouaké, 42.
- Elouard J.-M. (1983). Impact d'un insecticide organophosphoré (le Téméphos) sur les entomocénoses associées aux stades préimaginaux du complexe *Simulium damnosum* Theobald (Diptera: Simuliidae). Thèse Université de Paris-Sud, Orsay, No. 2686.
- Gibbs D.G. (1973) The Trichoptera of Ghana. *Deutsche Entomologische Zeitschrift* (Neue Folge), **20**, 363-424.
- Gibon F.M. & Statzner B. (1985) Longitudinal zonation of lotic insects in the Bandama River system (Ivory Coast). *Hydrobiologia*, **122**, 61-64.
- Glass L.W. & Bovbjerg, R.V. (1969) Density and dispersion in laboratory populations of caddisfly larvae (*Cheumatopsyche*, Hydropsychidae). *Ecology*, **50**, 1082-1084.
- Goedmakers A. & Pinkster S. (1981) Population dynamics of three gammarid species (Crustacea, Amphipoda) in a French chalk stream. Part III. Migration. *Bijdragen tot de Dierkunde*, **51**, 145-180.
- Hart D.D. (1983) The importance of competitive interactions within stream populations and communities. *Stream ecology* (Eds J. R. Barnes and G. W. Minshall), pp. 99-136. Plenum Press, New York.
- Hynes H.B.N. & Williams T.R. (1962) The effect of DDT on the fauna of a Central African stream. *Annals of Tropical Medicine and Parasitology*, **56**, 78-91.
- Itlis A. (1982) Peuplements algaux des rivières de Côte d'Ivoire. I. Stations de prélèvement, méthodologie, remarques sur la composition qualitative et biovolumes. *Revue d'Hydrobiologie Tropicale*, **15**, 231-239.
- Jansson A. & Vuoristo T. (1979) Significance of stridulation in larval Hydropsychidae (Trichoptera). *Behaviour*, **71**, 167-186.
- Kaiser P. (1965) Über Netzbau und Strömungssinn bei den Larven der Gattung *Hydropsyche* Pict. (Ins., Trichoptera). *Internationale Revue der Gesamten Hydrobiologie*, **50**, 169-224.
- Lévêque C., Dejoux C. & Itlis A. (1983) Limnologie du fleuve Bandama, Côte d'Ivoire. *Hydrobiologia*, **100**, 113-141.
- Lévêque C., Odei M. & Pugh Thomas M. (1977) The Onchocerciasis Control Programme and the monitoring of its effect on the riverine biology of the Volta River Basin. *Ecological Effects of Pesticides* (Eds F. H. Perring and K. Mellanby), pp. 133-143. Linnaea Society Symposium Series, No. 5.
- Marlier G. (1962) Genera des Trichoptères de l'Afrique. *Annales Musee Royal de l'Afrique centrale*, Série in 8, Sciences Zoologiques, Ter-vuren, no. 109.
- Mogel R., Rieder N. & Statzner B. (1985) Ein Gerät zur Freilandbeobachtung des nächtlichen Verhaltens von benthischen Bachtieren, mit Befunden aus der Gattung *Hydropsyche* (Trichoptera, Insecta). *Carolinea*, **42**, 121-128.
- Nielsen A. (1948) Postembryonic development and biology of the Hydroptilidae. *Biologiske Skrifter det Kongelige Danske Videnskabernes Selskabs, Copenhagen*, No. 5 (1), 1-200.
- O'Hop J. & Wallace J.B. (1983) Invertebrate drift, discharge, and sediment relations in southern Appalachian headwater streams. *Hydrobiologia*, **98**, 71-84.
- Peckarsky B.L. (1983) Biotic interactions or abiotic limitations? A model of lotic community structure. *Dynamics of Lotic Ecosystems* (Eds T. D. Fontaine and S. M. Bartell), pp. 303-323. Ann Arbor Science, Ann Arbor.
- Pierrot J.-P. (1984) Étude expérimentale de la niche écologique larvaire de quelques espèces d'*Hydropsyche* (Trichoptera, Hydropsychidae). Thèse, Université C. Bernard Lyon I.
- Sattler W. (1958) Beiträge zur Kenntnis von Lebensweise und Körperbau der Larve und Puppe von *Hydropsyche* Pictet (Trichoptera) mit besonderer Berücksichtigung des Netzbaus. *Zeitschrift für Morphologie und Ökologie der Tiere*, **47**, 115-192.
- Schröder P. (1976) Zur Nahrung der Larvenstadien der Köcherfliege *Hydropsyche instabilis* (Trichoptera: Hydropsychidae). *Entomologica Germanica*, **3**, 260-264.
- Schuhmacher H. (1970) Untersuchungen zur Taxonomie, Biologie und Ökologie einiger Köcherfliegenarten der Gattung *Hydropsyche* Pict. (Insecta, Trichoptera). *Internationale Revue der Gesamten Hydrobiologie*, **55**, 511-557.
- Statzner B. (1982) Population dynamics of Hydropsychidae (Insecta; Trichoptera) in the N'Zi River (Ivory Coast), a temporary stream partly treated with the insecticide Chlorphoxim. *Revue d'Hydrobiologie Tropicale*, **15**, 157-176.
- Statzner B. (1984) Keys to adult and immature Hydropsychinae in the Ivory Coast (West-Africa) with notes on their taxonomy and distribution (Insecta: Trichoptera). *Spixiana*, **7**, 23-50.
- Statzner B., Dejoux C. & Elouard J.-M. (1985a) Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams (Ivory Coast). I. Introduction: review of drift literature, methods, and experimental conditions. *Revue d'Hydrobiologie Tropicale*, **17** (1984), 319-334.
- Statzner B., Elouard, J.-M. & Dejoux C. (1985b) Field experiments on the relationship between drift and benthic densities of aquatic insects in tropical streams. II. *Cheumatopsyche falcifera* (Ulmer) (Trichoptera: Hydropsychidae). *Journal of Animal Ecology*, **55**, 93-110.
- Statzner B. & Gibon F.M. (1985) Keys to adult and immature Macronematinae (Insecta: Trichoptera) from the Ivory Coast (West Africa) with notes on their taxonomy and distribution. *Revue d'Hydrobiologie Tropicale*, **17** (1984), 129-151.
- Townsend C.R. & Hildrew A.G. (1976) Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *Journal of Animal Ecology*, **45**, 759-777.

APPENDIX 1. Independent variables used in the drift models in Appendix 2 and 3. From all variables of Table 1 those with the best correlation to the dependent variables were chosen after the calculation of product moment correlation coefficients: three variables from the abiotic group and four variables from the biotic group. These variables were ranked in order of decreasing correlation to the dependent variable (from left to right). If models in Appendix 2 or 3 did not reach significance ($P > 0.05$), data were omitted from this appendix. Note that the dependent variable was either RAW or LN transformed (see Appendix 2 and 3). If the correlation was significant (** $P < 0.01$; * $P < 0.05$) nothing was stated for positive and - was stated for negative relationships. PD: peak drift; ND: night drift; DD: day drift.

		Drift transport area ⁻¹ (drift h ⁻¹ 0.1 m ⁻²)							
<i>Cheumatopsyche falcifera</i>									
Larv. I	PD(n=14)	VEL	TMP	MON	CCO	CDI	CFA	ADI	
	ND(n=14)	VEL	TMP	TRB	ADI	CCO	OWN	CDI	
	DD(n=14)	OWN*	VEL*	TMP*	CDI*	CFA*	TRB	ADI	
Larv. II	PD(n=13)	VEL**	-CCO**	TMP*	CFA*	CDI*	OWN	TRB	
	ND(n=13)	TMP*	VEL*	CCO	TRB	ADI	CFA	CDI	
	DD(n=13)	TMP**	VEL**	TRB**	CFA*	CDI*	OWN*	ADI	
Larv. III	PD(n=14)	TMP**	VEL**	OWN**	CDI**	CFA**	TRB**	-ADI**	
	ND(n=14)	VEL**	TMP**	CFA*	CDI*	-CCO*	MON	OWN	
	DD(n=14)	OWN**	CDI**	CFA**	VEL**	TMP**	TRB*	-CCO*	
Larv. IV	PD(n=14)	TMP**	VEL**	OWN**	CDI**	CFA**	-CCO**	MON**	
	ND(n=14)	OWN**	VEL**	TMP**	CDI**	CFA**	-CCO**	MON*	
	DD(n=14)	CFA**	CDI**	OWN**	VEL**	TMP**	-CCO**	TRB*	
Larv. V	PD(n=14)	VEL**	OWN**	CDI**	CFA**	TMP**	-CCO**	MON*	
	ND(n=14)	OWN**	CDI**	CFA**	VEL**	TMP**	-CCO**	MON*	
	DD(n=14)	CDI**	OWN**	CFA**	VEL**	TMP**	-CCO**	TRB**	
All larvae togeth.	PD(n=25)	OWN**	TMP**	MON**	VEL**	CCO	CPE	OHY	
	ND(n=25)	OWN**	TMP**	MON**	VEL**	CCO	OTT	CDI	
	DD(n=28)	OWN**	TMP**	VEL**	MON**	CDI	CCO	ADI	
<i>Cheumatopsyche digitata</i>									
	PD(n=14)	-TRB*	CCO*	OWN*	VEL	MON	CFA	OTT	
	ND(n=14)	CCO**	OWN**	-TRB**	-VEL*	TMP	CFA	OTT	
<i>Aethaloptera dispar</i>									
	PD(n=9)	OWN**	OHY**	CPE**	CFA**	TMP**	VEL	TRB	
	ND(n=9)	CPE**	CFA**	OWN**	CDI**	TMP*	VEL	MON	
<i>Chimarra petri</i> group									
	PD(n=18)	ADI**	OWN**	OHY**	MAL**	TRB	VEL	DIS	
	ND(n=18)	OWN**	ADI**	OHY**	MAL**	TRB	VEL	DIS	
	DD(n=16)	OTT**	DIS**	ADI**	TRB	MAL	OWN	MON	
<i>Orthotrichia</i> spp.									
	PD(n=23)	ADI**	CPE**	OHY**	MAL**	TMP	TRB	MON	
	ND(n=23)	CPE**	ADI**	OWN**	OHY**	TRB	DIS	TMP	
	DD(n=25)	OWN**	DIS**	CFA	VEL	CDI	TRB	CCO	
Drift rate (% h ⁻¹)									
<i>Cheumatopsyche falcifera</i>									
Larv. I	ND(n=14)	OWN	TRB	TMP	VEL	CDI	CFA	ADI	
Larv. IV	PD(n=14)	DIS	OTT	CPE	OHY	MAL	VEL	TRB	
	ND(n=14)	-DIS*	-OTT*	MAL	CPE	OHY	TRB	TMP	
	DD(n=14)	CCO	TRB	DIS	ADI	MAL	CPE	MON	
Larv. V	PD(n=14)	-MAL*	-CPE*	-OTT*	OHY	DIS	VEL	TRB	
	DD(n=14)	CCO	ADI	TRB	DIS	MAL	MON	CPE	
All larvae togeth.	PD(n=25)	OTT**	DIS	VEL	TMP	CDI	OHY	MAL	
	ND(n=25)	OTT*	DIS	OHY	TRB	VEL	MAL	CPE	
	DD(n=28)	OTT*	VEL	CDI	TMP	OWN	DIS	CCO	
<i>Aethaloptera dispar</i>									
	PD(n=9)	-TMP*	-OTT*	DIS	OWN	CPE	CDI	TRB	
	ND(n=9)	-TRB*	-TMP*	DIS	OTT	OWN	CPE	CDI	
<i>Chimarra petri</i> group									
	DD(n=16)	OTT**	DIS	CDI	TRB	OHY	CCO	MON	
<i>Orthotrichia</i> spp.									
	PD(n=23)	-TRB**	CDI*	CCO	VEL	CPE	OHY	DIS	
	ND(n=23)	CPE**	OHY**	ADI**	MAL*	MON	TMP	DIS	
	DD(n=25)	CFA	MON	OWN	CDI	VEL	CCO	TMP	

APPENDIX 2. Drift transport area⁻¹ (drift h⁻¹ 0.1 m⁻²; RAW: untransformed, LN: as natural logarithm) versus the appropriate independent variables of Appendix 1. We showed the cumulative percentage variation explained in the best-fitting drift model after the stepwise introduction of independent variables (chosen according to the highest F-prime) in forward stepwise multiple linear regression. Detailed information was only given for significant models until the last independent variable with a significant relationship was introduced and for the complete model (ALL). Statistics referred to the moment a variable was introduced into the model.

	PD	ND	DD
<i>Cheumatopsyche falcifera</i>			
Larvae I	LN VEL:21ns -#CDI:58** ALL:69ns	RAW VEL:19ns -#CDI:47* ALL:58ns	LN +#OWN:42* ALL:46ns
Larvae II	LN +#VEL:52** ALL:73ns	RAW +#TMP:36* CDI:44ns -#OWN:76** -#VEL:88** ALL:93**	LN +\$TMP:68*** ALL:91*
Larvae III	LN +\$TMP:77*** ALL:86:*	RAW +#VEL:46** ALL:83*	LN +\$OWN:79*** ALL:80*
Larvae IV	LN +\$TMP:91*** ALL:93**	LN +\$OWN:89*** -#CDI:92*** -#TMP:96*** ALL:97***	LN +\$CFA:91*** ALL:93***
Larvae V	LN +\$VEL:91*** ALL:95***	LN +\$OWN:95*** ALL:95***	LN +\$CDI:98*** +#VEL:99*** ALL:99***
All larvae together	LN +\$OWN:70*** +#CPE:78*** ALL:80***	LN +\$OWN:79*** +#MON:83*** ALL:86***	LN +\$OWN:88*** ALL:90***
<i>Cheumatopsyche digitata</i>	RAW -#TRB:41* ALL:68ns	RAW +\$CCO:68*** +#TRB:84*** +#TMP:92*** ALL:96***	ns
<i>Aethaloptera dispar</i>	LN +\$OWN:94*** ALL:99ns	LN +\$CPE:90*** OWN:93*** +#CDI:97*** ALL:99ns	Few data
<i>Chimarra petri</i> group	RAW +\$ADI:96*** +\$OWN:98*** +#DIS:99*** -#MAL:99*** ALL:99***	LN +\$OWN:96*** ADI:96*** -#MAL:99*** ALL:99***	RAW +\$OTT:76** +#DIS:85*** +#MAL:91*** ALL:93***
<i>Orthotrichia</i> spp.	RAW +\$ADI:68*** +#TMP:78*** -#MAL:86*** -#TRB:90*** ALL:92***	LN +\$CPE:62*** +\$OWN:78*** +#TMP:83*** ALL:87***	LN +\$OWN:41*** +#CFA:53*** ALL:63**

+ # or - # = significant ($P < 0.05$) respectively + \$ or - \$ = very highly significant ($P < 0.001$) positive or negative relationship of the dependent variable to an independent variable; ns ($P > 0.05$), * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$) = significance (ANOVA) of the whole model. PD: peak drift; ND: night drift; DD: day drift.

APPENDIX 3. Hourly drift rate versus the appropriate variables of Appendix 1. See Appendix 2 for further details.

	PD	ND	DD
<i>Cheumatopsyche falcifera</i>			
Larvae 1	ns	RAW OWN:18ns TRB:20ns ADI:28ns TMP:29ns VEL:30ns CDI:30ns -§CFA:99***	ns
Larvae II	ns	ns	ns
Larvae III	ns	ns	ns
Larvae IV	LN DIS:20ns OHY:40ns +§MAL:68** ALL:77ns	RAW -#DIS:36* TRB:42* OHY:49ns -#OTT:76** ALL:79ns	RAW CCO:10ns TRB:20ns MAL:33ns MON:38ns ADI:43ns CPE:48ns -#DIS:89*
Larvae V	RAW -#MAL:35* ALL:61ns	ns	RAW CCO:10ns TRB:20ns MAL:34ns MON:38ns ADI:44ns CPE:49ns -#DIS:91**
All larvae together	LN +§OTT:30** -#OHY:55*** -§VEL:79*** -#CDI:86*** -#TMP:90*** -#DIS:94*** ALL:95***	RAW +§OTT:20* +§OHY:37** ALL:50ns	RAW +§OTT:15* ALL:37ns
<i>Cheumatopsyche digitata</i>			
	ns	ns	ns
<i>Aethaloptera dispar</i>			
	LN -#TMP:51* ALL:99ns	RAW -§TRB:97*** ALL:99*	few data
<i>Chimarra petri</i> group			
	ns	ns	RAW +§OTT:40** ALL:55ns
<i>Orthotrichia</i> spp.			
	LN -#TRB:29** +§OHY:46** VEL:53** CCO:59** -#CPE:67** ALL:72**	RAW +§CPE:36** ALL:44ns	RAW CFA:14ns -#TMP:29* ALL:35ns