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THE NON-PHENOMENON OF STREAM DRIFT

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JES

Abstract

A comparison was made between insects found in the water column and those found in the different areas of the stream substrate. The substrate may be divided into different habitats according to the speed of the current over it. The current will usually pick up animals in an area with fast current, and dump them in a slow area, so the drifting animal is carried from one habitat to another. Sampling the insects in the substrate of the different habitats, and those found in the current, revealed that the insects most likely to be found drifting are those living in the largest number of substrate habitats.

Drift can be explained in evolutionary terms; those whose specific habitats would be lost if they drifted, have evolved so they are almost never washed downstream. Those to whom drifting is not such a disaster, insofar as they will be all right when deposited, drift to a small extent. Drifting will harm them too, as they are more likely to be preyed on in the current, and it is time wasted. These two factors keep the drift rates small for everything.

Since the microhabitats are not constant in one general habitat, the results do not indicate anything about the microhabitat of the insects that do, or don't, drift. Either the drifting animals are flexible in microhabitat choice, or their microhabitat can be found in a variety of different currents.

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Relatively little is known about the ecology of streams. Limnologists have studied lakes, much more extensively, though streams are the more permanent geological habitat. (Hynes 1970) As a result any new phenomenon observed in streams is eagerly examined as possibly elucidating a new principle by which streams may be understood. Such a phenomenon is the drift downstream of benthic stream invertebrates, primarily insect immatures.

Drift has been demonstrated by many workers (Anderson 1967, Bailey 1966, Elliott 1968, Minshal & Winger 1968, Waters 1968). Elliott(1967) did not find any increase in drift with spate conditions of increased water flow in the stream. In general, however other workers did find increased drift during spates (Waters 1972). This drift, termed catastrophic drift, is considered quite different from the behavioral drift which occurs all the time, with lows during the winter, and during daylight hours. Waters (1961) noted that there was very little drift in the winter. Most workers who reported the existence of drift reported that it occurred after dark, with peaks just after dusk and just before dawn (Waters 1962, Anderson, 1967, Elliott 1965).

It seems logical that animals living in the stream bottom continually subject to the current would occasionally get swept away by it. In fact it is remarkable that the animals in the stream bottom can stay there at all. However the situation is not quite as simple as it might seem. Ambühl (1959) illustrated that there exists a boundary layer of water that is turbulent but without current. This layer, which is right at the bottom of the stream on the rocks, is thick enough so that animals might be completely protected from current action by it. It is several millimeters thick almost everywhere, with even bigger protected areas behind rocks and along the banks of the stream. Steinmann (in Hynes 1970) lists adaptations which stream dwellers exhibit. Some are for clinging and staying in one place in spite of the current, some are to squirm down between the rocks to get away from the current, and some are flattening, which has variously been interpreted as for staying within the boundary layer on top of rocks, or for sliding inbetween them. It could be for both, since there are animals, especially those that drift, that are hidden from light during the day, and then come out to the tops of rocks at night. Since an ecologically important boundary layer does exist the evolutionary adaptations of animals to the current would be in terms of the boundary layer.

Animals living in the bottoms of streams are adapted to stay there. The existence of a boundary layer of currentless water makes conditions less stringent than it would seem at first. So why does drift occur at all? A certain amount of drift can be accounted for by the inability of less fit animals to avoid being carried off by the current. But the number of animals caught in drift nets were thought too great to be accidental behavior of a minority of individuals. Waters (1966) compared the number of individuals caught in a drift net to a square foot bottom sample taken under the net. (The sampler was a Surber sampler.) He found that there were far more insects in the drift net than in the square foot sample. From this he concluded that there were far more insects drifting than could be attributed to the physical action of the current. He thought it must be a behavioral response to something.

Elliott did not agree with Waters. (Elliott 1968) He compared the amount of drifters to the volume of water that passed through the net. When looked at this way relatively few animals are drifting at any one time. The highest percentage of animals found in the water column was at night when 0.11% of the bottom fauna were calculated to be in the water column. Though this is a large number of individuals, it indicates that drifting is a minor event in the general population of benthic insects. Yet the number of drifters is high enough to indicate that drifting is not a severely detrimental thing to happen to an insect. If it were those insects that never drifted, and were best adapted to never be disturbed into the current would be the ones whose reproduction would be greatest. Their hold-fast traits would be passed on to future generations. Then now, after much evolution, there would be very little drift. This is not the case. Apparently drifting is not all that detrimental to the individual since a significant amount of drift occurs. It could be that under certain conditions animals actively detach themselves and drift, or it could be that drift is the accidental result of separate behavior. Since it is not that terrible of a thing to happen to an insect as far as survival goes, it would not be especially avoided if other behavior was desirable that might result in drift. Desirable is meant in terms as the best thing that the animal can do as far as the passing his genes on to the largest number of superior offspring. So drift could be an indication of other behavior.

It is in this context that drift could reveal principles relating animal behavior to varied conditions in streams. The daily pattern of drift was the first clue that drift is an indicator of something. From there it remained to find out what. Drift samples could be examined to see if there is any homogeneity to what drifts. It was found that certain animals are more likely to be found in drift samples than others (Hynes 1970, Elliott 1967 and others). Full-grown nymphs were most likely to be found in drift nets, though other stages were found (Elliott 1967). Most insects found in the benthos were also found to drift, though some were more frequently found in drift than others in a way that varied independently of the frequency of the animal in the benthos (Elliott 1967).

That the full-grown nymphs are most often found in drift nets can be explained by their size. Since they are the largest animals they will have the hardest time staying in the boundary layer. The daily rhythm and differential frequency of drifters can be explained either by concluding that some animals actively drift at certain times, or that some other behavior of certain animals makes them suseptible to drift. There must also be some as yet unrevealed reason why this behavior takes place mainly after dusk and before dawn. Many stream insects are negatively phototropic (Chaston 1967, Hynes 1970, Elliott 1967). They come out of the crevices at night to feed either on algae growing on sun-exposed rocks, or on the animals that feed there. So it could be that just after dusk and just before dawn is the time that the insects are making the biggest move. Not only will they be moving around more then, but they will have to be adapting to new current conditions. Perhaps it takes them some time to adjust to holding on more tightly, or crouching lower to avoid the current or resist it. This is a logical explanation for drift; others have been proposed that look at it in terms of the entire stream instead of individual behavior.

One of the first explanations of drift was that it was part of a colonization cycle. (Müller in Elliott 1967) More eggs would be laid upstream; then as it got crowded enough insects would drift downstream to evenly populate the stream. Elliott (1967) did tests which would seem to disprove this hypothesis. He took Surber samples at several places along a stream over a year and found that the upper areas were in no way depopulated as the season wore on. For Müller's hypothesis to hold there would have to be large numbers of animals drifting to distribute upstream insects. Elliott did not observe this. A further condition necessary for colonization is the upstream migration of adults. The evidence of this is not even worth mentioning for it is statements such as twenty adult mayflies observed heading upstream. Elliott (1967) found no pattern of upstream migration in mayflies. He concluded that any that is observed could be due to the wind patterns in that particular river valley; it is not anything that is significant. So the colonization theory of drift must be discarded.

Waters (1966) hypothesized a correlation between drift and productivity of the stream. He thought that drift increases when the stream bottom becomes crowded. The mechanism by which this happens could be either a voluntary launching into the current, or a jostling crowd in which some members were knocked off into the current by others. Whichever explanation held, drift would indicate dense bottom fauna. This would be an easy way to compare the productivity of different streams. But, once again, Elliott's findings disagreed with those of Waters. He found no relation between bottom density and drift density. (Elliot 1967) He suggested that this would always be the case if drift samples were correlated with the amount of water that flowed through the net. Looked at in this way the percentage of drifting animals is so low that the number of drifters would not be a sensitive enough figure to reflect what was happening in the entire benthic population.

It is important to know exactly how far a drifting animal drifts once he is caught by the current, for if the distance is not great, then coupled with the knowledge of how few animals drift at any one time, drift could be considered a relatively unimportant phenomenon. It could be that drift studies will elucidate no new principles in stream biology. Drift could be only an interesting, but minor happening in stream ecology, something curious yet expected by any amateur first considering the stream habitat. Using a series of successive drift nets Waters found drift greatly reduced far downstream from the first nets. He concluded that insects drift around 50-60 meters a night. (Waters 1965) This is far shorter than the length of most streams, so animals would have to drift repeatedly to colonize downstream. This points to a far larger percentage of benthic animals drifting than is in fact the case. If on considers that for recolonization 50% of the population (supposedly concentrated upstream) must drift <u>at least</u> 60 meters, then at present drift percentages per night this drift would take 454 nights. That is longer than the entire life cycle of most drifters.

Sixty meters is probably close to the distance from one slight bend in the stream to another. Or, if there are no bends it could well be considered the distance in which most of the water that was the fastest moving has come into contact with slower water. This distance does support the hypothesis that drift is a happening of no great import; that it is a minor consequence of other things which might be more interesting to study.

So far it seems as if most of the evidence supports a non-theoretical interpretation of drift. But there was one study done by Minshal and Winger (1968) that made drift look alot more important. They studied drift in a small stream that was undergoing flow reduction (artificially controlled). They found that the slower the water flowed,, and the less water there was in the stream the greater were the numbers of drifters. This can hardly be accidental drift since it is presumably easier to stay in place when the current is slower. They even reported seeing animals of the genera Baetis and Ephemerella actively launching themselves into the current.

This is an entierely differen t phenomenon from that in normal streams. More work must be done in this situation to explain what is really going on. Minshal and Winger suggested that the drift might be the results of respiratory stress caused by the disruption of diffusion gradients around the animal. This could lead to increased movements and drifting. It has also been observed in general that thigmotaxis is reversed when there is very low current. The animals then swim around on their own. But this one situation is quite outside the general scope of drift covered in this paper.

Any work done on drifting is cursed with the general problems of stream analysis. One of the biggest problems is that of estimating the biomass of the stream bottom. It was found that 73 Surber samples were necessary to get a 95% confidence level as to the biomass of a single riffle (Needham and Usinger 1956). Further studies indicated that perhaps even more samples would be necessary. This indicates a discrepancy between whatpeople see as a uniform area, and what animals percieve as a whole variety of diverse microhabitats. Perhaps the most important work to be done in streams now is to determine what makes animals choose to be where they are. Egglishaw (1964) did an elegant study to see if the aggregation of animals in detritus was due to the presence of the detritus or to the fact that the current and water action acted similiarly on the two. He found that animals actively chose the detritus, and did not aggregate in similiar situations where there were rubber bits instead of detritus.

Cummins (1962 and personal communication) used a technique of photographic analysis to determine what size particle was typical when there was a certain surface appearance. He took a photograph of the area, then collected all of the sediment and correlated a grid of the photograph with the particles. This worked best for the surface rocks and least well for the sands all the way under. This technique could be used in conjunction with collecting all the animals in the area to perhaps get a corelation between the appearance of a square and what might be found there. But it is probable that this would be only the roughest sort of indicator for a photograph of the bottom will probably not show anything that the animals are responding to very directly. Nonetheless it is in this sort of work that stream knowledge will be advanced; present information on the non-phenomenon of drift indicate that future work on drift will not be worth the time and effort when there are so many more important things to be studied that are more likely to reveal something important.

Introduction

When an insect drifts it moves with the current. Its own motions are insignificant, so it will leave the current only when it is thrown into an area without a strong current. Such areas are found along the very bottom of the stream, along the sides where plants drag in the water, and in the eddies and back washes that result from bends and indentations in the shore. How much of the water that flows down a stream is involved in these currentless areas? Are they stagnant areas that keep the same water for a long time, or are they continually interacting with the mainstream? The more water that is involved in these areas the more frequent will be the dumping of an insect from the current.

Drift can be better understood if it is known precisely what factors operate on the drifting animal. The study of the motion of water downstream will give a good indication of how far an insect will drift once he is caught by the current. The study of a riverbend was undertaken because it seemed that in a bend there was the most turbulence, and the resultant high level of interaction between still water and water moving straight downstream.

If an animal is carried into the current where it is the fastest and dumped where it is the slowest, it is likely that the two places will be different. An examination of the streambed divided it into five rough habitat types, ranging from the slowest to the fastest currents. (Table A) It was hypothesized that those animals most likely to drift would be those found in the greatest number of habitats. Animals that were only found in one or two

Table A

Characteristics of Four Maple River Habitats

	Depth	Current Speed	Substrate size (largest particle)
Fast Riffle	1 ft	10*	4"-6" diameter
Run	2-4 ft	7	2"-4" diameter
Riffle	1-2 ft	5	1"-2" diameter
Detritus	0-1.5 ft	0-2	silt

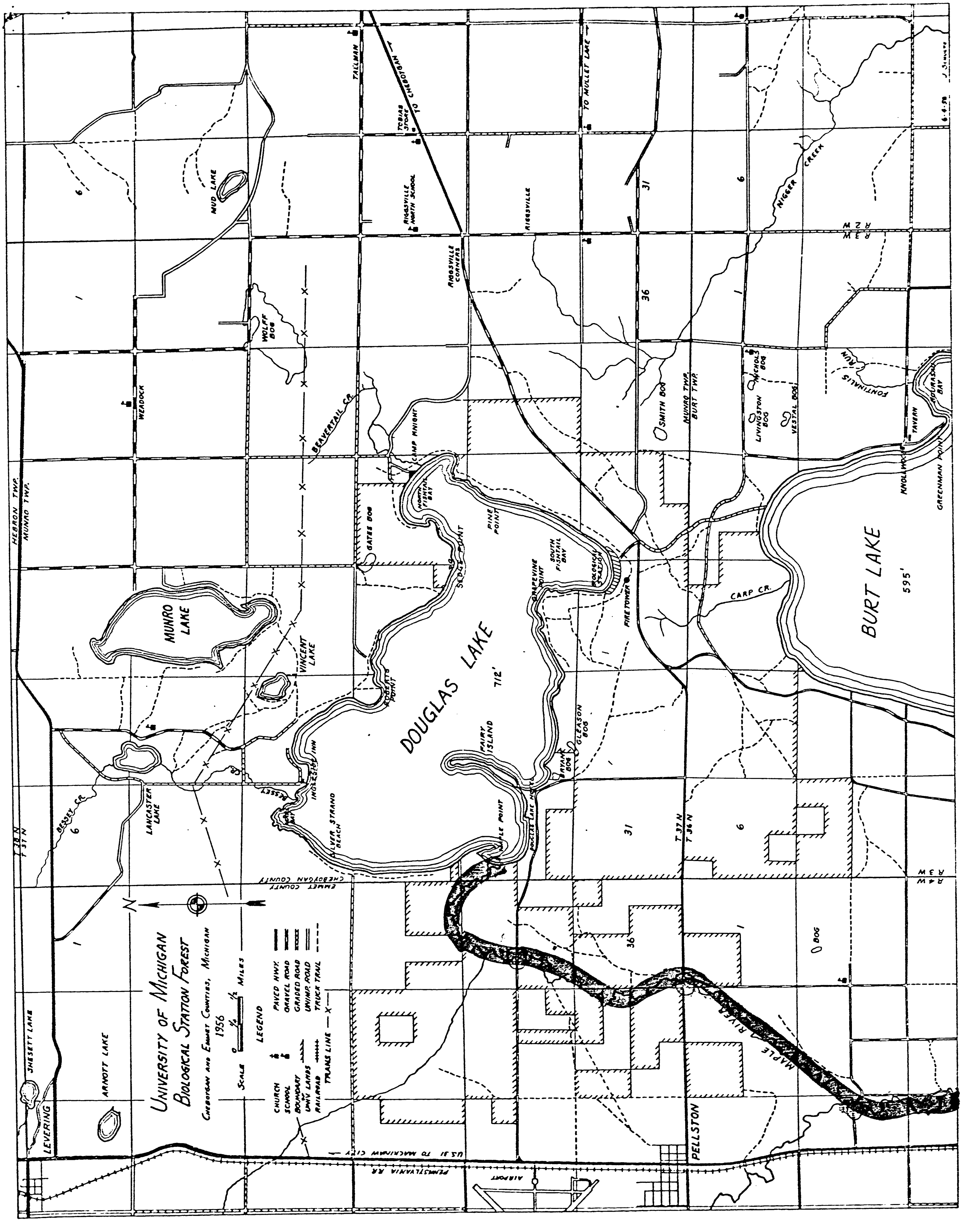
*current speed numbers are only in relation to one another habitats would either not be in the area most suseptible to the current, or would not be able to live in the deposition area. If they are not able to live in the habitat they are deposited in, they would have to crawl along the bottom to a better habitat without getting caught in the current again. They will very likely get caught in the current again since it happened once. Drifting would have an adverse effect on their survival possibly divorcing them from a habitat they can exist in, so there would be a selective pressure against drifting. Those animals adapted to stay where they were would contribute more genes to future populations.

Animals were collected from the five habitats and their distribution compared to test this hypothesis. Special attention was given to animals found to drift. The five habitats in order of decreasing current were fast riffle,run, riffle, sand, and detritus. Sand was eliminated because no animals were found there. Since a streambed is known to be composed of a whole series of microhabitats that vary every few centimeters, or from one side of a rock to another, one habitat includes many microenvironments. Likewise one specific microhabitat recognized by the insect could occur in more than one habitat. This will be reflected in the finding of one insect in several different habitats. It also means that perhaps the insects that drift are not necessarily more flexible in their environmental needs, but that their microhabitat is ubiquitous, or independent of current. This must be remembered, but will not effect the conclusions of the study because it still means that those insects will be most likely to drift. It only means that it cannot be assumed that it is they that are flexible in their environmental requirements.

Maple River, located in Emmet County, Michigan, (Fig. A) has two main branches. All of the work was done on the East Branch, which is the smaller and faster of the two. The first location, at Douglas Lake Road, is about a mile and a half from the exit of the river from Douglas Lake. The Riggsville Road location is another mile downstream. The Woodlawn Road location is about a mile and a half further downstream. That location was used only for the category fast riffle. A fast riffle did not occur elsewhere, but all three other habitats occurred at both of the other locations.

The East Branch of the Maple River is a fine trout stream. (All future references to the Maple River are to be understood as referring to the East Branch.) The bottom is alternately sandy, cobbled or rocky. There are wide, slower stretches with sandy bottoms, deep rocky curves around bends, and dark pools over five feet deep. Dead winter grasses drag in the stream along some of the bank. Along the edges are thickets of Cornus stolonifera, Salix sp. and Alnus rubra. These sometimes lean far out over the water, or fall in. Dead leaves and twigs collect against the fallen branches. At Douglas Lake Road Maple River passes through higher land with an open grove of Populus tremuloides. Below

Figure A


University of Michigan
Biological Station Forest
Cheboygan and Emmet Counties, Michigan
1956
Scale 0 ½ 1 Miles
Legend
Church
School
Boundary
Univ. Lands
Railroad
Trans Line
Paved Hwy.
Gravel Road
Graded Road
Unimp. Road
Truck Trail
N
DOUGLAS LAKE
712'
BURT LAKE
595'
MUNRO LAKE
VINCENT LAKE
LANCASTER LAKE
MUD LAKE
ARNOTT LAKE
SHESETT LAKE
LEVERING
PELLSTON
TALLMAN
TOBIAS STORE
TO CHEBOYGAN
TO MULLET LAKE
RIGGSVILLE
RIGGSVILLE NORTH SCHOOL
RIGGSVILLE CORNERS
WEADOCK
WOLFF BOG
BEAVERTAIL CR.
CAMP KNIGHT
NORTH FISHTAIL BAY
GATES BOG
SEDGE POINT
PINE POINT
SOUTH FISHTAIL BAY
GRAPEVINE POINT
BIOLOGICAL STATION
FIRETOWER
ROBERTS POINT
FAIRY ISLAND
GLEASON BOG
BRYANT BOG
DOUGLAS LAKE HOTEL
MAPLE POINT
INGLESIDE INN
BESSEY
BESSEY CR.
SILVER STRAND BEACH
SMITH BOG
MUNRO TWP.
BURT TWP.
NICHOLS BOG
LIVINGSTON BOG
VESTAL BOG
FONTINALIS RUN
NIGGER CREEK
TAVERN
KNOLLWOOD
GREENMAN POINT
MONRADNOCK BAY
CARP CR.
MAPLE RIVER
BOG
HEBRON TWP.
MUNRO TWP.
CHEBOYGAN COUNTY
EMMET COUNTY
T 38 N
T 37 N
T 37 N
T 36 N
R 3 W
R 2 W
R 4 W
R 3 W
US 31 TO MACKINAW CITY
PENNSYLVANIA RR
AIRPORT
6
1
6
1
31
36
6
1
31
36
6
1
J. Stouffer
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Woodlawn Road *Tsuga canadensis* shadows the river.

The character of the stream is uniform until the dam at Woodlawn Road swells it into a reservoir. The fast riffle below the dam is not found elsewhere. The presence of the dam probably had an effect on the river downstream but it was not considered to effect the present study. Numbers of organism were not counted, only kinds, which is something that the dam would not have an effect on. The fast current is probably the determining factor in species composition below the dam.

Most of the field work was done the second two weeks in March, 1973, though some work was done the third week in January, and the third week in April. During the two weeks in March the stream rose by nearly a foot. This flooding directed the course of field work, making some things impossible to do while at the same time providing unique opportunities to study drift into newly submerged areas. One islet, suberged after the first three days of March field work, was especially studied because all the approaches to it were sandy smooth. This made it unlikely that any insects had approached the area except by drifting. In fact, because of a failure of the drift nets, the insects found on the islet were considered to be those that drifted.

Procedure

Water sampling and collecting were done at three locations, where Maple River crosses Douglas Lake Road, Riggsville Road, and Woodlawn Rd. Currents were studied only at a bend near Douglas Lake Road.

Dissolved oxygen in the water was determined by the Alsterberg (Azide) midification of the Winkler method. Alkalinity was determined using a Bromocresole-Methyl Red mixed indicator test. pH was calculated on a Beckman pH meter. (Table 1)

Sampling of the stream bottom for particle size analysis was accomplished by forcing an eighteen cm diameter stovepipe ten cm into the stream bottom. The stones around it were cleared and a shovel put under the stovepipe so the contents could be emptied into a bucket. The bottom materials were then dried and weighed. Cobbles and pebbles were removed and the remaining material was put through seives from two tenths of a centimeter to fifty-three microns. Percentages of the total weight were then calculated. (McCormick 1973, unpublished)

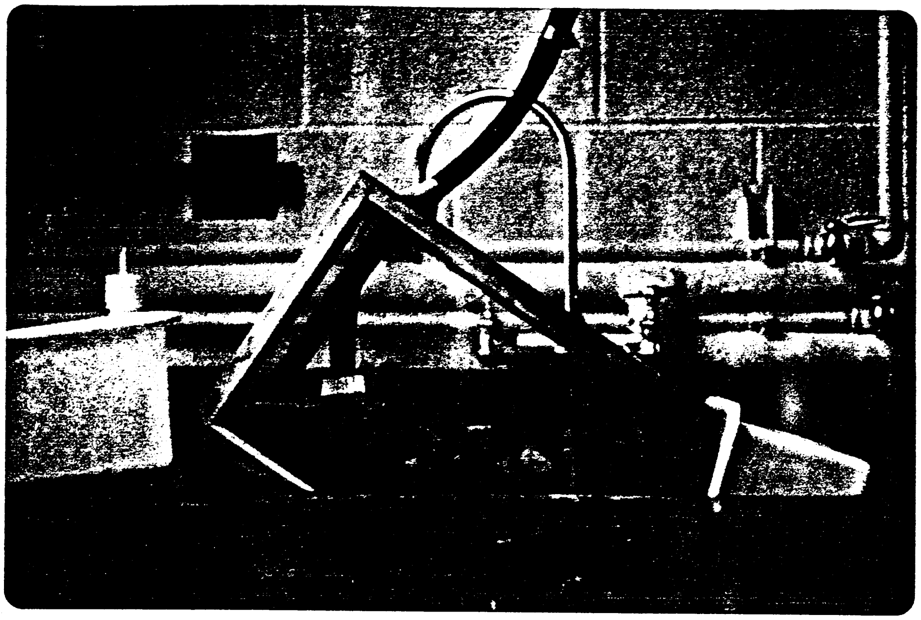
The methods of collecting varied from one habitat to another. In the riffle and the run a hand-screen was held downstream and the upstream substrate was kicked up. Any animals dislodged were caught in the screen. The screen contents were dumped into a white enamel pan so that the insects could be sorted through and picked out. Detritus areas were sampled with a net on the end of a pole that scooped up substrate and water. Sorting was done in an enamel pan. This sort of net was used in the fast riffle too. Both techniques were used to sample the flooded islet. An area that was smooth sandy bottom was sampled by both methods but nothing was found so that habitat was eliminated from the study. Since nothing was found there it was considered to be outside the choice of possible habitats.

Fluorescene dye colors everything it touches bright green. A capful of the powder was diluted with a bucket of water. Then a cup of the dye was thrown across the stream. The progress of this green line was watched as it moved downstream. It was recorded by running downstream and taking photographs. The currents in slow shore-clinging waters were tested by putting about a tablespoon of dye in the water.

The currents were observed and photographed from both sides of the stream. The dye was put in again and again until a good diagram of the currents could be drawn.

Movement

Figure 10



Artificial stream. A piece of glass fitted in the aquarium is the false bottom. Lake water comes from the red tubing and surges into the reservoir at the left. The water overflows into the stream, providing a uniform current.

of the current around individual rocks was observed by putting dye in an artificial stream set up in an aquarium in the laboratory. (Fig. 10) The currents around the rocks were observed and photographed.

Insects were identified by the author to genus except in the cases where the possible error in carrying identification that far was great. In those cases identification was taken only to family.

Results

The water chemistry and substrate composition at the three locations was rather uniform. The fast riffle at Woodlawn road contained a little more oxygen, explained by the great turbulence. But as with most streams oxygen was high enough in all three cases that the difference would probably not effect any organisms. (Table 1) The sampling station at Douglas Lake Road was in a run, that at Riggsville Road a riffle, and that at Woodlawn road a fast riffle. Any difference between the three habitats is probably not due to water chemistry. The substrate sample at Woodlawn Road contained less of the very fine particles than did the other two. This could possibly have an effect on organisms but even these differences are small enough so that another explanation must be looked for if animal population differences are found.

Thirty-seven different insects were distinguished in the sampling. (Table 2) Most of these were found in some abundance, but a few are represented by only one specimen. *Acroneuria*, *ParaLeptophlebia*, *Aeschna*, *Rhyacophila*,

Table 1

Oxygen Concentration

Location	Temp. °C	mg/1	D.O. mg/1 x 2	Percent Saturation
Douglas Lk. Road	1°	6.50	13.00	95%
Riggsville Road	1°	6.68	13.36	96.5%
Woodlawn Road	2°	6.80	13.60	99%

pH, Alkalinity, CO_2

Location	pH	Alkalinity(mg/1$CaCO_3$)	CO_2
Douglas Lake Road	7.8	126.8	3.0ppm
Riggsville Road	8.0	127.2	1.9ppm
Woodlawn Road	7.8	111.8	2.4ppm

Composition of Streambed

Size(Diameter)	Percent of Douglas Lake Rd. Sample	Percent of Riggsville Rd. Sample	Percent of Woodlawn Rd. Sample
cobble $\geq$ 6.4cm		31	17
pebbles $\geq$ 0.4cm	45	53	61
granules $\geq$ 0.2cm	15	6	16
v. coarse sand 0.1cm	5	2	2
coarse sand 500μ	11	3	2
med. sand 250μ	14	4	3
fine sand 105μ	3	0.3	$<$0.1
v. fine sand 53μ	0.6	0.3	$<$0.1
silt 53μ	1	0.4	$<$0.1

All of the above data was taken the third week of January 1973. Most of the calculations were done by Tom McCormick who was working on a concurrent project on Maple River at the time. January field work was done with Tom McCormick and Chris Muhich.

Table 2

Insect Immatures found in Maple River Jan.-April

- Plecoptera
  - Perlidae
    - *Acroneuria*
    - *Paragnetina*
    - *Phasganophora*
  - Taeniopterigidae
    - *Taeniopteryx*
  - Isoperlidae
    - *Isoperla*

- Ephemeroptera
  - Heptageniidae
    - *Stenonema*, *Epeorus*
  - Baetidae
    - *Baetis*
  - Leptophlebiidae
    - *Leptophlebia*
    - *Paraleptophlebia*
  - Baetiscidae
    - *Baetisca*

- Trichoptera
  - Limnephilidae
    - *Pycnopsyche*
    - *Neophylax*
    - *Platycentropus*
  - Hydropsychidae
    - *Hydropsyche*
    - *Cheumatopsyche*
  - Philopotamidae
    - *Chimarra*
  - Rhyacophilidae
    - *Rhyacophila*
  - Helicopsychidae
    - *Helicopsyche*
  - Glossosomatidae
    - *Glossosoma*
  - Phryganeidae
    - *Ptilostomis*

- Odonata
  - Aeschnidae
    - *Boyeria*
    - *Aeschna*
  - Calopterygidae
    - *Calopteryx*
  - Gomphidae
    - *Ophiogomphus*

- Diptera
  - Rhagionidae
  - Chironomidae
  - Tipulidae
    - *Tipula*
    - *Pedicia*
  - Simuliidae
  - Tabanidae

- Hemiptera
  - Corixidae*

- Coleoptera
  - Gyrinidae*
  - Dytiscidae*
  - Elmidae*

- Megaloptera
  - Sialidae
    - *Sialis*
  - Corydalidae
    - *Nigronia*

* adults

and Sialis are all represented by only one specimen. Either they are not abundant in Maple River, or there was something about the sampling techniques used that missed them. It is certainly possible that there were other insects that are in Maple River during the winter that were missed because they are very rare, or because they are so small they passed right through the net. The ten hours (approximately) spent collecting on Maple River are considered adequate to collect almost all of the insects occurring in the river (Dave Otte personal communication).

Table 3 shows the distribution of the insects collected in Maple River. The fast riffle had far the fewest insects but the ones that it did have generally occurred in several different places; they seemed to be able to live about anywhere, or at least to find their microhabitat in all of the general habitats. The one exception to that is the detritus habitat, where only two fast riffle dwellers were found. Perhaps the slow current in the riffle area doesn't provide enough oxygen, or not enough volume of water passes over the filter feeders that occur in the fast riffle to allow them to live in a stagnant detritus area.

If the number of insects unique to a riffle, a run, or detritus is subtracted from the total number of insects occurring in each place, you get eleven or twelve, a constant. (Table 4) If the same is done with the insects found on the flooded islet the number sixteen is obtained. This is substantially higher than the other differences. It suggests that drift is coming from more

Table 3

Distribution of Insects in Maple River

	Fast Riffle	Riffle	Detritus	Run	Flooded Islet
Plecoptera					
Acroneuria		x			
Paragnetina		x			
Taeniopteryx			x		x
Isoperla		x	x	x	x
Phasganophora		x	x	x	x
Ephemeroptera					
Ephemerella		x	x	x	x
Epeorus	x				
Stenonema			x	x	x
Baetis		x			x
Leptophlebia			x		x
Paraleptophlebia					x
Baetisca			x	x	x
Trichoptera					
Pycnopsyche		x	x	x	x
Cheumatopsyche	x	x	x	x	x
Glossosoma	x	x			
Neophylax		x			
Ptilostomis		x			x
Rhyacophila					x
Platycentropus			x		
Chimarra		x			
Hydropsyche	x	x		x	x
Helicopsyche		x			
Odonata					
Calopteryx			x		
Boyeria			x		x
Aeschna			x		
Ophiogomphus				x	
Diptera					
Rhagionidae	x	x	x		
Chironomidae	x	x		x	x
Tipula		x	x		x
Pedicia		x		x	
Simuliidae	x	x		x	x
Tabanidae			x		
Hemiptera					
Corixidae			x		
Coleoptera					
Elmidae		x			
Gyrinidae			x		
Dytiscidae			x		
Megaloptera					
Nigronia				x	
Sialis				x	

Table 4

Uniqueness of Insect Distribution

Insects occurring everywhere (excluding fast riffle)

1. Isoperla
2. Phasganophora
3. Ephemerella
4. Pycnopsyche
5. Cheumatopsyche

Insects occurring only in riffle

1. Acroneuria
2. Paragnetina
3. Neophylax
4. Chimarra
5. Helicopsyche
6. Elmidae

Insects occurring only in detritus

1. Platycentropus
2. Calopteryx
3. Aeschna
4. Corixidae
5. Tabanidae
6. Gyrinidae
7. Dytiscidae
8. Sialis

Insects occurring only in run

1. Ophiogomphus
2. Nigronia

Insects occurring only in flooded islet

1. Paraleptophlebia

Insects occurring only in fast riffle

1. Epeorus

	Fast Riffle	Riffle	Detritus	Run	Flooded Islet
Total Number	7	17	20	14	18
Number Unique To Each Habitat	1	6	8	2	2
Difference Between Above Numbers	6	11	12	12	16

Table 4 cont.

Uniqueness of Insect Distribution

Insects not at Islet that do occur in more than one other place

1. Glossosoma
2. Platycentropus
3. Rhagionidae
4. Pedicia

Insects not at Islet that occur in only one place

1. Acroneuria
2. Paragnetina
3. Epeorus
4. Neophylax
5. Chimarra
6. Helicopsyche
7. Calopteryx
8. Aeschna
9. Ophiogomphus
10. Tabanidae
11. Corixidae
12. Elmidae
13. Gyrinidae
14. Dytiscidae
15. Nigronia
16. Sialis

Frequency of Insects at Combined Places

Number of Insects	Occurring in number of Habitats
18	1
7	2
4	3
7	4
1	5

Frequency of Insects occurring at Flooded Islet at other locations

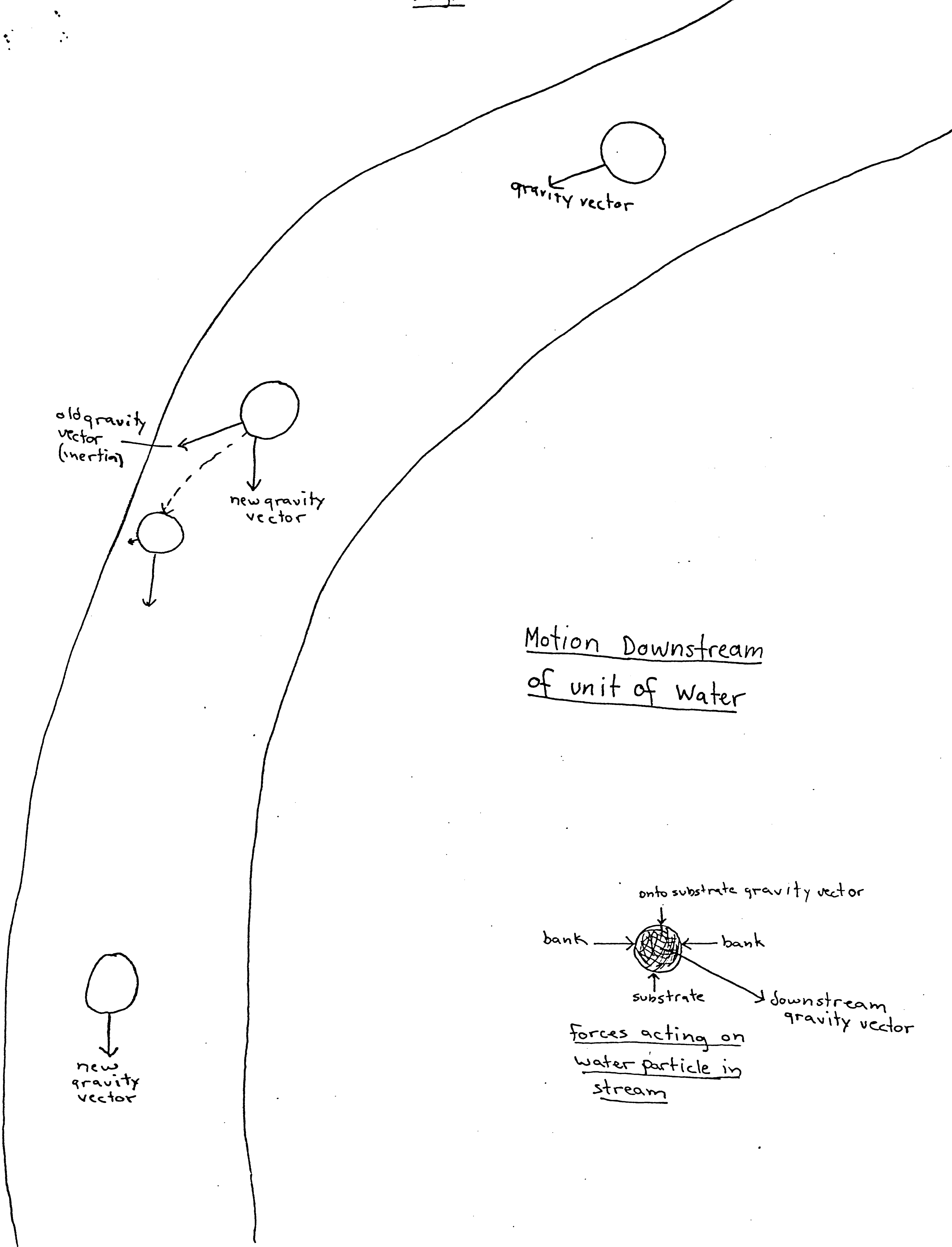
Number of Insects	Occurring in number of Habitats
2	1
5	2
3	3
7	4
1	5

Ratio of Insect number occurring in Flooded Islet and in 0 to 4 other habitats to total number occurring in 1 to 5 habitats. (# in second table over #insects in first table)

2/18=.111
5/7=0.715
3/4= 0.75
7/7= 1.0
1/1= 1.0

than one habitat. In fact only four insects are not found on the islet that do occur in more than one other place. The other sixteen insects not found at the islet are all unique to their respective habitats. (Table 4) This suggests that perhaps animals with greater environmental flexibility (or who can find their microhabitat in a variety of settings) are the ones that are the most likely to drift. This is further substantiated when the progression relating the insects found at the flooded islet to those found in the most other habitats is examined. Only two insects were found only at the flooded islet, and there was only one of each. Since they must have come from somewhere they probably represent insects missed elsewhere. From there the fraction of islet insects occurring in a set number of habitats to the total number occurring in that number of habitats increases. All of the insects that occur in four or five habitats are found at the islet. (Table 4) This could mean that they can live in all the habitats and are prone to drift because there is no selection against insects carried from their original habitat. Or it could merely mean that these insects are drifting because their microhabitat is especially disturbed by currents and they get pulled into the current easily, and are then dumped by the current all over the place. If this is the case, then the specimens collected in various habitats could be there only because of the flood conditions, not because this is their habitat. This second explanation is not as likely because of the great numbers of benthic insects. Those just dumped in area would

be a very small fraction of the total

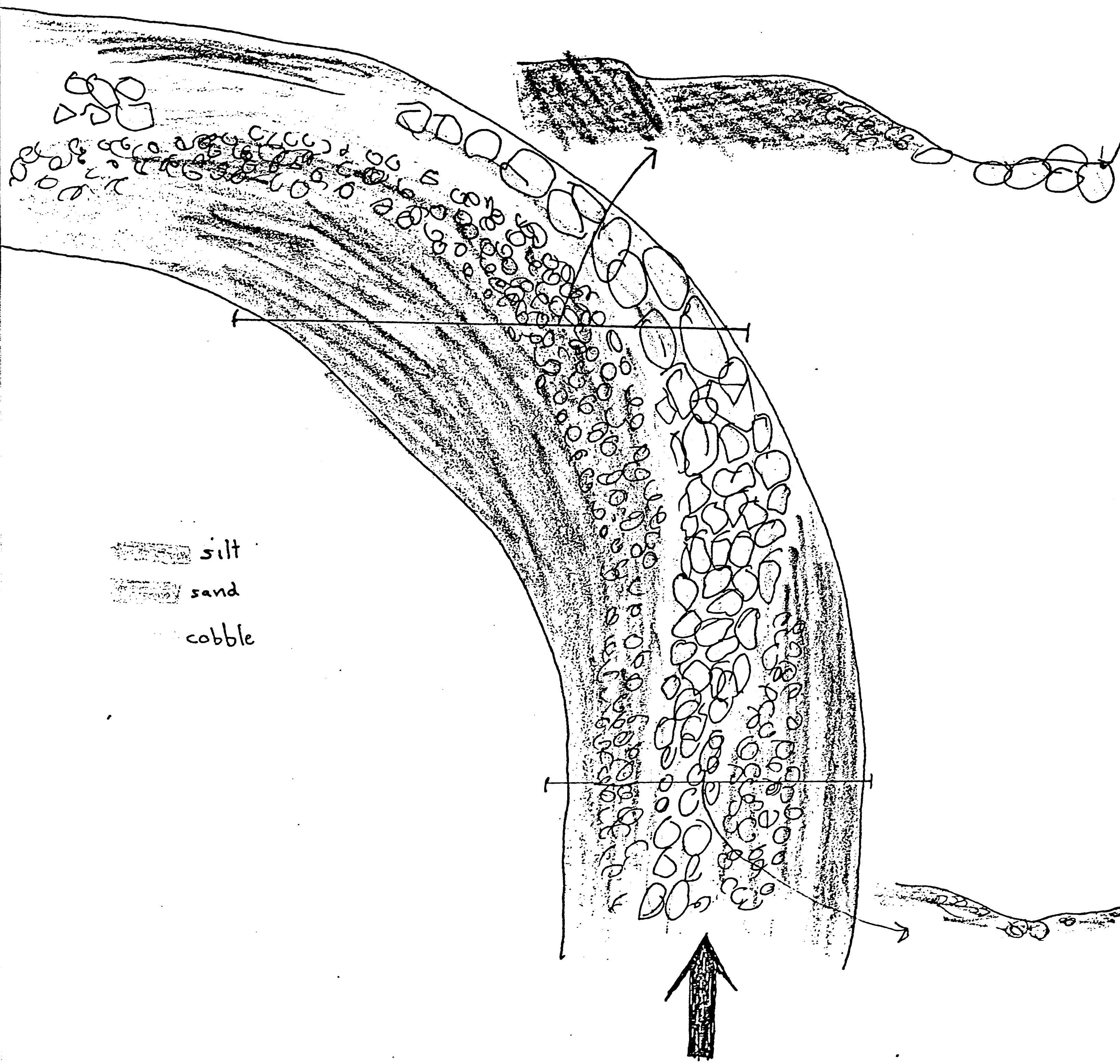


Motion Downstream of unit of Water

forces acting on water particle in stream

Figure 2

Diagram of a Bend in Maple River



insects found there. Therefore it would be unlikely that they would be uniformly collected to such a degree that the above-discussed progression would be apparent.

The path that water takes flowing downstream is a straight line wherever possible. So the general picture of the flow around a bend is that all the water smashes into the outer bank, careens along the far outer edge, then slowly regains the center channel. This motion represents a change indirection for most of the water, for the direction downhill has changed slightly. While in the bend there are two unbalanced forces acting on the water: the new downstream gravity vector, and the inertia from the old gravity vector. The path of the water will be somewhere between the two. (Fig. 1) The change in direction of each water particle means that they will jostle each other more than when they are all going in one direction. This will result in added turbulence. A larger part of the water will be involved in interaction with still water than in the straight part of the stream. This still water is mainly on the inside of the bend (Fig 2). Some water that was fast passes over this area and would drop insects from the current. The currents in the outside of the bend are very complex, for while there is great turbulence there is also a strong current. Some of the water that goes around the bend will rub right up against the shore and drop insects but the rest will be shielded from the bank by this water and will spin right around. So while a greater portion of the water will drop insects in a bend than elsewhere, it is possible for an insect to get carried around more than one bend. The general turbulence of the stream and the increased turbulence

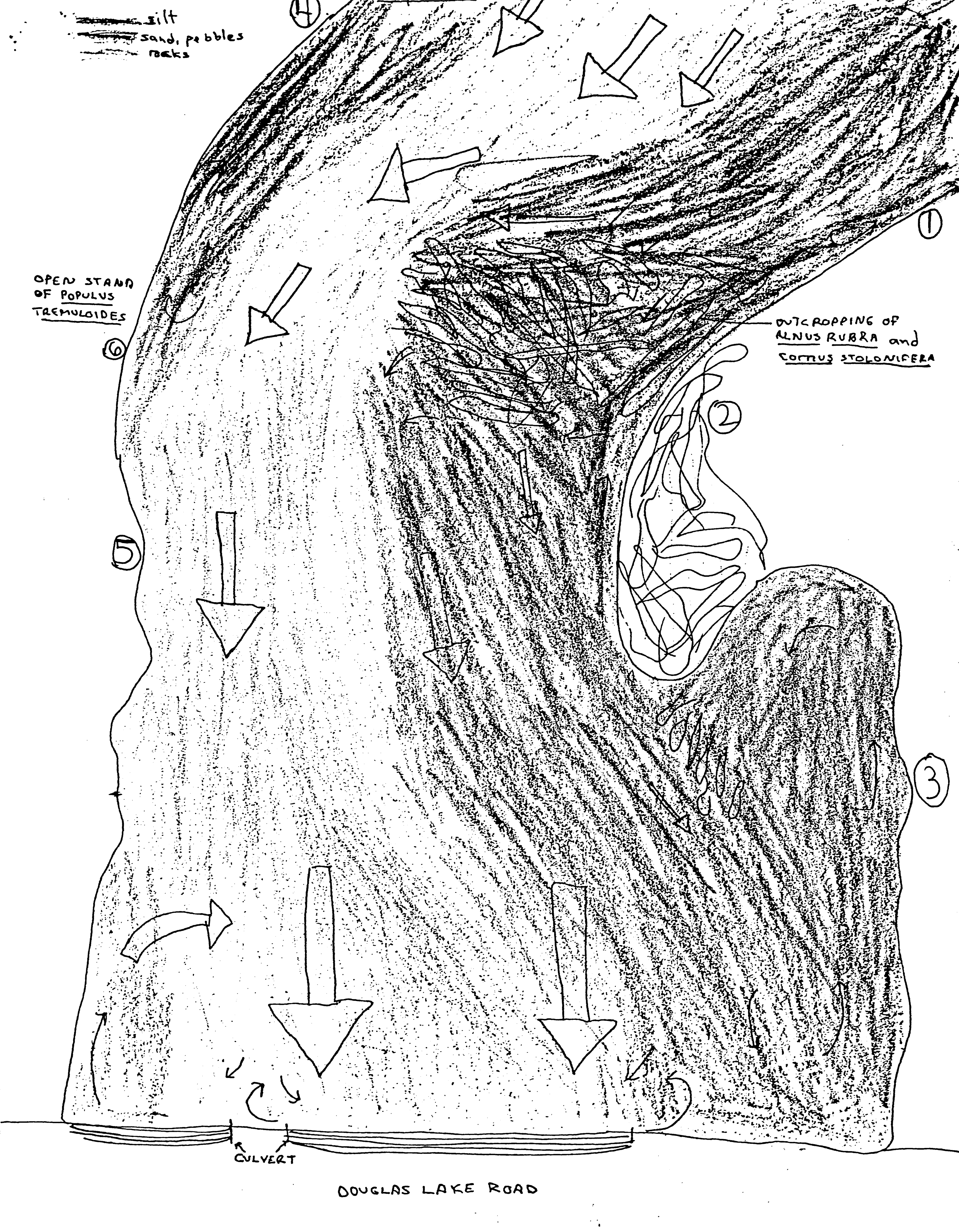

silt
sand, pebbles
rocks
4
1
OPEN STAND OF POPULUS TREMULOIDES
6
OUTCROPPING OF ALNUS RUBRA and Cornus STOLONIFERA
2
5
3
CULVERT
DOUGLAS LAKE ROAD

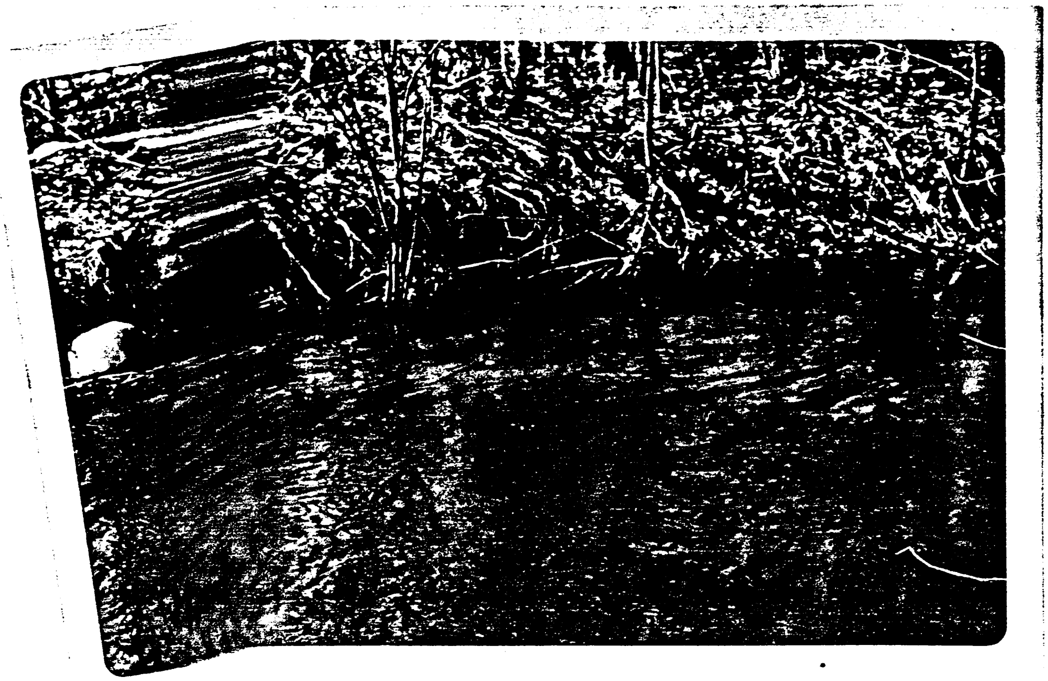
Figure 4

The dye is thrown in at site 1 (Fig. 3). The center water moves faster so the dye from there is nearly out of sight. The water that comes to the bushes is slowed down. Most of it does not flow through the branches but flows to the center past the obstruction.

Figure 5

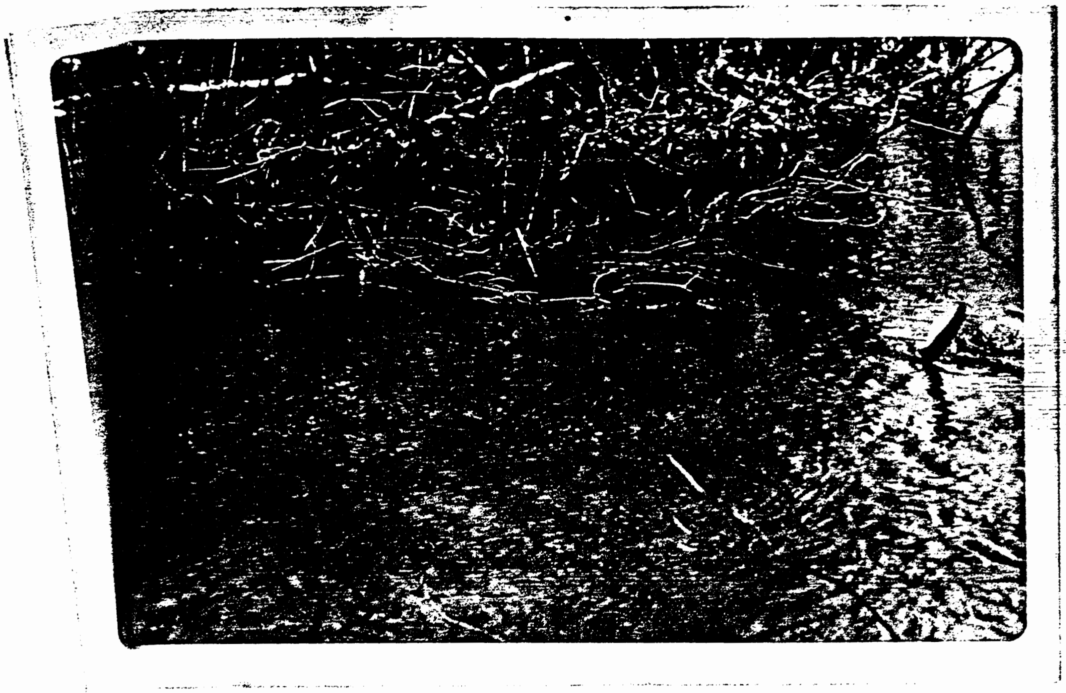
The dye was thrown in at site 1 (Fig. 3) and the photograph taken from site 2. This shows how most of the water is moving in the middle of the stream. The darker green in the bushes shows that some water flows through there, but the current is much slower.

Figure 6



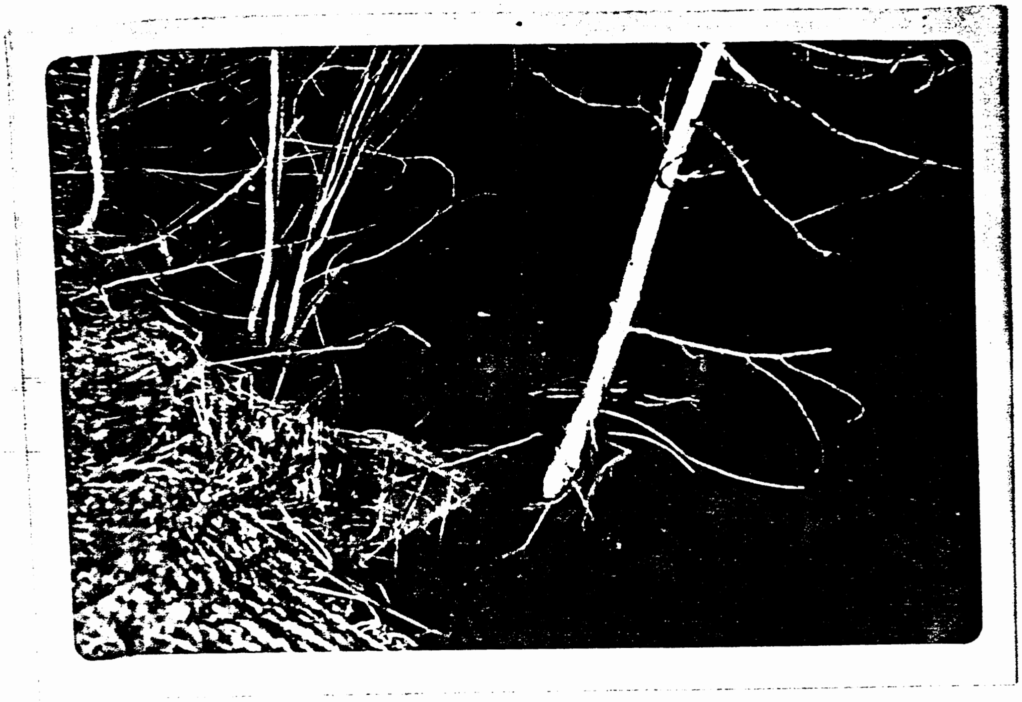
The dye was thrown in at site 1 (Fig. 3). The photograph was taken at site 3. Most of the water is passing around the far side of the bend, very close to the outer shore.

Figure 7



D[illegible]d photograph from site 4 (Fig. 3). Most of the w[illegible] before the bend is moving in the center of the stream.

Figure 8



Dye is thrown in at site 4 (Fig. 3). Photograph is taken from site 5. The water that was in the center of the stream at site 4 is now on the very outside of the bend.

Figure 9

Photog[illegible]a taken at site 6 (Fig. 3). Dye lingers in still water [illegible]nt along the banks long after the rest of the colore[illegible] ater has flowed downstream.

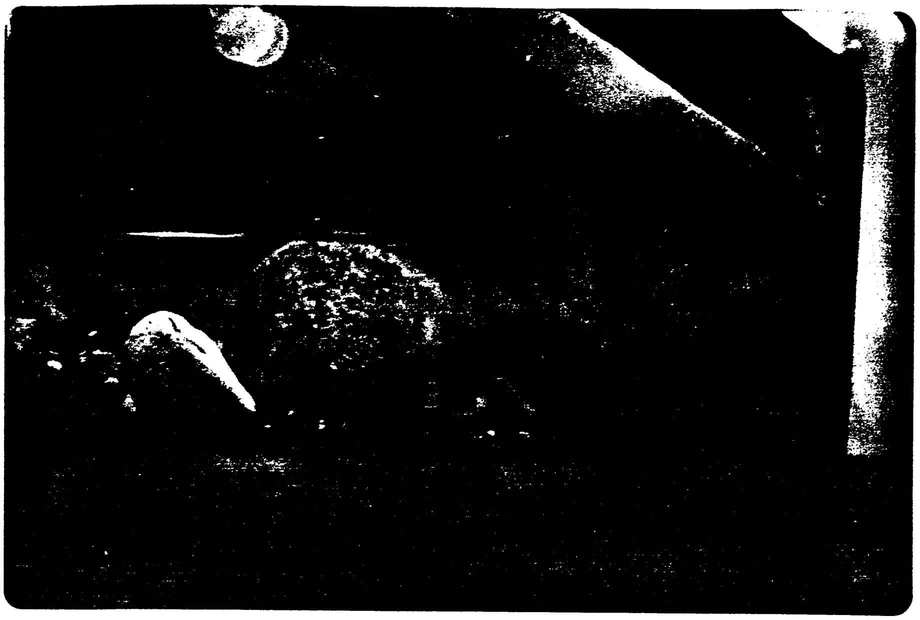
at bends make it likely that the insect would not get carried indefinitely far.

The current speed and the substrate are interrelated. (Fig. 2,3) The faster the water the larger are the stones. Presumably anything smaller would be tumbled away.. Underneath the rocks, and protected from the direct action of the current there may be smaller particles.

The artificial stream was first set up to observe the currents around rocks. Then a slow and a fast area were made. The slow area had more detritus in it; it was isolated from the fast current by surrounding it with bigger rocks. (Fig.) Insects were released in the various areas with the intent of observing whether or not they moved from one area to another. (Table 5) This was not possible because all of the insects were washed out of the stream and down the drain. This loss was an advantage insofar as it was observed that the insects were most likely to be washed away when the current speed was changing. The pump that brought lake water into the stream did not have a uniform pressure so when it surged on insects would drift. If the current was constant there was no (or very little) drift even when the current was very strong.

The observation of drift when the current changes correlates with the observation of drift peaks at dawn an d dusk. It is at this time that the insects move from one part of the rocks to another, and thereby change the current speed that they are exposed to. The current around rocks was observed at two different speeds and depths. It was found that when the

Figure 11

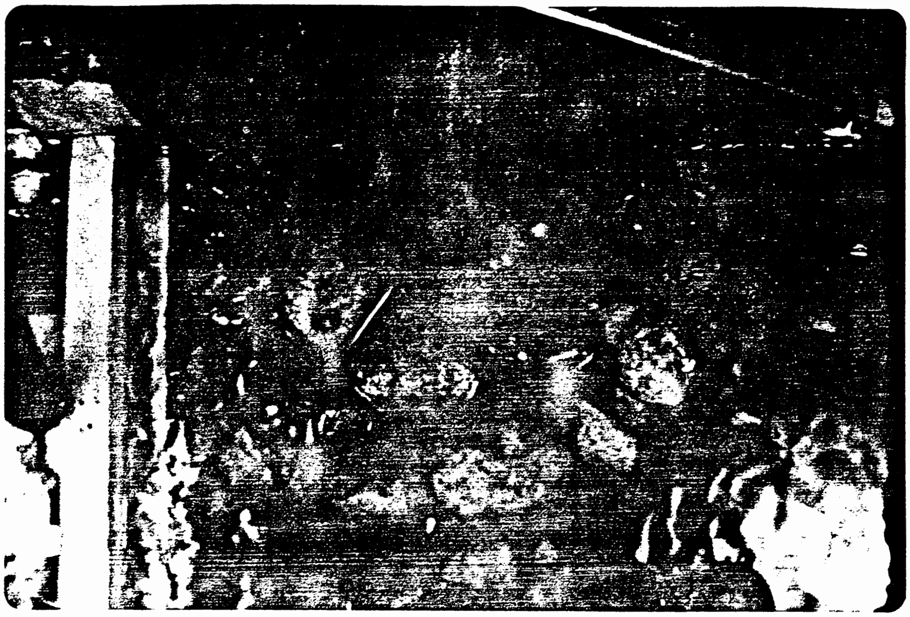


A large rock creates an area of slower current behind it. This is indicated by the presence of dye there when it has been washed away elsewhere. Current moves left to right.

Figure 12

Dye stays caught around nooks in the rocks and pieces of dead leaves over three minutes after the dyed water elsewhere had washed down the drain.

Figure 13



Two habitats were created in the stream, a slow, detritus-filled one, and a faster area. The presence of dye in the detritus area shows that it is, in fact, slow.

Table 5

Insects placed in the Artificial Stream.

- 19 Ephemeroptera

- 18 Trichoptera
    - 4 Neophylax
    - 10 Pycnopsyche
    - 4 Hydropsyche

- 6 Plecoptera
    - 3 Phasganophora
    - 3 Isoperla

- 2 Odonata
    - 2 Boyeria

- 2 Hemiptera
    - 2 Corixidae

- 5 Diptera
    - 5 Rhagionidae

- 1 Coleoptera
    - 1 Elmidae

water was shallow there was a general turbulence and lack of layering. There was no boundary layer. When the water was deeper (twice as deep) turbulence was restricted to the area around the rocks and a little on top. But the main body of water flowed smoothly over the top in a layer. There was considerable exchange between the two layers but the area right around the rocks was protected from the current. The faster the flow the more pronounced was the layering. The slower the flow the more likely that there was general turbulence, exposing more of the rocks to the current. (Fig.) This is the opposite of what would be expected at first, but if deeper, faster water did not create a substantial protected area the animals that lived there would be exposed to a formidable current. That they are not is evident by examining their morphological adaptations to the current. (Hynes 1970)

Dye reveals the current around a rock about two inches in diameter to be turbulent in front and back. The larger turbulent area is behaind the rock. There is a very little turbulence on the top. The swirling of turbulence indicate the boundary layer for it is not a stagnant area, but one where the current does not take one direction. (Fig.)

Discussion

The results support the hypothesis that drift is a non-phenomenon, merely explainable by the current. Those animals most likely to drift were found to be those occurring in the most general habitats. A change in the current was found to vastly increase drift (if the change was an increase in current). The results are fairly accurate, though some factors could have introduced error. Collecting in the five different habitats was good for the most common species, but it could have been off for the rarer ones. Since the common animals were concentrated on, and unique animals discounted to an extent, this probably was not all that important. If an animal was common in one habitat and rare in another,it would have been collected in the common habitat and even if missed in the rare it would be all right because where it is rare it is probably less suited to live.

Drift nets that worked would possibly have caught more drifters. The mesh on the nets that were used was so fine the currents around the nets made them inoperable. A substantial part of the stream water did flow by the island so it was probably a good random seive that sampled drift.

The currents in the stream were probably measured rather innaccurately. The test was only qualitative using the green dye. Since the dye was released by throwing it over the water, the surface water would be the most colored. If the water 2/3 of the way down behaved very differently from the top third, that would not be reflected in this study. However the substrate is an accurate reflection of the current that flows over it, and that could be accurately observed.

It is possible that an artificial stream that is one to five inches deep behaves differently than a stream that is one to five feet deep. But this difference is more likely to be quantitative than qualitative, so the general description of what happens around the rocks is probably accurate. It is things like the depth of the fast layer, and the area of the boundary layer, and the current speed necessary to achieve layering that would change.

It would have been desirable to distinguish more precisely between the five habitats. This could be done measuring current speed over the five areas, taking micro oxygen samples at the substrate level, and possibly quantifying the amount of detritus in each habitat. That would be difficult because streams vary so much from one square foot to another. In fact this variation is so great, further stream work must concentrate on understanding this variation so that quantitative sampling of some sort or another is possible. Until the sampling problems are explained quantitative sampling in streams is a joke. Perhaps the whole emphasis of stream research has to focus down to the centimeter, and define the differences in microhabitats and what determines them.

Conclusion

The phenomenon of stream drift represents the indirect effects of many other behavior patterns when carried out in a flowing environment. Drift is a direct indicator of nothing but current. Other things should be studied if any deep understanding of stream life interactions is to be gained.

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