

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

*1. Introduction : review of drift literature,
methods, and experimental conditions*

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SUMMARY

A review of the drift literature shows that the phenomenon of drift of benthic stream macroinvertebrates still poses many unanswered questions. The following factors govern natural drift in very diverse ways: sunlight; moonlight; current velocity; discharge; turbidity; substratum; oxygen; water temperature; ion concentration; abundance of organic matter, food, and predators; parasitism; molting processes; benthic density and behaviour of the drifting taxon. Instars or size classes of a taxon exhibit differences in drift intensity. The phenomenon of drift is further complicated by the three phases of drift movement: entrance, travel, and settling. Thus the only way to specifically explain the drift of benthic organisms is to arrange the governing factors into a hierarchical system.

A compilation of distances travelled in the drift and especially drift rates points to possible artifacts occurring in laboratory experiments and emphasizes the necessity of experimental field work under quasi-natural conditions.

We carried out 24 such trials in streams in the Ivory Coast (West Africa) using trough systems (metallic or PVC gutters) to establish the quantitative relationship between insect drift and the various abiotic factors and properties of the benthic community. 790 drift samples were obtained, representing a continuous survey of more than 600 hours. In total 161,000 specimens were examined. Using this broad data base we hope to make a useful contribution to the existing knowledge on: i) the general phenomenon of drift; ii) specific topics related to drift in the tropics; iii) the validity of drift collections as monitored in the study area through the Onchocerciasis Control Programme in order to indicate possible effects of regular insecticide treatments against larval Simulium damnosum s.l. on the non-target benthos.

This introduction to a series of publications about these trials describes our methods and the prevailing experimental conditions.

KEY WORDS : Population dynamics — Lotic insects — Insecticides — Running waters — Africa.

RÉSUMÉ

RECHERCHES EXPÉRIMENTALES SUR LA RELATION ENTRE LA DÉRIVE ET LA DENSITÉ BENTHIQUE
DES INSECTES AQUATIQUES DANS LES EAUX COURANTES TROPICALES (CÔTE D'IVOIRE).

1. INTRODUCTION : REVUE DE LA LITTÉRATURE SUR LA DÉRIVE, MÉTHODOLOGIE ET CONDITIONS EXPÉRIMENTALES

Une revue de la littérature concernant la dérive des macroinvertébrés benthiques met en évidence un grand nombre de questions relatives à ce phénomène, qui restent en suspens. Parmi les principaux facteurs qui influent sur le phénomène de dérive, il faut citer les suivants: l'éclairement solaire et lunaire, la vitesse du courant, le débit

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des cours d'eau, la turbidité, la nature des substrats présents, la teneur en oxygène, la température, la composition ionique de l'eau, l'abondance de matière organique, de nourriture, de prédateurs, le parasitisme, le taux de mue, la densité benthique et le comportement des taxons en dérive. Le stade de développement d'un taxon ou sa taille sont également des éléments qui influent sur son intensité de dérive, ce qui montre à quel point le phénomène de dérive est complexe, d'autant qu'à cette complexité initiale, il faut ajouter une complexité secondaire liée à la cinétique même du phénomène qui comprend trois phases bien distinctes : l'entrée d'un organisme dans la dérive, son transport et son éventuelle réimplantation. En définitive, seul un système hiérarchisé de facteurs est en mesure d'expliquer la dérive spécifique des organismes benthiques. L'examen des données publiées concernant les distances de transport ainsi que la quote-part de dérive mettent en évidence l'existence d'artefacts dans les expérimentations de laboratoire, prouvant la nécessité de réaliser dans ce domaine, un travail de terrain en conditions semi-naturelles.

Dans ce contexte, nous avons effectué 24 expérimentations dans les cours d'eau de Côte d'Ivoire, à l'aide de systèmes canalisés (appareils en fer ou matière plastique, en forme de gouttières). Nous avons ainsi récolté 790 échantillons de dérive (pendant plus de 600 heures), la faune testée représentant un total de 161 000 individus. Ce matériel très abondant nous a permis d'étudier un certain nombre de facteurs expliquant de façon globale le phénomène de dérive en milieu tropical. D'autre part, il a été possible de rechercher la validité d'une récolte de la dérive telle qu'elle est réalisée actuellement en Afrique de l'Ouest, dans le cadre de la surveillance écologique de routine des cours d'eau traités pour contrôler les populations larvaires de *Simulium damnosum* s.l., vecteur de l'onchocercose (Programme OMS de lutte contre l'onchocercose).

Cette note est la première d'une série relative à nos résultats expérimentaux et présente essentiellement les méthodes de terrain mises en œuvre et les conditions d'expérience.

MOTS-CLÉS : Dynamique des populations — Insectes lotiques — Insecticides — Eaux courantes — Afrique.

1. INTRODUCTION

Benthic macroinvertebrates which are dislodged from the stream bottom become part of the drift. What factors govern this drift is a frequently studied question in stream ecology and still remains largely open (see section 2.); this is no surprise, since the complex mechanisms involved in the longitudinal dispersion of even non-living materials (MANGELSDORF & SCHEURMANN, 1980; DIETRICH, 1982; BEER & YOUNG, 1983; BRIDGE & DOMINIC, 1984) are complicated by the specific, biological reactions of an organism.

A considerable number of papers have tried to provide answers to these questions using an experimental approach, most of them were laboratory studies. Although field work on this subject is preferable (GOEDMAKERS & PINKSTER, 1981), the statement of TOWNSEND & HILDREW (1976) that surprisingly little experimentation on drift in the field has been carried out is still valid.

Therefore we communicate the results of field trials on invertebrate drift carried out in streams in the Ivory Coast (West Africa) between 1977 and 1981. Our data are based on 24 reiterations of the following procedure: a gutter containing natural substrata colonized with benthic macroinvertebrates was exposed in a riffle. After a specific period nets were fixed in front of and at the downstream end of this device and the drift of organisms was collected at intervals, usually over periods of about 24 or 48 h. In total more than 600 hours of drift were

recorded. Abiotic factors considered as potential drift regulators were simultaneously monitored. At the end of the trial all animals remaining in the gutter were collected. From all these tests we obtained 790 drift samples and about 161,000 macroinvertebrates, almost exclusively insects. Hence we produced a broad "in situ" data base to relate drift to abiotic factors as well as to the quality and quantity of a quasi-natural benthic community.

This is the first of a series of papers, pointing out unanswered questions in stream drift and specifying which of these questions we will tackle. Furthermore it describes the methods applied and the experimental conditions of our study. The subsequent publications will consider smaller systematic groups of insects, e.g. a single species, family, or order. The drift of single instars of a species, of species or a group of species will be dealt with in relation to abiotic factors and their benthic abundances. A final paper will summarize the previous ones and deal with the synecological aspect of stream drift, e.g. functional group aspects such as prey drift versus benthic density of predators and vice versa.

Thus, we hope to contribute to the existing knowledge about: i) the general phenomenon of drift; ii) specific topics related to drift in the tropics; iii) the validity of drift collections as monitored in the study area through the Onchocerciasis Control Programme (OCP) in order to indicate possible effects of regular insecticide treatments against larval *Simulium damnosum* s.l. on the non-target benthos.

2. CURRENT KNOWLEDGE ON THE PHENOMENON OF DRIFT

Since the 1920's it has been known that benthic organisms are transported downstream in the drift (McATEE, 1925; BORGH, 1927, cit. in MÜLLER, 1954; NEEDHAM, 1928). The hypothesis of the colonization cycle (MOTTRAM, 1932, cit. in MÜLLER, 1982; MÜLLER, 1954, 1982) — in insects a compensation of downstream drift through upstream flight — its importance for the population dynamics of stream insects, and other recolonization mechanisms (WILLIAMS & HYNES, 1976) stimulated much detailed work on drift. It soon became evident

that natural drift — toxic effects of pollutants or insecticides will be largely excluded from our considerations here — exhibit a diel and/or an annual periodicity. With few exceptions this was repeatedly confirmed (see CHASTON, 1972; WATERS, 1972; BOURNAUD & THIBAUT, 1973; MÜLLER, 1974; ADAMUS & GAUFIN, 1976) and is now accepted to be a general pattern. It is further evident that drift varies vertically and horizontally through the cross-section of a stream (WATERS, 1962a, 1965; BESCH, 1966; WENINGER, 1968; CRISP & GLEDHILL, 1970; ELLIOTT, 1970; CLIFFORD, 1972; CELLOT, 1982; ECKBLAD *et al.*, 1984) and represents a specific food source for fish (e.g. ELLIOTT, 1973; METZ, 1974;

TABLE I

Relationship between the drift of benthic macroinvertebrates and abiotic as well as biotic factors. +: positive, -: negative, 0: no relationship between the drift and an increase of the factor, +e: drift density dependent. VEL: current velocity; DIS: discharge; TRB: turbidity; OXY: oxygen; TMP: water temperature; ION: ion concentration; MON: moonlight; FOD: abundance of food; PRE: abundance of predators or disturbances by other species; OWN: benthic density of the taxon considered in the drift. See appendix for codation of references

taxon	VEL	DIS	TRB	OXY	TMP	ION	MON	FOD	PRE	OWN	reference
field drift studies											
Tricladida	-	-			-					0	42/44
Gammarus		0			+0	+	-				0 20/27/31/38/43/44/59/64
Baetis	-0	+ -0	+0	0	+ -0		-0		+0	+e0	2/5/9/15/22/32/42/45/48/49/51/59 61/62/64
Heptageniidae	0	+ -		0	0	+	0		0	+0	2/5/15/21/23/32/49/51
Ephemera	-	+ -0			0	+	-0		0	+e	2/5/9/23/24/49/51
other Ephemeroptera		+	+				-			+e	22/24/32/62
Nemoura	-	-0			0	0	0			+	23/42/51
Capniinae		0			0	0	0			0	51
other Plecoptera		+0	+0		+	+0			0	+e?0	2/5/23/37/46/53
Elmidae	0	+	0	0	0					+0	5/15/62
Hydropsychinae	0	+	+	0	+		-0			+0	5/11/15/51/52/62
other Trichoptera	+	+					-		0		2/5/19/42/59
Simulium	-0	+ -	+0	-0	0		-0		+	+e0	1/15/42/44/45/50/62
other Simuliidae		+0	+0		+ -	+	0		+0	+e0	2/16/23/44/48/51
Chironomidae		+0	+		0	+	+0		-0	0	2/5/16/23/29/45/51/62
other Diptera		0	+		-		0			0	46/51
artificial stream studies											
Gammarus (1)	-	+0		-	+ -	-		-		0	26/40/41/56
Gammarus (2)	-					+		-	-	0	57/63
Baetis	+ -0						(-)	-0	+	+0	4/7/8a/12/13/14
Ecdyonurus	-				-					0	28
Ephemera	+0		+0				(-)	-0		+	3/6/7/8a/10/25
other Ephemeroptera								0	+	+	3/12/25
Perlodidae	+	+					(-)	0		0	7/12/54
other Plecoptera	+0						(-)			+e	3/7/58
Hydropsychidae							-			+e	25/52
Potamophylax					+			-			47
Simuliidae							(-)			+	7/25

(1) European (2) North American

WANKOWSKI, 1981; DUNBRACK & DILL, 1983; RINGLER, 1983; BACHMAN, 1984). However, many other questions related to stream drift remain controversial (Tabl. I). Besides the abiotic factors mentioned in Table I substrate quality is also considered to be an important factor affecting drift (CORKUM *et al.*, 1977; CORKUM & CLIFFORD, 1980; WALTON *et al.*, 1977; WILLIAMS & MOORE,

1982). Especially substrate, velocity, discharge, and turbidity can be regarded as a complex of factors (e.g. turbulence) affecting drift.

The main biotic factor thought to influence drift is the benthic density itself. The pollution of a stream (BESCH, 1966; CHUTTER, 1975) or the benthic excess production of a species (WATERS, 1962a, 1966, 1981; PEARSON & KRAMER, 1972) are supposed to be

reflected in the *drift concentration* (individuals per unit volume of water) or *drift transport* (individuals passing a point per unit of time). Drift concentration and transport are easily determined in the field with a net exposed in the stream for a certain time. In order to relate these measurements to benthic densities, one must know whether the *drift rate* (percentage of the benthic population which drifts per unit area and time) is constant or not. In a stable abiotic environment drift rate will be constant, if the rate of drift-inducing interactions in a group of organisms does not increase with increasing benthic density: in this case drift is *not "density dependent"*. If increasing densities cause a higher or lower rate of such interactions in the benthos and thereby a higher or lower drift rate, drift is — per definition — *"density dependent"* (MURRAY, 1982; CHANG & SELL, 1984; to avoid further linguistic confusion we will use this term as defined above). Both density dependence and independence of drift have been reported in the literature. But it is also stated that drift hardly reflects benthic densities (Tabl. I). We assume that a main reason for this variability is the relationship between the initial benthic density and the environmental carrying capacity, which can vary from one experiment to another: thereby the emigration pattern should be determined (WILEY, 1981).

Other biotic parameters, e.g. abundance of food or predators, also influence drift in diverse ways. Experimental enrichment of artificial streams with organic matter decreases drift (WARREN *et al.*, 1964) or does not affect drift (MUNDIE *et al.*, 1983). Parasites increase (LEHMANN, 1967; STATZNER & BITTNER, 1983) or decrease (ADLER *et al.*, 1983) the drift of their hosts. Drift can be reduced (TOBIAS & THOMAS, 1967) as well as increased (NEVEU, 1974) or remain unaffected (WENINGER, 1968; KURECK, 1969) by the molting process of larval insects.

In conclusion, both abiotic and biotic factors influence drift in various ways even in the same genus (Tabl. I). This is not surprising since the first thing we can expect are species specific differences within a genus. Furthermore, it is known that even instars or size groups of a species exhibit differences in their drift behaviour (ANDERSON, 1967; ELLIOTT, 1967b, 1968, 1971b; WENINGER, 1968; BISHOP & HYNES, 1969; THOMAS, 1969, 1970b; RÜHM, 1970; OTTO, 1971; COWELL & CAREW, 1976; MADSEN, 1976; ALLAN, 1978; WOTTON *et al.*, 1979; FJELLHEIM, 1980; HALL, WATERS & COOK, 1980; BAILEY, 1981; O'HOP & WALLACE, 1983). Even for a size group of a species a factor such as current velocity may govern drift very differently. If we extend the model proposed by KOVALAK (1979) taking the phenomena described in papers reviewed here into account, the drifting

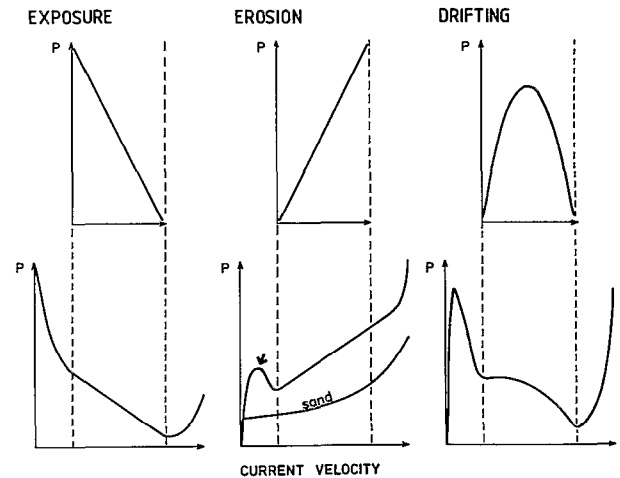


FIG. 1. — Hypothetical relationships between the probability of drifting (the proportion of benthos removed from an area of bottom per unit of time) expressed as the product of the probability of exposure and erosion at changing current velocities. Above: Based on reports that many stream insects move to more sheltered microhabitats as flow rate increases, KOVALAK (1979) assumes that $P\text{-exposure} + P\text{-erosion} = \text{constant}$ at any current velocity and that $P\text{-exposure} = P\text{-erosion}$ at the median current velocity. This results in an unimodal drifting curve. Below: From the literature reviewed in Table I it is evident that the assumptions of the Kovalak-model do hardly reflect natural conditions, especially not at extremely low and high current velocities (outside the areas marked by dashed lines). Our model assumes that there are frequent changes in exposure at very low velocities, due to the numerous vertical migrations from the crevices of the substratum to the upper surfaces. At very high velocities the substratum will begin to be moved and exposure will increase again. No erosion occurs at zero velocity. The peak in $P\text{-erosion}$ at low velocities arrow is due to the organisms, own activities. Since the relationship between a critical velocity and the particle size of sand, which starts to move, is exponential (MANGELSDORF & SCHEURMANN, 1980, p. 80), we assume that $P\text{-erosion}$ for the organisms is not linear at very high velocities. The resulting probability of drifting is much more diverse than in the Kovalak model

curve is no longer unimodal (Fig. 1). Our model is only one of several possibilities and will only apply to species exhibiting the assumed biological reactions in a stream where the substratum offers crevices and starts to move at high velocities. The effects of changing velocities on drift results as determined in the field (PEGEL, 1980) can further complicate this pattern. We do not propose that such simple models can adequately describe drift but this example demonstrates that the range of one particular factor studied can cause some of the diversity in Table I.

Others factors may show different relationships to drift via behavioural particularities of the species

involved (WILEY & KOHLER, 1984). A rise in the abundance of a predator, e.g., will increase the drift of the prey if it mechanically disturbs its benthic prey (CORKUM & CLIFFORD, 1980). It will decrease the drift if the predator feeds on drifting prey (KUBICEK, 1970) and if it reduces exposure of its prey to the current (CHARNOV *et al.*, 1976; STEIN & MAGNUSON, 1976; WILLIAMS & MOORE, 1982). PECKARSKY (1983) supposed that the relative roles of biological interactions and physical-chemical factors in structuring stream communities depend on the physical harshness of a running water. We agree with that view, since biological interactions in the benthos will seldom be reflected in the drift under the extreme current conditions shown in Figure 1.

Another source of complication is that the drift movements of a group of organisms are related to their entrance rate into the drift, the distances travelled therein, and their mode of resettlement on the stream bottom (ULFSTRAND, 1968; PEGEL, 1980).

If an organism's entrance into the drift is related to an increase in its exposure to current velocity it is usually impossible to decide whether the specimen entered actively or passively. Vertical migrations to the upper surfaces of the substratum as well as locomotory activities within the benthos are frequently studied (see references in STATZNER & BITTNER, 1983) in order to explain (see HANEY *et al.*, 1983) diurnal drift patterns. However, a considerable number of experiments (e.g. BOHLE, 1978; WILEY & KOHLER, 1981; KOHLER, 1983; GRAESSER & LAKE, 1984; STATZNER & MOGEL, 1984, *in print*) have shown that the erodibility of specimens and thereby their entrance rate into the drift does not automatically rise with increasing exposure to current velocity of benthic animals migrating on the surface of the stream bottom.

The mean distance travelled by drifting animals determined experimentally (Tabl. II) appeared to be quite long except for caddis larvae with a heavy case and specimens in relatively shallow water. Even longer (more than 500 m) drift distances are reported through a final-cut strip mine pit (VINIKOUR, 1981). However, under undisturbed conditions in the field much shorter drift distances have been observed during the day for *Baetis* (STATZNER & MOGEL, *in print*) and the long distances reported in Table II are probably partly due to handling of the experimental organisms. Models considering these distances are based on rates of drifting organisms returning to the bottom. In most cases the resettlement rates are reduced at higher current velocities (which, in our view, would be better described through turbulence parameters). Marking and recapture experiments in the field also report on considerable

downstream movements (e.g. LEHMANN, 1967; NEVES, 1979; GOEDMAKERS & PINKSTER, 1981).

The mode of resettling is another variable process which is mainly influenced by the morphology and the behaviour of an organism in relationship to the physical environment (WATERS, 1964, 1965; MADSEN, 1966, 1968, 1969; ELLIOTT, 1967a; HOBROUGH, 1973; LUEDTKE & BRUSVEN, 1976; TOWNSEND & HILDREW, 1976; STATZNER & STECHMANN, 1978; WALTON, 1978; CIBOROWSKI & CORKUM, 1980).

All the factors so far mentioned determine the number of organisms exported from a given area by drift (Tabl. III). Drift rates of Linnephilidae — cased caddis larvae exhibiting short drift distances — are relatively low. It is interesting to note that drift rates are relatively low in studies, where the organisms were hardly handled and the conditions were quasi-natural. Although the complexity of drift allows no definite conclusion, this points to probable artifacts in laboratory studies on drift and stresses the need for field trials on this subject.

Experiments relating drift to benthic densities have so far been based on three types of design: laboratory or outdoor stream tanks stocked with organisms just before the start of the test (e.g. HILDEBRAND, 1974; BOHLE, 1978), stream tanks fed with river water which are partly or completely colonized by the organisms themselves (e.g. KURECK, 1969; SCHWARTZ, 1970), and enclosures of stream segments (e.g. MELJERING, 1972b). A real problem is the choice of the appropriate size of the experimental device or the enclosed area, and a compromise between the following extremes must be found. Very small stream tanks (e.g. MUIRHEAD-THOMSON, 1978) allow the accurate estimation of the benthic density and almost every specimen that drifts will be registered. However, such a mini-stream tank represents a very artificial environment and bears the risk of behavioural artifacts: synecological drift studies are completely impossible. Very large stream tanks fed and colonized through an adjacent stream (e.g. THOMAS, 1970a) reduce the risk of behavioural artifacts, but the accurate estimation of the benthic density is difficult and not all organisms that drift will appear in the posterior drift net if the distances travelled are shorter than the length of the stream tank. Then problems arise to relate drift to an unit of benthic area.

Thus, in conclusion, drift of benthic stream invertebrates is a very complicated phenomenon governed by a large number of factors with different intensities, i.e. some factors are potentially more important than others. Therefore a hierarchical system of factors is expected to affect the drift of an organism in a very specific way.

TABLE II

The distance (m) or time (sec at a velocity of about 0.3 m/sec) drifted by living benthic invertebrates under light (L) or dark (D) conditions. We indicate mean values or range of mean values at different velocities and/or dates. See appendix for codation of references (numbers in brackets)

field experiments	
Polycelis felina (18): 3.2-20.0 m (L)	Chloroperla spp. (18): 1.8-16.9 m (L)
Ancyclus fluviatilis (18): 3.1-19.4 m (L)	Elmidae (18): 3.1-19.8 m (L)
Erpobdella octoculata (18): 1.8-3.6 m (L)	Elmidae (39): 7.3 m (L)
Gammarus pulex (18): 1.0-5.6 m (L); 1.0-5.7 m (D)	Rhyacophilidae (39): 19.3 m
Gammarus limnaeus (60, 39): 28.5 m (D)	Hydropsyche spp. (18): 2.0-11.5 m
Baetis tricaudatus (8b): 2.1-9.4 m (L)	c) Agapetus fuscipes (18): 0.1-1.9 m (L)
Baetis rhodani (18): 1.0-5.6 m (L)	c) Oxyethira albiceps (39): 9.8 m (L)
Baetis vagans (60, 39): 21.6 m (D)	c) Olingia feredayi (39): 0.5 m (L)
Rhithrogena semicolorata (18): 1.8-17.5 m (L)	c) Pycnocentropus sp. (39): 5.6 m (L)
Ecdyonurus venosus (18): 1.6-10.6 m (L)	c) diverse Trichoptera (18): 0.1-2.1 m (L)
Deleatidium sp. (39): 8.0 m (L)	Simulium spp. (18): 2.1-16.6 m (L)
Ephemerella ignita (18): 3.5-5.8 m (L)	Chironomidae (18): 3.2-19.6 m (L)
Ephemerella inermis (8b): 2.3-17.5 m (L)	Chironomidae (39): 8.0 m (L)
Amphinemura sulcicollis (18): 3.2-20.1 (L)	total benthos (55): 2 m (L, D)
Protonemura meyeri (18): 1.8-20.1 m (L)	total benthos (39): 10.7 m (L)
Leuctra spp. (18): 1.8-17.2 (L)	
laboratory experiments	
Baetis sp. (34): 2.5 sec (L)	Pteronarcella badia (33): 1.7-4.5 m (L); 2.0-3.8 m (D)
Ecdyonurus venosus (28): 0.3-2.6 m (L)	Brachyptera risi (36): 8 sec (L)
Heptagenia fuscogrisea (35): 26 sec (L)	Arcynopteryx sp. (33): 0.9 m (L); 0.9-1.3 m (D)
Heptagenia sulphurea (35): 7 sec (L)	c) Brachycentrus sp. (33): 1.7-2.2 m (L); 2.3-6.3 m (D)
Ephemerella ignita (34): 15 sec (L)	c) Potamophylax cingulatus (47): 0.05-0.5 m (L)
Ephemerella grandis (33): 0.9-2.4 m (L); 1.0-3.7 m (D)	

c) caddis larvae with cases

TABLE III

Drift rates (%) of benthic macroinvertebrates. Note that experimental periods, handling procedures of organisms, and the benthic area from which drift was fed varies between studies. See appendix for codation of references (numbers in brackets)

1) Gammarus fossarum (41): 1-8 per 24h
Gammarus (26): low-75 per 24h
1) Baetis rhodani (18): 21 per night
Baetis rhodani (4): 63-65 per 24h
Baetis tricaudatus (8a): 61-77 per 24h
Baetis vagans (14): 15-90 per 5h darkness
Ecdyonurus venosus (28): 30-90 per night
Stenonema spp. (3): 19-39 per 12h darkness
Ephemerella inermis (8a): 88 per 24h
Ephemerella needhami (25): 29-51 per night
Ephemerella serrata s.l. (25): 30-54 per night
Ephemerella spp. (3): 3-32 per 12h darkness
Tricorythodes spp. (25): 13 per night
2) Paraleptophlebia mollis (15): 5-20 per 5h darkness
2) Protonemura (17): 52 per 24h
1) Diura bicaudata (54): 2-10 per 24h
1) Isoperla goertzi (54): 5-13 per 24h
2) Isoperla (17): 39 per 24h
2) Elmidae (adults) (17): 52 per 24h
2) Elmidae (larvae) (17): 28 per 24h
2) Hydropsyche (17): 31 per 24h
2) Hydropsychidae (25): 23-36 per night
2) Polycentropus (17): 21 per 24h
2) Limnephilidae (17): 11 per 24h
1) 3) Limnephilidae (3): 2-12 per 12h darkness
Odalgmia frigida (30): 0.1 per 24h
Simuliidae (25): 19 per night

- 1) under almost natural conditions
 2) mean of rates of 24-h-period 1-5
 3) older larvae; younger ones: higher!

3. SPECIFIC TOPICS FACED IN OUR DRIFT STUDY

Our experimental approach enabled us to study this hierarchy of factors under almost natural conditions. We will evaluate the importance of most of the factors listed in Table I for the drift in single and multiple variable models. Of the factors mentioned in Table I we will neglect ion concentration and oxygen since they are relatively constant in the large rivers we have studied (RAI, 1974; ILLIS & LÉVÊQUE, 1982). Other factors not checked were parasitism and food of primary consumers. The seasonal availability of the latter — as far as periphyton and algal drift are concerned — can be extracted from ILLIS (1982, 1983). Substrate size and nature was kept relatively constant in the trials. Exuvial drift was controlled in some tests. The direct effect of moonlight on drift was studied through exposure — cover experiments. In addition we will take moonphases into account, since it is known that the phenology of insects can be influenced by them in African inland waters: this phenomenon appears in lakes (HARTLAND-ROWE, 1955; MACDONALD, 1956; CORBET, 1958, 1964; CORBET *et al.*, 1974; DEJOUX, 1976) but not in a Central African stream (STATZNER, 1976; KOPELKE, 1981).

This possible effect of moonphases on drift is one example of a topic specifically related to the tropics

as is the relative constancy of night length and water temperature. Most of the streams we have studied exhibit a high annual variation in discharge and turbidity (ILTIS & LÉVÊQUE, 1982). In the rainy season they can discharge several hundred m³/sec and in the dry season the riffles remain as small trickles between long pools or, in some cases, flow ceases completely, a fact that may lead to characteristic drift effects (DANCE & HYNES, 1979). During minimum discharge the lotic benthic fauna is highly concentrated on the rapids (STATZNER, 1982; LÉVÊQUE *et al.*, 1983) and this plays an important role in the question of density dependence of drift. Since specimens drifting out of the rapids during these periods can, to some extent, be considered as loss for the populations (DENDY, 1944; VINIKOUR, 1981) we intend to evaluate whether special adaptive strategies occur that reduce drift rates and mortality.

Thereby we hope to increase the knowledge on drift in latitudinally comparable areas (VAN SOMEREN, 1952; BISHOP, 1973; CHUTTER, 1975; HYNES, 1975; MILLS, 1976; COWELL & CAREW, 1976; ELOUARD & LÉVÊQUE, 1977; BAILEY, 1981; MCKILLOP & HARRISON, 1982; TURCOTTE & HARPER, 1982; DUDGEON, 1983), which is frequently based on purely descriptive studies that consider only higher taxa. We made a considerable effort to overcome problems one always has to face in classifying tropical stream invertebrates. We finally successfully identified most groups to the species level (frequently coded names: DEJOUX *et al.*, 1981b) and members of two abundant families, Hydropsychidae (Trichoptera) and Simuliidae (Diptera), even to instars (ELOUARD, 1978; STATZNER, 1984; STATZNER & GIBON, 1984).

A third aspect we will tackle bears on the Onchocerciasis Control Programme (OCP), which tries to suppress human onchocerciasis through insecticide treatments of rapids against the vector *Simulium damnosum s.l.* in our study area (DAVIES *et al.*, 1978). Possible effects on the non-target fauna are monitored in the OCP, and one of the methods applied is drift net sampling (LÉVÊQUE *et al.*, 1977; DEJOUX, 1983; ELOUARD, 1983). These 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 concentration. Animals are usually counted on the family level. While we sampled the total water column above the bottom in our trials, OCP drift is collected 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 quotient night drift: day drift are expected to reflect long

term effects — if they exist — of the insecticide applications on the benthic community, i.e. drift concentrations are used as an indicator to reflect the ecological condition of the benthos. We can carefully evaluate whether this is possible or not in general as well as in detail, since 11 of our trials ran in stream reaches untreated by insecticides in the OCP for a long period, while 13 were carried out in places previously treated with abate or chlorphoxim. In the latter case 5 to 6 days passed between the previous insecticide application and the beginning of a trial, i.e. none of the tests communicated in this series ran under the acute toxic effects occurring immediately after insecticide treatments (cf. DEJOUX & ELOUARD, 1977; DEJOUX, 1978, 1983, 1984; DEJOUX & TROUBAT, 1982; TROUBAT & LARDEUX, 1982; ELOUARD, 1983).

4. METHODS

The objectives for our experimental design were i) to work *in situ* under quasi-natural conditions and thereby to reduce the risk of behavioural artifacts; ii) to register most of the drift events, i.e. the length of the experimental device should be shorter or in the range of the mean distances travelled by drifting organisms (see Tabl. II); iii) to allow proper estimates of benthic densities, i.e. the area of the experimental device should be small enough to be completely sampled at the end of a test. To fulfil these requirements at the conditions of the hydrology and stream morphology in the study area *in situ gutter systems* were developed (DEJOUX, 1975; TROUBAT, 1981), which were modified as our experimental experience increased (Fig. 2).

Type A is a simple U-shaped gutter made of galvanized iron. To allow a better handling it is built in two parts, the anterior one is 2 m long, the posterior one is 1 m long. The front net is polyhedric, its length is 0.8 m, its greatest width is 0.5 m. The height of the gutter above the substratum is adjustable.

Type B is a modification of type A. In order to maintain a relatively high discharge through the gutter two lateral influx pipes are added.

Type C follows the general aspect of type B but is made of round plastic pipes; the central one is cut at about 2 cm above its maximal width. Due to its small size and light weight it is easy to handle and to transport. It can even be fixed under a small helicopter and then used in places with difficult land and water access. Better anchorage is achieved by fixing some ballast to the adjustable supports.

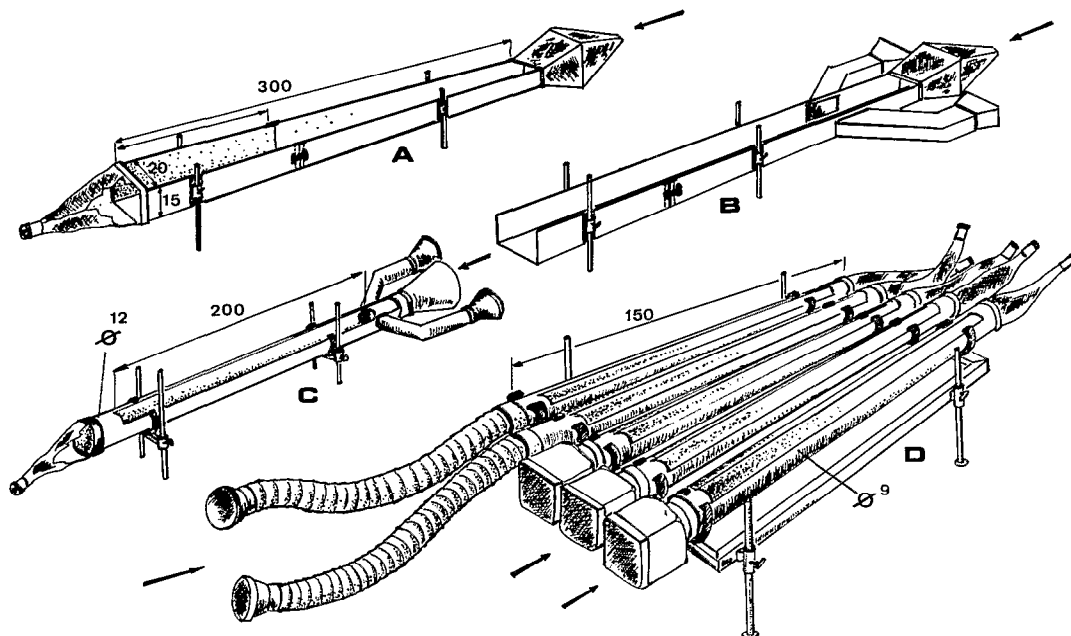


FIG. 2. — The four different types of gutters used in our trials (units: cm; see text for further details)

Type D was constructed for numerous standardized field experiments, usually for testing insecticides. Five small polyethylene pipes are fixed on an iron support and can be separately moved in three axes. Thereby the discharge through a pipe can be precisely adjusted. Special filter nozzles can be fixed at the upper end or can be replaced by flexible plastic tubes of 2 or 3 m length, in order to supply water from places with a suitable current velocity. Using these anterior tubes it is possible to emerge the pipes and even their support. Thereby discharge through the gutter can be directly determined by sampling the water flowing through it at the end and the experimental techniques are easier, especially at periods when the water level in the stream frequently changes.

In spite of the morphological "evolution" of our gutter systems the principle of our test remained the same:

The gutter, open at the front and back ends, was fixed within a rapid so that the side walls lay parallel to the main direction of flow and emerged from the water. This semi-isolated channel was then stocked with natural substrata (stones, gravel, sand, dead leaves, pieces of wood) colonized with invertebrates from the stream bottom. It was thereby possible to construct a "gutter ecosystem" within a few minutes without direct handling of the organisms. Then a period of adjustment followed to allow the organisms to regain their appropriate microhabitats and to

overcome the stress of manipulation. During this time natural drift added and exported organisms to and from the gutter community and in several cases oviposition occurred in the gutter. The period of adjustment was ended by fixing the nets in front and at the end of the gutter. At the beginning of our work this exposure period lasted only a few hours before we began sampling. However, we realized from other studies with briefly exposed gutters that drift on the first night could be distinctly higher than on the second night. We interpreted this as an artifact, since several groups react to physical disturbances not immediately, but after sunset (BROOKER & HEMSWORTH, 1978; SCULLION & SINTON, 1983). We therefore extended the exposure periods previous to the trial to a minimum of several days.

The front net of the gutter, which is meant to prevent the import of drifting organisms into the gutter, was adapted to ensure a high discharge through the gutter after the closure. It was regularly brushed during the tests to avoid clogging. The net of the collecting tube at the downstream end of the device could be quickly changed and allowed a continuous collection of the drift from the gutter divided into scheduled time periods. These periods varied in length due to other, parallel conducted experiments. Drift samples taken immediately after the closure of the gutter were not considered in the analyses.

At the end of a trial all the material remaining in the gutter was collected. All samples were preserved in the field (ethanol 70-80 %) and the organisms were later sorted in the laboratory with the help of a stereomicroscope. Mean mesh size of nets used in the experimental procedures ranged from 0.20 to 0.28 mm, i.e. even small instars or forms of benthic insects were collected (cf. BARBER & KEVERN, 1974).

By adding the appropriate drift samples to the numbers of organisms remaining in the gutter at the end of a test we were able to calculate the benthic density of a taxon or, e.g., one of its instars in theory at any time during the trial. In practice, however, the population structure of a taxon changes during a trial through, e.g. hatching, molting, emergence, and predation. To keep these changes relatively moderate and because of occasionally very high drift rates (depopulation of the gutter!) our trials usually ran over about 24 h. Only 4 tests monitored drift for over about 48 h.

During the tests we registered water temperature (mercury thermometer), transparency (Secchi-disk), and discharge through the gutter (with a digital flowmeter just in front of the net collecting drift, a reach of the gutter never stocked with substrate; or, in small gutters, by sampling the through-flowing water for a specific period). Water temperature, discharge, and transparency, which will be used as an indicator of turbidity, will be expressed as mean values. The mean velocity above the substratum was estimated from discharge data and the approximate mean cross section of the reach stocked with substratum. Moonphases were taken from calendars and, in two tests running parallel over two nights with a full moon and a clear sky, each of the gutters was covered to exclude moonlight for one night.

Since night length is relatively constant in the study area — the annual variation is about 45 min — we did not determine the exact time of dawn and dusk and will treat the drift in the following constant time periods:

morning drift (MD): 6.00 - 10.00
 day drift (DD): 10.00 - 16.00
 afternoon drift (AD): 16.00 - 19.00
 night drift (ND): 19.00 - 6.00

A fifth drift item is the "peak drift" (PD), which occurred at the time the drift of a taxon (or instar)

reached its maximum in a 24-h-period. If drift is density dependent (see 2.) this should appear at the best in the peak drift.

5. EXPERIMENTAL CONDITIONS

ILTIS & LÉVÊQUE (1982) give a physico-chemical description of the streams we have studied. More details of the specific experimental places are considered in DEJOUX *et al.* (1981a), STATZNER (1982), DEJOUX (1983) and ELOUARD (1983), and we pointed out the essentials of our study area in section 3. Almost all tests were performed in the Bandama basin (exception: Bagoué), the majority of them in stream reaches, which are faunistically relatively uniform (DE MENORA, 1981; LÉVÊQUE *et al.*, 1983; GIBON & STATZNER, *in print*).

Table IV summarizes our experimental conditions. The number of organisms tested varied considerably from one test to another, an essential fact to test whether drift is density related or not (note that the area covered with substratum was not constant and that other features may also be important in setting the carrying capacity). Discharge through the gutter and mean velocity therein also varied to some extent. Velocities, however, were never extremely low or high compared to those found in the streams. Turbidity was relatively low in most trials since the gutter technique can be used easily only at periods of relatively stable, low discharge, when turbidity is low in the study area. Mean water temperature ranged from 26 to 30 °C: this seems to be quite a small range for someone familiar with temperate streams. However, for tropical streams in the approximate same altitude and latitude, which have a relatively stable temperature, this is quite a large range.

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TABLE IV

Summary of experimental conditions. TEST: number of trial; TYP: type of gutter; LOC: location; EXP: exposure time for colonization previous to trial; DATE, SEASON: 1st day of trial, hydrological season; NORG: initial number of organisms tested ($\times 1000$); NSAM: number of drift samples; AREA: area stocked with substrate (m^2); DIS: mean discharge through the gutter (m^3/h); mean velocity in the gutter (cm/sec); TRB: turbidity (Secchi-disk) (cm); TMP: mean water temperature ($^{\circ}C$); MON: moon phase; PTI: previous insecticide treatments (last treatment: 5 to 6 days before the beginning of a trial)

TEST	TYP	LOC	EXP	DATE SEASON	NORG	NSAM	AREA	DIS	VEL	TRB	TMP	MON	PTI
G1 ¹⁾	B	Maraoue	14 d	21/01/78	24.4	108	0.36	5.93	16	>100	30	○	untreated
G2 ²⁾	B	Entomokro	14 d	id	26.2	108	0.36	12.13	34	>100	30	id	id
G3 ³⁾	A	N'Zi	2 h	13/06/77	1.0	13	0.40	4.06	11	53	29	●	Abate: 1974-Dec.76
G4 ³⁾	A	Tinbe	2 h	id	0.9	13	0.40	2.90	8	53	29	id	id
G5 ³⁾	A	N'Zi	2 h	20/06/77	1.4	15	0.40	5.77	16	23	28	●	id + Chlorphoxim, 14/06/77
G6 ³⁾	A	Tinbe	2 h	id	2.7	15	0.40	6.78	19	23	28	id	id
G7 ³⁾	A	N'Zi	1.5 h	27/06/77	0.6	6	0.40	3.96	11	16	28	●	untreated
G8 ³⁾	A	Bocanda	1.5 h	id	0.8	6	0.40	4.71	13	16	28	id	id
G9 ⁴⁾	A	Bagoue	4 h	28/03/77	6.1	15	0.56	17.28	48	>100	29	○	untreated
G10 ⁴⁾	A	Koutu	4 h	id	3.6	15	0.56	11.06	31	>100	29	id	id
G11	C	Maraoue	7 d	13/08/78	3.7	54	0.24	2.58	20	40	27	●	untreated
G12	D	Kennedy	5 d	03/09/81	11.8	54	0.12	1.09	17	>100	26	●	untreated
G13	C	Bouake	7 d	19/12/78	1.5	57	0.24	5.46	42	>100	28	●	untreated
G14	B	Entomokro	5 d	19/12/79	8.9	18	0.56	15.12	42	>100	28	●	Abate: 9 months
G15	D	Entomokro	5 d	18/02/80	3.4	23	0.12	3.84	59	>100	30	●	Abate: 11 months
G16	D	Maraoue	5 d	id	1.4	31	0.12	3.84	59	100	30	id	id
G17	U	Entomokro	5 d	id	2.7	23	0.12	3.84	59	100	30	id	id
G18	D	id	5 d	id	3.1	25	0.12	3.84	59	100	30	id	id
G19	D	id	5 d	id	4.0	53	0.12	3.84	59	100	30	id	id
G20	D	Maraoue	5 d	21/04/80	14.1	52	0.12	5.33	82	100	32	●	Abate: 13 months
G21	D	Yaoukro	5 d	id	8.6	39	0.12	5.33	82	100	32	id	id
G22	D	id	5 d	id	8.8	16	0.12	5.33	82	100	32	id	id
G23	D	id	5 d	id	11.1	15	0.12	5.33	82	100	32	id	id
G24	D	id	5 d	id	10.2	16	0.12	5.33	82	100	32	id	id

1) not exposed to moonlight: 25-26/01/78; 2) id: 24-25/01/78; 3) large fluctuations in stream water level; 4) extremely low discharge in the stream

APPENDIX

Data of Table I to III were taken from the following publications. Sometimes this was done from figures and the data are then approximate ones

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|--------------------------------|------------------------------|----------------------------------|
| 1 Adler et al., 1983 | 22 Gyselman, 1980 | 44 Müller, 1966 |
| 2 Allan, 1982 | 23 Hall, Likens et al., 1980 | 45 Neveu & Echaubard, 1975 |
| 3 Bishop, 1969 | 24 Haney et al., 1983 | 46 O'Hop & Wallace, 1983 |
| 4 Bohle, 1978 | 25 Hildebrand, 1974 | 47 Otto, 1976 |
| 5 Brooker & Hemsworth, 1978 | 26 Hughes, 1970 | 48 Pearson & Franklin, 1968 |
| 6 Butz, 1973 | 27 Iversen & Jessen, 1977 | 49 Radford & Hartland-Rowe, 1971 |
| 7 Chaston, 1969 | 28 Keller, 1975 | 50 Reisen, 1977 |
| 8a Ciburowski, 1983 a | 29 Kubicek, 1970 | 51 Reisen & Prins, 1972 |
| 8b Ciburowski, 1983 b | 30 Kureck, 1969 | 52 Schuhmacher, 1970 |
| 9 Ciburowski & Clifford, 1983 | 31 Lehmann, 1967 | 53 Schwarz, 1967 |
| 10 Ciburowski et al., 1977 | 32 Lehmkuhl & Anderson, 1972 | 54 Schwarz, 1970 |
| 11 Cloude & Stewart, 1974 | 33 Luedke & Brusven, 1976 | 55 Townsend & Hildrew, 1976 |
| 12 Corkum & Clifford, 1980 | 34 Madsen, 1966 | 56 Vobis, 1973 |
| 13 Corkum & Pointing, 1979 | 35 Madsen, 1968 | 57 Wallace et al., 1975 |
| 14 Corkum et al., 1977 | 36 Madsen, 1969 | 58 Walton et al., 1977 |
| 15 Cowell & Carew, 1976 | 37 Madsen, 1976 | 59 Waters, 1962 b |
| 16 Crisp & Robson, 1979 | 38 Marchant & Hynes, 1981 | 60 Waters, 1965 |
| 17 Elliott, 1967 a | 39 McLay, 1970 | 61 Waters, 1966 |
| 18 Elliott, 1971 a | 40 Meijering, 1972 a | 62 White, 1976 |
| 19 Fjellheim, 1980 | 41 Meijering, 1980 | 63 Williams & Moore, 1982 |
| 20 Goedmakers & Pinkster, 1981 | 42 Minshall & Winger, 1968 | 64 Wojtalik & Waters, 1970 |
| 21 Gore, 1977 | 43 Müller, 1963 | |

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