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Fluctuations of Aquatic and Terrestrial Invertebrates in Drift Samples from Convict Creek, California

Introduction

Cyclic drift patterns for various aquatic and terrestrial insects in lentic environments should be of primary concern to workers involved in studies of feeding habits and behavioral activities of fishes inhabiting these environments. Waters (1965) divided stream invertebrate drift into three categories: (1) "catastrophic" drift (due to an unusually severe disturbance), (2) "constant" drift (due to an accidental dislodgement), and (3) "behavioral" drift (due to endogenus insect behavior patterns). While most drift organisms appear to be "night" rather than "day" active (Müller, 1966), others appear to be more sensitive to the vicissitudes of stream flow (Anderson and Lehmkuhl, 1968). Many authors (Tanaka, 1960; Waters, 1962; Müller, 1966; Elliott, 1967; and Pearson and Franklin, 1968) have observed a dramatic post-sunset increase in aquatic drift organisms from streams from various geographic regions.

The experimental stream sections at the Sierra Nevada Aquatic Research Laboratory, Bishop, California provide an excellent opportunity for a study of the diurnal drift patterns of aquatic and terrestrial insects in both a riffle and a pool. Also, observations were made of changes of drift abundance and type by artificially altering the water flow and velocity through these areas.

Materials and Methods

The Sierra Nevada Aquatic Research Laboratory, a facility of the Bureau of Sport Fisheries and Wildlife, Division of Fishery Research, is located on Convict Creek on the eastern slope of the Sierra Nevada Mountains in California (lat. 37°37′N, long. 118°50′W) at an elevation of 2195 m (Fig. 1-A). Convict Creek heads from snow-fed lakes encompassing Convict Creek Basin near the precipitous eastern escarpment (average crest elevation 3600 m) and drains an area of 60 km^2. Convict Creek eventually empties into Crowley Lake (elevation 2070 m), a reservoir for the Los Angeles Department of Water and Power.

Convict Creek is normally very clear, has a rocky substrate derived from glacial outwash material, and is nearly devoid of vascular aquatic vegetation. Although the surrounding terrain to the study area is vegetated with xeric shrubs, the creek is canopied for most of its length with *Populus tremuloides, Betula fontinalis,* and *Salix* spp.

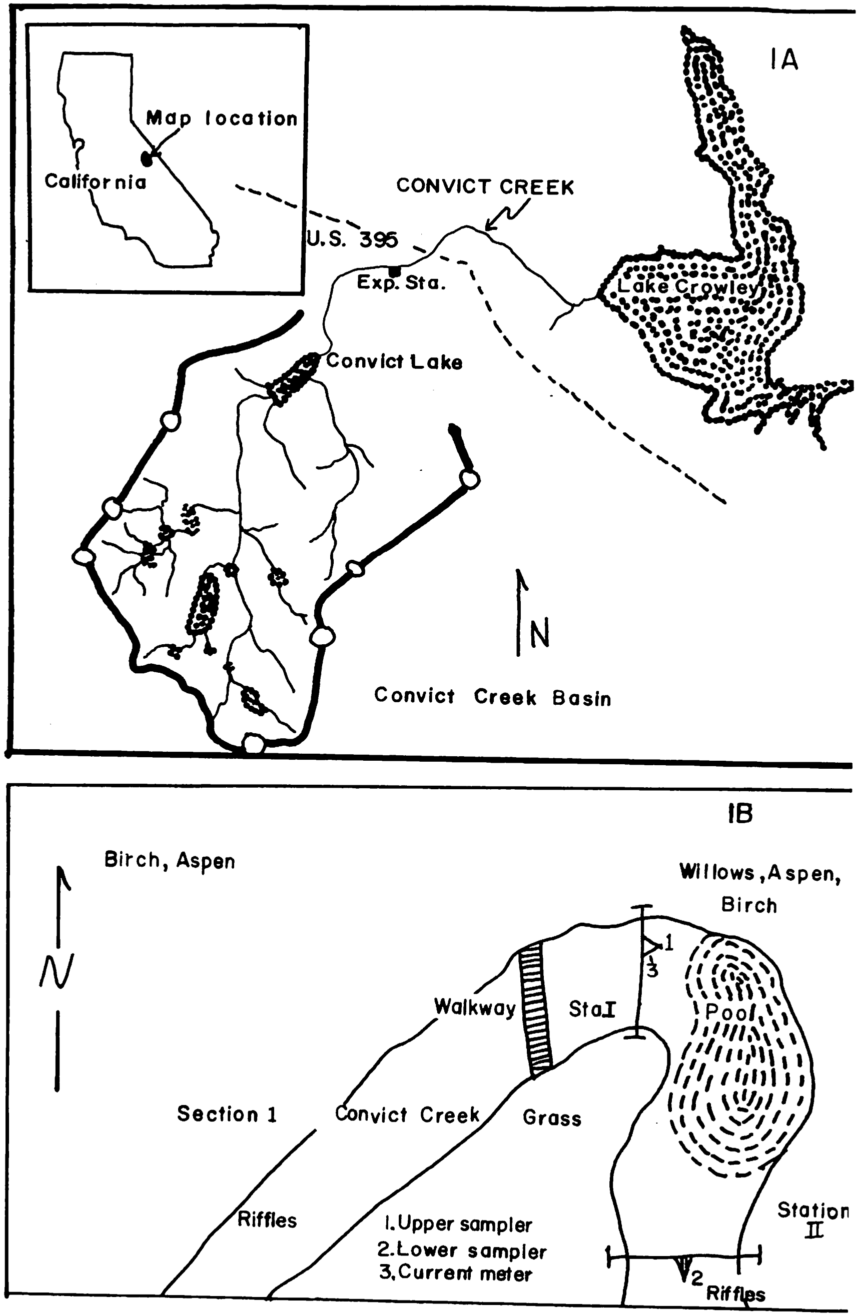

Figure 1. A: Convict Creek watershed and location of U.S. Fish and Wildlife Experime
Station. B: Diagram of sampling locations.

Further description of the lakes in Convict Creek Basin is provided by Reimers *et al.* (1955), and of investigations of Convict Creek by Maciolek and Needham (1951), Reimers (1957), Kennedy (1955 and 1967), and Jenkins (1969).

The main channel of Convict Creek within the grounds of the research area is divided into two 0.8 km sections which are further subdivided in half. An area of study was selected in stream section I and consisted of one riffle-pool complex (Fig. 1-B). The riffle area extends almost continuously upstream for 50 m from sample Station I. Sample Station II was located at the beginning of another riffle area and at the downstream side of a pool. The pool was typical of a more mature stream with a heavily undercut bank and various bars and deeps. The deepest point in the pool was approximately 1.4 m. Sample stations were established by placing sawdust evenly across the entire width of the stream 8 m upstream from the pool and then observing areas of greatest flow. The sawdust entered the pool mainly at the area where Station I was established. The sawdust was well distributed by several turbulent eddies and only a small, rather even proportion emerged at the area where Station II was established.

Aquatic and terrestrial[1]-drift organisms were collected in Surber samplers suspended in the area of maximum current velocity. The sampler rested on the substrate so that the sample area was approximately .07 ± .01m². Samples were collected for one hour, placed in 50 percent ethanol solution, and examined within 12 hours of collection. Drift samples were divided into three main classes: organisms of aquatic origin, terrestrial organisms, and egg masses. The aquatic and terrestrial classes were sorted to order or family, recombined, blotted with filter paper for 30 seconds, and weighed to the nearest .001 of a gram. Egg masses were similarly weighed.

Air and water temperatures were continuously monitored at the research station. The water temperature probe was located approximately 50 m upstream from the study area. Current velocity was measured with a Gurley Current Meter three times every hour. The base plate of the current meter was fixed in the stream bed approximately 10 cm from the upstream edge of the Surber sampler at Station I.

Preliminary experiments were conducted at Station I with two Surber samplers located 30 cm apart. Samples were collected from 1000 hours on July 19 until 1700 hours on July 20; from 1700 until 2000 hours on July 27 and August 9; from 0400 until 0900 hours on July 28 and August 10; and from 1100 until 1900 hours on August 12, 1966. The final experiment was conducted with one Surber sampler placed at each Station for a 24-hour period from 1700 hours on August 18 until 1700 hours on August 19.

Results

Results of a preliminary experiment established that a peak in aquatic drift organisms occurred around sunset (Table 1). Mayflies (Ephemeroptera: *Baetidae*: Immatures) were the dominant aquatic organisms while chironomids and crane flies (Diptera: *Chironomidae* and *Tipulidae*: Adults) were the most common terrestrial organisms observed in this postsunset peak. Subsequent experiments were designed to ascertain the causes of this increase in drift activity. Water velocity in this and the other three stream sections could readily be altered by diverting water into or from the other sections. Water velocity was increased by 18 percent at 1800 hours on August and a 32 percent increase in organisms (by weight) was observed from the next sample period (Table 2). However, this increase in stream flow did not appear t cause an increase in bottom-originated organisms, while it did increase terrestrial organisms. These terrestrial organisms included adult forms of black flies (Diptera *Simuliidae*), chironomids, and crane flies. This qualitative increase in organisms wa most likely due to the greater amount of bank vegetation being submerged because o increased stream depth and flow. Subsequent decreases in water velocity did no prevent the observed increase in drift activity at sunset. The mayfly (immatures was the most dominant aquatic insect found in the 2000- to 2100-hour sample, although chironomids (adults) and crane flies (adults) were the most common terrestrial organisms. There was no correlation between water velocity and weigh of organisms ($R^2 = .03$), but a positive correlation did exist between water temperature and weight of organisms ($R^2 = .85$).

The experiment involving changes in water velocity was repeated because of the confounding effect that sunset had on the numbers of organisms present. This next test was conducted during the early afternoon to eliminate this effect. Water velocity was increased 78 percent at 1200 hours on August 12 (Table 3). An immediate in-

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[1] Terrestrial insects were defined as those insects which dropped into the stream and became incorporated into the drift material.

TABLE 1. Effect of time on aquatic drift organisms at Station I. Sunset was at 1945 hour

Date	Time (hours)	Sample weight (grams) Sampler 1	Sampler 2
7-19	1100	.045	.125
7-19	1200	.035	.075
7-19	1600	.020	.045
7-19	1700	.015	.040
7-19	1900	.025	.050
7-19	2000	.165	.235
7-20	0900	.100	.145
7-20	1000	.053	.080
7-20	1600	.032	.045
7-20	1700	.034	.048

TABLE 2. Effect of increasing and decreasing stream flow on drift organisms on August 9. Sunset was at 1935 hours.

Sample Period	Water Temperature (°C)	Water Speed (m/sec)	Organisms (grams)	Number of Organisms Eggs	Aquatic	Terrestrial
1700-1800	20.3 - 20.3	0.45	0.025	0	10	28
1800-1900	20.3 - 20.0	0.53	0.033	0	3	60
1900-2000	20.0 - 19.4	0.50	0.085	0	6	92
2000-2100	19.4 - 19.1	0.47	0.268	57	72	118

TABLE 3. Effect on drift organisms by altering the water velocity. August 12.

Sample Period	Water Velocity (m/sec)	Organisms (grams)	Number of Organisms		
			Eggs	Aquatic	Terrestrial
1100-1200	0.43	0.074	0	10	20
1200-1300	0.76	0.101	0	82	33
1300-1400	0.83	0.088	0	30	31
1400-1500	0.84	0.079	--	----	----
1500-1600	0.81	0.060	--	----	----
1600-1700	0.76	0.048	2	16	17
1700-1800	0.34	0.009	0	5	4

crease in number and weight of organisms was observed, 39 and 282 percent respectively. The greatest proportion of this increase was noted in aquatic chironomids (immatures: from one to 49) and crane flies (immatures: from six to 18), whereas the number of terrestrial organisms only increased from 20 to 33, a 65 percent change which represents an increase proportional to the increase in stream velocity. However, after this initial surge, the numbers and weight of organisms returned to or below pretreatment (1200 hours) levels. By reducing the water velocity at 1700 hours a further decrease in the number of organisms was observed in the sample. In this case, a correlation existed between water velocity and weight of organisms ($R^2 = .41$). A negative correlation was found between water temperature and weight of organisms ($R^2 = .53$). This correlation is opposite to the positive one found for August 9.

The final experiment consisted of a 24-hour sampling period at Stations I and II (Fig. 1-B). Results from these samples were very striking (Fig. 2). There was an explosive increase in the amount of drift organisms approximately one-half hour after sunset (sunset was defined as the time the sun completely disappeared from view behind the Sierra crest) for both sample stations. The majority of drift organisms were aquatic insects although egg masses and terrestrial insects showed some increase at this time. Aquatic insects were the dominant forms through the hours of darkness. At sunrise, there was a sudden drop in the drift of aquatic insects and egg masses.

One sample taken at Station I from 2300 to 2400 hours (Fig. 2) showed a secondary increase, mainly in aquatic insects, which could have been caused by disappearance of the moon (2245 hours), consequently, an almost total reduction light. The sample at Station II did not respond to this change in light. The consı and relatively low level for all three classes from samples at Station II might have b caused by (1) the low and even discharge across the base of the pool, (2) the tuı lent mixing action of the pool and the settling out of some organisms, (3) remc of organisms at Station I, and (4) by fish which inhabited the pool. This p contained a mixed population of brook trout (*Salvelinus fontinalis*) and raint trout (*Salmo gairdneri*). These fish were observed to be feeding during the ni at a position in the pool where the sawdust had been observed to roll and tumble

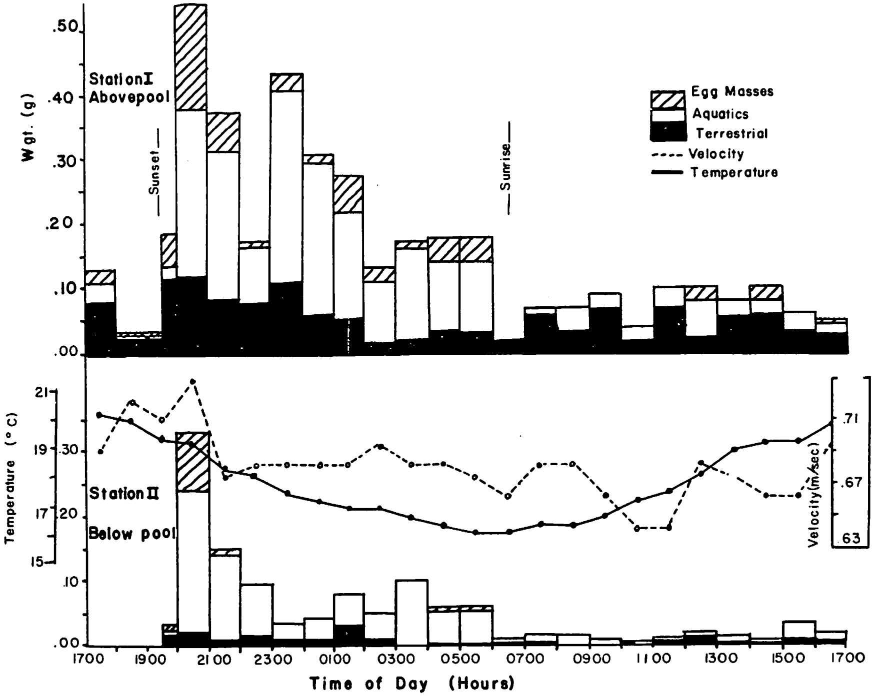

Figure 2. Time course for drift samples from Stations I and II (Fig. 1-B), water temperature, and velocity on August 18 and 19, 1966 at Convict Creek.

Throughout the daylight hours, the drift of terrestrial and aquatic insects remai at a low level while egg masses were collected in only a few samples. There wa decrease of chironomids (adults) in the samples after 2100 hours and a correspond increase of the mayfly (immatures). At sunrise, the presence of mayflies was c siderably less than during the night. Caddisflies (Trichoptera: *Rhyacophilidae* *Limnophilidae*: immatures) and beetles (Coleoptera: *Elmidae*: immatures) were more prevalent during conditions of darkness.

Over the 24-hour period, a total of 1755 organisms was counted from the th classes for all samples taken at Station I, and only 912 organisms from Station II. all 48 samples, aquatic insects comprised 68.1 percent of the total collected, terrest insects 25.0, and egg masses 6.9.

Discussion and Conclusions

Aquatic and terrestrial organisms appeared to be principally "night" active in Con Creek. Jenkins (1969) observed a similar pattern from another section of Con Creek on August 12 and 13, 1966. Aquatic mayflies and both aquatic and terrest chironomids and crane flies were the organisms that showed the greatest respo during the period of sunset. Similar results were noted by Pearson and Frank (1968) and by Anderson and Lehmkuhl (1968).

Reduction in light intensity (Tables 1, 2 and Fig. 2) had a dramatic effect both the numbers and weight of organisms sampled. Possibly the activity of aqua organisms was even sensitive to changes in moonlight (2300 to 2400 hour samp Fig. 2). Hughes (1966) and Elliott (1967) maintain that the absence of light cau disorientation of many aquatic organisms, hence their potential to drift, and theref a passive rather than an active response. In contrast, Holt and Waters (1967) demc strated a negative photoactic response in certain "night" active organisms.

An increase in water velocity in the stream section increased the terrestrial dr This appeared to be proportional to the increased flow through the sampler (Tables and 3). However, an extreme increase in stream flow resulted in an appreciable incre in aquatic insects (Table 3). The number of these aquatic insects decreased rapi in the second hour following this increase in water velocity (1300 to 1400 hou Table 3), while the number of terrestrial insects remained constant. This type of dr pattern probably is included in Waters' (1965) definition of "catastrophic" dri In the absence of abnormal fluctuations in water velocity, the weight of drift organis was not correlated with diurnal changes in stream velocity caused by repeated thawi and freezing of upper elevation snow. Similarly, water temperature did not appe to influence drift except perhaps between 1700 and 2100 hours (Table 2). This is evidently a correlative rather than a causative relationship. The absence or presence of light was the dominant factor controlling the magnitude of aquatic drift organisms.

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Literature Cited

Anderson, N. H., and D. M. Lehmkuhl. 1968. Catastrophic drift of insects in woodland stream. Ecology 49: 198-206.
Elliott, J. M. 1967. Invertebrate drift in a Dartmoor stream. Arch. Hydrobiol. 63: 202-237.
Holt, C. S., and T. F. Waters. 1967. Effect of light intensity on the drift of stream invertebrates. Ecology 48: 225-234.
Hughes, D. A. 1966. The role of responses to light in the selection and maintenance of microhabitat by the nymphs of two species of mayfly. Anim. Behav. 14: 17-33.
Jenkins, T. M., Jr. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim. Beh. Monogr. 2: 57-123.
Kennedy, H. D. 1955. Colonization of a previously barren stream section by aquatic invertebrates and trout. Progressive Fish Culturist 17: 119-122.
————. 1967. Seasonal Abundance of Aquatic Invertebrates and Their Utilization by Hatchery-Reared Rainbow Trout. U.S. Bureau of Sport Fisheries and Wildlife. Tech. Paper No. 12. 41 pp.
Maciolek, J. A., and P. R. Needham. 1952. Ecological effects of winter conditions on trout and trout foods in Convict Creek, California. Trans. Am. Fish. Soc. 81: 202-217.
Miller, K. 1966. Die Tagesperiodik von Fliesswasserorganismen. Z. Morph. Ökol. Tiere 56: 93-142.
Pearson, W. D., and D. R. Franklin. 1968. Some factors affecting drift rates of Baetis and Simulidae in a large river. Ecology 49: 75-81.
Reimers, N., J. Maciolek, and E. P. Pister. 1955. Limnological study of the lakes in Convict Creek Basin, Mono County, California. U.S. Fish and Wildlife Service, Fishery Bulletin 56: 437-503.
Tanaka, H. 1960. On the daily change of the drifting of benthic animals in stream, especially on the types of daily change observed in taxonomic groups of insects. Bull. Freshwater Fisheries Res. Lab., Fisheries Agency Tokyo 9: 13-24.
Waters, T. F. 1962. Diurnal periodicity in the drift of stream invertebrates. Ecology 43: 316-320.
————. 1965. Interpretation of invertebrate drift in streams. Ecology 46: 327-334.

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Comparative Food Habits of Four Species of Stream-Dwelli Vertebrates (Dicamptodon ensatus, D. copei, Cottus tenuis, Salmo gairdneri)

When two or more species occupy the same habitat and have the same requireme
for food and space, supposedly limited in supply, then these species are in di
competition. Ultimately, the least adapted species may be excluded from the c
petitive arena. This is a simplification of Gause's Principle (1934) or Hard
"competitive exclusion principle" which states that complete competitors cannot occu
the same niche (Smith, 1966). If the niches (niche is defined here as the residen
and nutritional requirements of an organism) only partially overlap, then the organis
involved may coexist, and often behavior mechanisms serve to establish partial exc
sion. For example, MacArthur (1958) found that several species of warblers w
similar food habits were able to coexist in the same wood by a combination of ad
tations including partitioning of the forest canopy and selective feeding by at le
one species.

Four species of cold-blooded vertebrates often occur together in northweste
streams. These are: *Dicamptodon ensatus* (Pacific giant salamander), *Dicamptod*
copei (Cope's salamander), *Cottus tenuis* (slender sculpin), and *Salmo gairdn*
(rainbow trout). Only the branchiate, larval forms of the two salamanders are
interest in this study.

Casual observations suggested that the habitats of these four species were simil
especially among smaller individuals. Individuals of all species take cover und
rocks and logs and in crevices, and often individuals of two or more of the speci
can be found sharing the same hiding place. In light of these observations, it w
thought that a comparative study of the food habits of these four species within
single section of a stream would help to reveal the role that each of the species h
in the stream community, and that possible exclusion mechanisms might be foun

The food of *S. gairdneri* is generally known through a widely scattered literatur
Bailey's (1952) study of the food of *Cottus bairdi* suggests that freshwater cotti
are largely opportunistic feeders, although he gave no information on availabilit