

Downstream Drift in Madeiran Levadas: Tests of Hypotheses Relating to the Influence of Predators on the Drift of Insects

by

Björn MALMQVIST

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On the Atlantic island of Madeira, mobile invertebrate predators such as perlid and periodid stoneflies as well as a native fish fauna are absent, permitting tests of hypotheses concerning the influence of predators on the nocturnality of drift. Here, species and size composition of the drift, in addition to drift lengths, were studied in two man-made waterways (levadas). It was found that the following insects dominated in the drift: *Baetis rhodani* (Ephemeroptera), *Dixa tetrica* (Diptera), Chironomidae (Diptera), and Simuliidae (Diptera). Wind increased the drift density, evidently by causing large amounts of terrestrial plant material to enter, especially in the more open streams. It seems likely that the drifting material caused the benthic animals to drift either through direct mechanical action or via indirect effects, such as visual disturbance.

Rainbow and brown trout were successfully introduced into the island of Madeira in 1961. In a levada with trout, *B. rhodani* drifted significantly more by night. In another levada devoid of fish there was no difference between daytime and nighttime drift density. The size composition in the drift of *B. rhodani* was skewed so that larger nymphs dominated by night in the presence of fish. Where fish did not occur there was no difference in size distribution between night and day. This is in accordance with an expected "risk of predation" being greater on larger insects in the light because of size-selective feeding by the fish. *Dixa tetrica* drifted significantly more by night in the fishless levada in which the population had a size composition that was biased towards larger larvae. In the other levada containing fish there were no diurnal patterns in drift numbers. This is in accordance with a previous report in which a dixed has been shown to occur in the drift to a higher extent at pupation.

A set of experiments demonstrated that the drift distance of *B. rhodani* was less than 20 m in a channelized stream having a current velocity as high as 2.0 m s^{-1} , and that nymphs of *B. rhodani* will drift upon a visual disturbance.

B. MALMQVIST, Department of Ecology, Animal Ecology,
University of Lund, S-223 62 Lund, Sweden.

INTRODUCTION

Considerable effort has been devoted to the study of the downstream drift of freshwater invertebrates (see reviews in Waters 1972, Müller 1974, Wiley and Kohler 1984, Statzner et al. 1984). Certain aspects such as the rhythmical diel patterns are fairly well understood while others still call for critical studies. No doubt drift is a complex phenomenon that is related to many different factors. Among these, food abundance, physico-chemical parameters of the water, and predators have important consequences for the drift-prone animals, such as amphipods and larval Ephemeroptera, Diptera, Plecoptera, and Trichoptera. Statzner et al. (1984) listed 16 different factors governing drift.

The risk of predation by fish is a possible explanation for the nocturnal rhythm of drift. Allan (1978, 1984) suggested that large insect larvae ought to drift less during daytime to avoid being preyed upon by fish, since visual predators feed size-selectively on larger prey. He found support for this contention in his studies, and further support has been provided by Newman and Waters (1984), Skinner (1985), and Andersson et al. (1986).

Invertebrate predators also influence drift, although in a quite different way than do fish. Widely foraging invertebrate predators such as perlid and perlotid stoneflies also may influence drift, partly through unsuccessful attacks that cause prey animals to drift (Malmqvist 1986, Malmqvist and Sjöström 1987). Baetid mayfly nymphs are one group that typically shows a drift response.

In the present study I test the following hypotheses: 1) Drift is arrhythmic in the absence, and nocturnal in the presence, of fish, 2) Where fish occur, large insects are more nocturnal in their appearance in the drift than are small insects. In addition, I investigate whether drift may be initiated in response to a visual disturbance. Little evidence exists concerning this matter among aquatic insects (e.g. Allan 1983); however, Malmqvist and Sjöström (1987) noticed that nymphal *Baetis rhodani* Pict. drifted away from approaching stonefly predators before contact under daylight conditions, but only upon physical contact in darkness as registered by use of infrared video technique. This behaviour suggested that, in day light, the mayflies were able to see and escape from the predator before an attack was elicited.

The present investigation was carried out on the island of Madeira, an Atlantic island with general features rendering it particularly interesting for drift studies. Madeira has a depauperate fauna, without predacious stoneflies and rhyacophilid Trichoptera. Further, there is no native freshwater fish fauna. Only recently, in 1961, rainbow trout (*Salmo gairdneri* Richardson) and brown trout (*Salmo trutta* L.) have been successfully introduced from northern Portugal (MacCrimmon 1971). Furthermore, the only abundant mayfly in running waters on Madeira is *Baetis rhodani*, a species that is widely distributed in Europe and northern Africa (Illies 1978), and whose drift behaviour has been especially well studied (e.g. Müller 1966, Elliott 1968, Ulfstrand 1968, Bohle 1978, Malmqvist 1986, Malmqvist and Sjöström 1987). In addition to *B. rhodani* there exists a single observation of a subimago *Centroptilum* sp. on Madeira (Classey 1966) and in lentic waters *Cloeon dipterum* L. has been found (Eaton 1871).

It is not clear for how long *B. rhodani* has occurred on Madeira. Wollaston found this mayfly species on the island in 1865 (Eaton 1871). *B. rhodani* may be indigenous on Madeira but the possibility that it has been introduced unintentionally by humans can not be excluded (Brinck and Scherer 1961). Alternatively, immigration of *B. rhodani* took place from Africa, which must have involved a flight over open sea, a distance of > 550 km.

STUDY SITES

Madeira has an extensive network of channelized waterways, *levadas*, for irrigation and other purposes. These artificial streams are usually narrow and fast-flowing. Two such streams belonging to separate water systems were chosen for the drift studies in the Arieiro mountains. The levada site at Ribeira das Cales was situated at an elevation of 1140 m, 6 km N of Funchal, and only 1.5 km southwest of the second site 1 km W of Poiso (Levada do Blandy), 1480 m above the sea level. Trout were frequently observed at Ribeira das Cales, while no fish occurred at the levada near Poiso, neither at the study site nor further upstream in the system. Some features of the two levadas are given in Table 1. In addition, while the vegetation at the site near Poiso was quite open, dominated by grasses, *Ulex* sp., *Vaccinium maderense*, and scattered conifers (*Pinus* sp.), the valley around the levada at Ribeira das Cales had a richer flora dominated by laurel trees, heather, *Mimosa*, *Eucalyptus*, *Salix*, *Rubus*, etc. The water temperature differed little between sites and occasions of drift sampling, with a range of 9.5 - 11.0°C. The drift experiments were carried out 21 to 14 days before the full moon.

The weather during the drift recording and experiments was variable; on 1 and 3 December it was not overcast and winds were weak, 7 and 8 December were cloudy, and on the 7th there were strong westerly winds.

MATERIALS AND METHODS

Drift was estimated on four dates, viz. 1, 3, 7, and 8 December 1986. On each date samples were taken at both sites, twice during daytime, usually at noon and between 5.00 and 6.00 p.m., and once after nightfall (7.00-8.00 p.m.), about one hour after sunset. Highest drift rates are usually found in the beginning of the dark period (Bournaud and Thibault 1973, Allan and Russek 1985), though sometimes there is a higher peak at dawn (Müller 1966). The drift nets were in place for one hour, except at the Poiso site on 7 December when relatively high amounts of leaves entered the drift nets. To avoid reduced sampling efficiency through clogging of the nets the sampling time for the second and third collections on that date were reduced to 30 minutes.

Each net filtered a large proportion of the passing water and therefore was not replicated. At the Poiso site ca. 50% of the water passed through the net, and at Ribeira das Cales the corresponding value was ca. 16%. The drift nets were 1 m long, and mesh width was 0.20 mm. The diameter of the opening of the nets was 13 cm. Drift samples were sorted fresh and the animals were preserved in 80% ethanol.

Identification and measurements were made using a binocular stereo microscope with an eye-piece micrometer.

The disturbance experiment was performed over a homogeneous 300 m section

of the levada near Poiso, where current velocity was 2.0 m s^{-1} and water temperature was $10\text{-}11^\circ\text{C}$. A visual disturbance was created by moving a hand-net ca. 20 cm above the water surface along 20 m of stream. The drift rate of mayflies, blackflies, and caddisflies was recorded for 5 min as in the previously described drift sampling. The hand-net was moved back and forth over the water approximately twice per metre while walking from the drift-net in an upstream direction at a distance of about 1 m from the side of the stream, and again while walking back to the drift net. This procedure lasted for 90 seconds. Prior to each disturbance event the control drift level was estimated during a 5 min exposure, when I walked along the stream although without the net. The whole procedure was repeated three times at 30 min intervals. After such a set of six measurements the disturbance experiment was repeated at another four 20 m sections, each time upstream from the previous experimental sections, over the course of two days.

RESULTS

The total number of drifting animals is given in Fig. 1. On 7 December the numbers were much higher than on other occasions, especially at the Poiso site. This increase of drift was doubtless a consequence of strong winds on that day carrying leaf material, especially of *Vaccinium maderense*, that was continuously being trapped in the stream channel. The subsequent drift of leaf material dislodged animals through direct abrasion or in an indirect way (see the disturbance experiment below).

A high proportion of the drifting animals was of terrestrial origin. On average only ca 75% of drift collections in Ribeira das Cales, and 50% at Poiso, consisted of aquatic animals (Fig. 1).

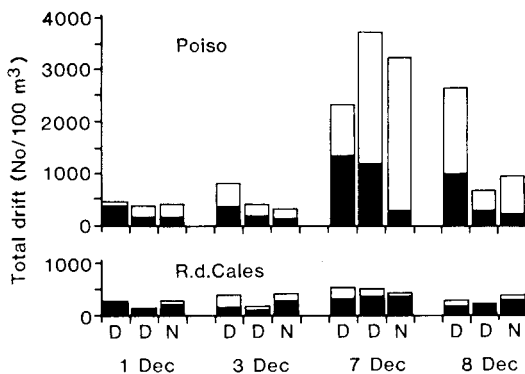


Fig. 1. The total drift, including both aquatic (black) and terrestrial (white) animals, on the four dates. For each date the first two bars represent daytime drift numbers (D), and the third nighttime drift numbers (N).

Table 1. Characteristics of the study streams.

Characteristics	Ribeira das Cales	Poiso
stream type	levada	levada
elevation (masl)	1140	1480
current velocity (m s ⁻¹)	0.4	2.0
depth (m)	0.25	0.04
width (m)	0.36	0.20
pH	6.85	6.80
conductivity (mS m ⁻¹)	9.2	7.0
fish	trout	none

Baetis rhodani, *Dixa tetrica* Peus, simuliids of the species *Simulium (Eusimulium) azorense* Carlsson, *Simulium (s.) intermedium* Roubaud, and chironomids were the dominant aquatic animals in the drift. In total, nearly 3000 individuals of aquatic invertebrates belonging to 18 taxonomic groups were identified and measured.

The drift density of the four most common taxa by day and by night are given in Table 2. Nymphs of *B. rhodani* drifted on average in significantly higher numbers by night than by day in Ribeira das Cales. At Poiso this tendency was reversed, although not significantly so. Significant differences in drift numbers between day and night could be detected for neither simuliids nor chironomids. *D. tetrica* drifted in significantly higher numbers by night at the Poiso site, while the population in Ribeira das Cales showed no differences between night and day.

The only significant difference in mean size between day and night drifting individuals was found in Ribeira das Cales for *Baetis rhodani* [mean \pm 95% confidence intervals: 8.9 ± 0.46 (day) and 12.2 ± 0.53 (night), $t = 9.04$, $P < 0.0001$, $df = 273$, Tab. 3]. The mean size of drifting *Baetis rhodani* showed also on each date highly significant differences between day and night (t -tests, 1 December $P = 0.0021$, other dates $P < 0.001$, Fig. 2). The mean head width of this species was nearly 40% larger by night than by day at this site where fish occur. Also the size distributions of drifting *Baetis rhodani* differed considerably between day and

Table 2. The average drift density (numbers/100 m³) by day and by night at the two sampling sites and the difference between the sites (One-way Anova after transformation, * = $P < 0.05$, ** = $P < 0.01$. The day with strong drift caused by wind blown leaf material is excluded from the Poiso data (7 December). This means that $N = 8$ for R. d. Cales (day), $N = 4$ for R. d. Cales (night), $N = 6$ for Poiso (day), and $N = 3$ for Poiso (night).

Taxon	R. d Cales					Poiso				
	day		night		F	day		night		F
	mean	SD	mean	SD		mean	SD	mean	SD	
<i>Baetis rhodani</i>	77	36	194	41	19.7**	102	77	56	5	0.71ns
<i>Dixa tetrica</i>	13	9	18	3	1.25ns	16	14	61	15	8.76*
Simuliidae	12	8	10	11	0.25ns	90	79	34	32	1.71ns
Chironomidae	87	64	55	20	0.96ns	83	67	34	6	1.93ns

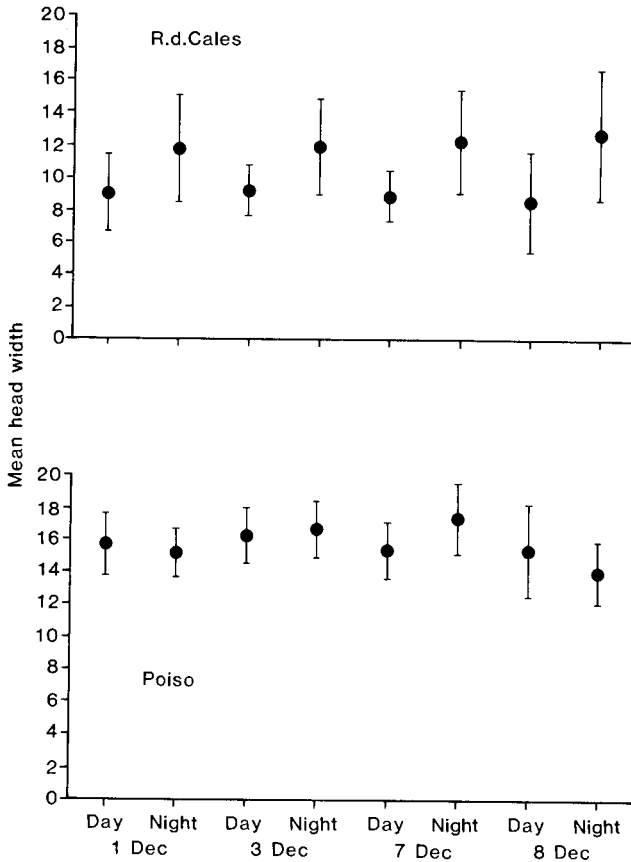


Fig. 2. Mean head width of *Baetis rhodani* at the two sites. Vertical bars represent 1 S.D. The 95% confidence limits range maximally between 7.57 and 10.16 units by day (0.37 - 0.50 mm), and 10.48 and 14.06 units by night (0.51 - 0.69 mm) at the site with fish (Ribeira das Cales).

night. Large nymphs were virtually absent from the drift during the day (Fig. 3). At the Poiso site there was a more narrow range of size classes (10-21 units, i.e. 0.49-1.03 mm) than in Ribeira das Cales (range: 4-22 units, i.e. 0.20-1.08 mm), and, contrastingly, daytime drift was higher for most size categories (Fig.3). There was no tendency for large nymphs to drift more frequently at night, which they clearly did within the same size range in Ribeira das Cales.

The disturbance experiment showed that drift decreased exponentially from the manipulated section with successive bouts of disturbance (Fig. 4). This decline indicated that virtually all drift originated from within the 20 m section upstream of the drift net, since drift, both when disturbed and when not, approached a value

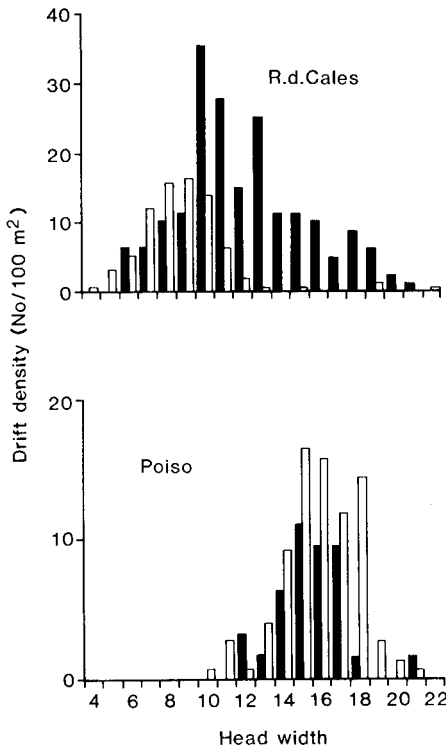


Fig. 3. The size distribution in terms of head width (each unit equals 0.049 mm) of drifting *Baetis rhodani* from the levada with fish (Ribeira das Cales) (top) and from the fish-less site at Poiso (bottom), at night (black bars) and at day (white bars). Data from Poiso from the day with heavy leaf drift have been omitted.

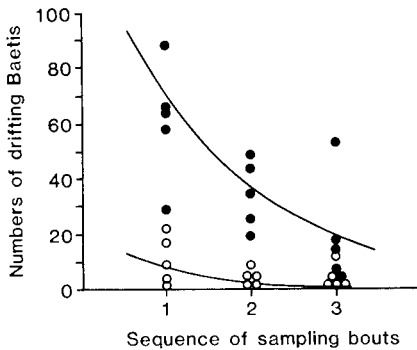


Fig. 4. The drift of *Baetis rhodani* when visually disturbed (black symbols) and when undisturbed (white symbols) in five separate disturbance experiments, each of which contained three bouts of disturbance at 30 min intervals. Each estimate of drift upon disturbance was preceded by an equally long (5 min) record of “undisturbed” drift. The curves are exponential and have the equations: $Y_{\text{dist}} = 131.6 \cdot 10^{-0.28x}$, $R = 0.97$, and $Y_{\text{undist}} = 23.6 \cdot 10^{-0.47x}$, $R = 0.98$.

Table 1. The mean head width of the dominant aquatic insects in the drift. Each length unit equals 0.049 mm.

Taxon	Ribeira das Calés										Poiso							
	Day					Night					Day/night		Day		Night		Day/night	
	N	mean	SD	N	SD	N	mean	SD	N	SD	size ratio	N	mean	SD	N	mean	SD	size ratio
<i>Baetis rhodani</i> ¹	121	8.9	2.53	154	3.35	385	15.5	1.81	35	15.9	0.73	385	15.5	1.81	35	15.9	2.03	0.97
<i>Dixa terrica</i>	21	5.4	1.63	14	1.74	37	8.9	1.33	33	9.3	0.96	37	8.9	1.33	33	9.3	0.89	0.96
Simuliidae	19	13.8	2.93	8	3.20	206	11.8	1.72	21	12.5	1.00	206	11.8	1.72	21	12.5	1.47	0.94
Chironomidae	144	4.2	0.67	43	0.78	166	4.5	0.86	16	4.4	0.98	166	4.5	0.86	16	4.4	0.62	1.02

¹ If the day with high leaf drift at Poiso were to be excluded from the material the average head width would be 15.9 at day, and 15.5 at night.

of zero after successive drift sampling. The response to the visual disturbance was unexpectedly strong, and after the three bouts of disturbance the sections seemed virtually depleted of mayfly nymphs. Larvae of Trichoptera and Simuliidae were not affected by the disturbance and occurred in low but unchanged numbers in both records of drift (means for disturbance: Trichoptera = 1.8, Simuliidae = 1.9; means for undisturbed samples: Trichoptera = 1.8, Simuliidae = 2.2).

DISCUSSION

Drift densities for Madeiran animals were similar to European reports (cf. for example Armitage 1977). The drift of *Baetis rhodani* nymphs was perhaps most interesting, since comparable data are available from many European studies. These mayflies drifted in relatively large numbers despite the absence of searching predators, such as stonefly nymphs, either be it as a result of accidental dislodgement, active dispersal to locate better foraging habitats, or for yet other reasons. The present study was not designed to separate these forces. However the support for Allan's (1978, 1984) risk of predation theory, found in the bias towards greater number of large *B. rhodani* nymphs drifting by night in levadas containing fish (Figs 2 and 3), implies that drift has an active component.

A reduced catch of drifting mayfly nymphs by day could theoretically be the result of a higher predation pressure from trout. In the daylight, these could detect and capture the drifting *Baetis*, large individuals in particular, more efficiently. Although I observed fish on a number of occasions in Ribeira das Cales I never saw any fish at the location of the drift net and for a short distance upstream, i.e. in the section where most *B. rhodani* must have entered the drift. I therefore assume that there was only a low density of trout. It seems very unlikely that these should have been able to remove > 150 *Baetis* nymphs per hour, provided daytime drift would equal nighttime drift at no predation. It is, however, reasonable to believe that selective predation by trout may have contributed to the observed pattern. A similar justification was given by Allan (1978) to the assumption that the increased nocturnal drift was a consequence of insect behaviour and not of fish performance. In another study, he found that the pattern remained after the removal of trout (Allan 1982).

The observation that *B. rhodani* drift is nocturnal in the presence of fish and aperiodic or slightly diurnal in the absence of fish is consistent with the view that the usual nocturnal rhythm is a predator avoidance mechanism. It is tempting to believe that mayflies on Madeira, where they would have no long history of experience with native fish, should not show adaptive behaviour to the presence of fish. One must however consider that *B. rhodani* probably is a fairly recent immigrant, since it is, in contrast to many Madeiran freshwater insect species, conspecific to a widely distributed continental species. In addition, it seems realistic to believe that intense selection pressure due to fish predation could cause a rapid evolution of suppression of drift under lighted conditions. Nocturnality is

widely spread over different freshwater habitats and taxonomic borders, and is generally believed to have evolved as a defence against predation.

While there is no doubt that different populations of *B. rhodani* exhibit different patterns of drift in separate but adjacent water systems, one can hardly disregard the possibility of a certain amount of gene flow between the populations, which have an aerial adult stage. The drift behaviour reported herein, and possibly also other activities, of *B. rhodani* may thus be a reactive response to the prevailing conditions in the respective habitats, rather than a genetically fixed behavioural pattern.

It may be reemphasized that the present study showed that *B. rhodani* drifted despite the absence of searching invertebrate predators. Malmqvist (1986) and Malmqvist and Sjöström (1987) found that perlotid and perlotid stoneflies might contribute to as much as 60 - 70% of the nightly *Baetis* drift numbers where such stoneflies are abundant. Obviously the remaining fraction of the drift was due to other factors than disturbance by predators. Factors influencing drift entry include the present observation that stream drift may be an indirect consequence of wind. In addition to direct physical abrasion it is possible that the comparatively extensive leaf drift can have elicited visual responses in *Baetis rhodani* leading to drift in a similar way as it did in the disturbance experiment.

Dixa tetrica showed an opposite drift pattern to that of *B. rhodani* nocturnal at Poiso, not so in Ribeira das Cales. Elliott and Tullett (1977) showed that increased drift in another species, *Dixa puberula* Loew., was correlated to the phase of pupation. In the present study, the size distribution of drifting dixids indicated considerably larger individuals at the Poiso site than in Ribeira das Cales, suggesting that the explanation of Elliott and Tullett (op.cit.) could be valid also in the present material.

The disturbance experiment demonstrated first that visual disturbance may cause substantial drift in *Baetis rhodani*, and second, that the drift distance was probably considerably less than 20 m. Drift distances have been estimated for *Baetis rhodani* and other baetid nymphs in a number of investigations (Waters 1965, Madsen 1966, Elliott 1967, 1971, Larkin and McKone 1985). The advantage of the present technique is that the insects were allowed to enter the drift freely, while in other investigations some sort of handling of the animals preceded the entry, possibly increasing both stress and the subsequent estimates of drift distances. The drift distances reported here are relatively short, in agreement with previous reports, although it should be kept in mind that at current speeds at 2 m s⁻¹ one might have expected longer distances.

In conclusion, this study demonstrated that nymphs of *Baetis rhodani* on Madeira show an adaptive response in their drift behaviour to the presence of fish, both in terms of diel rhythm and in body size. Furthermore, it was found that drift may be an indirect consequence of strong winds, and that it may be elicited through visual disturbance only.

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