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Invertebrate Drift in the Snake River, Wyoming*

by

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Abstract

Drifting invertebrates were collected hourly during 24-hour sampling periods at two stations in the Snake River. The greatest number of invertebrates was collected on 8 and 15 July 1966 at station 1 between 9:00 p. m. and 12 midnight, then the numbers gradually decreased until the low daylight drift rate was reached at dawn. On 26 and 27 August 1966 at station 2 ,the diel periodicities of drifting invertebrates were different than at station 1. Many species increased their drift rates slightly during the first hour of darkness but also exhibited a higher drift peak later in the night.

Drift indices for 25 taxonomic groups of invertebrates were established from the ratio of standing crop, estimated from Surber samples, to numbers drifting. There was more apparent correlation between species life cycle stage and numbers drifting than between species abundance and numbers drifting.

Introduction

Drifting invertebrates in streams were first reported more than a quarter century ago but they have been extensively studied only during the last decade. Early research indicated invertebrate drift was a normal process even in the absence of swift currents (Dendy, 1944). Müller (1954) reported drift was caused by competition for food and space and was an important mechanism for population dispersal. Waters (1965), after finding that high drift rates occurred

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with a diel periodicity and did not deplete the stream bottom, coined the term, behavioral drift, to distinguish it from constant and catastrophic types. WATERS also reported that drift appeared to remove excess production and regulate population densities. Drift was later shown to be exogenously controlled by light intensity (HOLT & WATERS, 1967 and BISHOP, 1969) and to be density dependent (DIAMOND, 1967 and PEARSON & FRANKLIN, 1968). Since a small proportion of the bottom fauna was found to be drifting at any one time, ELLIOTT (1967) concluded that the organisms probably lose their footing or are dislodged by their cohorts and the quantity of drifting organisms is dependent on population size and competition for food and space.

In 1966 I studied drift in the Snake River in Grant Teton National Park, Wyoming as part of an ecological and classification study of the invertebrates. I recorded diel periodicities and calculated drift indices for 25 taxonomic groups of invertebrates during the summer when the flow exceeded 3,000 cubic feet (84.9 m^3) per second. Drift indices, which are an indicator of a species tendency to drift under the prevailing conditions of competition and carrying capacity, were calculated from the relationship of the standing crop of a species in a riffle to the number drifting in the riffle.

METHODS

The standing crop of invertebrates in the riffles was estimated from five Surber 1-ft^2 (.093 m^2) samples taken by standard techniques (NEEDHAM & NEEDHAM, 1962). Even though the Surber sampler underestimates standing crop (KROGER, 1972), the foot-square data appear sufficient for determining drift indices.

Samples of drifting invertebrates were collected with a modified net and frame (Figure 1) described by WATERS (1962). The portable frame consisted of two 5-feet (1.52 m) parallel iron rods joined by 1-foot (.305 m) spacer rods; stabilizing rods were welded across the front of the frame and two iron rods were welded upright to the base rods to hold the net. The frame was anchored to a large rock to prevent displacement by the swift current. A Surber sampler with the 1-foot square frame removed was attached to the iron upright rods with metal rings. The time required to remove, empty and replace the net was less than 2 minutes.

Hourly drift samples were collected from two locations in 1966. At station 1, a riffle 1 mile (1.6 km) downstream from Jackson Lake Dam, a 24-hour drift series was obtained on July 8 and another on July 15. The sampler was placed on the gravel bottom in 2 feet

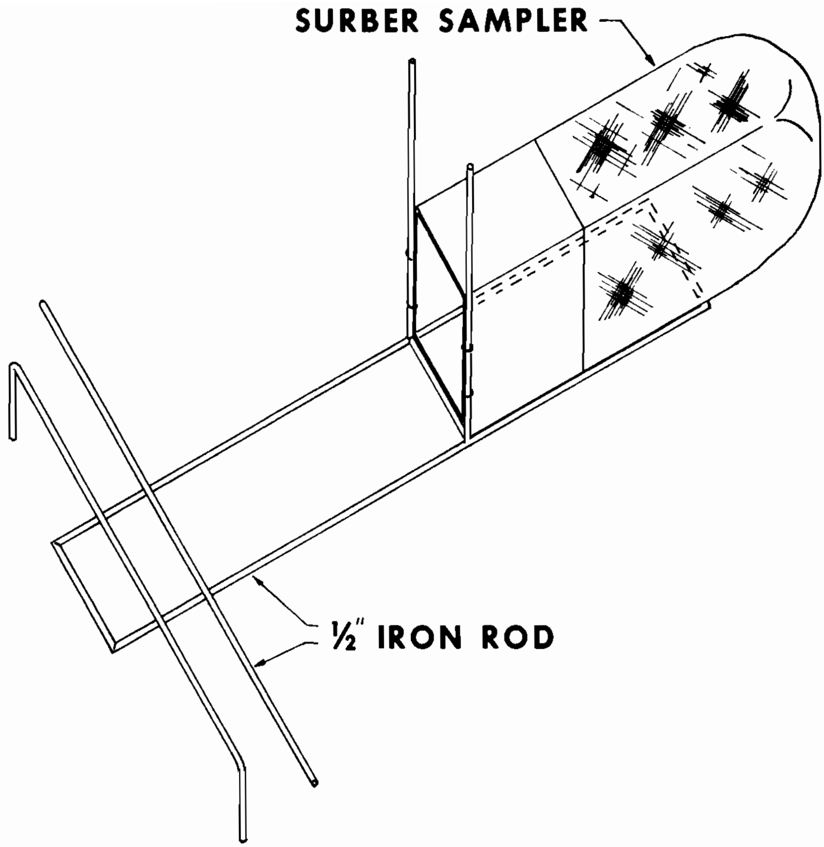

Fig. 1. Frame and net used to collect drift samples.

(.61 m) of water about 20 yards (18.29 m) from shore where current speed was 4 feet (1.22 m) per second. On these dates it became dark by 9:30 p.m.; both nights were moonless. At station 2, a riffle in a side channel of the Snake River 4 miles (6.4 km) north of Moose, Wyoming, a 24-hour drift series was collected on August 26 and another on August 27. The sampler was set on the rubble stream bed in 10 inches (.25 m) of water about 15 yards (13.72 m) from shore where current speed was 3.3 feet (1.01 m) per second. It became dark by 8:00 p.m. on these dates; the moon was visible until about 2:00 a.m.

Species drift indices were calculated by dividing the average number collected in the drift net during the 24-hour periods by the number collected in five Surber foot-square samples taken over the entire riffle. Pupae and emerging nymphs were eliminated from the foot-square and drift samples. All invertebrates were preserved in museum fluid and identified with the aid of a reference collection from the Snake River (KROGER, 1970).

RESULTS

Diel periodicities of drifting organisms were the same in the two 24-hour drift series collected at station 1 and the data from both series were combined (Table I). The number of drifting *Ephemerella inermis* EATON, *Simulium*, sp. and *Hydropsyche* sp. increased greatly during the first hour of darkness and then gradually declined until sunrise when the low diel rate was reached (Figure 2). The increase

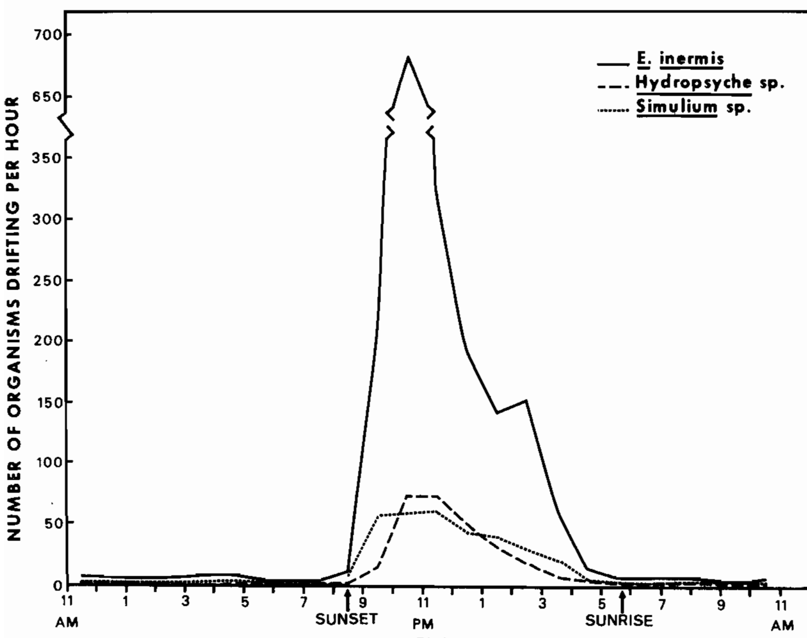

Fig. 2. Average number of *E. inermis, Simulium* sp. and *Hydropsyche* sp. collected in a drift net on July 8 and 15, 1966.

and gradual decline illustrated the same diel periodicity exhibited by *Gammarus pseudolimnaeus* BOUSFIELD and *Baetis vagans* McDUNNOUGH in a small Minnesota stream (WATERS, 1962) and is typical of drift that occurs during short summer nights (MÜLLER, 1965). Two stoneflies, *Alloperla* sp. and *Isoperla* sp., also showed the same diel periodicity but few were collected because *Alloperla* sp. was scarce in

TABLE I

Average number of organisms collected hourly during two 24-hour drift series from July 8 to 9 and July 15 to 16, 1966 at station 1. Also included are the number collected in five Surber 1-ft² (.093 m²) samples taken on July 12 and the calculated drift indices.

Time	Alloperla	Isoperla	Ephemerella inermis	Hydropsyche	Chironomidae	Simulium	Acarina	Total aquatic invertebrates per hour	Fish	Terrestrial insects
11 a m			7	1	3	1	2	14	1	1
12			5	1	1	2	1	10		
1			3	1	2	1	1	8	1	
2			5	1	5	1		12	1	1
3			7		5	2	2	16		
4			8	1	6	4		20	2	1
5			5	2	2	2	1	12	1	1
6			4	1	3	2	2	12	1	
7			3	2	4	3	1	13		
8			12	2	6	8	1	29	2	1
9		3	217	16	2	57		295	1	1
10	2	8	682	74	4	59	1	830	11	1
11 p m		2	326	73	8	61	1	471	20	1
12	1	1	191	49	3	43	1	289	42	1
1	1	1	143	32	6	40		223	23	
2	1	1	153	19	5	30		209	12	1
3			65	8	3	23		99	8	
4			15	4	2	6		27	1	
5			6	3	1	2	1	13	1	2
6			7	2	4	3	3	19		
7			8	2	1	3	2	16	1	
8			6	3	3	4	2	18	1	1
9			4	1	2	2	2	11		1
10			7	1	2	2	1	13		1
11 a m										
Total	6	16	1,889	299	83	361	25	2,679	130	15
Five 1-ft² sample total	1	1	186	130	37	414	0	769	—	—
Drift index	6.0	16.0	10.2	2.3	2.2	0.9	*	3.5	—	—

* No value

this riffle and most of the abundant *Isoparla* sp. had previously emerged. Small fish also followed the same drift pattern as the insects. Water mites, Acarina, and chironomids were the only aquatic organisms collected at station 1 that did not follow the typical periodicity.

At station 2 the diel periodicities of drifting organisms were similar in each 24-hour drift series and the data from both series were also combined (Table II). The mayfly, *Paraleptophlebia packii* NEEDHAM, and caddisflies, *Hydropsyche* sp. and *Arctopsyche* sp. had an alternans type drift patterns, that is one low peak of drift just after dark and another higher peak later in the night (Figure 3). This double peak pattern is typical of drift during longer nights in spring and autumn (MÜLLER, 1965). The drift of mayflies, *Ephemerella grandis ingens* EATON and *Rithrogena hageni* McDUNNOUGH closely resembled that in figure 3. Stoneflies, *Petronarcella badia* (HAGEN), *Isogenus* sp. and *Acronuria pacifica* Banks had two peaks also, but the first was very slight.

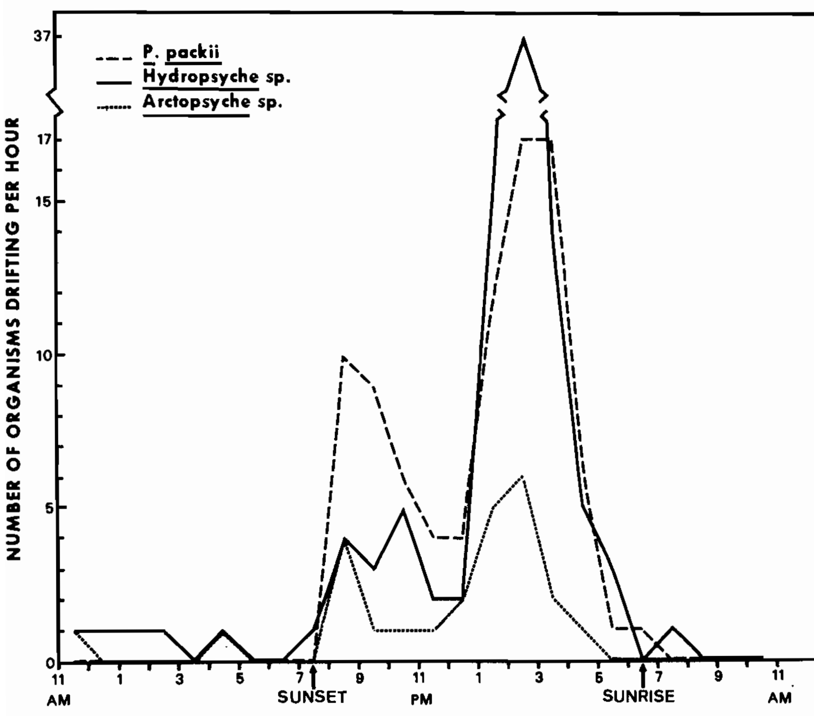

Fig. 3. Average number of *P. packii*, *Hydropsyche* sp. and *Arctopsyche* sp. collected in a drift net between August 26 and 28, 1966.

TABLE II

Average number of organisms collected hourly during two 24-hour drift series from August 26 to 28, 1966 at station 2. Also included are the number collected in five Surber 1-ft² (.093 m²) samples taken on September 2 and the calculated drift indices.

Time	Pteronarcela badia	Alloperla	Isoperla	Isogenus	Arcynopteryx	Acronuria pacifica	Claassenia sabulosa	Ephemerella inermis	Ephemerella tibialis	Ephemerella grandis ingens	Baetis tricaudatus	Baetis bicaudatus	Paraleptophlebia packii	Rithrogena hageni	Hydropsyche	Arctopsyche	Polycentropous	Brachycentrus	Hydroptila	Limnephilidae	Glossosoma montana	Chironomidae	Simulium	Metachela	Acarina	Total aquatic invertebrates per hour.	Fish	Terrestrial insects
11 a m									6	2	4	16		1	1	1	1	1	1			5	3			42		46
12		1		1		1			3	1	1	10			1		1					6	1			27		54
1		1							2	2	2	8			1		1	1				2	1			21		118
2		1		1					3	1	1	2			1							2				12		231
3		1							1	1								2				1				6		352
4		3							2	1	1	10			1	1						4	1			24		26
5		1							4	1	3	5										1	1			16		22
6	1	1							6	2	1	11										4	1			27		16
7						1			4	2	15	44		1	1							3	1			72	2	7
8				1		1			1	5	50	76	10	2	4	4		2	1			9	1			167	2	24
9	1			1					1	5	27	41	9	3	3	1	1		1			14	2			110	3	4
10	1									2	28	20	6		5	1	1	2				5	2			73	2	11
11 p m	1									1	21	11	4	1	2	1						9	3			53	2	3
12				1		1			1	1	13	8	4		2	2						1				34	1	2
1	4			6	1	2			1	4	23	12	12	2	15	5						5				92	1	6
2	8			27	1	2			1	7	23	18	17	4	37	6	1	3				3	1			160	3	6
3	15			50		1			1	5	41	25	17	7	14	2	1	1				1				181	2	4
4	5			5						1	30	22	6		5	1		1				2				78	1	2
5	1	1								1	4	7	1		3								1			19	1	3
6											1	4	1				1	1				2				10		4
7										1	4	8			1		2					3	1			20		3
8										1	5	7		1			1	1								16		13
9										1	1	10					1					1	1			15		23
10									1	1	4	13					1	1				2				23		25
11 a m																												
Total	37	10	0	93	2	9	0	0	38	49	303	388	87	22	97	25	13	16	3	0	0	85	21	0	0	1,298	20	1,005
Five 1-ft² sample total	9	1	4	1	8	16	9	7	1	192	15	172	5	67	611	83	10	122	4	24	143	562	24	5	8	2,103	—	—
Drift index	4.1	10.0	0.0	93.0	0.3	0.6	0.0	0.0	38.0	0.3	20.2	2.3	17.4	0.3	0.2	0.3	1.3	0.1	0.8	0.0	0.0	0.2	0.9	0.0	0.0	0.6	—	—

The stonefly, *Alloperla* sp., and the mayfly, *Ephemeralle tibialis* McDunnough drifted mainly during the daylight hours. *E. tibialis* was emerging and some of its drift may have been of a preemergence type, although no subimagoes were collected. Waters (1968) reported a caddishfly, *Oligophebodes sigma* Milne, had a day active drift periodicity which was controlled by water temperature changes.

Even though mayfly nymphs, *Baetis bicaudiatus* Dodds and *Baetis tricaudatus* Dodds* were emerging, a distinct drift periodicity was indicated. Emerging nymphs and subimagoes were recovered only between 11:00 a.m. and 8:00 p.m. and were not included in Table II. Both species exhibited the bigeminus drift pattern, that is a high drift peak during the first hour of darkness and a second peak of less magnitude later in the night (Figure 4). *B. bicaudatus* also had a third peak of less significance at 11:00 a.m. Waters (1969, personal

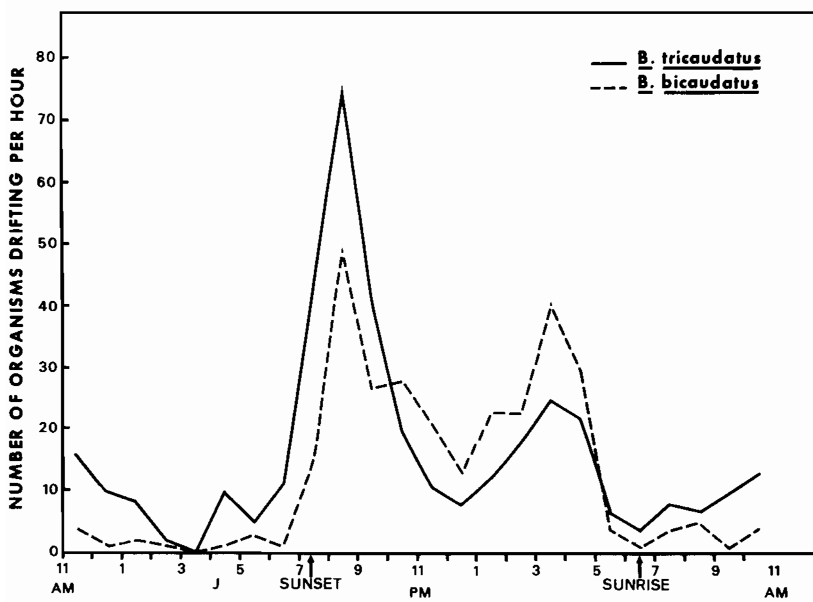

Fig. 4. Average number of *B. bicaudatus* and *B. tricaudatus* collected in a drift net between August 26 and 28, 1966.

communications) observed that both species in Utah streams had two peaks, but *B. tricaudatus* exhibited the alternans type with the second peak higher than the first.

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* Also includes some *Baetis intermedicus* Dodds which could not consistently be distinquished from *B. tricaudatus*.

Differences in diel drift patterns of invertebrates collected on 8 and 15 July at station 1 and 26 and 27 August at station 2 were evident for several taxonomic groups. The stonefly, *Alloperla* sp. drifted during the night at station 1 and during the day at station 2. The reason for the differences may be a species trait since adult collections of *Alloperla* at the two stations indicated different species occupied each area. Chironomid and simuliid drift also differed at the two stations. At station 2 chironomids which usually do not exhibit drift periodicities (WATERS, 1969) had a distinct peak of drift early in the night whereas at station 1 they appeared to drift at random. In contrast, simuliids which drifted equally during day and night in a Minnesota stream in August (WATERS, 1962), appeared to drift at random at station 2 whereas at station 1 they had a distinct diel periodicity. The reasons for these changes in drift patterns are not known.

Second peaks of drift which occurred for many species at station 2 between 1:00 and 4:00 a.m. may have been related directly to the moons disappearance behind the mountains at about 2:00 a.m., after which the nights became much darker. WATERS (1962) also reported increased drift after the sky changed from moonlit to overcast. Second peaks were lacking at station 1 where no apparent change in light intensity occurred during the nights.

The number of terrestrial insects and emerging aquatic insects collected at station 2 was much higher than at station 1. More terrestrials were collected at station 2 because the net extended above the water surface, collecting all the insects that floated, and because a rainstorm knocked many terrestrial insects into the water. During and immediately after the storm, 844 winged ants (Hymenoptera) were collected. The orders Hemiptera, Homoptera and Diptera were also well represented in the drift samples. Most of the more than 800 emerging aquatic insects collected in the drift net at station 1 and 10,000 at station 2 were chironomids and mayflies.

Even though periodicities of some species could not be determined because too few drifted, drift indices were calculated for all species whose total number collected in the combined drift and Surber samples was greater than four (Tables I and II). *Glossosoma montana* Ross, a stone-cased caddisfly, was the only abundant insect which was not collected in drift samples, and therefore had a drift index of zero. Other less numerous invertebrates that did not drift and had drift indices of zero were the stonefly, *Claassenia sabulosa* (BANKS), the caddisflies, Limnephilidae, and the dipteran, *Metachela* sp. Water mites, Acarina, did not drift at station 2 where they appeared abundant in the foot-square samples, but they did at station 1 where none were collected in the foot-square samples.

Drift indices of 10 or greater were calculated for the three stoneflies, *Alloperla* sp., *Isogenus* sp., and *Isoperla* sp., and the four mayflies, *E. inermis*, *E. tibialis*, *B. tricaudatus* and *P. packii* all of which, except *Isogenus* sp., were in or approaching their periods of emergence. Only emerging *B. tricaudatus* nymphs, however, were collected in the drift net. Other effects of extreme life cycle stage differences on drift indices were evident for *Isoperla* sp. and *E. inermis*. At station 1 where they had indices greater than 10, the nymphs were mature when the the samples were collected. At station 2, where they had indices of zero, the drift samples were taken when only recently hatched nymphs were present in the River. Evidently, drift increases in later life cycle stages in many species (WATERS, 1969).

The average drift indix at station 1 was six times greater than at station 2 which had three times the standing crop biomass of invertebrates and more than twice the numbers as at station 1. I concluded the average drift index may have been higher at station 1 because the standing crop of invertebrates in the unproductive gravel substrate of the riffle exceeded the carrying capacity to a greater extent than at station 2 where the riffle was composed of a more productive rubble substrate. WATERS (1966) reported drift rate may be a function of production beyond the carrying capacity of the stream bed. Differences in species composition, in life cycle stages and in time when samples were collected at the stations, no doubt also affected the average drift indices.

DISCUSSION

The relationship of drifting invertebrates and the feeding habits of trout suggests that nighttime drifting may have evolved as a protection mechanism. After examining many trout stomachs, I became convinced that during the summer, tiout fed almost entirely on drifting insects, terrestrials and adult or emerging aquatics. Even though the terrestrial insects constituted less than 1 percent of the total drift in the Snake River, they made up about one-half the mass of food in trout stomachs. A high incidence of terrestrial insects in the stomach contents of trout was also found by WARREN et al. (1964). If immature aquatic insects drifted primarily during daylight as terrestrials and emerging and adult aquatics do in the summer, I believe the percentage of immatures utilized for fish food would greatly increase. The possibility of artificially increasing invertebrate drift to make more food available to trout has been discussed by MINSHALL & WINGER (1968).

Drift indices, as I calculated, may be misleading at times because a species drift rate is not necessarily a function of its abundance at the drift nets location (WATERS, 1965). A species that does not normally inhabit riffles but does drift through them will have a high drift index because standing crop samples from the riffles which are used to calculate drift indices, will contain very few of the species. For example, *P. packii* had a high calculated drift index because many individuals drifted through the riffle even though the species did not inhabit the swift-water area where the drift net was located and where most foot-square samples were collected. This burrowing mayfly normally inhabits slow-water areas where silt is deposited, such as at the edges of riffles or in pools. A few *P. packii* were obtained in the foot-square collections because one sample was taken in the slow-water area near shore so as to be representative of the entire riffle.

Drift indices and periodicities evidently fluctuate with changes in physical factors such as water temperature and current velocity and biological factors such as life cycle stage, growth rate and population density (WATERS, 1969). To gain a better understanding of the effects of these multiple factors on invertebrate drift in a stream, bottom and drift samples should be taken simultaneously and at short intervals during the entire life cycles of all species present. These sampling methods should show when during each species life history and under what prevailing conditions that drift patterns and rates change.

ZUSAMMENFASSUNG

Dahintreibende, wirbellose Tiere wurden während 24-stündigen Untersuchungsperioden stündlich an zwei Stationen im Snake River gesammelt. Die grössten Anzahlen von wirbellosen Tieren wurden auf Station 1 am 8. und 15. Juli 1966 zwischen 21 und 24 Uhr gefunden. Danach verminderten sich die Zahlen allmählich bis sie bei Morgendämmerung die niedrigsten Werte des Tagesdrifts erreichten. Am 26. und 27. August 1966 waren die täglichen periodischen Zyklen der treibenden Invertebraten auf Station 2 ganz anders als die auf Station 1. Viele Arten erhöhten ihre Driftgeschwindigkeit etwas in der ersten Stunde der Dunkelheit und hatten ausserdem noch einen Höchstdrift später in der Nacht.

Ein Driftindex für 25 taxonomische Gruppen wirbelloser Tiere wurde nach dem Verhältnis von Standing Crop zur Anzahl dahintreibender Tiere aufgestellt, berechnet auf Grund von Surber Proben. Es bestand eine grössere Wechselbeziehung zwischen der Stufe im Lebenszyklus der Arten und der Anzahl der Treibenden, als zwischen dem Artenquantum und der Anzahl der Treibenden.

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