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CATASTROPHIC DRIFT OF INSECTS IN A WOODLAND STREAM[1]

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Abstract. The effect of early fall rains on the downstream drift or displacement of insects was studied for two seasons by collecting the entire streamflow at one point through a drift net. Drift rate increased within 24 hr after the start of each rainy period, with the increase approximately proportional to the increase in stream flow. Freshets due to less than 1 in. (2.5 cm) of rain caused a fourfold increase in numbers and fivefold to eightfold increase in biomass. Major components of the drift were Ephemeroptera, Plecoptera, Diptera and terrestrial insects.

Plecoptera and Ephemeroptera retained the day–night periodicity of behavioral drift during freshets, but drift of Chironomidae (Diptera) was attributed to catastrophic and constant drift. Mean weight per individual of several taxa was greater at night than day, in freshet than nonfreshet periods, and in drift compared with benthos samples.

Though catastrophic drift due to fall freshets displaced large numbers of individuals, the standing crop of the benthos increased during the fall because of hatching. The drift may be beneficial in dispersing aggregations of young larvae. Removal of allochthonous food by increased water flow could be more detrimental to benthos populations than the direct mortality caused by catastrophic drift.

Introduction

The insect fauna of lotic habitats possesses morphological and behavioral adaptations to resist displacement by the unidirectional flow. The denuding effects on insect populations of floods and scouring by ice have been documented by many workers (e.g., Needham 1928; Moffett 1936; Allen 1951; Müller 1954). However, the influence of increased water velocity due to normal seasonal rainfall on the bottom fauna has only rarely been subjected to quantitative studies. In Waters' (1962) study of downstream drift in Minnesota, he noted a large increase in drift of the amphipod *Gammarus limnaeus* Smith and the mayfly *Baetis vagans* McDunnough due to a heavy rain. The most striking change, however, was a fiftyfold increase of larvae of the dipteran *Dixa* sp. Waters pointed out that even slight increases in depth and velocity would be expected to have a marked effect on these larvae because they are associated with the surface film and with wet areas near the water's edge. Elliott (1967a) showed that although more animals were collected in a drift net during a severe spate, the density of

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drifting organisms per unit volume of water sampled did not increase (surface velocity increase of 1.35 to 2.50 m/sec). However, a few specimens of snails, dragonflies, and caddisflies were collected at the height of the spate that were not collected at any other time during his 17-month study.

Waters (1965) subdivided the overall phenomenon of downstream drift into three components: 1) behavioral drift, a result of some behavioral characteristic of the animal, such as a response to changes in light intensity, which causes the diel periodicity in drift; 2) catastrophic drift, that which occurs as a result of floods or other physical disturbance; and 3) constant drift, composed of occasional individuals of all species that for various reasons lose their hold on the bottom and drift in low numbers without any regard to diurnal periodicity.

The present study was initiated to provide data on the magnitude of the catastrophic component of the drift when stream levels begin to increase during the first fall rains.

Procedures

The experiments were conducted in Oak Creek, a small stream in the eastern foothills of the Coast Range in Benton County, near Corvallis, Oregon. The stream is shaded by a dense canopy of deciduous trees and shrubs.

In the experimental area, there is a series of riffles and pools. The riffles are composed of gravel and small rubble. The pools are about 1 m deep with silt bottoms. The typical flow regime of streams in this area is characterized by several peaks due to winter and spring rains between October and April, and then very decreased flows during the dry summer and fall. Estimated maximum flow for Oak Creek is about 2,800 liters/sec (100 ft^3 per second), but typical flows would range from 3–6 liters/sec, in late summer and fall, to 400–700 liters/sec in the winter and spring flood periods.

Equipment for continuous gauging of stream flow was not available. Depth and width of the creek were measured daily and velocity was measured on several occasions with a Gurley Pygmy current meter. However, as the flow increases within a few hours after rainfall commences, the velocity measurements were inadequate for calculating daily stream flow. The watershed is relatively steep and once the ground is saturated, runoff into the stream occurs rapidly after the onset of rain. Stream flow also decreases shortly after cessation of a rainy period. Rainfall records were thus used as an index of stream discharge.

The entire surface flow of the creek was channeled through one trap (20 cm wide by 30 cm high) at the base of a riffle, and the drifting organisms were collected in a net with a mesh size of 0.333 mm (Fig. 1). The trap was emptied daily for about 5 weeks before and during the rains in late September and October 1965. Collections were discontinued in November when high water washed out the weir.

FIG. 1. Drift trap in Oak Creek, Benton Co., Oregon, with diversion wings to funnel entire stream flow through trap.

During 1965 the effects of the first three fall freshets were monitored. The rainfall records from Corvallis, 8 km to the east, only approximate conditions at the creek since rainfall is probably higher in the watershed than in the valley at Corvallis. This was particularly evident for the first freshet period. Our observations at the field site indicated rain for 2 days, some of it heavy, before the first rain was recorded at Corvallis.

In the 1966 collections the traps were emptied at least every 12 hr (0800 and 2000 hr), so that day and night samples could be compared. In addition, a rain gauge was installed near the sampling site, so rainfall records reflected more closely the precipitation in the watershed.

Bottom samples were taken in both years in a transect across a riffle about 4.5 m above the drift trap. A modified Hess-type sampler that enclosed the area to be sampled was used (Lattin 1956). The collecting net was of 0.116 mm mesh. The samples were taken before, during and after the period of drift-net collecting.

Collecting and sorting procedures were hampered somewhat by the tremendous quantities of fallen leaves that were collected. Sometimes it was necessary to empty the net two or three times in a 24-hr period to prevent clogging. Samples from October 3 and 4, 1965 were discarded because of unexpected overflow. At peak intervals there were 20 liters of leaves collected in 24 hr. The trap also clogged and overflowed in the night sample on October 21–22, 1966, so an unknown portion of the collection was lost.

The organisms were removed from leaves by rinsing the leaves individually in water or dilute alcohol. The insects were picked from the debris and counted and measured under a stereoscopic microscope. Body length data were converted to dry weights with a conversion table obtained by measuring freshly killed specimens in 0.5-mm size classes and weighing after 48 hr drying at 70°C.

24-Hr Collections 1965

Each of the freshet periods caused a marked increase in the total drift of insects (Fig. 2). The major components of the drift were Ephemeroptera, Plecoptera, Diptera, and terrestrial insects. The terrestrial component was somewhat greater

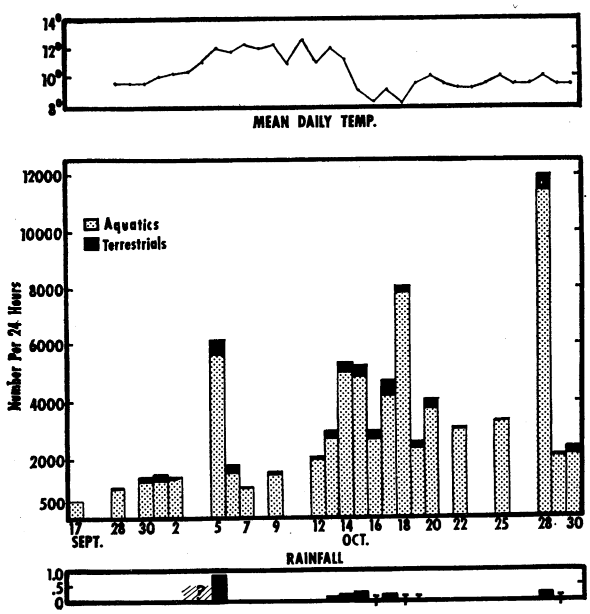

Fig. 2. Total number of insects drifting per 24 hr in Oak Creek, Benton Co., Oregon, before and during the first fall rains, 1965. Under rainfall, T = trace; ? = rain at field site but none recorded at weather station.

during the first freshet period than in previous collections. It was composed of duff inhabitants that were trapped as the water level rose, and arboreal insects carried into the stream on additional leaf fall that was caused by the rain.

The first freshet, resulting from more than an inch of rain, increased the total number of drifting insects by a factor of four, from a base level of 1,500 per 24 hr to more than 6,000. The flow during this interval increased from about 3 liters/sec to approximately 15 liters/sec. The drift rate dropped to normal within 24 hr when the rain stopped on October 6, and remained thus until the second period of rain. The second freshet resulted from almost a week of intermittent rain (October 13–19), and the increase in drift began even with the 0.12 in. of rain on October 13. A third freshet caused a peak drift of almost 12,000 insects per 24 hr on October 28. The drift rate dropped to below 3,000 per 24 hr when the rain stopped. We estimate that peak flows during both of these freshets were about 25–40 liters/sec. The density of total insects in the drift was largely unchanged in nonfreshet and freshet periods; fourfold to sixfold increases in stream discharge resulted in about fourfold increases in drift collections.

During October there was a tenfold increase in density in benthos samples even though catastrophic drift displaced large numbers of insects. The mean density of three bottom samples was: on September 25, 334 per 0.1 m^2; on October 22, 3,426 per 0.1 m^2. The autumnal increase is attributed to the hatching of eggs, both of multivoltine species and of the univoltine winter-growing species. These density increases coincide with the general decrease in the water temperature and the great increase in the amount of available allochthonous food. Inspection of the temperature data indicates no direct relationship between daily drift rate and mean water temperature (Fig. 2).

Ephemeroptera

At least eight genera of mayflies were collected in drift or bottom samples, but only *Baetis* and *Paraleptophlebia* were major components of the drift samples. The effects of the freshets were readily apparent on mayfly drift, but the magnitude of the effects was not as great as it was for Plecoptera and Chironomidae.

There are three species of *Baetis* in Oak Creek, *B. tricaudatus* Dodds, *B. bicaudatus* Dodds, and *B. parvus* Dodds, but the larvae were not separated to species for this study. The pattern of drift rate of *Baetis* spp. was consistent in the three freshet periods (Fig. 3). Prefreshet rates

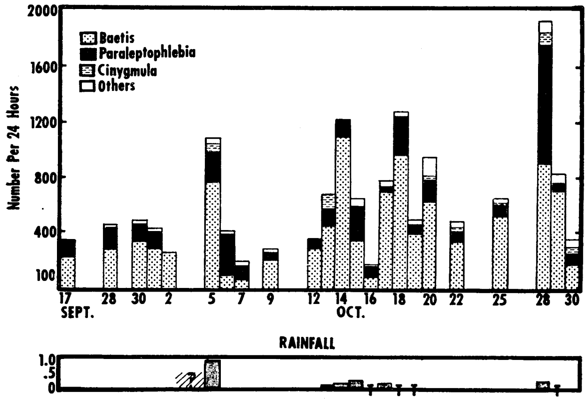

FIG. 3. Total number of Ephemeroptera drifting per 24 hr in Oak Creek, Benton Co., Oregon, before and during the first fall rains, 1965.

ranged between 200 and 300 per 24 hr and increased by about a factor of three as a result of the rainfall. The correlation between numbers of *Baetis* drifting and rainfall in the previous 24 hr was highly significant ($r = 0.75$, $P < .001$). A characteristic pattern for this genus was for drift rates to drop rapidly to very low numbers when the water levels decreased. However, this decrease was not statistically significant. There was no correlation between drift rate of *Baetis* and the rainfall in the previous 24–48 hr ($r = 0.12$).

Of the four species of *Paraleptophlebia* in Oak Creek, both *P. debilis* (Walker) and *P. temporalis* (McDunnough) are present in the fall. The numbers of *Paraleptophlebia* spp. did not increase in response to increased water levels as much as those of *Baetis* spp. except for the tenfold increase that occurred on October 28, resulting in a collection with similar numbers of *Paraleptophlebia* and *Baetis* (Fig. 3). Bottom samples on October 22 had 372 *Paraleptophlebia* spp. per 0.1 m^2 (75% less than 2 mm), compared with 7 per 0.1 m^2 on September 25. Thus, mid-October was the hatching period and many young larvae were displaced by increased water levels. Though there was a large increase in numbers drifting during the third freshet, there was no increase in the drift to benthos ratio.

Plecoptera

Two genera in the suborder Filipalpa, *Capnia* and *Nemoura,* were exceptionally abundant in the drift collections. Ball (1946) recorded six species of *Nemoura* and eight of *Capnia* in Oak Creek, but the larvae have not been described, so discussions have to be at the generic level. It is probable that minor numbers of other genera of Cap-

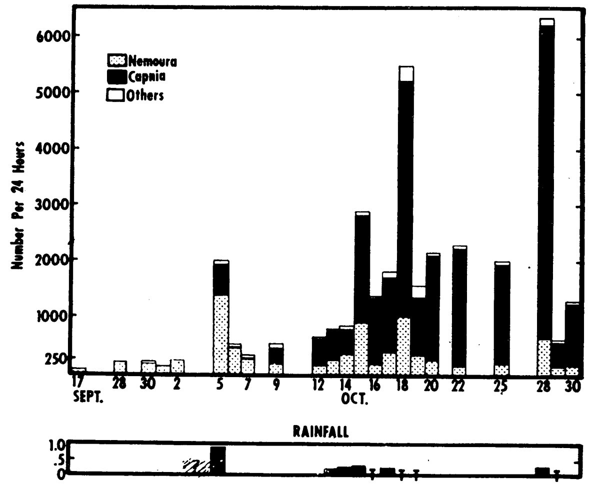

FIG. 4. Total number of Plecoptera drifting per 24 hr in Oak Creek, Benton Co., Oregon, before and during the first fall rains, 1965.

niidae and of Leuctridae were also counted as *Capnia.*

Nemoura was the most numerous plecopteran during the first weeks of the study (Fig. 4). The drift rate increased by a factor of six on October 5, whereas during the second and third freshets the increases were only two to three times greater than the interfreshet drift levels.

Capnia larvae only occurred in very small numbers in either bottom or drift samples up to the first freshet (Fig. 4). Thereafter, *Capnia* became very numerous and the catastrophic drift was particularly marked. For the last half of October, *Capnia* accounted for about 50% of the total insects in the drift samples compared with about 10% for the first half of the month.

Diptera

The two major families of Diptera in the drift were Chironomidae and Simuliidae, with the former being more than five times as numerous as the latter (Fig. 5). The chironomids were primarily of the subfamily Orthocladinae. Larvae, pupae and emerging adults were all abundant in the drift. Diptera accounted for about one-third of the total number of insects, and fivefold increases in drift rate occurred at each freshet. The chironomids and simuliids represent two distinct habitat groups—the former are associated with the leaf debris, whereas the latter occur on rocks in fast water, but the drift of both families increased to a similar degree with the increases in stream discharge.

DAY AND NIGHT COLLECTIONS 1966

Results for 1965 clearly showed the effects of increases in stream discharge on the downstream

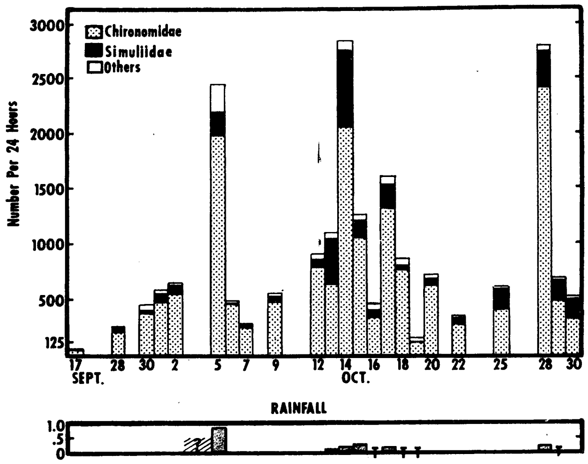

FIG. 5. Total number of Diptera drifting per 24 hr in Oak Creek, Benton Co., Oregon, before and during the first fall rains, 1965.

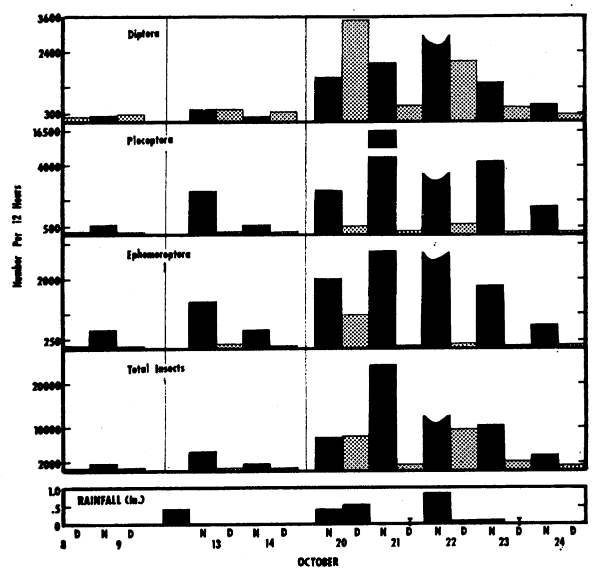

FIG. 6. Comparison of numbers of insects in day and night drift collections in Oak Creek, Benton Co., Oregon, 1966. Curved line for Oct. 22 indicates incomplete collection.

displacement of insects. The objective in 1966 was to determine whether behavioral day-night periodicities were maintained even during periods of high water.

The effects of freshets in 1966 were similar to those in 1965 (compare Fig. 2 and Fig. 6), though the prefreshet drift rate was slightly higher in 1966. In periods without rain (October 8–9, 13–14, and 23–24) the drift rate was three to four times as high at night as during the daylight hours. The rain on October 12 increased this ratio slightly to 5.4:1. The heavy rains of October 19–20 resulted in a large increase in drift but high stream discharge also kept the daytime drift equal to the night drift (Fig. 6). However, the peak occurred during the night period after the rains had ceased (24,000 per 12 hr), followed by a 95% decrease in drift rate in the following day period (1,800 per 12 hr). The effects of the heavy rain during the night of October 21 are evident in the increased drift rates. There was considerable overflow of the trap during this period, so there is an underestimate of the total drift. The same trend occurred as in the previous rainy period; increase in water levels resulted in high drift rates for more than 24 hr, but during the second daylight period the drift rates had dropped to low levels (Fig. 6).

Ephemeroptera and Plecoptera were two orders that retained the behavioral day–night periodicity during high water periods (Fig. 6). The night: day ratio of drift rate was much higher during freshets than during periods of normal water flow. By contrast, the Diptera (more than 90% Chironomidae) did not exhibit this periodicity. The numbers of Diptera decreased or increased in a manner very closely related to the amount of rainfall recorded in the previous 24 hr. During freshet periods the chironomid component in the day collections tended to mask the diel periodicity of the total insect drift rate (Fig. 6).

BIOMASS RELATIONSHIPS

The effect of catastrophic drift expressed as numbers of individuals drifting has important implications in population dynamics and regulation, but from the viewpoint of production ecology the biomass relations are more meaningful.

In Figure 7 the mean weight of specimens drifting during the 1965 freshets is compared with weights during intervals of lower water levels. A pooled mean was obtained for each of the three rainy periods and compared with mean weights for the pre-, inter-, and postfreshet periods. There was a tendency for larger individuals to be collected in the catastrophic drift. This was particularly evident for *Baetis* where mean weight was about 50% higher at each freshet. The Chironomidae exhibited a similar relationship, though the percentage increase of the first freshet was only 12%. *Nemoura* and *Paraleptophlebia* had marked increases in weight at the first freshet, but thereafter life-history considerations complicate the relationship. The apparent decrease in mean weight per specimen of *Paraleptophlebia* was due to hatching of eggs of *P. temporalis* during mid-October, and a decrease in large individuals because of emergence of *P. debilis* adults. The weight increases for *Nemoura* during the second and third freshet reflect a period of rapid

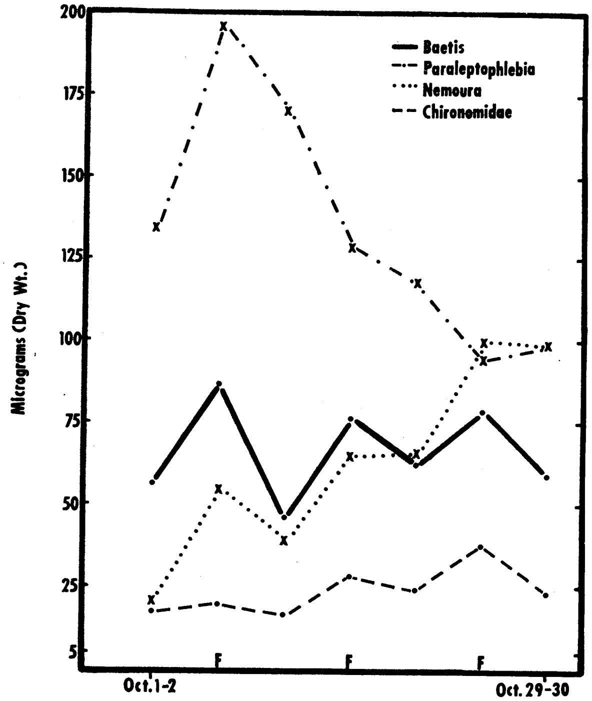

FIG. 7. Comparison of mean weight per individual of four taxa of insects in drift collections from freshet (F) and nonfreshet periods, Oak Creek, Benton Co., Oregon.

growth of the larvae during October. The growth rate from October 5 to 28 might have been somewhat less than is suggested by Figure 7 because mortality due to displacement was probably greater for the smaller size classes. Thus, the slope of the line for *Nemoura* could reflect the effects of growth plus selective mortality. The weight increase for *Capnia* (Fig. 8) also indicates very rapid growth or mortality of small larvae throughout October.

The biomass and numbers of *Capnia* drifting

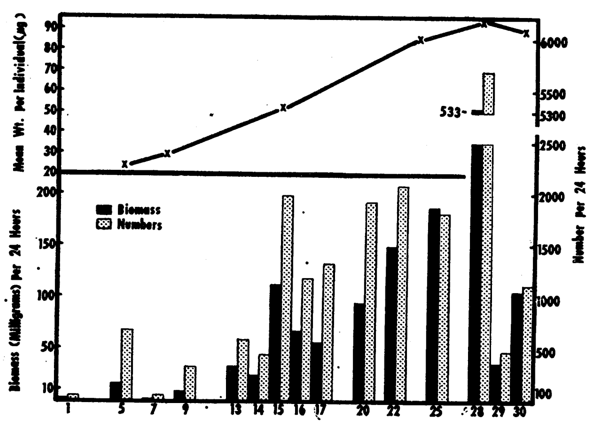

FIG. 8. Biomass and numbers of *Capnia* spp. in drift collections in Oak Creek, Benton Co., Oregon, 1965. Points on mean weight line are averages for several days.

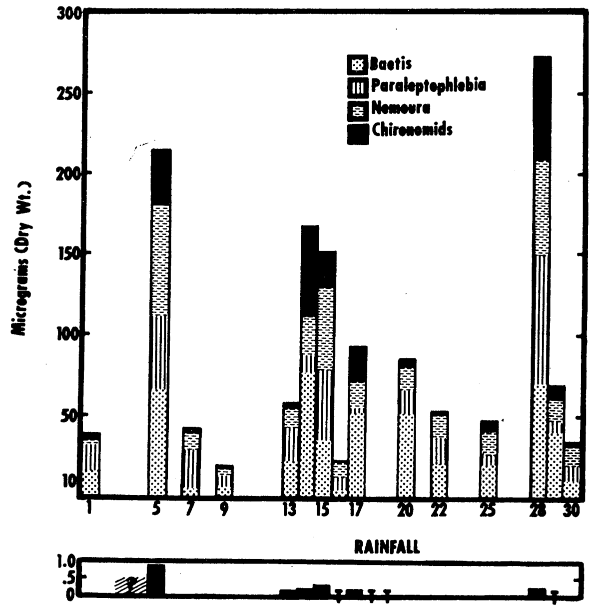

FIG. 9. Biomass of four taxa of insects in drift collections in Oak Creek, Benton Co., Oregon, 1965.

per 24 hr are graphed in Figure 8. Of the five major groups, this genus accounted for over one-half of the biomass and slightly less than 50% of the numbers in 1965. In contrast with the other dominant taxa, both the numbers and biomass of *Capnia* increased in drift collections during the interfreshet period of October 20–25. The biomass of the drift of four other important groups is illustrated in Figure 9. The general trend was the same as for the numbers of individuals drifting (Fig. 2–5). The magnitude of differences in drift biomass between nonfreshet and freshet periods was greater (fivefold to eightfold increase) than in the numbers of individuals drifting because more of the larger specimens were collected during freshet periods.

The mean weights per individual of four major taxa are compared for day and night in Figure 10. The specimens collected at night were heavier than those collected during daytime, as previously suggested (Anderson 1966). This is particularly evident for *Paraleptophlebia,* where all the day collections were quite consistent and had a mean weight of 40 mg, whereas the night collections ranged from 78 to 240 mg per individual. The Chironomidae also were significantly heavier in night collections than in the day collections. There was considerable variation in mean weights for *Baetis* and *Capnia* even between consecutive samples, but the nighttime weights were, with few exceptions, larger than the daytime weights. As shown (Fig. 7), specimens collected during freshet periods were larger than those collected during

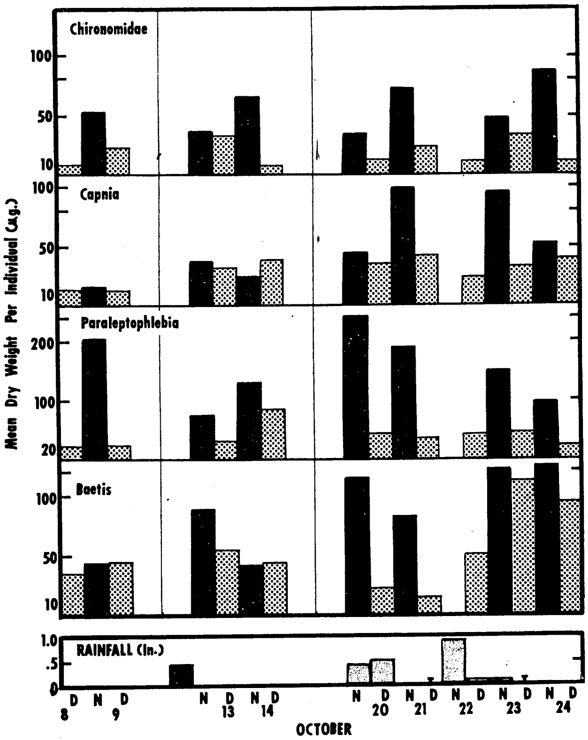

FIG. 10. Comparison of mean weight per individual of four taxa of insects in day and night drift collections, Oak Creek, Benton Co., Oregon.

normal winter flows. Even during the high water of October 19–20 and 22–23, when stream discharge was high both during night and day, the mean weights were greater during the night.

On the basis of the present data no attempt was made to establish confidence limits for the magnitude of differences in weights between freshet and nonfreshet periods, or for day vs. night. Body length measurements, from which the weights were estimated, were not normally distributed. In addition, each of the taxa considered represented a complex of species and the differences in mean weight would depend upon the species composition of samples. As the proportion of each species was not known, and may vary between samples, it was only practicable to indicate major differences. Table 1 indicates the probability for comparisons of mean body weight for night vs. day collections and freshet vs. nonfreshet collections. Paired data were compared and a nonparametric sign test was used to establish the probability level. For the five dominant groups the mean weight was significantly greater at night than during the day, and under freshet as compared with nonfreshet periods. The difference for some of the genera was not significant ($P > .05$) because of the small number of samples, but the same trend was apparent for each

TABLE 1. Paired sign test comparing mean weight per individual in freshet: nonfreshet periods, and day and night. Oak Creek, Benton County, Oregon

Taxon	Weight greater at night (1966 data)			Weight greater during freshets (1965 and 1966 data)		
	Yes	No	P	Yes	No	P
Baetis	5	2	0.227	5	0	0.031
Paraleptophlebia	7	0	0.008			
Nemoura	3	2	0.500	5	0	0.031
Capnia	6	1	0.063	4	0	0.062
Chironomidae	7	0	0.008	4	1	0.156
Total	28	5	0.00003	18	1	0.00004

TABLE 2. Comparison of mean weight per individual (µg dry wt) in drift and benthos samples, Oak Creek, Benton County, Oregon, 1966

Taxon	October 12			October 24		
	Benthos[a]	Drift Day	Drift Night	Benthos[a]	Drift Day	Drift Night
Baetis	33	49	88	47	94	121
Paraleptophlebia	31	53	78	60	42	128
Capnia	23	35	38	18	40	97
Chironomidae	16	28	37	22	24	49

[a]To compensate for finer mesh in sampler, specimens under 1 mm in length are not included in mean weights.

group. *Paraleptophlebia* was not included in the freshet: nonfreshet comparison because emergence of *P. debilis* and hatching of *P. temporalis* during October obscured any relationship.

There was a major difference between the weights of individuals collected in the drift samples and benthos samples. In Table 2 mean weights per individual are compared for night and day drift, and for benthos samples for two dates during interfreshet periods. As the benthos samples were taken with a very fine mesh net, which may retain smaller size classes than did the drift net, all individuals less than 1 mm were excluded in calculating mean weights for the benthos samples. This is considered to be an overcorrection for mesh selectivity in that many individuals under 1 mm were collected in the drift net. However, even with this compensation, mean weights in the drift samples were consistently greater than in the benthos samples.

DISCUSSION

The autumnal rains that are characteristic of western Oregon have a pronounced effect upon stream populations. Minor freshets resulting from 1 to 2 in. of rain are a normal feature of the flow regime. The effects on the fauna result from the increase in width, depth and velocity of water, and are in part due to habitat displacement. The increased flow tends to flush out the accumulation of fallen leaves that form the habitat of many species of insects. In addition, even the minor increases in flow, from 3 to 40 liters/sec as discussed here, have a scouring effect in that the displaced detritus removes such forms as the Simuliidae from their exposed positions on the rocks in midstream.

Catastrophic drift may be too strong a term to describe the effects of these minor freshets because gravel and rubble were largely undisturbed. However, the fourfold increase in numbers of insects drifting and the biomass increase of fivefold to eightfold, due to the increase in stream flow, would obviously reduce the standing crop unless balanced by colonization from upstream areas. The results indicated the magnitude of the increase in drift for the entire stream at one point, since all of the water passed through one trap. Precise drift density relationships could not be obtained from the data, but our calculations suggested that the number of insects drifting per unit volume of water was similar before and during freshets. This result is in agreement with Elliott's (1967a) statement that a rise in water velocity does not increase the density of animals in the drift.

It is particularly interesting that the Ephemeroptera and the Plecoptera retain their characteristic day-night periodicity of drift even during periods of high water. This indicates that behavioral drift continues under all conditions discussed in these experiments. It also means that it becomes extremely difficult to partition the magnitude of the behavioral and the catastrophic components of the drift.

Although it may be argued from the above that Waters' (1965) concept of components of drift becomes vague under certain conditions, the pattern of drift for Chironomidae indicates that the component concept provides a useful framework for comparing the drift patterns for various taxa. The close relation between the numbers of chironomid larvae collected and the amount of rainfall recorded suggests that the downstream drift of these larvae is due almost entirely to the catastrophic and constant components of the drift. Many species of chironomids have been shown to have marked rhythms of daily emergence (see review by Pálmen 1955). Emergence rhythms of species of the subfamily Orthocladinae can sometimes be detected by peaks in the number of pupae collected in the drift traps. However, we have been unable to detect any consistent diel patterns of drift of chironomid larvae. Though, in part, this is due to the fact that all stream collections will represent larvae of several species, it also seems that there is no pronounced behavioral drift of chironomid larvae (Anderson 1966).

Elliott (1967a, b) did not partition drift into behavioral and catastrophic components. His hypothesis of the mechanisms causing drift combined all factors that would result in individuals being carried downstream by the current. Resolution of the contrasting views as to whether drift is an active (Müller 1963) or a passive process (Elliott 1967a) cannot be achieved until experiments indicate whether individuals swim from the benthos or if they are swept away by the current. In either case, species behavior patterns are responsible for the microdistribution and activity that results in the typical nocturnal peak in drift, and the term behavioral drift should be retained to describe a component of the drift process.

Few detailed reports have been published on the difference in drift activity of various size classes of insects. Müller (1966) reported the highest drift activity for baetid mayflies occurred immediately before emergence and for simuliids shortly before pupation. Elliott (1967b) found that large nymphs of mayflies and stoneflies were often predominant in the drift and that there was a strong correlation between periods of rapid growth and drift rate. Anderson (1967) found that the caddisfly, *Amiocentrus aspilus* (Ross), had different peaks of activity depending upon the size of the larvae; large larvae were night-active, whereas the early-instar larvae were day-active. In the present study we have found that larger individuals of Ephemeroptera, Plecoptera and Diptera occur in night drift as compared with the day and also under high water conditions as compared with low water. In addition, in both day and night drift samples the mean weight of larvae of each of these taxa was greater than in the benthos samples (Table 2).

Hughes (1966) found under laboratory conditions that disorientation was caused by absence of an overhead light source and suggested that disorientation at night may be a contributing mechanism to the night peak in drift. To explain the size differences between day and night, the degree of disorientation would have to increase with age. There are no experimental data to support this idea. Hughes (1966) found that the final instar of *Baetis harrisoni* Barnard did not exhibit as strong a dorsal light response as did earlier instars. Disorientation, however, could increase up to the penultimate instar and give a result consistent with the above.

Mature larvae in the water column should be able to resist downstream displacement to a greater degree than small larvae because of the superior swimming ability of the former. On this basis one would expect mean size to decrease in relation to increased water level. However, drift acts as a "mixing" process and increased flow tends to flush out individuals from the previously slow, shallow backwaters near shore. Recently we have found that small larvae of *P. debilis* occur in the riffle area, whereas the large larvae are more common in slow water (less than 3 cm/sec) along the bank. Thus, our benthos samples would be biased towards the smaller size classes for this species because samples are taken where current velocity is fast enough to sweep the specimens into the collecting net. In addition, the large larvae would not be exposed to displacement until stream volume increased to the extent of covering their habitat with several cm of water. The accumulated organic debris would then be displaced by the current and the larvae would be transported as a component of the catastrophic drift when this critical level was reached.

The above interpretation is offered to explain the differences obtained between weights of individuals in day and night samples and also between drift and benthos samples. At present it is difficult to decide whether either the benthos samples or the drift samples provide a reliable measure of the size class or weight distribution of the populations. A comprehensive interpretation of the reasons for differences in the sizes of individuals drifting under various conditions will require detailed knowledge of the life cycle, behavior and microhabitat preference of each species under consideration, and of the effect of physical factors such as velocity and scouring action of the substrate and debris.

The nonbehavioral drift has both beneficial and detrimental effects on the fauna. The increase in stream flow coincides with a period when the eggs of several species are hatching, and the drift aids in dispersing aggregations of young larvae. Undoubtedly, many individuals perish from mechanical injury (Needham 1928) but much of the transport is effected as packets of leaves and debris, so all specimens are not necessarily exposed to this hazard or to increased predation by fish or other predators that hunt their prey by sight. Factors that have not yet been quantified are the distance traveled and the eventual deposition site of transported larvae. It is probable, however, that a majority of the individuals transported downstream will not lodge in habitats that are suitable for completion of their life cycle. Increased stream discharge removes large quantities of allochthonous material (Warren *et al.* 1964). Removal of this food supply may well be the major effect of the fall and winter rains on the stream invertebrates of this area.

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