

ECOLOGICAL FACTORS INFLUENCING
MACROINVERTEBRATES IN THE PINE RIVER

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ABSTRACT

ECOLOGICAL FACTORS INFLUENCING MACROINVERTEBRATES IN THE PINE RIVER

By

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Influences of substrate, macrophyte growth and detritus on macroinvertebrate standing crop distribution, numbers and biomass (ash-free dry weight), as well as seasonal variations in standing crop were investigated in a marginal trout stream.

Seasonal maxima and minima in numbers and biomass are given for ephemeropterans, chironomids, simuliids, other dipterans, trichopterans, and trichopteran Helicopsyche borealis, coleopterans, water mites and plecopterans. Percentage pupae and/or average weight/individual are given for each group and are discussed in relation to population changes. Annual production is estimated, 654 g/m^2 , by using Waters' constant turnover ratio 3.5.

Ephemeropterans show no consistent relationship to large or small substrates, either numbers or biomass. Numbers of dipteran larvae do not show a definite relationship to substrate size, reflecting the relationship of chironomids and simuliids, but a larger biomass is associated with larger

substrates, reflecting the association of larger dipterans. Higher numbers and biomass of trichopterans are associated with larger substrates. The trichopteran Helicopsyche borealis also shows the preceding relationship. Numbers of coleopteran larvae show no relation to substrate size, but biomass is greater in large size substrates. Biomass and numbers of water mites are generally associated with larger substrates, whereas there is no relationship in plecopterans.

Larger numbers and biomass of ephemeropterans, dipterans (chironomids and simuliids but no others) and trichopterans are associated with macrophyte beds; this is attributed to drifting species and those that have summer generations. Macrophyte growth seems to reduce numbers and biomass of H. borealis, but no differences are observed in coleopterans or plecopterans.

In a substrate substitution study, ephemeropterans, chironomids, coleopterans and oligochaetes are significantly related to smaller substrates, whereas dipterans (less chironomids) and trichopterans are not significantly related to substrate type. Significantly higher numbers are related to low and medium food levels rather than high. The relationship to smaller substrates may be related to a reduction in interstitial space (as compared to the large substrates) and the lack of spacial heterogeneity in large substrates. Higher numbers related to low and medium food levels is suggested

due to low oxygen levels below the substrate's surface in the high food levels or due to detritus being in large packets with a great deal unavailable to invertebrates.

For the clam Sphaerium striatinum, highest numbers (1005/m²) and biomass (3.54 g/m²) occur during summer and fall, whereas lowest are observed in late winter. Higher numbers and biomass are generally associated with smaller substrates with no differences between macrophyte and riffle habitats. The majority of the young are extruded when they are 3.6 to 3.8 mm in length. Maximum size reached is 13.5 mm, but growth could not be interpreted from length frequency histograms. Adults contain as high as four young, but the majority contain two.

ECOLOGICAL FACTORS INFLUENCING MACROINVERTEBRATES
IN THE PINE RIVER

By ¹⁹⁷⁰
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INTRODUCTION

There has been increasing interest in stream ecology in recent years, not only because of problems in pollution but also in an attempt to increase knowledge concerning the dynamics of stream ecosystems to better understand natural influences and to predict consequences of human activities. An understanding of the dynamics of the benthic fauna, in relation to physical and biological aspects of the stream, is a prerequisite to this knowledge.

There have been numerous studies on benthic faunas, but many study a few specific species, lack information concerning relationships to the biological or physical components of the stream or are so broad in scope as to give a general overview of ecological relationships. Percival and Whitehead (1929), Jonasson (1948), Minckley (1963), Cummins (1964a,b), Cummins and Lauff (1969), Egglshaw (1969), Mackay and Kalff (1969) have demonstrated influences of substrate and macrophytes on the distribution of standing crop of benthic fauna. Nelson and Scott (1962), Egglshaw (1964), Minshall (G. W., 1967), Mackay and Kalff (1969) have demonstrated that detritus is also an important factor in distribution and support of standing crops. There have also been a number of studies on

seasonal changes of standing crops of benthic organisms in streams (Hynes, 1961; Minckley, 1963; Egglshaw and Mackay, 1969; and others). But the majority of these studies have dealt with numbers, ignoring or giving little reference to biomass, and with numerical estimates being based only on insects caught in large meshed screens, ignoring young individuals that may make up 50% or more of the total fauna (Jonasson, 1955; Macan, 1958; Maitland, 1966).

This paper is concerned with the influence of substrate, food (detritus) and macrophytic growth on macroinvertebrate standing crop distribution. Food manipulations under field conditions have demonstrated the existence of food limitation in a number of populations (Eisenberg, 1970); therefore, an experiment was conducted in the stream to determine the effect of a food (detritus in the present case) and substrate substitution on distribution of numbers to strengthen field data and determine quantitatively the effects and interaction of the two factors. This study is concerned also with seasonal variations in standing crop, numerical and biomass, with emphasis on estimating the total population of those organisms studied. From this data an attempt is made at estimating annual production.

These previous objectives evolved from a concern about the multiple use of rivers for hydroelectric installations, flood control, and recreation that has become extensive in

the United States, and because there is a need for documentation of biological and physical conditions before a stream is altered by a dam. Therefore, this work is part of a series of ecological studies on the Pine River which will provide information that will lead to a better understanding of the ecological effects of such alteration of stream ecosystems.

STUDY AREA, METHODS AND MATERIALS

The study was conducted from June 1968 to October 1969 in the Pine River, Montcalm County, Michigan. The stream above the study area drains about 259 km² (100 mile²) of which approximately 70% is agricultural, the rest aspen-oak hardwoods. The stream is alkaline, averaging about 200 ppm CaCO₃, with summer daytime temperatures ranging from 17-25 C. It has a gradient of 0.95 m/km (5 ft/mile). Discharge ranged from 0.96 m³/sec (34 CFS) to 1.39 m³/sec (45 CFS) in the summer but was somewhat larger during spring runoff.

The sampling site was a riffle area 200 m in length with an average width of 10 m, downstream from the Tamarack Road crossing (edge of Secs. 8-17, T-12N, R-5W). Six samples, selected randomly from a random numbers table, were taken with a Petersen dredge having an area of 651 cm² at biweekly intervals throughout the spring, summer and fall months. During the winter months samples were taken only twice, in late November and early March. Although six samples were taken on each date, all were not used.

The samples were placed in buckets with 10% formalin added and taken to the laboratory. Excess liquid was poured through No. 30 and No. 60 mesh (0.5 mm and 0.246 mm mesh

openings, respectively) Tyler sieves placed in sequence. The invertebrates were removed by the sugar flotation technique (Anderson, 1959). The remaining material was placed in a white enamel pan and examined for remaining invertebrates. The material in each sieve was placed in separate jars and 75% ethyl alcohol added. It often was necessary to deal with only part of a sample because of large amounts of detritus which floated on the sugar solution; therefore, two or three subsamples were taken from each (number of ml subsampled varied depending on the total amount of the sample), picked under a dissecting microscope, enumerated, and the total number estimated in each by simple proportion and averaged to give a mean estimate in the sample. These estimates were added to give an estimate of the total number of invertebrates in the sample and expressed as the number/m² or biomass/m². Ash-free dry weights were determined by placing the subsamples in small planchets and drying at 105 C for 48 hours. The subsamples were then placed in a dessicator and allowed to cool to room temperature, weighed to the nearest 0.01 mg, then ashed at 600 C for one hour, again allowed to cool to room temperature in a dessicator, and reweighed. Errors introduced by inorganic gut contents are avoided by this technique (Scott and Nelson, 1962).

In order to determine the various substrate particle sizes present, samples of the stream bottom were taken immediately adjacent to the area sampled for invertebrates.

The sampler, a cylinder 8.5 cm in diameter, was pushed into the substrate to a depth of approximately 7.5 cm. The upper end was enclosed to prevent the loss of silt and clay. Once the sampler was in place in the substrate, a thin metal plate was forced under the end, the sample removed and placed in a container. In the laboratory, substrate samples were analyzed for particle size distribution by a combination of two methods: the settling velocity method for silt and clay, and dry sieve analysis for the substrate materials 1.16 mm and greater (Cummins, 1962).

For the settling velocity method, each sample was agitated vigorously after water was added. The resulting silt and clay suspension was decanted. This process was repeated three to six times depending on the amount of silt and clay. The suspension was then placed in gallon glass jars, allowing the silt component to settle. The water, still containing the clay suspension, was siphoned through a Foerst centrifuge. At this time the precipitated clay and silt were placed in separate porcelain dishes. The remainder, consisting of coarse substrate, silt and clay fractions were oven dried at 105 c.

Dry sieving of each sample involved the use of a mechanical shaker (Ro-Tap) and nine U. S. Standard Sieves with the following openings: 16, 8, 4, 2, 1/2, 1/4, 1/6 mm. In addition, a single square of heavy wire was constructed with an opening of 32 mm. The weights of each of these 12 particle

size fractions were determined for each sample to the nearest 0.01 g. Following Cummins' technique (1962) the sediment size classes were converted to the phi scale.

RESULTS AND DISCUSSION

Factors Influencing Standing Crop Distribution

Field Observations

Differences in standing crop and faunal relationships in respect to substrate (see Cummins, 1964b, and Cummins and Lauff, 1969, for reviews) and aquatic plants (Percival and Whitehead, 1929; Whitehead, 1935; Frost, 1942; Jonasson, 1948; Minckley, 1963) have been observed. In this study in order to investigate substrate size as a factor in macro-invertebrate standing crop distribution the median phi value was used to characterize the substrate from which benthos was taken (Cummins, 1962). Samples were divided into two categories according to phi values: those that were taken from an area in which phi was 2.7 or less--termed small, and those from an area of more than 2.7--termed large. Because either the large or small category lacked samples in many collections, data were combined from two consecutive dates (except the last collection, 24 June 1969, which had samples in both categories) giving nine time periods (TP₁-TP₉). Average standing crop was determined when more than one sample was represented.

Prior studies have compared the faunal composition or numerical standing crops occurring in macrophytes with that of

other habitats of the stream. In this study macrophytes (three species of Potamogeton) were growing in portions of the riffle area in late May, being sparse at first with little standing crop (biomass). They became dense, with maximum standing crop in August, and again reached a low standing crop in October. As plants grew the current decreased in the lower portions of the water column with a corresponding deposition of detrital and inorganic materials through the summer. To investigate this growth of macrophytes on the distribution of invertebrate standing crops, on the dates when samples were taken in macrophytes the average standing crop was determined for those samples taken in riffle areas and compared with the standing crops obtained from macrophytes.

As indicated in Tables 1 and 2, there seemingly was a difference in numbers/m² and biomass/m² of ephemeropteran nymphs between the two types of substrates, but neither high biomass nor numbers was consistently related to either substrate type. At TP₁ there were, on the average, more individuals and a larger biomass in the smaller substrates, but at TP₂ this association was reversed. TP₃ showed a higher number of individuals but a lower biomass associated with the smaller substrate. During TP₄ both numbers and biomass were associated with smaller substrates. At TP₅ there was a high number of nymphs in larger substrates, and, except for TP₆ which had only one sample representing the smaller substrates, this was maintained through TP₉. Biomass also showed the same pattern

Table 1. Average estimate of individuals/m² at each time period (TP) associated with small and large substrates from a riffle area of the Pine River (n = number of samples).

n	TP-1		TP-2		TP-3		TP-4		TP-5		TP-6		TP-7		TP-8		TP-9		TP-10	
	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large
Ephemeroptera	3,212	589	1,790	3,767	2,571	1,918	5,321	3,816	2,471	2,811	3,159	1,874	4,318	7,596	2,676	6,733	6,085	7,752		
All Diptera	26,340	13,831	58,811	93,919	59,889	23,685	53,876	50,763	97,279	83,692	44,010	68,022	46,819	47,361	35,449	39,459	36,671	41,704		
Chironomidae	22,692	10,628	57,065	89,571	59,119	22,687	55,393	47,143	93,125	81,154	42,546	63,385	40,350	43,944	29,926	33,939	34,568	37,516		
Simuliidae	343	2,595	45	36	0	4	314	42	566	280	271	716	5,068	1,059	2,719	908	30	653		
Other Diptera	3,305	608	1,700	4,312	770	994	2,169	3,578	3,588	2,248	1,195	3,921	1,400	2,358	2,805	2,602	2,073	3,554		
Trichoptera	8,661	3,250	6,256	9,277	1,000	5,434	4,117	9,905	2,262	3,459	2,689	4,312	3,052	5,195	2,233	3,987	2,918	8,949		
H. borealis	343	75	1,479	0	882	2,436	924	2,239	468	278	201	584	565	1,003	412	485	371	683		
Coleoptera	1,220	1,517	1,487	3,364	2,802	1,918	1,170	1,624	1,868	2,709	4,923	2,717	1,364	1,864	2,219	1,061	1,299	778		
Hydracarina	1,048	166	1,266	1,955	3,122	1,667	2,414	3,964	2,342	2,102	289	3,912	2,037	3,019	1,646	4,465	766	1,406		
Plecoptera	18	181	111	213	495	12	1,060	433	220	886	308	270	1,017	174	658	895	154	31		
TOTAL	40,339	19,334	69,661	112,495	69,879	54,663	66,968	70,505	106,442	95,639	55,387	81,107	58,607	65,199	44,881	55,600	47,893	63,620		

Table 2. Average estimate of biomass (g/m^2) at each time period (TP) associated with small and large substrates from a riffle area of the Pine River (n = number of samples).

n	TP ₁		TP ₂		TP ₃		TP ₄		TP ₅		TP ₆		TP ₇		TP ₈		TP ₉	
	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large
	2	3	1	2	1	3	2	1	4	2	1	4	3	4	3	4	3	3
Ephemeroptera	0.184	0.201	0.026	0.140	0.022	0.062	0.150	0.064	0.268	0.349	1.542	1.255	0.810	2.191	0.098	0.269	0.147	0.211
All Diptera	0.311	0.229	0.676	0.941	0.263	0.288	0.458	0.672	0.742	0.976	1.543	2.744	0.967	1.358	0.660	0.981	0.677	0.878
Chironomidae	0.195	0.179	0.161	0.459	0.236	0.198	0.308	0.282	0.466	0.613	1.204	1.470	0.670	0.697	0.442	0.754	0.136	0.649
Simuliidae	0.703	0.078	0.001	0.000	0.000	0.000	0.013	0.000	0.024	0.022	0.044	0.004	0.051	0.007	0.071	0.006	0.001	0.028
Other Diptera	0.112	0.031	0.115	0.202	0.026	0.089	0.137	0.390	0.252	0.342	0.297	1.270	0.246	0.653	0.147	0.221	0.370	0.201
Trichoptera	1.821	0.175	0.463	0.622	0.121	0.725	0.454	0.794	0.307	0.970	0.730	0.797	1.155	2.353	0.828	2.268	0.794	1.649
<i>H. borealis</i>	0.219	0.050	0.031	0.000	0.045	0.039	0.023	0.091	0.047	0.029	0.011	0.018	0.117	0.125	0.095	0.110	0.201	0.362
Coleoptera	0.085	0.097	0.131	0.264	0.039	0.168	0.039	0.080	0.052	0.261	0.443	0.266	0.072	0.124	0.059	0.033	0.076	0.042
Hydracarina	0.039	0.004	0.023	0.037	0.026	0.020	0.031	0.052	0.028	0.029	0.012	0.567	0.020	0.041	0.015	0.043	0.038	0.019
Plecoptera	0.022	0.007	0.001	0.001	0.025	0.000	0.008	0.023	0.096	0.034	0.299	0.030	0.010	0.211	0.005	0.014	0.002	0.000
TOTAL	2.430	0.963	1.421	1.912	0.673	1.262	1.141	1.685	1.442	2.678	4.371	5.149	3.035	6.277	1.664	3.639	1.633	2.813

from TP₅, larger in larger substrates except for TP₆. These observations are in contrast to the relationship Pennak and Van Gerpen (1947) found, more nymphs in larger substrates. Macan (1957) observed that more and smaller nymphs were generally associated with smaller substrates and observed a migration in some species when they became large and prior to emergence. Although the relationship between standing crops and substrate type, in the present study, was not consistent from TP₁ through TP₆, from TP₇ through TP₉ numbers and biomass were higher in the larger substrate at a time when nymphs would be largest. Thus it may be possible that there is no definite relationship until nymphs are large, at which time they move to a larger substrate.

A comparison between macrophyte beds and riffles shows that on 23 June the number of mayfly nymphs/m² was higher in macrophytes (Table 3), but there were more occurring in riffles on 8 July. On 22 July nymphs occurred in both areas in about equal numbers. Concurrently the biomass/m² on the first date was a little greater in macrophytes, but on 8 and 22 July solid substrates contained a larger amount of biomass. From 2 September until 6 October the numbers of organisms inhabiting macrophytes were much higher than in solid substrates. Biomass was greater in macrophyte beds on 2 and 16 September but about equal on 6 October. On the last date both biomass and numbers were about equal in both types of habitat. Mayflies have previously been observed to inhabit plants.

Table 3. Average estimate of numbers/m² and biomass (g/m²) (in parentheses) in macrophyte beds (present) and in riffles (absent) during summer and fall 1968 (n = number of samples).

DATE	EPHEM- EROPTERA	ALL DIPTERA	CHIRO- NOMIDAE	SIMUL- IIDAE	OTHER DIPTERA	TRICHO- PTERA	H. BOREALIS	COLEOP- TERA	HYDRA- CARINA	PLECOP- TERA	TOTAL	n
June 23	Present	32,155 (1,336)	6,933 (1,136)	24,832 (1,177)	273 (0.022)	415 (0.0715)	12 (0.013)	995 (0.080)	107 (0.005)	24 (0.007)	34,454 (2,132)	1
	Absent	8,433 (0.218)	8,104 (0.176)	158 (0.004)	617 (0.037)	2,662 (0.218)	146 (0.075)	1,477 (0.073)	203 (0.006)	166 (0.007)	15,814 (2,572)	3
July 6	Present	84,236 (0.000)	85,586 (0.004)	24 (0.000)	616 (0.015)	8,080 (0.510)	177 (0.114)	2,357 (0.140)	747 (0.011)	1,458 (0.033)	99,335 (1,250)	1
	Absent	53,723 (0.216)	26,478 (0.200)	3,943 (0.024)	3,246 (0.139)	9,543 (2,357)	166 (0.121)	1,280 (0.110)	983 (0.005)	42 (0.022)	43,113 (2,908)	2
July 22	Present	58,720 (0.004)	47,484 (0.132)	8,684 (0.110)	2,582 (0.033)	9,510 (0.668)	36 (0.048)	1,247 (0.036)	2,745 (0.022)	115 (0.001)	75,113 (1,414)	1
	Absent	59,224 (0.004)	56,202 (0.123)	36 (0.001)	2,987 (0.136)	9,028 (0.556)	65 (0.037)	2,551 (0.163)	1,785 (0.030)	185 (0.001)	75,671 (1,586)	3
Sept. 2	Present	64,731 (0.004)	48,269 (0.030)	15,412 (0.138)	1,110 (0.021)	11,302 (0.863)	261 (0.004)	2,703 (0.160)	4,116 (0.035)	837 (0.003)	95,903 (1,912)	1
	Absent	44,257 (0.000)	42,386 (0.210)	53 (0.000)	1,268 (0.080)	6,229 (0.410)	752 (0.044)	2,517 (0.114)	2,401 (0.026)	431 (0.013)	58,981 (0,933)	4
Sept. 16	Present	89,636 (0.001)	68,344 (0.130)	19,128 (0.019)	1,561 (0.066)	15,330 (1,302)	0	2,739 (0.152)	3,745 (0.025)	1,030 (0.006)	122,372 (2,783)	1
	Absent	57,034 (0.163)	53,878 (0.277)	1,134 (0.000)	2,024 (0.223)	7,502 (0.314)	1,315 (0.063)	1,165 (0.048)	3,470 (0.058)	687 (0.002)	74,384 (1,227)	3
Oct. 6	Present	85,470 (0.009)	79,062 (0.160)	3,365 (0.160)	1,043 (0.013)	9,431 (2,337)	48 (0.001)	415 (0.025)	4,479 (0.031)	1,445 (0.021)	101,316 (3,333)	1
	Absent	88,845 (0.072)	56,086 (0.373)	715 (0.020)	2,043 (0.277)	3,124 (0.563)	266 (0.017)	881 (0.050)	1,843 (0.015)	1,526 (0.011)	68,654 (2,338)	2
Oct. 24	Present	78,722 (0.009)	76,765 (0.130)	1,244 (0.000)	705 (0.088)	3,187 (1,532)	432 (0.057)	1,005 (0.036)	1,406 (0.017)	918 (0.009)	87,348 (2,732)	1
	Absent	81,778 (0.004)	79,003 (0.000)	283 (0.012)	2,332 (0.233)	2,264 (0.222)	371 (0.032)	2,463 (0.135)	1,350 (0.027)	187 (0.001)	90,771 (2,311)	1

Whitehead (1935) found that many parts of the stream were repopulated from moss areas after the recession of winter floods, and Frost (1942) found extensive utilizations of mosses throughout the year. Maitland (1966) found many nymphs in macrophyte beds but not as high numerically as he found in riffle areas. In the present study there seemed to be not consistent numerical relationship with either riffle or macrophyte habitats from 23 June to 22 July; however, there was a higher average biomass in the riffle habitat possibly indicating that smaller individuals were utilizing the macrophytes. From 2 September to 6 October there was a large difference in standing crop between the two habitats, numbers and biomass being greater in the plants. By 24 October numbers and biomass were nearly equal, undoubtedly due to the fact that prior to this time plants had begun to die off and break loose from the bottom; thus areas that were inhabited by extensive growths of macrophytes were becoming more like a riffle habitat.

The disparity between large and small substrate in average numbers/m² of diptera was great in the first three time periods (Table 1), more dipterans occurring in the smaller substrates at TP₁ and TP₃ and more in larger substrates at TP₂. From TP₄ to TP₉ the differences were not great. At TP₄ and TP₅ there averaged more larvae in smaller substrates. There is a relationship between average biomass/m² and substrate type (Table 2); the first time period biomass was

greater in smaller substrates but associated with larger types at all other time periods.

Relationship between the number of chironomids and substrate type was identical to dipteran larvae taken as a whole, which one would expect since chironomids were the dominant member of the group. Biomass did not follow a similar pattern. More biomass was associated with smaller substrate type at the first, third and fourth time periods, but larger substrates contained more biomass at the other time periods.

Numbers of blackfly larvae did not show a constant relationship to substrate type. At TP₁ there were more associated with large substrate, but more were associated with small substrate in time periods 2, 4, and 5. At TP₃ there were no larvae from the small substrate and very few from larger substrate samples. At TP₆ there were more associated with large substrate whereas more were associated with small substrate at TP₇. At TP₈ and TP₉ more larvae were associated with large substrates.

Larger numbers of other dipteran larvae, excluding chironomids and blackflies, were generally associated with large substrate. At TP₁ more were associated with the small substrate, but higher numbers were in larger substrate from TP₂ to TP₄. Again at TP₅ there were more in small substrate. At TP₆, TP₇ and TP₉ large substrate contained more larvae, and at TP₈ there was a small difference between substrate

types with small containing a few more. Larger biomass was associated with large substrate at all time periods except the first in which the small type contained a higher biomass.

Numerically dipterans did not show a relationship to substrate size nor was there any relationship when chironomids, simuliids or other dipterans were considered separately. However, biomass of dipteran larvae as a whole did show a relationship, with a larger biomass in larger substrates. Biomass of chironomid and simuliid larvae did not show a relation to substrate type whereas the other dipterans did. Other dipterans consisted mostly of the large, robust larvae; thus dipterans taken as a whole reflect the association of biomass of these large individuals to substrate. Denham (1938) contrasted sand and gravel, finding more larvae in gravel but noted those occurring in sand were much smaller. Pennak and Van Gerpen (1947) found more chironomids in gravel and sand than in larger types and more simuliids on bedrock than other areas. However, they found more other types of dipterans associated with larger substrates. This association of the larger dipterans with the larger substrates is undoubtedly due to growths of algae and moss on the rocks, making refuges among the growth (Whitehead, 1935; Frost, 1942; Minckley, 1963).

Dipteran larvae as a whole utilized macrophytes extensively as a habitat (Table 3) with both biomass and numbers generally greater in these beds than in riffles; this

association was due to the high occurrence of chironomids and simuliids. Numbers of chironomid larvae were highest in riffle areas on the first and third dates but higher in macrophytes on the second date. Biomass was larger in riffle areas on the first date, larger in macrophytes on the second and about equal on the third date. From the fourth date, 2 September, to 6 October greater numbers of chironomid larvae were associated with macrophyte beds. On 24 October numbers of these larvae were still higher in macrophytes, but the disparity between the two habitats was not as great as on the previous dates. Chironomid biomass was higher in macrophyte beds from 2 September until the last date. Simuliids showed a definite preference for macrophyte beds, both in numbers and biomass. On all dates, except the second, numbers were greater and biomass higher in macrophyte beds than in riffles. In contrast to both chironomids and simuliids, other dipteran larvae occur in higher numbers and larger biomass in riffle areas; however, the disparity between numbers of larvae in macrophytes and riffles was not great on 22 July or 2 September.

The association of dipterans with macrophytes is obvious, particularly with biomass. This association is due to chironomid and simuliid larvae while other dipterans are associated with riffles, both numbers and biomass. Maitland (1966) found that in macrophytes, dipterans made up a higher percentage of the fauna than in other habitats. Jonasson

(1948) found simuliid larvae in high concentrations in Cladophora, particularly in early spring and fall.

Caddisfly standing crop showed a definite relation to substrate type, both numbers/m² and biomass/m² larger in the bigger substrates in all except the first time periods (Tables 1 and 2). In comparing macrophytic and riffle habitats in this group, on the first and second dates a higher number of individuals were associated with riffles (Table 3). Concurrently, biomass was greater in macrophytes on the first date but greater in riffles on the second date (Table 3). On 22 July numbers in both habitats were nearly equal, but biomass was greater in macrophytes. From 2 September to the last date there were more individuals and a greater biomass present in macrophytes than in riffle areas.

Although standing crop numbers of caddisflies showed variation in relation to substrate for the first three time periods, from TP₄ until the last more occurred in the larger substrates. Relationship of biomass is obvious, in all except the first time period, with more biomass being in larger substrates. Pennak and Van Gerpen (1947) compared numerical standing crops of three substrate types and found more caddisflies associated with the larger stones. Sprules (1947) found a similar relationship. However, Scott (1958) found the densest populations on medium-sized stones. An important factor causing differences between the two investigations could be attributed to the presence of moss and algae

cover on particular sizes of stone resulting in a microhabitat utilized by certain species (e.g., members of the families Hydropsychidae, Philopotomidae, Psychomyidae) (Percival and Whitehead, 1929; Scott, 1958). Another factor that would influence the relation to substrate type is movement of the larvae. Scott noted that several species migrated from gravel to larger stones upon pupation. Cummins (1964a) studied substrate relations in two Psychopsyche species. He showed that one species during early larval periods was associated with silt bottom habitats, then migrated to gravel-pebble substrates in the terminal instar. The other species showed no changes in substrate association as maturation occurred.

Standing crops of caddisflies, numbers and biomass, follow the same pattern as mayflies and dipterans in relation to plants; very little difference between the two habitats in early summer, much higher in plants during late summer and fall. When plants died off in late October, both habitats became nearly equal. From observations it was determined that utilization of macrophytes as a habitat was almost entirely due to Hydropsyche larvae. This association of Hydropsyche larvae with macrophytes was noted by Jonasson (1948), large populations being built up in Elodea beds during the summer. Minckley (1963) observed that Hydropsyche larvae avoided Myriophyllum beds in pool areas when there was little or no current.

The caddisfly H. borealis showed a similar relation to size of substrate type as did the group as a whole. TP₁ had more individuals and a higher biomass associated with smaller substrates. There was only one sample representing large substrates in TP₂ and this did not contain any specimens. In TP₃ and TP₄ there were more larvae in larger substrates whereas biomass was greater in the smaller substrate in TP₃ and greater in the larger substrates in TP₄. The TP₅ biomass and numbers were smaller in smaller substrates. In the last four time periods more nymphs and greater biomasses were associated with larger substrates. Thus, H. borealis seemingly demonstrates an affinity for larger substrates, both in numbers and biomass. Cummins and Lauff (1970) studied selectivity of substrate of this species in a laboratory situation and found that there was a tendency to select the largest substrate (16 mm). They noted that the larvae encountered locomotory problems on finer substrates but were quite mobile on silted substrates. Cummins and Lauff concluded from their study that substrate size is of secondary influence on micro-habitat selections and that food organisms are probably of prime importance. However, a selection of substrate may be made by the adult female while ovipositing as it is known that many species submerge to accomplish this (Pennak, 1953).

Growth of macrophytes seemingly influences the distribution of H. borealis; more larvae were associated with riffles

than macrophyte beds on all dates except the last (Table 3). Biomass was also larger in riffles in all cases except 22 July. No larvae occurred in the sample from macrophytes on 16 September. This association with riffles is in contrast to the caddisfly group as a whole. These larvae, in contrast to the majority of the larvae found in macrophytes, build stone cases and are attached to rocks. It is possible that adverse conditions arise from deposition of silt and detrital material in macrophytes.

Numbers of beetle larvae/m² demonstrated no consistent relation to substrate type (Table 1). More larvae were associated with large substrate at TP₁ and TP₂, but at TP₃ there were more in small substrates. TP₄ and TP₅ had more larvae and a greater biomass associated with larger substrates. Biomass and numbers were greater in small substrate at TP₆ as well as TP₈ and TP₉. At TP₇ larger biomass and greater numbers were associated with large substrate. Biomass being greater in larger substrates while numbers are fewer, indicates larger larvae inhabiting larger substrates. Maitland (1966) found higher numbers of beetle larvae occurring in areas of coarse gravel than in the larger stones, whereas Pennak and Van Gerpen (1947) found more associated with rubble (i.e., large stones) than with coarse gravel.

Comparing numbers of beetle larvae in relation to macrophyte or riffle habitat shows that there were more larvae associated with macrophytes on two dates, 8 July and

2 September; on all other dates higher numbers were associated with riffle habitat. On 23 June biomass was nearly equal in the two types of habitats, but macrophytes had a little higher biomass. On 8 July a higher biomass was associated with macrophytes. Higher biomass was associated with riffles on 22 July and 6 October; at the three other dates it was associated with macrophytes. There is little difference between plant and riffle habitats, which is similar to what Maitland (1963) observed; numbers of beetle larvae in plants were nearly equal to those in riffle areas. Frost (1942) and Minckley (1963) found large numbers of beetle larvae, mostly elmids, inhabiting moss which undoubtedly provides microhabitats.

Water mites occurred in higher numbers in small substrates at three time periods, TP_1 , TP_3 and TP_5 (Table 1). At all other periods there were higher numbers in large substrates. Biomass showed a similar relation to substrate in that it was higher in small substrates at TP_1 and TP_3 but associated with large substrates at all other periods (Table 2). Macrophytic habitat had a higher number of water mites associated with it from 22 July to 6 October (Table 3), whereas riffle habitat had more associated with it on the first two and last dates. Large biomass was not consistently associated with either habitat but alternated between the two types of habitat (Table 3).

There is no relation of water mites to substrate during the first three time periods, after which numbers and biomass are larger in bigger substrates. There seems to be no effect on standing crops of water mites by growth of macrophytes. Maitland (1966) found more mites occurring in macrophytes and among large stones than in other areas, and Frost (1942) found large numbers inhabiting moss. Jonasson (1948) found in areas adjacent to macrophytes that when the plants died there was an influx of mites which apparently did not occur here.

The first two time periods showed more stonefly nymphs associated with larger substrates with more associated with smaller substrates the next two periods. Concurrently there was a larger biomass in small substrates at TP₁ and TP₃ but larger in large substrates at TP₂ and TP₄. At TP₅ as well as TP₆ there were more nymphs in large substrates. At TP₆ numbers were nearly equal in the two types of substrates even though there were a few more in smaller substrate. At TP₇ and TP₉ more nymphs were in small substrates. In contrasting riffle and macrophytic habitats, higher numbers occurred in riffles on 23 June, 22 July and 6 October, with more occurring in macrophytes on the other dates. Biomass was nearly equal in the two habitats on two dates, 22 July and 24 October, greater in macrophytes on 8 July and 16 September and in the riffle areas on the other three dates.

In this study little can be said in regard to substrate relationships of stoneflies, undoubtedly due to small numbers present in the stream. Also little can be said in relation to the effect of macrophyte growth other than that there is no apparent adverse effect on standing crops by macrophytes. However, several studies (Percival and Whitehead, 1929; Pennak and Van Gerpen, 1947) have found more stoneflies in larger substrates, whereas Maitland (1966) found more associated with gravel than in a mixture of large and small particle sizes. Stoneflies have also been shown to utilize plants as a habitat (Frost, 1942), with large numbers utilizing moss, but Minckley (1963) found more individuals in riffle areas without moss or macrophytes than in those with plants.

Total numerical standing crop does not demonstrate a definite association with substrate type, generally reflecting the association of the major numerical group, dipterans (Table 1). Standing crop measurements that have been made in different substrate types in the past have usually been thought of as a demonstration of production, being higher in a particular substrate type (Pennak and Van Gerpen, 1947). However, these studies have usually been over a short period of time, the summer, and have used numbers as the measure of production instead of biomass. Present data show that there is a definite association of biomass to substrate type, larger at all except the first time period in the bigger substrates (Table 2). As mentioned previously, this is probably due to the growth of

moss and algae on some of the larger rocks diversifying the habitat, leading to more areas to be inhabited, particularly by larger dipteran (e.g., Tipulidae, Rhagionidae) and caddisfly larvae (e.g., Hydropsychidae).

An effect of macrophyte growth on total standing crop in numbers and biomass is evident (Table 3). During the early part of the growth phase of the macrophytes (May and June) there seems to be no difference in standing crops of invertebrates. However, when macrophyte standing crop is high (August to October), there are higher numbers and larger biomass of invertebrates in the plants. Growth of macrophytes as it occurred in this investigation brought about changes in the riffle habitat, changing current velocity and turbulence which in turn caused deposition of detritus and inorganic materials. Other studies indicate that in such a situation there would also be a change in the macroinvertebrate associations, through changes in abundance of various groups, distribution and diversity (Chutter, 1969; Cole, in press). As macrophyte standing crop decreased in fall, there was a removal of deposited materials and a return to riffle conditions, and this is indicated in the last collection date (Table 3). Growth of macrophytes also presents an unoccupied habitat to be colonized by drifting organisms and those that have a summer generation. It seems noteworthy that the macrophytes were colonized by groups of organisms that are noted for drifting and inhabiting denuded areas: Simuliidae, Baetidae and

Hydropsychidae (Waters, 1966; Chutter, 1968). Annual plants then act as a refugia for drifting organisms preventing the loss due to drift as presupposed in situations in which drifting of organisms occurs.

Substrate and Food Manipulation

Previous discussion focused on the relationship between macroinvertebrates and habitat types. However, other factors have been investigated (e.g., food, temperature, current and others) and have been shown to be important. One factor is detritus, both allochthonous and autochthonous, acting as a source of nutrition for primary consumers (Nelson and Scott, 1962; Hynes, 1963; Darnell, 1964; Minshall, G. W., 1967; Egglshaw, 1964). Therefore, it was decided to manipulate substrate and amount of detritus under natural conditions to quantitatively estimate the influence and interaction of these two factors on macroinvertebrate numbers. In an attempt to eliminate current as a factor, an area of relatively constant current and depth, varying between 0.12 m/sec and 0.28 m/sec (0.4 ft/sec and 0.9 ft/sec), and 15 cm and 27 cm (6 inches and 11 inches), respectively, was selected. Eighteen locations of about 0.27 m² (4 ft²) were selected and the stream bottom removed to a depth of about 23 cm (9 inches). This was a 2 x 3 factorial analysis design. Gravel and rock were obtained from a local gravel company and separated into large and small substrate types (see Table 4 for analysis of two

Table 4. Particle size distribution by weight of four samples, two from each size category, from substrates substituted in a riffle area of the Pine River.

Particle Size range in mm	Large		Small	
	Weight of Particle Size in Grams		Weight of Particle Size in Grams	
	Sample		Sample	
	1	2	1	2
16+	338.9	318.8	---	---
16-8	15.9	63.6	254.9	303.1
8-4	6.5	48.2	197.2	60.4
4-2	0.7	19.6	20.0	11.6
2-1	0.8	17.5	1.6	1.0
1-0.5	1.2	16.2	1.8	0.4
0.5-0.25	3.1	17.0	3.6	0.6
0.25-0.125	0.8	2.3	0.6	0.2
0.125-0.063	0.1	0.4	---	0.05

samples of each type). Dried Potamogeton (three species that were found in the stream) was added at levels of about 121 g/m^2 (11 g/ft^2), 484 g/m^2 (44 g/ft^2) and 847 g/m^2 (77 g/ft^2). In July each sample was placed at random in the stream according to a random numbers table and sampled with the Petersen dredge in October. Samples were placed in buckets, 10% formalin added and returned to the laboratory. Samples were processed as those taken throughout the year with the exception that a No. 60 mesh sieve was used and two subsamples per sample were taken.

Numbers of ephemeropterans, chironomids (data on this group was transformed to logs due to variance heterogeneity) and coleopterans were significantly different between substrate types and food levels; more individuals in each group were associated with small substrates (Tables 5 and 6). Orthogonal contrasts (Table 5) show that numerically there were significant differences between food levels within substrate types, for ephemeropterans and chironomids only within small substrates and for coleopterans in both substrate types. Oligochaetes were significantly associated with substrates (Table 5), but orthogonal contrasts show that within smaller substrates medium food level was different from high food level. Other dipterans and trichopterans were associated significantly with food levels. Orthogonal contrasts show in both groups that low food level was significantly different from medium and high with large substrates, and in dipterans

Table 5. Analysis of variance and orthogonal contrasts on numbers of organisms in six groups with food level and substrate manipulations in a riffle area of the Pine River. Data for Chironomidae were transformed to common logarithms. In contrasts L=large and S=small substrates, l, m, and h indicate low, medium, and high food levels, respectively.

Source	d.f.	Ephemeroptera			Chironomidae			Other Diptera			Trichoptera			Coleoptera			Oligochaeta		
		S.S.	M.S.	F ratio	S.S.	M.S.	F ratio	S.S.	M.S.	F ratio	S.S.	M.S.	F ratio	S.S.	M.S.	F ratio	S.S.	M.S.	F ratio
Substrate	1	331.4	331.4	21.2**	1.11	1.11	14.0**	3.5	3.5	0.97	3.31	3.31	0.8	9.0	9.0	6.9	306	306	4.9*
Food Level	2	273.3	136.2	8.7**	2.58	1.29	16.0**	51.5	25.7	7.14*	63.7	31.9	7.6**	34.4	17.2	13.1**	273	137	2.2
S x F	2	127.8	63.9	4.1*	0.33	0.17	2.2	5.6	2.8	0.78	3.5	1.7	0.4	3.47	1.7	1.3	246	123	2.0
L:l vs m & h	1	5.13	5.13	0.3	0.24	0.24	3.0	23.6	23.6	6.56*	32.0	32.0	7.6**	1.9	1.9	1.5	72	72	1.2
L:m vs h	1	9.2	9.2	0.6	0.32	0.32	4.2*	9.5	9.5	2.64	12.7	12.7	3.0	6.9	6.9	5.3*	1	1	0.02
S:l vs m & h	1	57.3	57.3	3.7	0.55	0.55	7.0*	3.4	3.4	0.94	9.2	9.2	2.2	19.4	19.4	14.8**	15.6	15.6	0.26
S:m vs h	1	328.7	328.7	21.1**	1.8	1.8	22.8**	20.5	20.5	5.69*	13.3	13.3	3.2	15.7	15.7	12.0	434	434	7.0
Pooled error	30	468.0	15.6		2.36	0.08					126.0	4.2		39.0	1.3		1857	61.9	
Error	12	134.5	11.19	1.23	0.72	0.6	0.66	41.0	3.42	3.6*	57.8	4.8	1.27	13.6	1.13	0.8	906	75.5	1.43
Subsampling error	18	273.5	15.19		1.64	0.09		17.0	0.94		68.6	3.81		25.7	1.4		951	52.8	

* Significant at the 0.05 level.

** Significant at the 0.01 level.

Table 6. Ninety-five per cent confidence intervals on average number of organisms per ml sample in six groups associated with different treatment combinations placed in a riffle area of the Pine River. L = large and S = small substrates, l, m, and h are low, medium and high food levels, respectively. Data for Chironomidae were transformed to common logarithms.

	Ephemeroptera			Chironomidae			Other Diptera		
	l	m	h	l	m	h	l	m	h
L	2.5 ±10.81	2.25 ±10.81	0.5 ±10.81	3.0 ±0.55	2.9 ±0.55	2.6 ±0.55	4.31 ±2.49	2.77 ±2.49	1.0 ±2.49
S	10.3 ±10.81	11.8 ±10.81	1.32 ±10.81	3.4 ±0.55	3.45 ±0.55	2.7 ±0.55	2.69 ±2.49	3.07 ±2.49	0.45 ±2.49
	Trichoptera			Coleoptera			Oligochaeta		
L	4.57 ±3.36	2.77 ±3.36	0.7 ±3.36	1.96 ±1.04	2.02 ±1.04	0.51 ±1.04	5.35 ±49.69	0.81 ±49.69	1.4 ±49.69
S	3.09 ±3.36	2.63 ±3.36	0.52 ±3.36	3.71 ±1.04	3.03 ±1.04	0.74 ±1.04	9.65 ±49.69	13.71 ±49.69	1.68 ±49.69

medium food level was significantly different from high within small substrates. Thus, from the preceding and Table 6, it is clear more individuals are associated with smaller substrates and with low and medium food levels than with high food levels. If there is no significant relationship, there is this tendency of higher numbers to occur in small substrates and in low and medium food levels.

Although there was no consistent numerical relationship to substrate type in many of the groups, results of substrate substitution are generally in contrast to the higher numbers in larger substrates found in other studies. Food manipulation also resulted in data one might not expect. Nelson and Scott (1962), Minshall, G. W. (1967), and Mackay (1969) have attributed the majority of energy utilized by stream benthos to allochthonous detritus, and Egglisshaw (1964) found that numbers were significantly related to the amount of detritus present in a stream. He also found the same relationship by placing trays containing various amounts of detritus in the stream.

Differences in numerical relationships to substrate type between substituted and undisturbed substrates may be due to dissimilarities in physical complexity. Natural substrates are a heterogeneous mixture of large and small particles with larger particles having an algal or moss covering. Smaller substrates are less heterogenous in makeup, no moss or algal covering for insects to inhabit or large rocks present.

Substrates substituted were more homogeneous than natural substrates; large ones consisted mostly of particle sizes bigger than 16 mm, resulting in relatively large interstitial spaces and not having algal or moss growths extensive enough for insects to inhabit. Smaller substituted substrates would reduce interstitial space size, in comparison to larger substrates, allowing greater numbers of insects to inhabit the area.

Large numbers of insects occurring in low and medium food levels rather than in high food levels may have two explanations. At high food levels there may be so much plant material present as to result in formation of aggregates. Therefore, material on the inside of the aggregate would be relatively unavailable to macroinvertebrates as a food source since the available surface area per unit weight of available food is decreased. But with low and medium food levels plant material is more dispersed and offers a larger surface area which insects can utilize. Another possibility is that at high food levels interstitial oxygen can not be maintained due to decomposition of plant material resulting in interstitial oxygen concentrations below tolerance levels for stream macroinvertebrates. Those macroinvertebrates found would, therefore, inhabit the surface and not interstitial areas.

Seasonal Variations in Standing Crop

The life histories of aquatic insects include a wide array of forms. Some have one brood a year, others several; some show rapid growth in fall and spring with little during summer or winter; others grow from fall through spring; some have overwintering eggs, and others have ova with a long period of hatching or a very short one (Harker, 1953; Macan, 1957; Scott, 1958; Hynes, 1961; Hartland-Rowe, 1964; Maitland, 1964, 1966; Minshall, J. N., 1967; Heiman and Knight, 1970; and others). Despite differences in life history forms that exist in macroinvertebrates, from the analysis of all samples obtained from the Pine River through the year, general patterns of standing crop in the various groups can be seen.

Mayflies show two periods of relatively low numbers and biomass, late spring-early summer (May-June) and late summer, 5-19 August (Figure 1, Tables 7 and 8). The low biomass and numbers in spring would be expected following emergence of spring emerging species. During spring, average weight/nymph ranged from 0.03 mg to 0.05 mg, but during the low period of late summer, average weight was smaller, ranging from 0.01 mg to 0.03 mg. Highest standing crop of numbers occurred during two periods, early fall (16 Sept. 1968) and spring (12 May 1969), whereas highest biomass occurred during spring (11 April to 12 May 1969); average individual weight ranged from 0.02 mg to 0.03 mg and 0.16 mg to 0.79 mg, respectively.

Figure 1. Seasonal changes in average estimate of standing crop, numbers/m² and biomass (g/m²), of various groups from a riffle area of the Pine River.

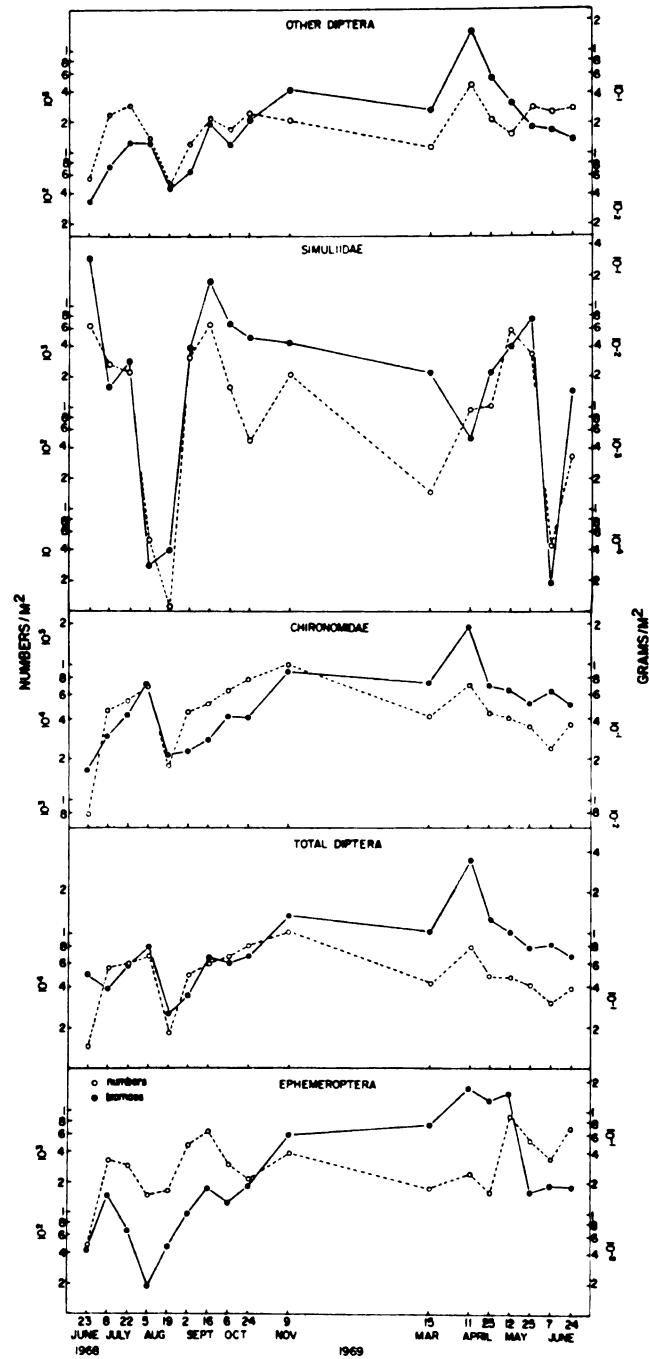


Figure 1

Table 7. Average estimate of individuals/m² in a riffle area of the Pine River on each collection date. Ranges are in parentheses.

DATE	NO. OF SAMPLES	EPHEMEROPTERA	ALL DIPTERA	CHIRONOMIDAE	SIMULIIDAE	OTHER DIPTERA	TRICHOPTERA	H. BOREALIS	COLEOPTERA	HYDRACARINA	PLECOPTERA	TOTAL
17-19 June	4	483 (1,90-758)	14,722 (6,928-36,527)	7,826 (6,552-10,647)	6,542 (83-24,832)	544 (275-948)	2,100 (415-5,838)	113 (12-390)	1,410 (758-2,832)	184 (107-332)	130 (12-367)	19,029 (8,933-44,714)
8 July	3	3,274 (5,773-5,773)	50,441 (15,383-97,583)	45,447 (14,644-85,386)	2,674 (24-24,832)	2,370 (415-6,078)	9,056 (5,071-14,016)	169 (0-296)	1,875 (1,067-2,393)	304 (201-1,765)	514 (24-1,458)	65,314 (24,171-122,485)
22 July	4	2,872 (1,633-3,777)	59,100 (33,401-102,567)	54,016 (32,687-83,571)	2,198 (12-8,694)	2,886 (1,202-4,512)	9,149 (8,708-9,510)	55 (12-118)	2,302 (1,460-3,376)	2,025 (1,954-2,745)	168 (12-330)	75,612 (46,758-122,295)
5 August	4	1,435 (913-2,534)	68,027 (54,558-82,562)	66,588 (54,496-73,630)	50 (0-153)	1,389 (442-2,719)	4,932 (1,406-8,116)	687 (71-1,457)	1,606 (786-1,961)	1,050 (821-1,600)	81 (12-182)	77,143 (58,476-96,755)
19 August	2	1,622 (908-2,275)	18,146 (14,137-21,861)	17,640 (14,273-21,307)	6 (0-12)	500 (134-875)	5,667 (4,388-6,546)	1,972 (553-3,412)	2,072 (174-3,963)	1,594 (486-2,701)	6 (0-12)	29,107 (21,023-37,187)
2 Sept.	5	4,548 (1,931-10,101)	49,361 (21,617-96,674)	44,002 (23,722-82,273)	3,125 (214-15,412)	1,237 (518-1,986)	7,244 (2,228-15,365)	654 (281-1,157)	2,577 (1,137-4,431)	2,744 (900-5,286)	414 (131-930)	65,841 (27,871-135,659)
17 Sept.	3	1,538 (3,818-3,172)	59,030 (34,863-91,650)	50,446 (36,421-78,344)	6,534 (11-19,128)	2,200 (1,457-3,579)	9,488 (3,170-15,393)	877 (0-2,239)	1,359 (1,458-2,796)	3,225 (1,967-5,394)	563 (154-1,093)	80,636 (47,464-124,562)
7 October	2	2,534 (1,732-4,374)	67,034 (46,446-86,567)	63,745 (44,786-73,962)	1,544 (617-5,375)	1,410 (1,043-1,880)	5,226 (1,183-9,181)	145 (71-462)	726 (415-883)	2,755 (925-4,479)	1,444 (1,116-1,537)	80,209 (52,833-106,113)
24 October	3	2,141 (1,239-2,844)	81,143 (43,563-111,678)	78,434 (42,867-104,516)	475 (0-1,244)	2,534 (703-5,888)	2,449 (1,318-3,206)	303 (0-569)	2,174 (1,005-3,834)	1,825 (2,410-2,410)	333 (47-918)	90,118 (48,122-125,118)
24 Nov.	2	3,732 (2,785-4,733)	101,085 (84,425-113,200)	98,128 (84,764-115,391)	560 (12-1,108)	2,100 (1,149-3,051)	4,672 (3,543-5,794)	468 (107-829)	2,355 (2,068-2,642)	2,686 (2,467-4,467)	1,618 (513-2,726)	116,211 (32,743-133,678)

1954	2	1,721 (294- 3,154)	41,755 (39,561- 44,010)	40,461 (38,576- 42,546)	147 (24- 271)	1,177 (1,161- 1,193)	1,705 (725- 2,688)	142 (63- 201)	4,215 (3,507- 4,923)	434 (299- 569)	190 (71- 309)	55,060 (44,443- 55,657)
11 April	3	2,435 (167- 4,603)	77,510 (48,231- 118,731)	71,722 (43,888- 107,563)	915 (160- 1,438)	4,842 (2,183- 9,455)	5,508 (1,090- 11,019)	750 (56- 1,706)	2,454 (1,002- 4,221)	5,027 (731- 11,139)	356 (185- 549)	35,240 (31,916- 150,522)
25 April	5	1,587 (17- 2,075)	47,130 (36,797- 56,504)	45,992 (34,277- 52,416)	1,057 (740- 1,503)	2,141 (1,750- 2,785)	3,699 (1,751- 5,189)	576 (296- 841)	1,177 (675- 1,683)	1,378 (540- 2,233)	174 (95- 267)	55,184 (40,455- 67,951)
12 May	4	8,853 (7,001- 18,776)	46,948 (35,113- 31,581)	40,315 (31,789- 62,838)	5,070 (706- 16,552)	1,563 (324- 1,688)	4,175 (1,503- 6,220)	886 (154- 1,576)	1,880 (1,138- 3,744)	3,267 (1,795- 5,462)	1,372 (628- 3,361)	67,075 (39,264- 113,523)
23 May	4	5,150 (754- 12,075)	40,711 (27,086- 61,501)	54,502 (24,413- 48,553)	3,568 (427- 9,206)	2,841 (2,189- 5,512)	3,456 (1,459- 7,441)	483 (190- 711)	2,164 (628- 4,965)	2,723 (1,288- 5,331)	1,228 (249- 2,369)	55,412 (51,454- 93,450)
7 June	3	3,436 (2,181- 1,765)	30,436 (18,444- 40,251)	27,838 (16,523- 36,943)	45 (0- 71)	2,555 (2,121- 3,187)	2,383 (789- 3,752)	391 (284- 462)	1,135 (892- 1,563)	3,027 (1,018- 5,279)	135 (24- 231)	40,552 (23,316- 55,850)
24 June	6	6,913 (4,580- 10,580)	50,187 (20,936- 52,121)	56,042 (24,543- 14,409)	332 (0- 1,836)	2,816 (357- 5,876)	5,353 (405- 9,645)	527 (178- 1,114)	1,038 (47,322- 2,322)	1,085 (0- 1,600)	93 (0- 344)	54,255 (32,915- 76,612)

Table 8. Average estimate of biomass (g/m²) in a riffle area of the Pine River on each collection date. Range in parentheses.

DATE	No. of Samples	EMPHEROPTERA	ALL DIPTERA	CHIRONOMIDAE	SIMULIIDAE	OTHER DIPTERA	TRICHOPTERA	H. BOREALIS	COLEOPTERA	HYDRACARINA	PLECOPTERA	TOTAL
13th 25 June	4	0.044 (0.007- 0.104)	0.498 (0.165- 1.437)	0.166 (0.136- 0.210)	0.208 (0.001- 1.177)	0.033 (0.024- 0.049)	0.342 (0.044- 0.715)	0.060 (0.004- 0.208)	0.099 (0.004- 0.173)	0.006 (0.004- 0.010)	0.007 (0.000- 0.021)	0.995 (0.267- 2.467)
8 July	3	0.144 (0.035- 0.264)	0.591 (0.167- 0.727)	0.301 (0.152- 0.504)	0.016 (0.001- 0.046)	0.074 (0.015- 0.176)	1.742 (0.510- 3.207)	0.119 (0.000- 0.477)	0.136 (0.106- 0.159)	0.007 (0.004- 0.011)	0.026 (0.000- 0.043)	2.445 (0.823- 4.412)
22 July	4	0.065 (0.022- 0.141)	0.577 (0.356- 0.950)	0.423 (0.263- 0.658)	0.029 (0.001- 0.110)	0.126 (0.093- 0.202)	0.569 (0.234- 0.752)	0.047 (0.014- 0.067)	0.192 (0.088- 0.274)	0.028 (0.009- 0.044)	0.001 (0.000- 0.003)	1.072 (0.711- 2.163)
5 August	4	0.019 (0.007- 0.047)	0.804 (0.551- 1.056)	0.684 (0.487- 0.843)	0.001 (0.000- 0.001)	0.120 (0.064- 0.212)	0.598 (0.245- 0.846)	0.014 (0.000- 0.033)	0.126 (0.046- 0.177)	0.022 (0.010- 0.030)	0.0004 (0.000- 0.0008)	1.569 (0.853- 2.156)
19 August	2	0.045 (0.010- 0.079)	0.302 (0.118- 0.539)	0.212 (0.116- 0.310)	0.045 (0.000- 0.001)	0.045 (0.002- 0.088)	0.590 (0.075- 1.105)	0.035 (0.023- 0.047)	0.206 (0.001- 0.411)	0.014 (0.007- 0.020)	0.0001 (0.000- 0.0003)	1.157 (0.234- 2.015)
2 Sept.	1	0.096 (0.013- 0.276)	0.342 (0.115- 0.749)	0.254 (0.134- 0.559)	0.040 (0.000- 0.198)	0.068 (0.021- 0.213)	0.566 (0.079- 1.494)	0.036 (0.004- 0.051)	0.138 (0.064- 0.186)	0.028 (0.005- 0.047)	0.011 (0.000- 0.049)	1.180 (0.314- 2.178)
16 Sept.	3	0.119 (0.061- 0.210)	0.662 (0.260- 1.508)	0.285 (0.173- 0.400)	0.173 (0.001- 0.519)	0.204 (0.057- 0.500)	0.777 (0.234- 1.502)	0.042 (0.000- 0.091)	0.087 (0.017- 0.165)	0.047 (0.024- 0.063)	0.003 (0.002- 0.006)	1.745 (0.571- 3.551)
6 October	2	0.126 (0.114- 0.150)	0.604 (0.343- 0.950)	0.415 (0.318- 0.494)	0.067 (0.012- 0.160)	0.122 (0.013- 0.276)	1.155 (0.503- 2.537)	0.012 (0.000- 0.027)	0.042 (0.025- 0.063)	0.020 (0.009- 0.040)	0.015 (0.003- 0.021)	1.962 (1.009- 3.512)
24 October	5	0.182 (0.084- 0.401)	0.676 (0.286- 1.134)	0.409 (0.199- 0.517)	0.049 (0.000- 0.200)	0.218 (0.088- 0.416)	0.490 (0.127- 1.532)	0.032 (0.003- 0.037)	0.184 (0.032- 0.296)	0.025 (0.017- 0.030)	0.053 (0.001- 0.185)	1.609 (0.487- 3.553)
29 November	2	0.589 (0.300- 0.878)	1.362 (0.947- 1.798)	0.893 (0.821- 0.966)	0.044 (0.001- 0.087)	0.425 (0.125- 0.745)	1.738 (0.672- 2.903)	0.052 (0.003- 0.102)	0.292 (0.259- 0.324)	0.032 (0.009- 0.055)	0.181 (0.018- 0.345)	4.244 (2.204- 6.303)

1963 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The peak in numbers on 8 July 1968 is believed to be an artifact because earlier collections gave estimates of biomass and numbers which are believed to be too low.

From the preceding an overall picture of the changes of the mayfly fauna with seasons may be deduced. In spring, emergence results in recruitment of many small nymphs; however, since there are still large individuals present, average weight/individual is maintained at a moderate level through most of the summer. The majority of mayflies in Michigan's trout streams have emerged by late August (Leonard and Leonard, 1962) at which time there are very few large nymphs in the stream; nearly all occur in the egg stage or as relatively small nymphs. As fall progresses biomass and numbers increase with growth and hatching of dormant eggs.

Maitland (1966) found that mayflies were most abundant in May to August and decreased throughout fall and winter. In a productive stream studied by Egglshaw and Mackay (1967) higher numbers of nymphs occurred during the winter months, but no significant changes were observed in two relatively sterile streams during the year. Comparisons among different authors as done here suffers because of differing methods (see Jonasson, 1955, and Macan, 1958, for a review of sampling methods) and differing objectives. But despite this, comparisons of the general results can be made and perhaps some conclusions drawn. In both of these studies the kicking method was used, catching the floating invertebrates in large meshed

nets. The present study used a fine meshed screen which retained many of the very smallest nymphs or larvae. It is therefore believed that collections in the present study give a more accurate description of the changes in the fauna.

Highest numerical standing crop of dipteran larvae occurred in late November, 1968, with another peak occurring in mid-April, 1969 (Figure 1, Table 7). However, biomass was largest in early spring with a lesser peak in late fall. Lowest numbers were found in late summer (19 August) and late spring-early summer (7 June). Biomass was also low at these times. Minckley (1963) found seasonal changes in abundance of dipteran larvae, but time of maximum abundance varied with habitat which changed as he progressed downstream. Maitland (1966) found the greatest numbers occurring in summer which undoubtedly is a reflection of his use of a large meshed screen in collections.

When the order is divided into chironomids, simuliids and all other dipterans, the trends in biomass, numbers and average individual weight are similar (Figure 1, Tables 7 and 8). However, it is not surprising that the seasonal variation of the order as a whole reflects that of the chironomids, the dominant group. Seasonal changes in chironomid larvae have been noted by other authors. Egglshaw and Mackay (1967) in studying a productive stream, found peak numbers in June and July with lows in late fall and late winter-early spring. Pupae occurred from May to October, but in higher numbers in

May, June and July. Allen (1951) found peak numbers in mid-winter with pupae present at all times. In one area on the River Susaa Jonasson (1948) found maximum numbers in spring due to newly hatched and overwintering larvae, with numbers decreasing appreciably in succeeding months. He found a smaller peak in numbers during late summer with lows occurring in fall and winter. At another area on the river he found that numbers increased from spring to late summer, followed by an appreciable decline. In the present study, peak numbers of chironomids occurred in late fall and early spring. Individual dipterans in late fall averaged 0.01 mg each, whereas in early spring they averaged 0.02 mg, indicating that the chironomid fauna as a whole consists of larger individuals which leads to highest biomass at this time. No pupae were present in late fall collections, whereas in early spring (11-25 April 1969) 1% to 2% of the chironomids collected were pupae. During the summer less than 1% were pupae.

Simuliid larvae are well-known for their patchy distribution and a tendency to drift which results in extreme fluctuations in numbers present in collections (Chutter, 1968; Ulfstrand, 1968). Perhaps, though, a general description of standing crops can be made. Maximum numbers and biomass occurred during early summer (23 June to 22 July 1968 and 23 June 1969). This is undoubtedly from hatching of overwintering eggs and growth of larvae (Ulfstrand, 1968). There was another peak in fall (16 September 1968) and at these two

peaks average individual weight ranged from 0.01 mg to 0.03 mg. There were minimums during late summer and early spring with larvae averaging 0.15 mg to 0.89 mg each. This may be partially due to sampling error. Pupae made up from 0.2% to 1% of the total population on collections prior to these low periods with only a few or none recorded at other times, thus indicating emergence and reproduction responsible for the lows. Frost (1942) observed a similar distribution of numerical standing crop in her study. Allen (1951) found that pupae were most abundant during the same seasons observed in this study but found no seasonal changes in larval abundance. Jonasson (1948) found high numbers of larvae in the spring but very few until fall when they were again abundant.

The majority of other dipteran larvae collected were large specimens of the families Rhagionidae, Empedidae, and Tipulidae with Dolichopodidae and Tabanidae taken in fewer numbers. Small larvae of the family Heleidae were also taken. Taken as a group these larvae demonstrated a low in numbers in late summer (19 August 1968) and late spring (12 May 1969) (Figure 1, Table 7). Biomass showed a low at two periods, late summer (19 August 1968) and late spring-early summer (23 June to 24 July 1968) (Figure 1, Table 8). Numbers increased on 23 June 1969 then stabilized, whereas biomass decreased. These trends are undoubtedly due to emergence of larvae and recruitment of young.

There were four major families represented in trichoptera: Hydropsychidae, Helicopsychidae, Glossosomatidae (Hydropsyche, Helicopsyche and Glossosoma, respectively) and Limnephilidae, with the latter occurring less frequently than the first three, while those of other families occurred infrequently. Caddisflies, numbers and biomass, showed several periods of maximum and minimum (Figure 2, Tables 1 and 2). But the low in both numbers and biomass in late fall (24 October 1968) may be due to sampling bias as biomass seems to be increasing prior to a winter decrease, and the trend in numbers is from a high in September to a winter low.

Average weight/individual and the percentage of pupae in the population showed seasonal trends. Percentage pupae in summer 1968 increased from 2% at 23 June to a high of 10% on 5 August after which there was a decrease until none were present on 6 October. Average weight/individual varied from 0.10 mg to 0.20 mg and dropped in early fall to 0.08 mg (16 September). Average weight then increased as fall progressed to a high of 0.38 mg on 29 November. By 15 March 1969 this had dropped to 0.23 mg and to 0.19 mg by 11 April at which time less than one percent of the population was pupae. Average weight increased to a high of 0.75 mg by 12 May then decreased to a low of 0.21 mg on 24 June. After the start of pupation in April the percentage of pupae increased to a high of 12% on 7 June then decreased to 1% on 24 June.

Figure 2. Seasonal changes in average estimate of standing crop, numbers/m² and biomass (g/m²), of various groups from a riffle area of the Pine River.

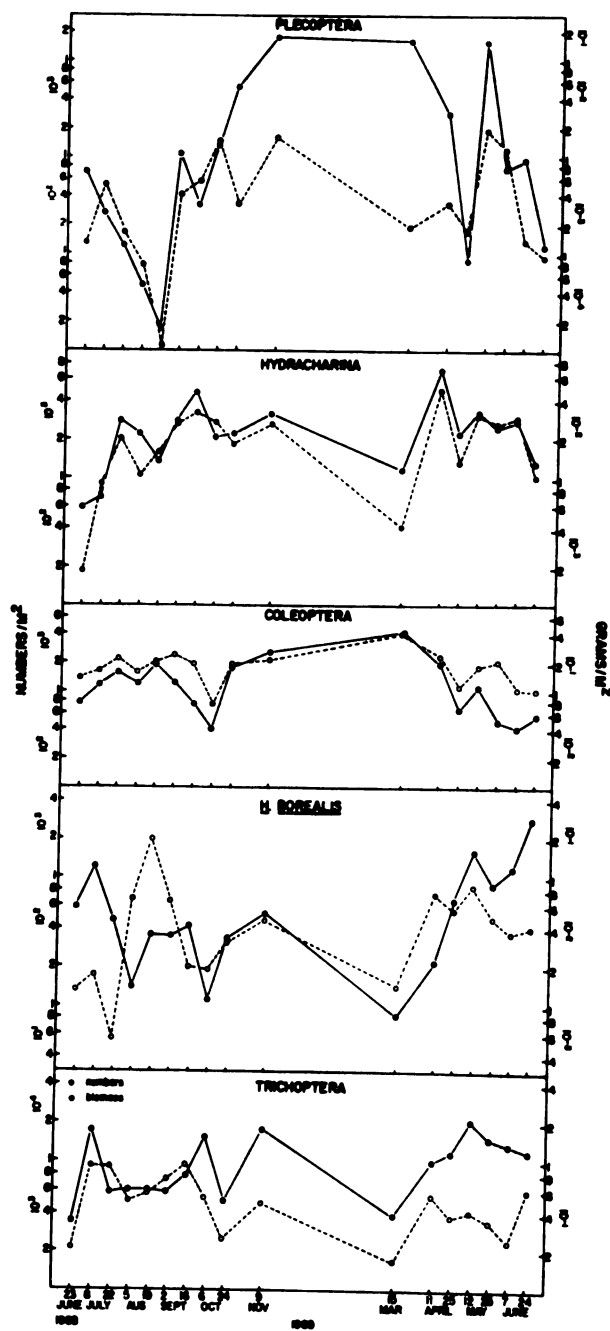


Figure 2

From the above, a general seasonal cycle may be inferred for trichopterans as a whole. Biomass and numbers are highest in spring prior to emergence due to gains in weight following winter senescence and the hatching of overwintering eggs. Emergence continues through the summer due to those species which emerge late and species that are multivoltine. As fall progresses there is less emergence and growth occurs leading to a high in biomass and numbers in fall. Numbers and biomass decrease due to winter mortality, and as temperatures increase at the end of winter, growth of larvae resumes and overwintering eggs hatch.

Seasonal variations in trichopterans have been noted by other authors. Frost (1942) and Hynes (1961) found a steady decrease in numbers as winter progressed to lows in late winter and early spring, with highest numbers occurring from summer to fall. Jonasson (1948) found no marked seasonal variation but noted largest numbers occurring from January to May. Minckley (1963) noted that in riffle areas there were periods of high populations, but these were different at various stations in the stream. But all highs occurred between January and May. Allen (1951) found that in the families Hydropsychidae and Rhyacophilidae average weight varied similarly to the variations noted in the present study: smallest in late summer-early fall and highest in late winter-early spring. Scott (1958) found that there was a common seasonal pattern to all species he studied, a summer minimum and a winter maximum.

Data were obtained for an individual species of trichopteran, Helicopsyche borealis (Figure 2, Table 7). Unlike the order as a whole, maximum numbers occurred in August 1968 with a decline to a low in late winter with a smaller maximum occurring in spring. Maximum biomass occurred in early summer, highest during June and July in both 1968 and 1969. Percentage pupae and average weight/individual varies seasonally. Average weight decreased from 0.49 mg on 23 June 1968 to 0.32 mg on 22 July, whereas percentage pupae in the population increased from 45% to 95%. Pupae were present in the collection on 2 September and 24 October, being less than one percent of the population, and absent until spring collections. Average weight increased from 0.01 mg on 5 August to 0.11 mg on 29 November then decreased to a low average weight of 0.03 mg on 11 April 1969. From this low, average weight increased to a high of 0.50 mg on 24 June. Percentage pupae increased from 1% on 25 April 1969 to 23% on 24 June.

The life history of H. borealis seemingly then is annual with two broods present. Emergence begins in late spring reaching a peak in early summer, resulting in a peak recruitment of young larvae in late summer. Ross (1944) states that there apparently is a continuous succession of generations, emergence occurring from May to September. This could coincide with embryonic development lasting between 9 and 25 days for trichoptera (Scott, 1958). Perhaps some larvae are produced in spring, grow and emerge in the fall, producing ova.

Mortality of larvae occurs through winter. Delayed hatching probably occurs in those ova produced in fall giving another period of recruitment and reduction of average individual weight along with the resumption of growth in spring.

The majority of the beetles collected were of the family Elmidae. Members of Psephenidae were collected only periodically. Therefore, seasonal variation in standing crops is mostly a reflection of elmid life histories. Maximum biomass and numbers occurred in late winter after which there was a decline (Figure 2, Tables 1 and 2). The extreme low in numbers on 6 October may be due to sampling error as the trend from the beginning of collections to winter was toward an increase in numbers. Pupation in both of these families occurs on the shores of the streams (Pennak, 1953; Leech and Chandler, 1956). Therefore, only adults and larvae were collected. Adult percentage of the population between 23 June and 22 July ranged from 2.5% to 5% and decreased as summer progressed to fall. No adults were collected from 6 October until the following spring when adults again began to appear in the population because of pupation, numbers increasing as spring progressed.

Average weight/individual increased due to growth from 0.05 mg on 23 June 1968 to 0.10 mg on 19 August, then decreased to 0.03 mg on 16 September probably because of recruitment of young and emergence of adults. Increase in average weight then occurred as young grew to a high on 29 November

of 0.11 mg which was maintained until 15 March 1969, after which average weight decreased to a low of 0.02 mg on 23 May, probably due to recruitment of overwintering young, and then increased to 0.06 mg on the last date, 24 June.

These two families of beetles, Elmidae and Psephenidae, are thought to have a two-year life cycle (Pennak, 1953; Leech and Chandler, 1956) and the data presented here seemingly support this thought. Perhaps, then, seasonal changes occur in the following manner. Pupation results in high numbers of adults in early summer with the production of ova which have an extended period of hatching, resulting in a gradual increase in larvae through summer. Concurrently, those larvae which will not pupate until the following spring grow, and as the number of young larvae increase through late summer, there is a decrease in average weight/individual and biomass. Growth of the population as a whole leads to an increase in biomass through late fall. With the advent of spring, mature larvae leave the stream to pupate leading to a decrease in average weight, numbers and biomass. Frost (1942) found that higher numbers of adults occurred during the winter at a time when larvae were lowest in numbers. Highest number of larvae in her study were found in July.

Although there are fluctuations in standing crops (biomass and numbers), there are obvious trends in standing crops of water mites (Figure 2, Tables 1 and 2). There is an increase from an early summer low to peak numbers and biomass in

fall. Following this there is a winter decrease, an increase in spring, followed by an apparent decrease in early summer. Maitland (1966) found the highest numbers of water mites in his samples from May to October, whereas Jonasson (1948) found the highest numbers in late winter and early spring; Jonasson attributed this to the migrations of individuals from decaying vegetation along the stream to the stony substrates. There is some confusion concerning whether water mites reproduce throughout the year or during late spring or early winter (Pennak, 1953). Present data seem to support the latter.

Stoneflies of the genus Taeniopteryx made up the majority of plecopterans collected, with Pteronarcys taken periodically. Nymphs did not occur in high numbers in this study which leads to obvious sampling errors in estimating standing crops through the year, and makes it very difficult to discuss seasonal changes. Spring and early summer emergence occurred in Pteronarcys, but this should not have caused the extreme low on 19 August 1968 as the majority of stoneflies collected were Taeniopteryx. This low may be due to two factors: one is sampling as previously mentioned. Secondly, it has been observed that benthic organisms may go as deep as 30 cm (Coleman and Hynes, 1970), presumably to escape particular rigors of the environment (Maitland, 1964). Possibly summer temperatures are a form of "rigor" for Taeniopteryx, a winter emerger (Frison, 1935); large numbers of adults were observed

on 15 March 1969. As temperatures decrease in the fall, Taeniopteryx emerges from the substrate and resumes growth leading to a high biomass in the winter. Emergence occurs in late winter resulting in a low biomass, but oviposition leads to an increase in numbers during spring.

In this study macroinvertebrates taken as a whole demonstrated fluctuations seasonally with peak numbers in late fall-early winter and a lesser maximum in spring; the largest biomass occurs in early spring before emergence commences. Changes in numbers reflect the changes in dipteran larvae as these were the predominant group numerically. For example, the extreme low on 19 August was due to few numbers of dipteran larvae present. The low estimate of both biomass and numbers on the first collection date, 23 June 1968, is not entirely a reflection of the fauna. Because it occurred in every group on this date, I feel this low is due to sampling error. The decline through winter may not be due entirely to winter mortality. Babcock (1954a, b) points out that insects may be found as deep as 12 cm and Coleman and Hynes (1970) have shown that insects may occur as deep as 30 cm in the substrate. It may be that insects seek the lower strata of the substrate to escape rigors of winter. As temperatures increase with the advent of spring, they return to the surface and, with hatching of overwintering eggs and resumption of growth, there is a spring increase in both numbers and biomass. In retrospect then, a general pattern of change may

be described. Lowest numbers and biomass are found in early summer, both increasing through fall. Both decrease due to winter mortality and possible vertical movement downward, but with warmer temperatures numbers again increase, due to hatching and a vertical movement upward, and biomass reaches a maximum before emergence.

The seasonal change observed in the present study is not entirely in accordance with that found by other authors. Maitland (1964) found peak numbers and biomass during summer months; however, he stated that the streams he studied were subject to extreme winter conditions and spates which led to low numbers during winter. Although flooding was observed in the present study, particularly during spring, there was no scouring of the bottom, which is a situation that has been shown to be an important factor to stream benthos (Minckley, 1963; Maitland, 1964, 1966). Egglshaw and Mackay (1967) found a maximum biomass in spring, but maximum numbers occurred in July and December through March. Jonasson (1948) found that maximum numbers occurred in spring. All of the above authors used large meshed screens which allow the loss of smaller nymphs, whereas I used a fine meshed screen which retained small nymphs and led to better characterization of the changes in numbers and biomass.

Annual Production Estimate

In past years the production of aquatic plants and fish has been measured. Recent years have seen an increase in the measurement of production of invertebrates but limited to single species and then to those that demonstrate certain types of life histories (see Mann, 1969, and Waters, 1969, for reviews). Presently there is particular emphasis on attempts to determine production of entire benthic faunas and by a means which is fairly simple. Hynes and Coleman (1968) have attempted to do this (see Fager, 1969, and Hamilton, 1969, for modifications and criticisms of the technique) by using length measurements of the fauna collected over a year's time. Waters (1969) has recently reviewed the literature concerning turnover ratio in freshwater invertebrates and found that it ranged from 2.5 to 5, averaging 3.5, which is comparable to the turnover ratios which Hynes and Coleman found with their method.

Although the present study was not designed to obtain an accurate estimate of production, perhaps a gross estimate may be obtained by using Waters' assumed constant, 3.5. It was felt that the results might be compared to the production estimate of Hynes and Coleman (1968) as well as estimates obtained in future studies. Average ash-free dry weight was 2.52 g. Multiplying by the constant gives an average of 8.0 g/m²/yr. But, as Waters points out, in a fauna which is

dominated by multivoltine species this ratio would be higher by two-or-threefold. Since the fauna in this study undoubtedly consists primarily of multivoltine species, mayflies, dipterans, and various species caddisflies, it seems reasonable to assume that the turnover ratio would be near seven (which assumes an average of two generations a year) in which case production of ash-free dry weight would be $17.7 \text{ g/m}^2/\text{yr}$. It was determined that dry weight is about 6.7 times greater than ash-free dry weight. Egglisshaw and Mackay (1967) found that wet weight of insects averaged 5.5 times dry weight. Together these two factors give an estimate of wet weight as being 37 times greater than ash-free dry weight. Multiplying this factor by the estimate of ash-free dry weight gives a production estimate $654 \text{ g/m}^2/\text{yr}$. This river is high in nutrient and primary production (Tesar, 1970) and is comparable in secondary production to that of 620 g/m^2 of another hardwater stream as determined by Hynes and Coleman (1968). Although Waters' turnover ratio is highly speculative, it would seem that an estimate of $654 \text{ g/m}^2/\text{yr}$ may be in the right order of magnitude. This is also a method which is much more simple and less time consuming than the one proposed by Hynes and Coleman.

Observations on *Sphaerium striatinum*

Three species of fingernail clams were represented in the collections: *Sphaerium striatinum*, *Pisidium compressum* and

P. fallax. Pisidium occurred infrequently; therefore, only S. striatinum will be considered in the following discussion.

Clams were picked from the decanted material which remained in the sieves and from the remaining gravel, then stored in 75% ethyl alcohol. Numbers and ash-free dry weight were expressed as for the other invertebrates. Ash-free dry weight was determined in the same manner as for the other invertebrates. Ash-free dry weight was determined in the same manner as for the other invertebrates. For growth studies the length of each clam was taken to the nearest 0.2 mm with an ocular micrometer. Those too large for the microscope's field were measured to the nearest 0.2 mm with a pair of dividers.

It was observed that after ashing young within the adults maintained their form and rigidity. Therefore, to determine numbers of young produced and time of reproduction, adults and young that they contained were measured from 23 June to 2 September 1968. After 16 September until the termination of the study the young were counted after ashing but no measurements taken.

Standing Crop and Habitat

Average number/m² was high on the first collection date, 23 June 1968, after which there was a decline followed by an increase on 5 August to the prior level (Figure 4, Table 9). Biomass and numbers increased to a high on 22 July but then decreased to an extreme low on 19 August. This decrease is

Figure 3. Seasonal changes in average estimate of total standing crop, numbers/m² and biomass (g/m²), from a riffle area of the Pine River.

Figure 4. Seasonal changes in standing crop of Sphaerium striatinum, numbers/m² and biomass (g/m²), in a riffle area of the Pine River.

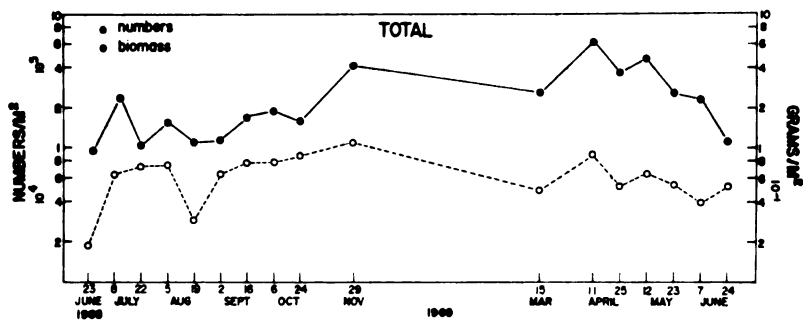


Figure 3

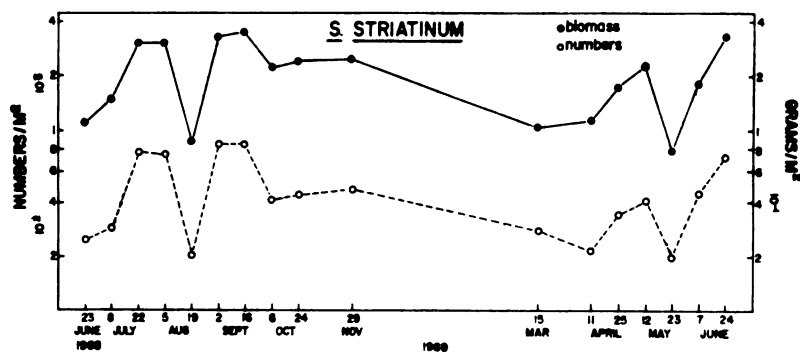


Figure 4

Table 9. Average number/m² and grams/m² of Sphaerium striatinum on each sampling date.
Two standard deviations in parentheses.

DATE	June 23 1968	July		August		September		October	
		8	22	5	19	2	16	6	24
NUMBERS	248 (248)	296 (660)	1561 (936)	764 (992)	201 (134)	848 (1342)	821 (1866)	410 (276)	455 (204)
BIOMASS	1.101 (1.296)	1.492 (3.892)	3.116 (5.504)	3.092 (2.90)	0.874 (0.70)	3.370 (6.570)	3.537 (7.578)	2.278 (2.190)	2.404 (1.758)
n	4	3	4	4	2	5	3	3	5

DATE	Nov. 29	March 15 1969	April		May		June	
			11	25	12	23	7	24
NUMBERS	498 (268)	278 (318)	213 (206)	344 (628)	409 (620)	192 (272)	442 (498)	719 (1682)
BIOMASS	2.535 (0.478)	1.024 (0.212)	1.141 (1.252)	1.739 (3.826)	2.249 (3.662)	0.764 (1.110)	1.809 (1.856)	3.330 (8.020)
n	2	2	3	3	4	4	3	6

undoubtedly due to sampling error as both numbers and biomass increased next sampling, reaching high in September. Through fall and winter there was a decrease in numbers and biomass, probably because of winter mortality, reaching a low on 11 April 1969. From this time the tendency of both was to increase, probably from spring reproduction. The extreme low on 23 May is again probably due to sampling error as the tendency from 23 March until termination of the study was to increase.

Biomass and numbers were associated with smaller substrates from TP₁ to TP₅ (Table 10) and during these periods the disparity between the average standing crops associated with the two substrate types was generally great. At TP₆ and TP₇ numbers and biomass were higher in larger substrates, but at the last two periods both parameters were again associated with smaller substrates. It should be pointed out that there is extensive overlap of standard deviations in each time period, thus the differences between standing crops of small and large substrates are insignificant statistically. However, perhaps the trend is meaningful in itself.

From Table 11 it can be seen that both highest numbers and largest biomass were associated with macrophyte and riffle habitats an equal number of times, both about equal on the last date. Even though there was only one sample obtained from macrophyte beds on each date, compared with means of samples from riffle habitats, I think the comparisons give an

Table 10. Relationship between average numbers/m² and biomass in grams/m² of Sphaerium striatinum and substrate type with time. Two standard deviations in parentheses; none is given when only one sample is present.

		TP 1	TP 2	TP 3	TP 4	TP 5	TP 6	TP 7	TP 8	TP 9
NUMBERS	Small	403 (770)	885 (652)	924 (200)	442 (260)	539 (520)	165 ---	358 (626)	352 (544)	1,047 (2,394)
	Large	193 (344)	165 ---	228 (102)	130 ---	441 (202)	258 (244)	411 (626)	229 (274)	391 (256)
BIOMASS	Small	2.064 (4.704)	3.734 (3.734)	2.905 (1.518)	2.315 (2.158)	3.126 (1.836)	0.948 ---	1.633 (3.554)	1.415 (2.146)	4.665 (11.672)
	Large	0.793 (1.624)	0.631 ---	0.956 (0.410)	0.654 ---	2.085 (1.060)	1.133 (1.006)	2.56 (3.694)	0.942 (1.136)	1.995 (1.774)

Table 11. Average numbers/m² and biomass in grams/m² of Sphaerium striatinum associated with habitat type. Two standard deviations in parentheses. Only one sample obtained from macrophyte beds on each date.

	Date	June 23	July 8	July 22	Sept. 2	Sept. 16	October 6	October 24
NUMBERS	Macrophytes	356 ---	142 ---	663 ---	1,884 ---	1,884 ---	355 ---	427 ---
	Riffles	213 (308)	373 (854)	805 (1,134)	589 (782)	291 (452)	438 (368)	462 (350)
BIOMASS	Macrophytes	1.789 ---	0.652 ---	1.624 ---	8.602 ---	7.832 ---	2.014 ---	2.50 ---
	Riffles	0.768 (1.692)	1.918 (5.104)	3.622 (6.346)	1.972 (2.322)	1.391 (2.080)	2.41 (3.026)	2.38 (2.010)

estimate of what effect macrophytes have on sphaeriid distributions.

The general trends in standing crops shown here, high during spring, summer and early fall with a general decline through winter months, are similar to those found by Foster (1932). Although he sampled approximately monthly, no comparison can be made with regard to standing crops as he did not sample a constant area.

The two extreme lows that occurred in the present study may be caused by high waters or sampling error. Minckley (1963) and Maitland (1964, 1966) have discussed the effect of spates in streams which leads to a reduction of the fauna by washing them away and destroying them. However, in the present case, even though water levels were about six inches higher than normal, I believe the lows are due to sampling because of the later return to prior levels, even though water levels were still high. Gale (1969) studied standing crops of sphaeriids in the Mississippi River from June to December, S. striatinum being present in substantial numbers. Highest numbers and biomass occurred in August, approximately 5,000/m² and 50 g/m² dry weight. Highest numbers in the present study were 1,005/m² during September. Highest biomass also occurred in September, 3.54 g/m² ash-free dry weight. If it is assumed the conversion factor of 6.7 to convert ash-free dry weight to dry weight is valid, an estimate here of 24 g/m² is given.

Herrington (1962) indicates that this species, most common of the genus, has a wide tolerance of habitat type, being present in sand, sandy-gravel, and muds of creeks, rivers, and lakes. In the present study the smaller substrate types seem to be preferred, generally having higher average standing crops. Gale (1969) comments that substrate type did not appear to greatly affect the abundance of sphaeriids (two species) except that fewer occurred in substrates of bare rock, gravel, or hard clay. It seems plausible that the relation to substrate type is due to physical effect. Larger substrate types contain rocks which occupy space that would be available if smaller rocks or sand were present. This would also be a possible reason for the differences between standing crops of Gale's study (where substrate consisted of sandy silt) and the standing crops of the present study.

There seems to be no adverse effects on S. striatinum distribution by extensive summer growth of macrophytes. This might be expected in a species which has a wide tolerance of habitats. This is in contrast to Gale's (1969) report that areas associated with vegetation generally supported low sphaeriid populations. However, it must be pointed out that he was dealing with very large standing crops, and areas of vegetation in his study may still have yielded populations equal to or greater than were found in the present study.

Growth and Reproduction

From Figure 5 it seems that the majority of the young are extruded when they are 3.6 mm to 3.8 mm in length; few smaller free-living young were found in the collections. Length measurements of young still contained by adults showed very few 4.0 mm or larger. The percentage distributions in Figure 5 also show that a bimodal curve is present in a number of samples, 8 July to 5 August, 2 September to 16 September 1968, and 23 May to 24 June 1969. However, no growth can be interpreted from these distributions as there are no changes in various size groups through the year. Numerous individuals reached a size of between 10 mm and 11 mm, with some being as large as 13.5 mm.

Table 12 shows the size of adult and number of young contained. The largest number of adults examined contained two young, with a substantial number containing one. A few adults contained 3 and 4 young. Smallest adults containing young from 23 July to 2 September were 7.4 mm and of those equal to or greater than this size the percentage containing young is shown in Table 13. It can be seen that the greatest percentage carrying young occurs from late fall to spring with the least occurring during summer and early fall.

Minimum size of free-living young and maximum sizes of young still within adults coincide; thus young are released when they reach a size of 3.6 to 4.0 mm. This is in accordance with Foster's (1932) findings. However, maximum size of adults

Figure 5. Length frequency distributions for collections of Sphaerium striatinum, by date, from the Pine River.

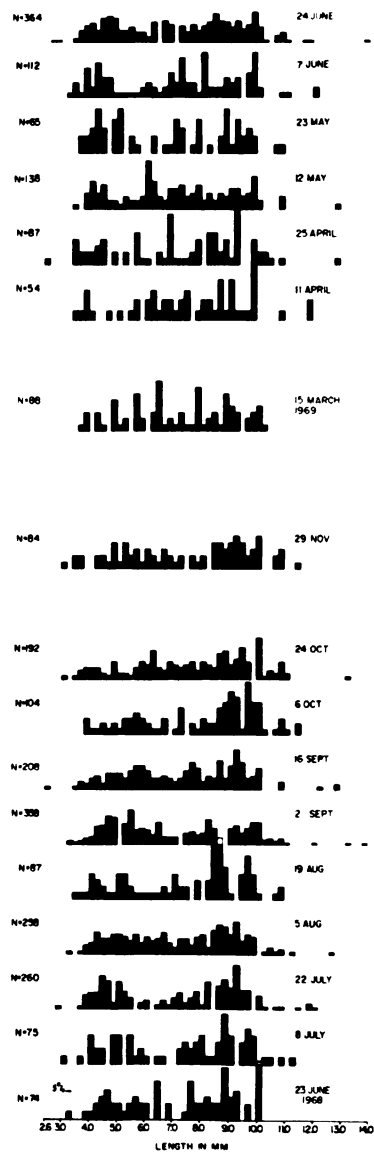


Figure 5

Table 12. Relationship between size and frequency of number of young contained in brood pouches of adult Sphaerium striatinum.

Number of Young	Adult Size in mm															Total				
	7.4	7.6	7.8	8.0	8.2	8.4	8.6	8.8	9.0	9.2	9.4	9.6	9.8	10.0	10.2		10.4	10.6	10.8	11.0
1	2		2		3	2	2		4		5	4	4	3			2			
2			2		3	4	6		10	4	13	8	2	19	2		2	2	2	
3									2			2								
4							2		2		2								2	8

Table 13. Percentage of Sphaerium striatinum population over 7.4 mm in length containing young by collection date.

DATE	1968	July		August		September		October		November
		8	22	2	19	2	16	6	24	
PERCENT	57	41	47	16	33	16	12	48	63	67

DATE	1969	April		May		June	
		11	25	12	23	7	24
PERCENT	76	75	68	66	72	55	52

in Foster's study was smaller; the largest specimen was 10 mm with the majority of the largest individuals being 9-9.5 mm.

Gilmore (1917) stated that the majority of adult S. striatinum contained two young, one in each pouch, with a few containing four. Foster (1932) obtained similar results but also found a few adults with one or three young, as found in the present study, and concluded this was due to the recent extrusion of young. The bimodal curves (Figure 5) seem to suggest that these sphaeriids live two years and from this and Table 12 the majority of reproduction and nurturing of young seems to occur during colder months with the majority of young being released in spring, summer, and fall. Monk (1928) reached a similar conclusion with this species. Foster arrived at different conclusions; finding a bimodal curve in size distributions, he attempted to show that it was due to periods of maximum extrusion of young during spring, summer and fall. It should be pointed out that these three studies were conducted in two divergent habitats, Foster's work in an oxbow lake and Monk's and the present study in streams, and the differences in conclusions about the life history of the clam may be derived from differences in life history response to habitat type.

GENERAL CONCLUSIONS

The effect of substrate size, macrophyte growth and detritus distribution was demonstrated in the present study. As a whole the benthic fauna does not demonstrate a definite association with either small or large substrates numerically, but biomass is higher in larger substrate sizes. Standing crop, biomass and numbers, is higher in macrophyte beds than in riffles when they are dense but the habitats are similar during early growth phase of the plants and in late fall when they have died back. Substrate-food substitution experiment showed that the majority of the groups were related to low and medium food levels and small substrate sizes. Although macro- or microdistribution of invertebrates may be related to a particular factor, the interaction of many factors is undoubtedly the most important aspect of the problem.

Most benthic invertebrate studies seem to disregard the problem of sampling technique, and in this case it was random. A stratified random sampling design, according to at least three substrate sizes and macrophyte beds, would have alleviated this problem and led to less variation in estimates of standing crops.

Coarse screens are normally utilized in benthic studies and miss many of the younger larvae which were obtained in this study by the use of a fine meshed screen. Compared to other studies the present study obtained substantially higher estimates of numbers of macroinvertebrates/m², the highest being 116,000; thus a more accurate estimate of standing crops and seasonal changes has been given.

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LITERATURE CITED

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