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Title: THE SEASONAL OCCURRENCE AND DISTRIBUTION OF STONEFLIES (PLECOPTERA) OF A WESTERN OREGON STREAM

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Plecoptera were collected from four sampling stations selected to represent a range of conditions on Oak Creek, a small woodland stream originating in the foothills of the Oregon Coast Range. The elevation of Site I was 700 ft. while the lowest site was located at 225 ft. Monthly benthos samples were taken for one year from a riffle and glide section at each site using a stovepipe sampler (6 in. dia.) and a standard tropical fish net. Samples were sorted in the laboratory and Plecoptera identified and placed into 1 mm size classes. Emergence of adults was measured for 13 months using a tent-shaped trap ($1 m^2$) at each site. Traps were checked once or twice weekly.

Forty-two species of Plecoptera were found in Oak Creek. The number of species is very large when compared with other studies. The stonefly fauna is fairly similar to that reported 35 years ago.

Thirty-seven of the 42 species complete emergence during the

spring. Temporal separation is marked in the emergence periods of Nemoura and Leuctra. Examples of split emergence periods and early emergence of males were found. Life cycle information is given for a number of species and genera.

Using the Shannon-Wiener function, diversity of emerging adults ranks by season as: Spring > Summer > Winter > Fall. The diversity of the sites on a yearly basis is: II > I > III > IV. Using a percentage of similarity index it is concluded that Sites I and II are very similar. Site III is intermediate while Site IV is quite different.

A number of examples of restricted distributions are cited. These examples illustrate that differences in longitudinal distribution are important in ecological segregation. Herbivorous stoneflies (suborder Filipalpia) comprise a greater proportion of the fauna at the upper site while predaceous stoneflies (Setipalpia) predominate in the lower areas.

Water depth and amounts of leaves and silt are important factors in determining the distribution of stoneflies. Most species are abundant in leaf drifts. Microhabitat selection does not appear to be rigorous.

The Seasonal Occurrence and Distribution of Stoneflies (Plecoptera) of a Western Oregon Stream

by

Cary Dean Kerst

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THE SEASONAL OCCURRENCE AND DISTRIBUTION OF STONEFLIES (PLECOPTERA) OF A WESTERN OREGON STREAM

INTRODUCTION

Plecoptera are one of the most abundant components of benthic communities in Western Oregon streams. For example, Anderson and Lehmkuhl (1968) record over 6000 Plecoptera nymphs in a daily drift sample from Oak Creek. Plecoptera have been found to be important as fish food (Dimick and Mote, 1934) and as bird food (Hamilton, 1933; Knappen, 1934). Stoneflies have at least once been found to be injurious to vegetation (Newcomer, 1918).

Basic information concerning species composition and life cycles is lacking on Oak Creek. The present study was undertaken to provide background information for further ecological work.

The objectives were:

1. To determine the species composition and seasonal succession of adult stoneflies at four sampling stations on Oak Creek.
2. To determine the life cycles of these stoneflies.
3. To determine the general habitat preferences of the nymphs.
4. To assess factors influencing species diversity and habitat partitioning by stoneflies through comparison of four sites on Oak Creek.

LITERATURE REVIEW

As this project involves the study of an order, much literature is of potential use. Jewett's (1959) excellent monograph on the stoneflies of the Pacific Northwest has been invaluable. Ricker (1943) published on the stoneflies of Southwest British Columbia. A thesis by Ball (1946) was concerned with the seasonal succession of stoneflies of Willamette Valley trout streams, particularly Oak Creek.

A recent work on the world fauna is the Katalog der rezenten Plecoptera by Illies (1966) which contains a very extensive bibliography. Older works on North American species include Claassen (1931) and Needham and Claassen (1925). Illies (1965) outlined the phylogeny and zoography of the Plecoptera. The eggs of a number of western species were described by Knight, Nebeker and Gaufin (1965a, 1965b).

Mr. R. Thut, Longview, Washington, is presently working on the biology of Plecoptera as well as other aquatic groups in Washington (Thut, 1968, 1969). Sheldon and Jewett (1967) studied the emergence of stoneflies in a Sierra Nevada stream while Kraft (1963) studied emergence in an Oregon stream. Chapman and Demory (1963) investigated the food habits of aquatic insect larvae in two Oregon streams. Others publishing on the biology and behavior of the order include: Brinck (1949), Percival and Whitehead (1929), Smith (1913, 1917), and Wu (1923). Hynes (1941, 1942, 1962) and Ulfstrand (1968) emphasized ecology in studies involving Plecoptera.

METHODS

Description of Oak Creek

Oak Creek originates in the foothills of the Oregon Coast Range in MacDonald Forest, Benton Co., and flows approximately ten miles before joining the Marys River at Corvallis. The soil in the area is Wapato silty clay loam (Ball, 1946). It is composed of 8-12 inches of heavy clay loam with a subsoil to 36 inches or more of clay or clay loam. The creek has cut well into the soil exposing bedrock in the upper areas. This bedrock is of the Siletz River volcanic series (Baldwin, 1959). It is early Eocene basalt with white crystals of zeolite minerals caused by warm solutions circulating throughout the rock as it cooled. The lower region of the stream flows through recent alluvium on the valley floor.

The Sites

Four sampling stations were selected on the stream representing a range of conditions. Site I was located in the upper region of the stream (Figure 1) in MacDonald Forest. Sites II and III were also located in MacDonald Forest. Site IV was at the Entomology Farm on the campus in Corvallis.

Some characteristics of the sampling stations are summarized in Table 1. The upper three sites are in an area forested with willow,

Figure 1. Map showing the location of the upper three sampling stations on Oak Creek, Benton Co., Oregon. Site IV, located at the Entomology Farm, is not shown. The numbers are elevations.

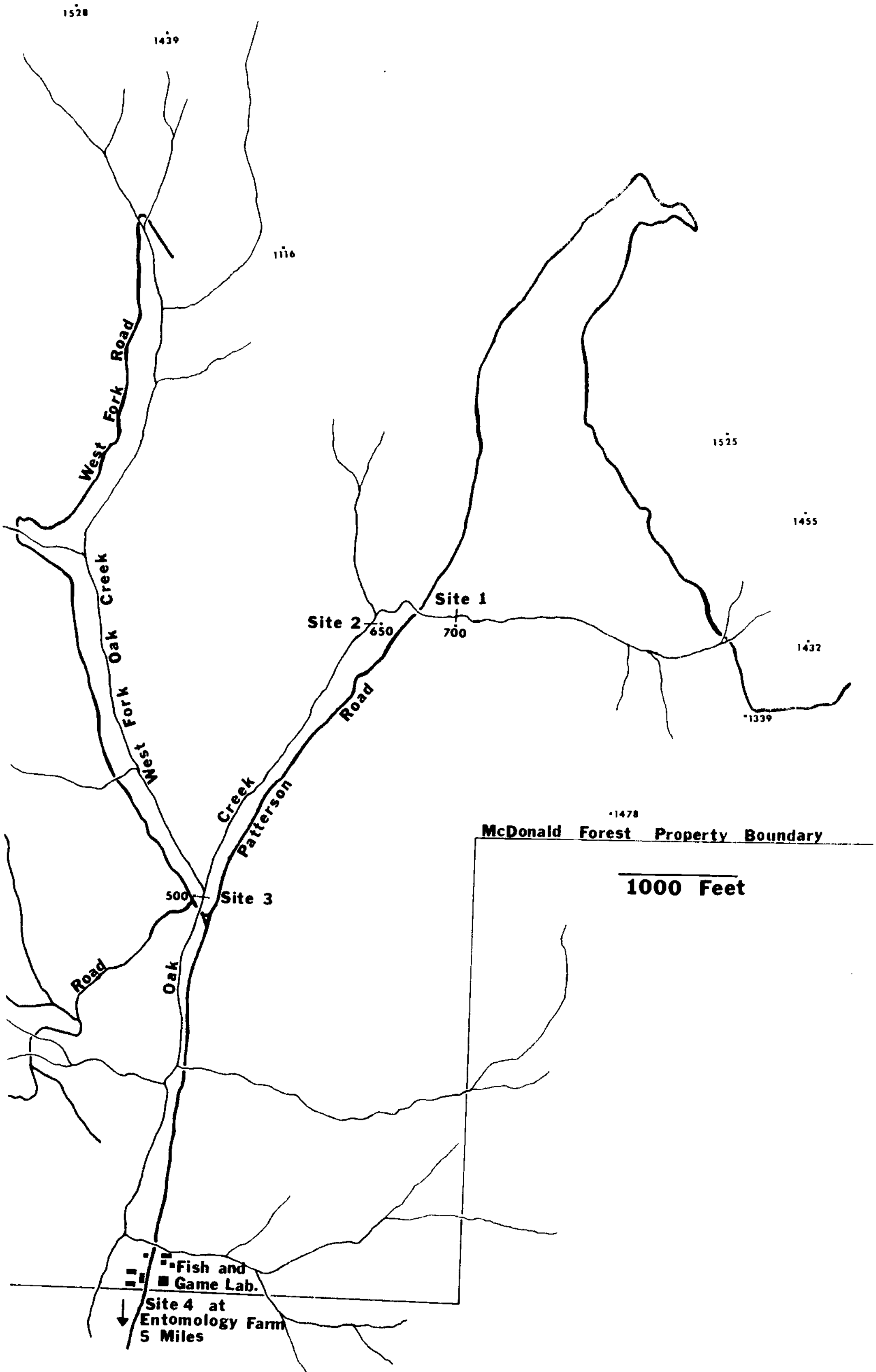

1528
1439
1116
1525
1455
1432
1339
1478
West Fork Road
West Fork Oak Creek
Site 1
700
Site 2
650
Patterson Road
Creek
Oak
Site 3
500
Road
McDonald Forest Property Boundary
1000 Feet
Fish and Game Lab.
Site 4 at Entomology Farm 5 Miles

Table 1. Some characteristics of the sampling sites.

	Site I	Site II	Site III	Site IV
Distance from Oak Creek Lab.	1.50 mi. upstream	1.25 mi. upstream	0.65 mi. upstream	5.00 mi. downstream
Elevation	700 ft.	650 ft.	500 ft.	225 ft.
Percent sunlight reaching water	10.43	18.39	13.04	84.78
Width*	3-7 ft.	3-7 ft.	3-18 ft.	6-20 ft.
Current speed*	0-2.40 fps	0-2.86 fps	0-4.86 fps	0-4.60 fps

*Range of measurements taken at times of benthos sampling.

alder, oak, and Douglas fir. Site IV is surrounded by agricultural land. There are several small impoundments between Sites III and IV. During the summer while flow was low Site IV was warmer than other sites and heavily silted. Figures 2-9 show the range of stream flow conditions during the year at the four sites. The stream is flushed during the winter rainy season. In addition, substrate was larger at the upper sites, with bedrock being found in spots at Site I.

Temperature was monitored continuously at Site III and is shown in Figures 11 and 12. In addition, temperature was recorded at the times of benthos sampling (Table 2).

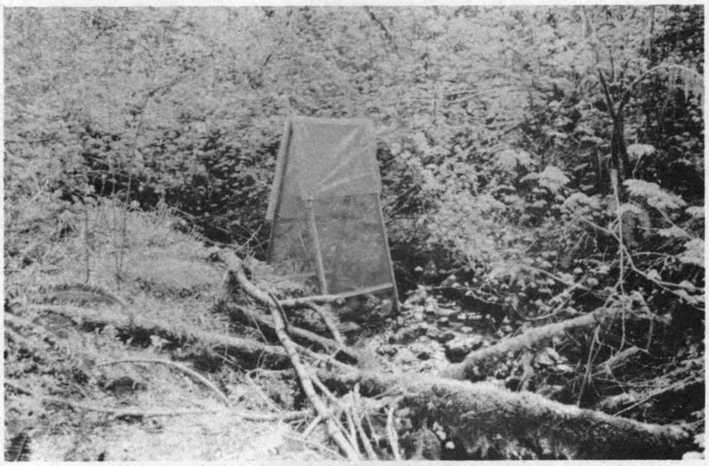
Emergence Traps

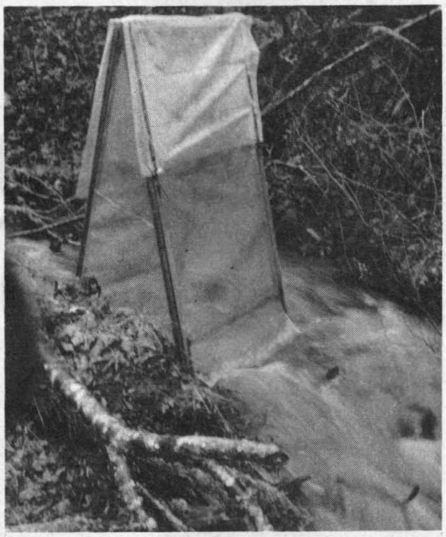
The emergence traps can also be seen in Figures 2-9. The traps were one square meter and were placed on a riffle at each site. They

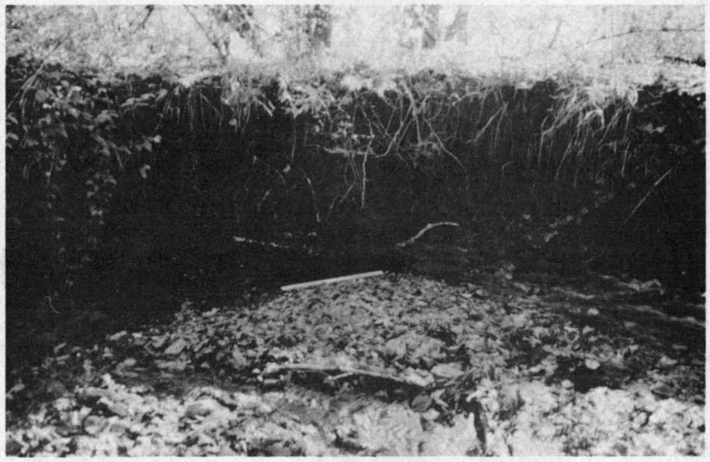
Figure 2. Site I at low flow. April, 1969.

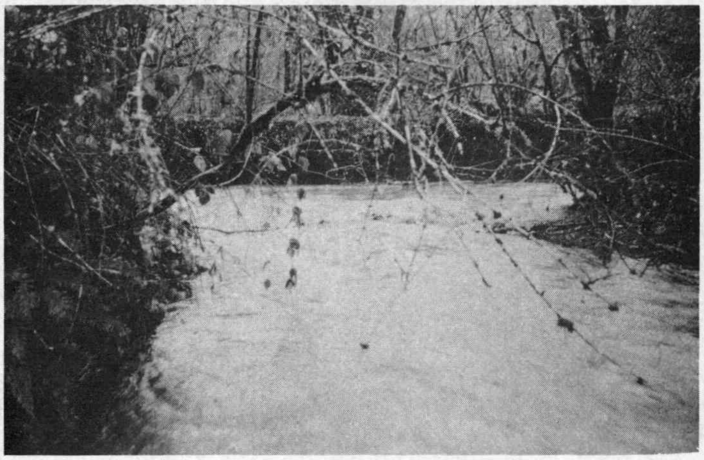
Figure 3. Site I at high flow. December, 1968.

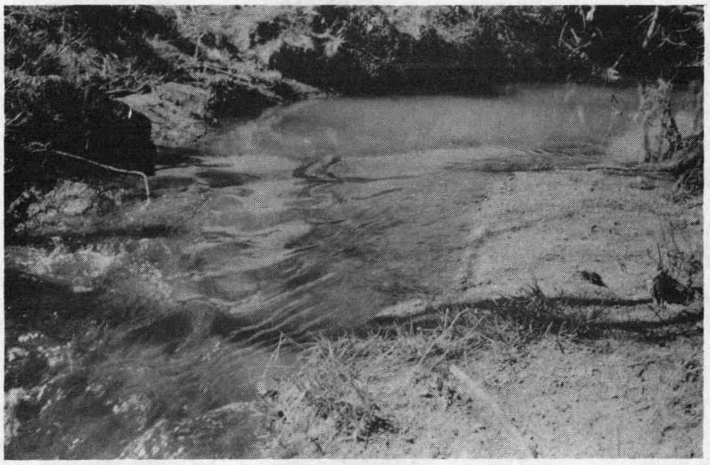
Figure 4. Site II at low flow. April, 1969.

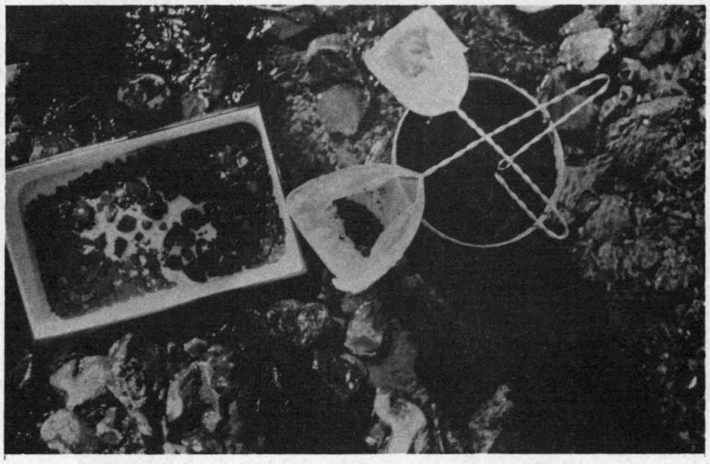












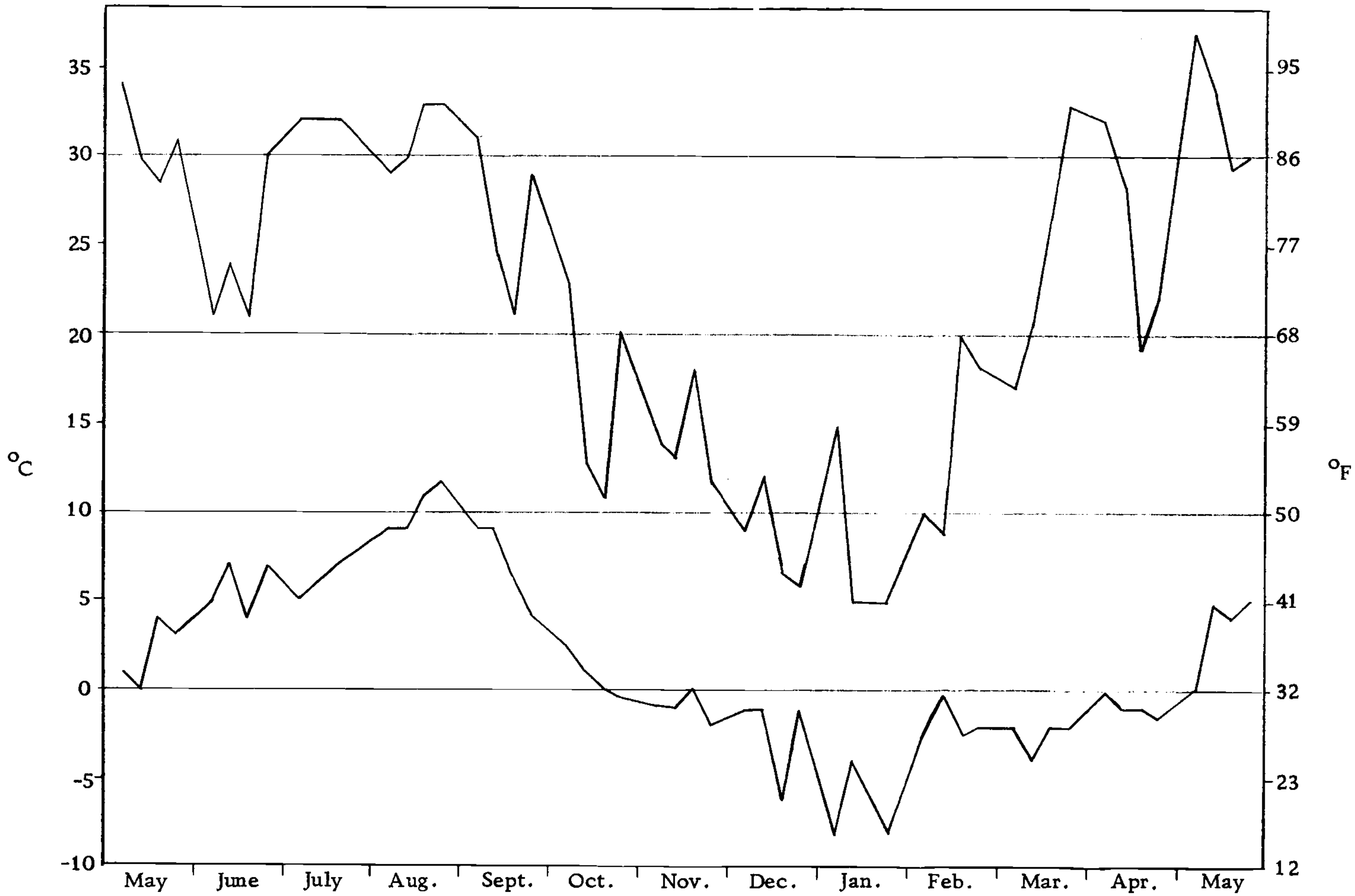


Figure 11. Weekly range of air temperature at Site III from May, 1968, through May, 1969.
*August, 1967, substituted for August, 1968, which was missing.

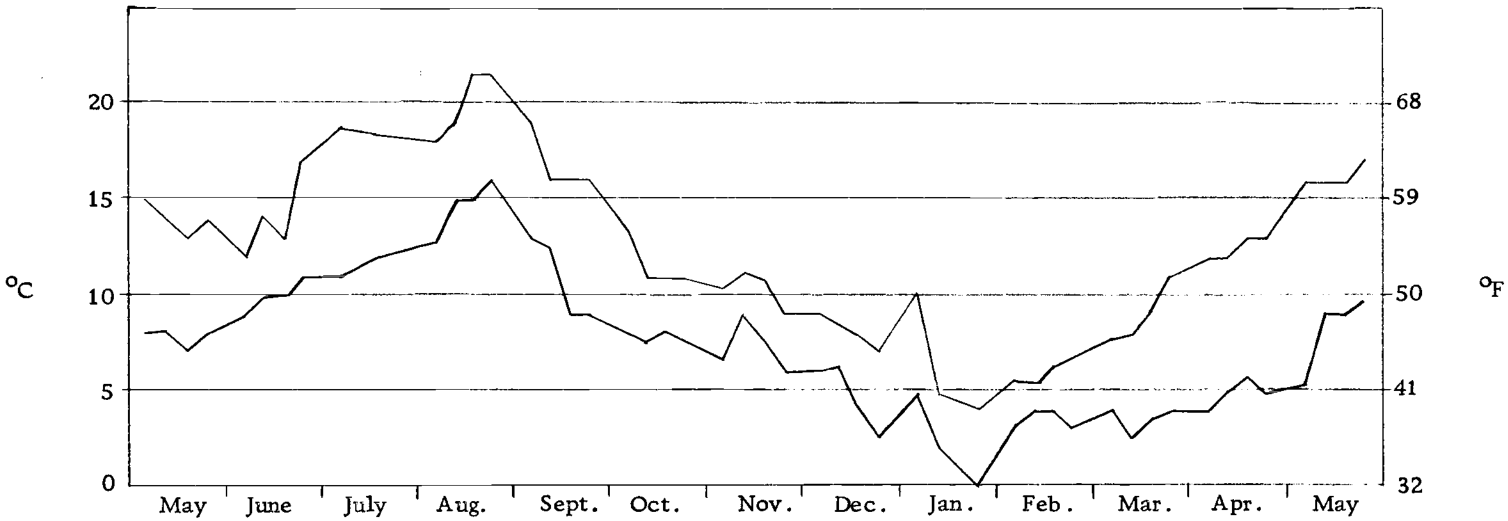


Figure 12. Weekly range of water temperature at Site III from May, 1968, through May, 1969.
*August, 1967, substituted for August, 1968, which was missing.

Table 2. Water and air temperatures (^{o}C) on benthos sampling dates at the four sites.

Date	Water				Air			
Site:	I	II	III	IV	I	II	III	IV
June 8, 1968	10.8	11.3	11.3	13.0	--	--	--	--
July 13, 1968	13.2	13.5	14.8	18.0	18.0	20.0	20.0	22.6
Aug. 20, 1968	10.5	12.5	13.5	16.5	14.2	14.0	17.0	19.5
Sept. 16, 1968	12.8	12.8	13.8	15.8	12.2	16.0	15.5	19.6
Oct. 16, 1968	8.8	10.6	10.6	10.6	10.0	13.3	15.5	17.0
Nov. 14, 1968	8.3	8.3	8.3	7.8	4.0	5.0	5.0	4.0
Dec. 15, 1968	8.3	7.8	7.8	--	8.5	6.0	5.0	4.0
Jan. 22, 1969	5.0	4.5	4.5	4.0	- 2.0	- 0.5	3.0	3.0
Feb. 17, 1969	5.5	5.5	6.2	6.5	4.0	6.0	8.0	10.0
Mar. 17, 1969	7.5	7.5	8.0	9.8	8.6	10.0	10.3	11.0
Apr. 17, 1969	8.0	8.5	8.5	10.0	11.0	10.0	9.0	11.0
May 16, 1969	10.0	10.5	13.0	15.5	13.3	16.0	22.0	22.0

were about two meters in height and covered with fiberglass window screen (mesh open. = 1.5 mm). The bottom edges of the screening were allowed to hang loosely into the stream to prevent escape of adults. This also allowed free flow of water so that modification of the habitat was minimal. One side of the trap opened to allow one to enter and aspirate the live material. Traps were checked twice a week during the major emergence periods (April, May, June, July) and weekly during the remainder of the year. Periods were sometimes longer during extreme weather.

The mature Plecoptera nymph crawls from the water to moult. Small Alloperla seem to remain close to the water while Kathroperla perdita Banks 1920 was found to a height of eight feet up trees. Thus, any structure rising above the water may be attractive for emergence. If traps were attractive, the area from which they attracted would be limited, and most nymphs would crawl up the outside of the trap. Data from traps will suffice for comparative purposes.

Benthos Samples

For sampling purposes, each site was divided into a riffle and glide section approximately six feet in length. Four benthos samples were taken from each riffle and glide section, for a total of 32 samples per month. The samples were taken beginning at one edge of the stream and working towards the other edge. Because of the irregular nature of the substrate sampling on a straight line transect was found to be impossible. Due to high water, quantitative samples could not be taken at Site IV during the winter. Qualitative samples were taken during these periods. Extreme weather conditions during January made it necessary to take one-half the normal number of samples.

Benthos samples were taken using a one-foot section of six-inch stovepipe. The pipe was forced into the substrate as in Figure 10. Substrate was scooped into a pan, and organisms remaining in the water were obtained using standard tropical fish nets (mesh open. = 0.2 mm). Using this method all size classes including eggs were obtained. The larger stones, leaves, and debris in the pan were washed. The organisms in the pan were washed into a net and preserved in 70% alcohol for sorting in the laboratory. The Plecoptera were identified as far as possible and measured in millimeter size classes. Mr. Stanley G. Jewett, Jr. of Portland, Oregon, identified many adult and some nymphal specimens.

Current speed was recorded for each sample, using a Gurley Pygmy current meter. Other data usually recorded for a sample included date, section, sample number, general habitat, water depth, distance from the shore, stone size, and amount of leaves, debris, and silt.

RESULTS AND DISCUSSION

Species Composition

Forty-two species of adult Plecoptera representing 15 genera were collected in the emergence traps on Oak Creek. A thesis by Ball (1946), concerned with the seasonal succession of stoneflies in Willamette Valley trout streams, listed 48 species. His collections were not made with emergence traps so the precise habitats are in doubt, but 36 species probably emerged from Oak Creek. He also collected from a number of other streams. Table 3 lists species composition as determined during the present study and as listed by Ball 35 years ago. Eighteen species collected in the present study were not taken by Ball while Ball lists 12 species not taken by me. Two of the species found by Ball and not recorded by myself, *Hastaperla brevis* and *Alloperla signata*, are not listed from the Pacific Northwest by Jewett (1959). Of the four species which Ball cites as common on Oak Creek, all are still common. However, *Alloperla fraterna*, listed by Ball as uncommon, and described from material collected by him, is now the most abundant species on the creek. Most changes seem, however, to be in rare species. Considering the probability of collecting a rare species, the stonefly composition of the creek is apparently little changed in the 35 years since Ball was doing his field work.

Table 3. Comparison of species of Plecoptera collected from Oak Creek by Ball (1946) and in the present study.

Species collected in both studies	
Peltoperla brevis	Brachyptera nigripennis
Nemoura californica	Pteronarcella regularis*
Nemoura obscura	Pteronarcys princeps
Nemoura interrupta	Isoperla mormona
Nemoura cinctipes*	Isoperla trictura
Nemoura oregonensis	Alloperla delicata
Leuctra infuscata	Alloperla borealis*
Leuctra forcipata	Alloperla coloradensis*
Leuctra occidentalis	Alloperla fidelis
Perlomyia utahensis	Alloperla fraterna
Perlomyia collaris	Acroneuria californica
Eucapnopsis brevicauda	Acroneuria pacifica

Species collected only by Kerst	Species collected only by Ball
Peltoperla quadrispinula	Nemoura dimicki
Nemoura cornuta	Megaleuctra complicata
Nemoura foersteri	Capnia excavata
Nemoura producta	Capnia projecta
Nemoura frigida	Capnia promota
Leuctra augusta	Capnia tumida
Leuctra sara	Isocapnia abbreviata
Capnia porrecta	Brachyptera pacifica
Isogenus misnomus	Brachyptera oregonensis
Isogenus nonus	Taeniopteryx maura
Calliperla luctuosa	Alloperla signata
Isoperla ebria	Hastaperla brevis
Isoperla marmorata	
Isoperla sordida	
Kathroperla perdita	
Alloperla pallidula	
Hastaperla chilnualna	
Acroneuria theodora	

*Recorded by Ball as common.

Forty-two species of Plecoptera is a large number for a small stream when compared with other investigations of small stream rithron biotopes (Table 4). Rithron biotopes are defined as having an annual temperature amplitude of less than 20°C, high oxygen content, and rapid current (Ulfstrand, 1968). Two additional conditions are that this biotope lies close to where the stream rises, and the water volume is small.

Table 4. Species abundance in small stream rithron biotopes. Modified from Ulfstrand (1968).

Area	No. species	Investigator
Wales	9	Jones (1948)
Central Germany	10	Illies (1952)
England	14	Macan (1963)
Swedish Lapland	15	Ulfstrand (1968)
England	16	MacKereth (1957)
Wales	19	Hynes (1961)
Central Germany	27	Dittmar (1955)
Oregon	28	Kraft (1963)
California	31	Sheldon and Jewett (1967)
Oregon	42	Kerst (1969)

Judging from Table 4, Oak Creek must be considered a stream productive in species. Some caution is justified as it is difficult to judge the intensity with which the other studies were conducted.

SEASONAL SUCCESSION

With 42 species of Plecoptera present in one small stream one asks, 'How do species partition the habitat to allow for this amount of diversity?' Some partitioning results from seasonal succession in emergence of adults. This provides reproductive isolation and allows nymphal growth periods to be staggered and thereby lessen competition for food and space.

Adult stoneflies can be taken during every month of the year on Oak Creek. Figures 13, 14, and 15 illustrate the seasonal emergence pattern on the stream. The total number of specimens of each species taken in the emergence traps is used as an indication of relative abundance. In the text, numbers listed in parenthesis after a species name indicate the total collected from all four traps during 12 months.

The spring emergence (April, May, June) is very large with all but five species completing their emergence during this period. Eighty-eight percent of the species, and 77% of the specimens, were taken during this period.

Temporal separation of species is largely absent in the suborder Setipalpia as all species emerged in the spring and early summer. This is confirmed by data from Kraft (1963) in Berry Creek, Oregon, and Sheldon and Jewett (1967) in Sagehen Creek, California.

In the suborder Filipalpia there is good temporal separation between the common species in the genus Nemoura. Nemoura cornuta

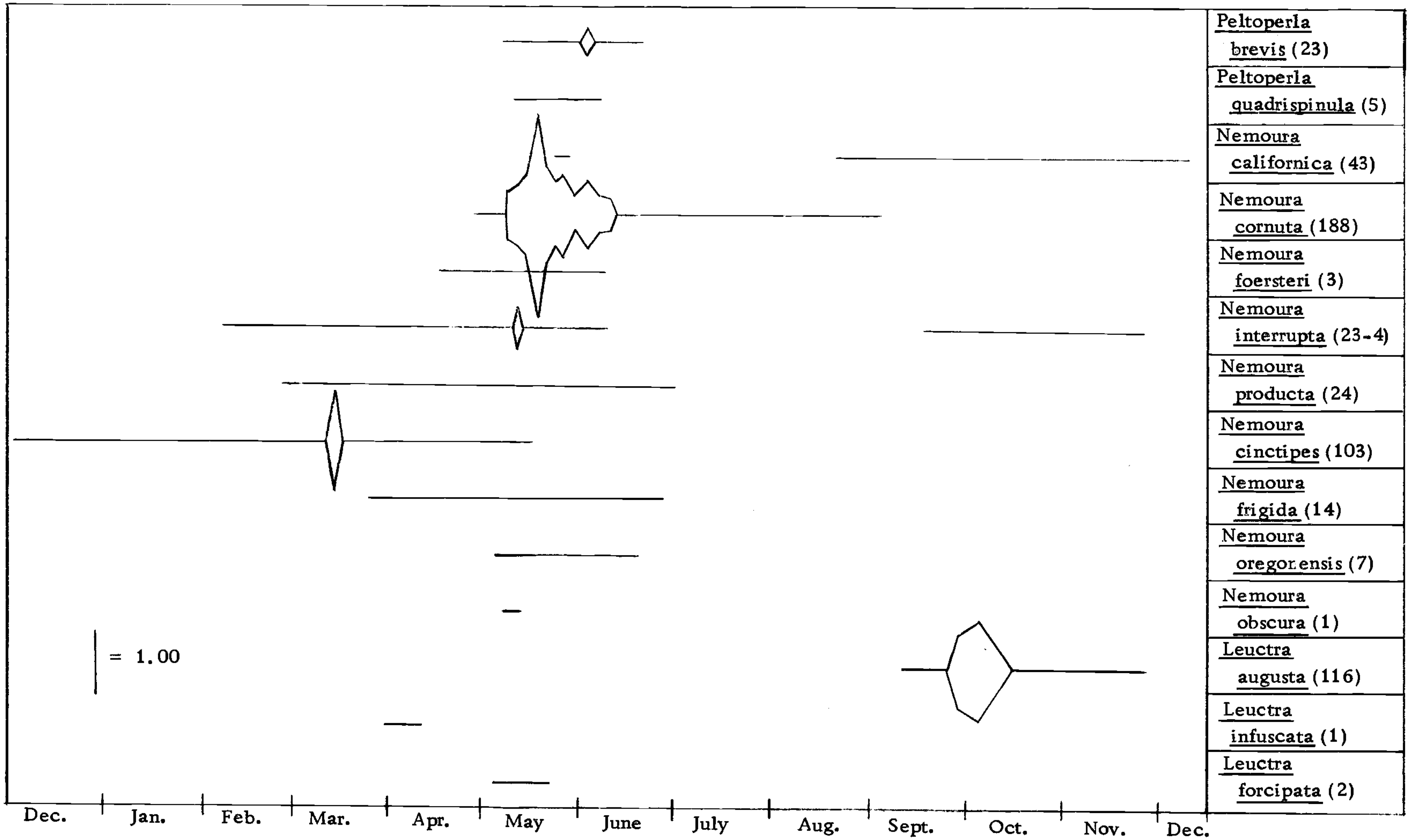


Figure 13. Seasonal succession and abundance of Plecoptera adults on Oak Creek expressed as no./m^2/day. —— < .5/m^2 day. Numbers are total per year for all four traps.

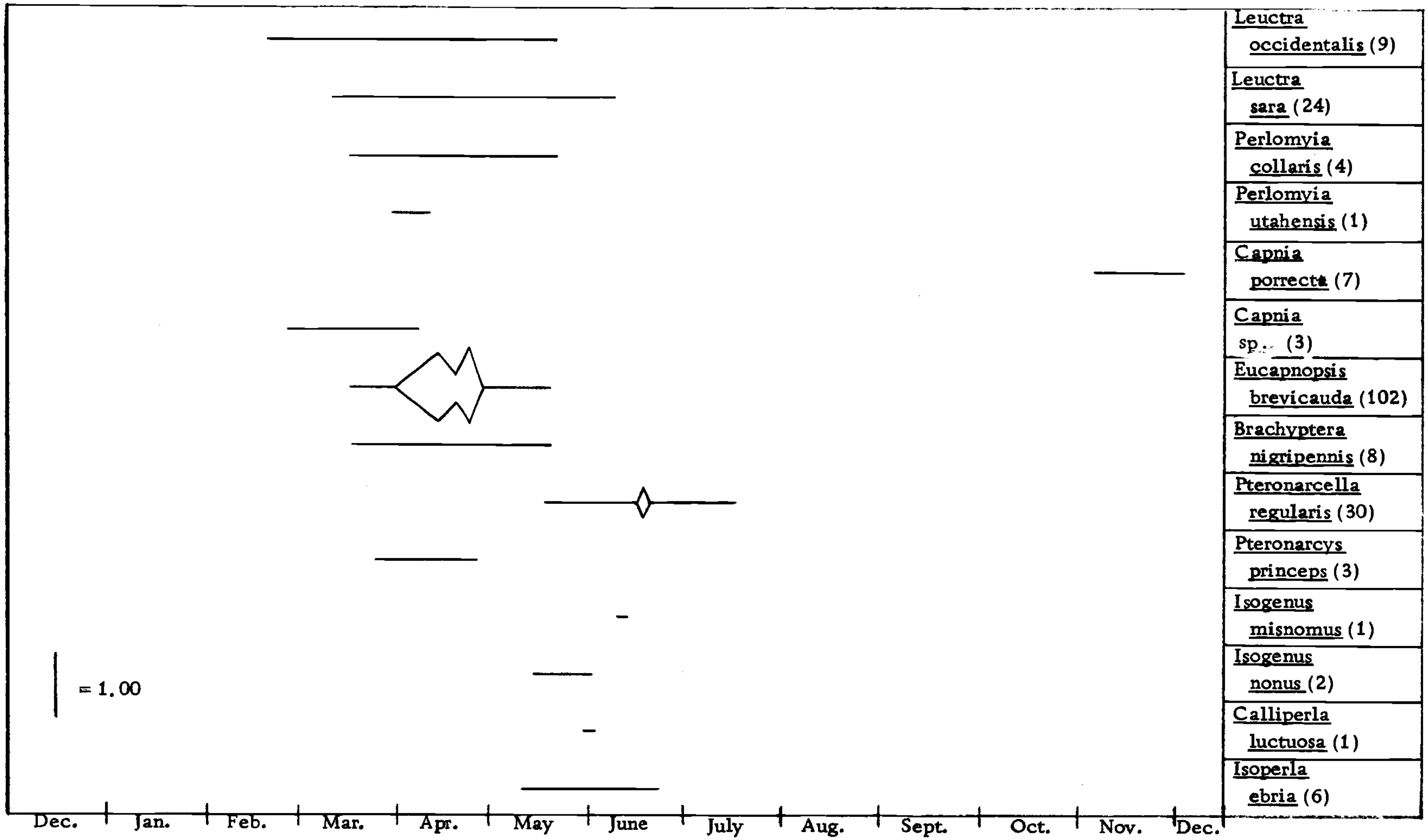


Figure 14. Seasonal succession and abundance of Plecoptera adults on Oak Creek expressed as no./m^2/day. —— <:5/m^2/day. Numbers are total for all four traps.

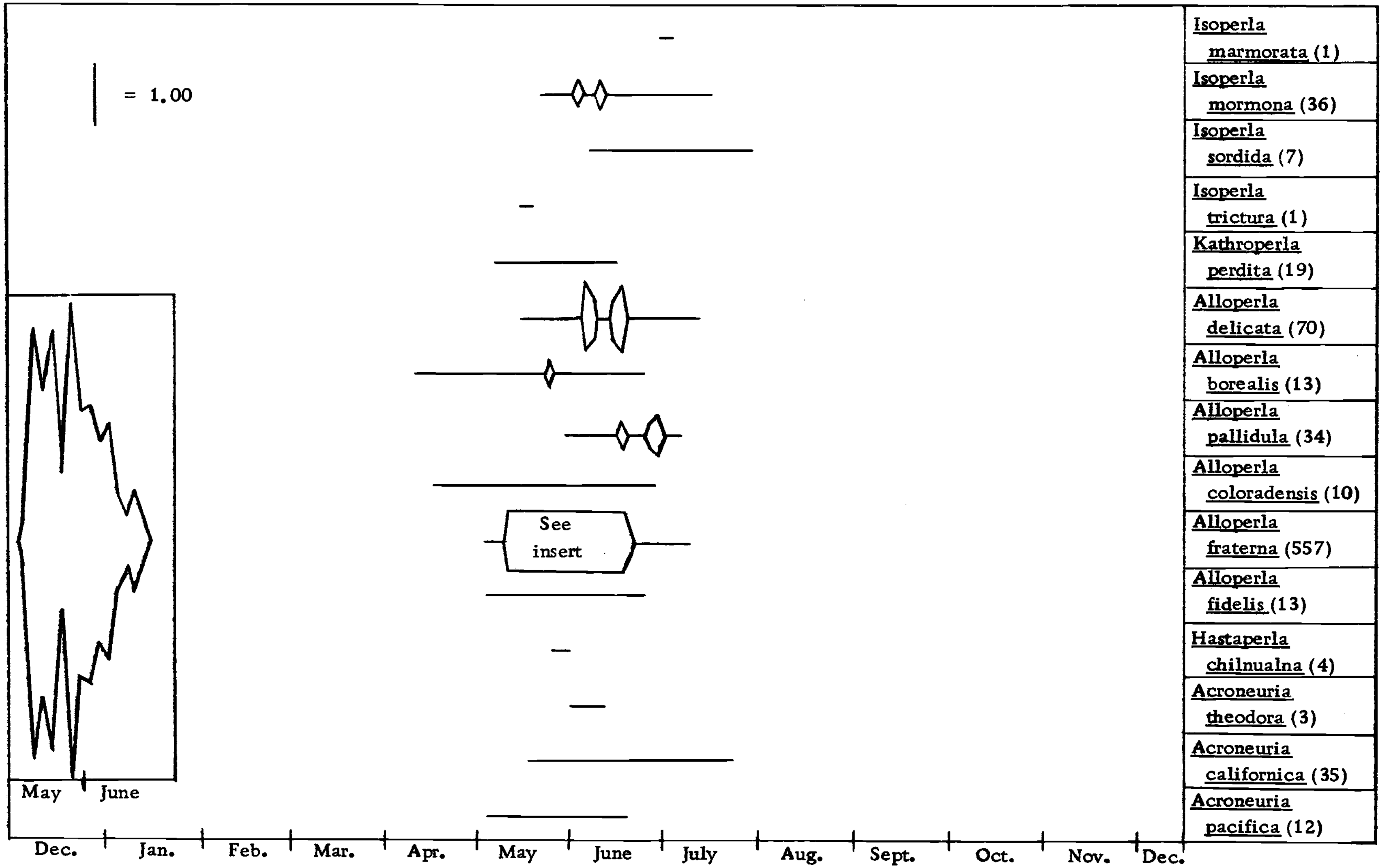


Figure 15. Seasonal succession and abundance of Plecoptera adults on Oak Creek expressed as no./m^2/day. —— < .5/m^2/day. Numbers are total per year for all four traps.

(188) emerges from May through August. N. californica (43) begins to emerge at the end of August and continues until the first of December. N. cinctipes (103) emerges from early December through early May when N. cornuta begins the cycle again. The importance of seasonal succession of closely related species is that nymphal growth periods probably are staggered. The genus Leuctra also shows some separation in time. The two common species, Leuctra augusta (116) and L. sara (24) have fall and spring emergence periods, respectively.

Two Nemoura species from Oak Creek show split spring-fall emergence periods. This type of emergence period has been documented for N. columbiana by Sheldon and Jewett (1967), for N. californica by Jewett (1959) and Ball (1946), and for N. cornuta by Kraft (1963). In Oak Creek, N. californica displays exactly the type of emergence described by Jewett (1959), being common in the fall and rare in the spring. N. interrupta also has a split emergence period on the creek being common in the spring and rare in the fall. If this species had two generations a year one might expect the size of the emergences to be similar unless mortality factors were quite different during different periods of the year. Considering the differences in the size of the emergences and the time required for growth, the broods do not overlap. The split type of emergence pattern would be advantageous where severe weather occurred during one of the periods. It also would provide a good mechanism for speciation.

N. cornuta has a large spring emergence beginning in April with scattered adults appearing until September. Kraft (1963) found this species to have a split emergence period in Berry Creek, Oregon, with almost no separation of the two periods. This species seems to be intermediate in the process of developing the split type of emergence period.

Another trait of stonefly emergence patterns is earlier emergence of males than of females. Sheldon and Jewett (1967) found sex ratios to be variable but last survivors were females. Brinck (1949) noted an early emergence of males in several species in Sweden. Using only the more common species, the changes in sex ratio of adults taken during approximately weekly periods are listed in Table 5. Towards the end of emergence periods nearly all specimens are female, so periods are only shown until females predominate in Table 5. It appears that N. californica, N. cornuta, and Leuctra augusta show earlier emergence of males. Alloperla delicata shows a moderate trend in this direction. The remaining six species show little in the way of trends. Thut (1968) also reported earlier emergence of males in N. californica but not in N. cinctipes in a Washington stream. He suggests that protandry may have been selected against in N. cinctipes due to extreme weather conditions during the time of emergence. N. cinctipes begins to emerge in winter.

Some caution is called for when making inferences from

Table 5. Comparison of female and male emergence times of 11 species of Plecoptera. Species represented by 25 or more specimens in emergence traps during 12 months have been listed.

Species	Sex	Week of emergence period								
		1	2	3	4	5	6	7	8	Total
Nemoura	F	0	0	0	1	1	5	3	1	11
californica	M	1	2	3	8	6	4	0	0	24
Nemoura	F	0	3	4	27	14	11	10	5	74
cornuta	M	1	9	24	32	15	14	6	1	102
Nemoura	F	1	0	1	5	0	0	0	1	8
cinctipes	M	1	0	2	9	0	1	1	0	14
Leuctra	F	0	1	16	21	4	4	4	3	53
augusta	M	2	5	18	25	7	3	0	0	60
Eucapnopsis	F	2	2	12	11	4	10	6	4	51
brevicauda	M	0	3	15	9	7	9	3	2	48
Pteronarcella	F	1	0	1	1	2	7	3	1	16
regularis	M	0	0	0	1	3	3	1	1	9
Isoperla	F	2	6	4	2	0	3	0	1	18
mormona	M	4	6	3	0	2	0	1	0	16
Alloperla	F	0	4	2	8	7	16	7	4	48
delicata	M	5	1	1	5	3	5	0	0	20
Alloperla	F	3	3	12	3	0	0	0	0	21
pallidula	M	4	4	3	0	0	0	0	0	11
Alloperla	F	1	23	104	73	73	57	52	26	409
fraterna	M	2	4	41	31	36	13	15	4	146
Acroneuria	F	1	2	5	3	1	6	2	4	24
californica	M	0	1	1	1	2	1	2	1	9

emergence trap data concerning sex ratios. Males are more active than females and may escape more readily, and males are shorter lived.

LIFE CYCLES

The determination of life cycles has been hampered by problems with the systematics of the nymphs. Further work is needed to find characters to separate species in the nymphal stages. For certain genera nymphs may prove to be indistinguishable. Thus, it was necessary in many cases to work at the generic level. Length-frequency graphs have been prepared for common species using information from all samples. These graphs also indicate the periods when adults and eggs are present.

Suborder Filipalpia

Nymphs in this suborder are herbivorous (Brinck, 1949; Chapman and Demory, 1963; Claassen, 1931; Frison, 1935; Hynes, 1941; Jones, 1949, 1950; Minshall, 1967; Wu, 1923). The adults that have been studied have been found to be herbivorous (Brinck, 1949; Frison, 1935; Hynes, 1941). Hynes (1942) found that an English species, *Nemoura variegata*, was herbivorous in the adult stage and required food to live and produce eggs. He generalized this pattern to the suborder Filipalpia. Eggs mature after the emergence of the adult, while in the Setipalpia mature eggs are present in the last nymphal instar.

Genus *Peltoperla* Needham 1905

Claassen (1931) found that the eastern species, *P. arcuata*, had a two year life cycle. Of the two species of *Peltoperla* adults taken from Oak Creek, *Peltoperla quadrispinula* Jewett 1954 (5) was rare while *P. brevis* Banks 1907 (23) was more common. The nymph of *P. quadrispinula* is unknown. All immatures in this genus were assigned to *P. brevis* as these nymphs were too common to represent the rare species. There is also a considerable size difference. The adults of *P. brevis* occur during May and June, but small nymphs were not found until January. This suggests that a period of six months is required for incubation of the eggs. Eggs should then be present from May to December. Small nymphs were present along with mature ones during March and April. This suggests a two year life cycle for *P. brevis*. Most rapid growth takes place during the fall. *P. quadrispinula* is much larger and may have a longer cycle.

Genus *Nemoura* Pictet 1841

A number of authors have published biological information on this genus. Brinck (1949) found the incubation time required for eggs of three Swedish species, *N. meyeri*, *N. avicularis*, and *N. erratica*, to be 21, 25, and 16 days at 15°, 15°, and $18^{\circ}C$, respectively. Hynes (1941) records the English species, *N. erratica*, as requiring 17-23 days for incubation of the eggs at $15^{\circ}C$. All species that have been studied are univoltine (Brinck, 1949; Minshall, 1968; Svenssen, 1966; Wu, 1923). Wu (1923) studied the complete life history of *N. vallicularia* which she found to pass through 22 instars.

The number of branches of the cervical gills provides the major character for separation of nymphs in this genus. The key given by Jewett (1959) was used, realizing that keys are only to be used for mature nymphs. When nymphs are small they have small, simple gills, but as the nymphs grow the gills also grow and branch. This makes separation quite difficult. The only solution seems to be familarity with a given study area. Nine of the 22 species of *Nemoura* known from the Pacific Northwest have been taken from the creek.

Nemoura californica Claassen 1923 and *N. cornuta* Claasen 1923. The data for *N. californica* (43) and *N. cornuta* (188) is shown in Figure 16. Both species have more than six branches to the cervical gills. Some separation is possible because of temporal differences in the life cycle.

Nemoura californica emerges during the fall. The eggs apparently take about six weeks to hatch since small nymphs appeared in samples the second month after emergence began. Thut (1968) reported that the eggs of this species probably require five months to hatch in a spring-fed stream in Washington with a constant $6^{\circ}C$. The water is well above $6^{\circ}C$ when the eggs of this species are present in Oak Creek, and the higher temperature could account for the difference

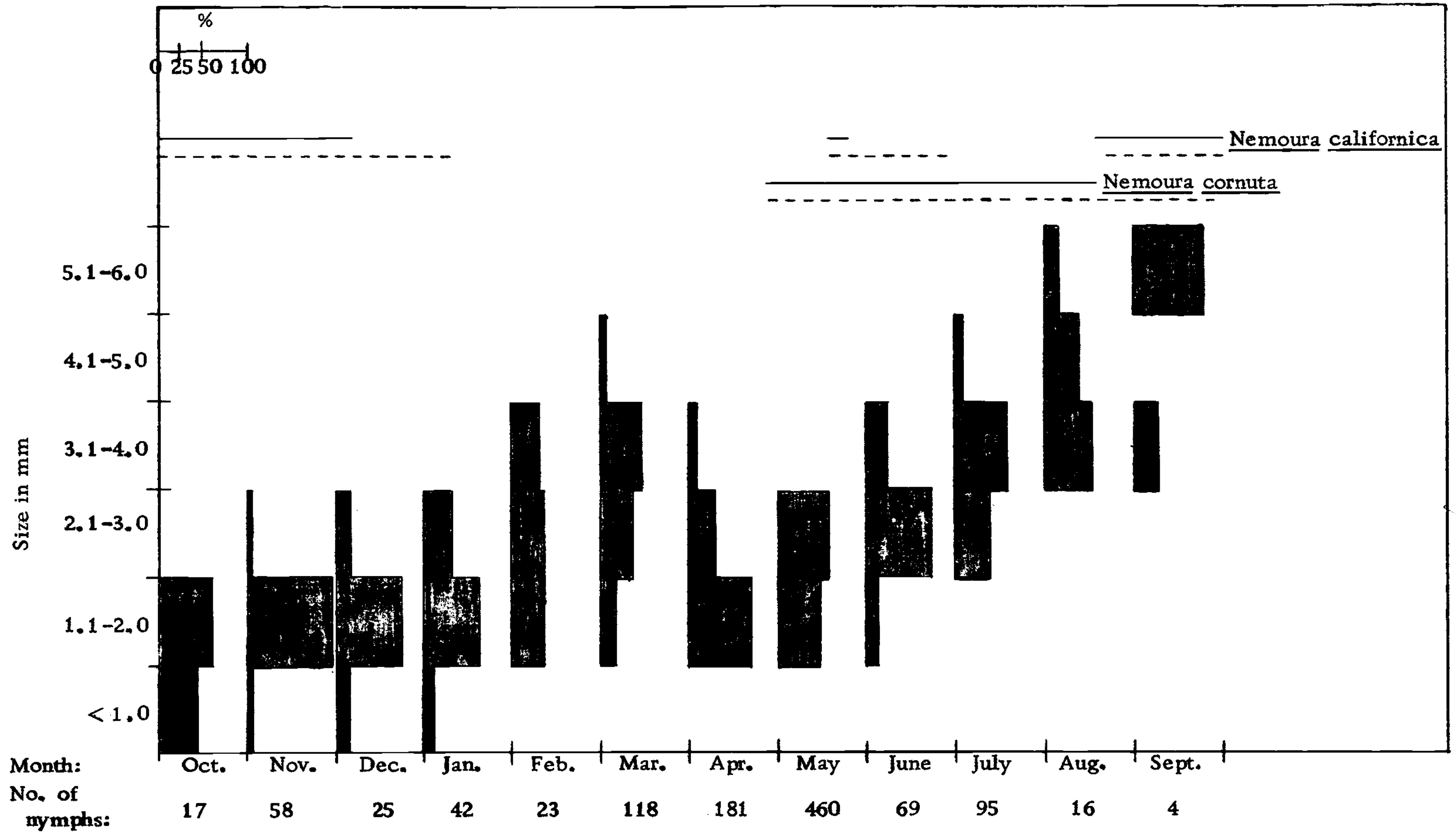


Figure 16. Length frequency of Nemoura californica and N. cornuta nymphs from benthos samples. Frequencies expressed as percentages. —— Adults present. --- Eggs present.

in incubation times. This species grows most actively during the summer and is univoltine.

The larger nymphs occurring in the spring are *N. cornuta* which has a spring and summer emergence period. The eggs apparently have an incubation time of five months. This is uncertain as some small nymphs were probably included with *Nemoura cinctipes*. *N. cornuta* grows most rapidly during the spring and is univoltine.

Nemoura nevadensis interrupta Claassen 1923 and *N. producta* Claassen 1923. These species cannot be separated in the immature stages and are very similar as adults. They have one year life cycles as shown in Figure 17. The eggs require between two and three months to hatch. The nymphs apparently grow little during the summer and have a period of rapid growth during the fall when leaves accumulate in drifts in the stream.

Nemoura cinctipes Banks 1897. *N. cinctipes* (103) along with *N. cornuta* (188) was a very common species in Oak Creek. The eggs of *N. cinctipes* apparently require less than one month to hatch. Small nymphs were not common until late spring. This could be due to fluctuations in the emergence pattern. *N. cinctipes* began emerging during December but the rate slowed down considerably during a period of severe weather during winter. Thut (1968) thinks the eggs of this species require five months incubation at 6°C.

The nymphs grow very little from January through August. Growth

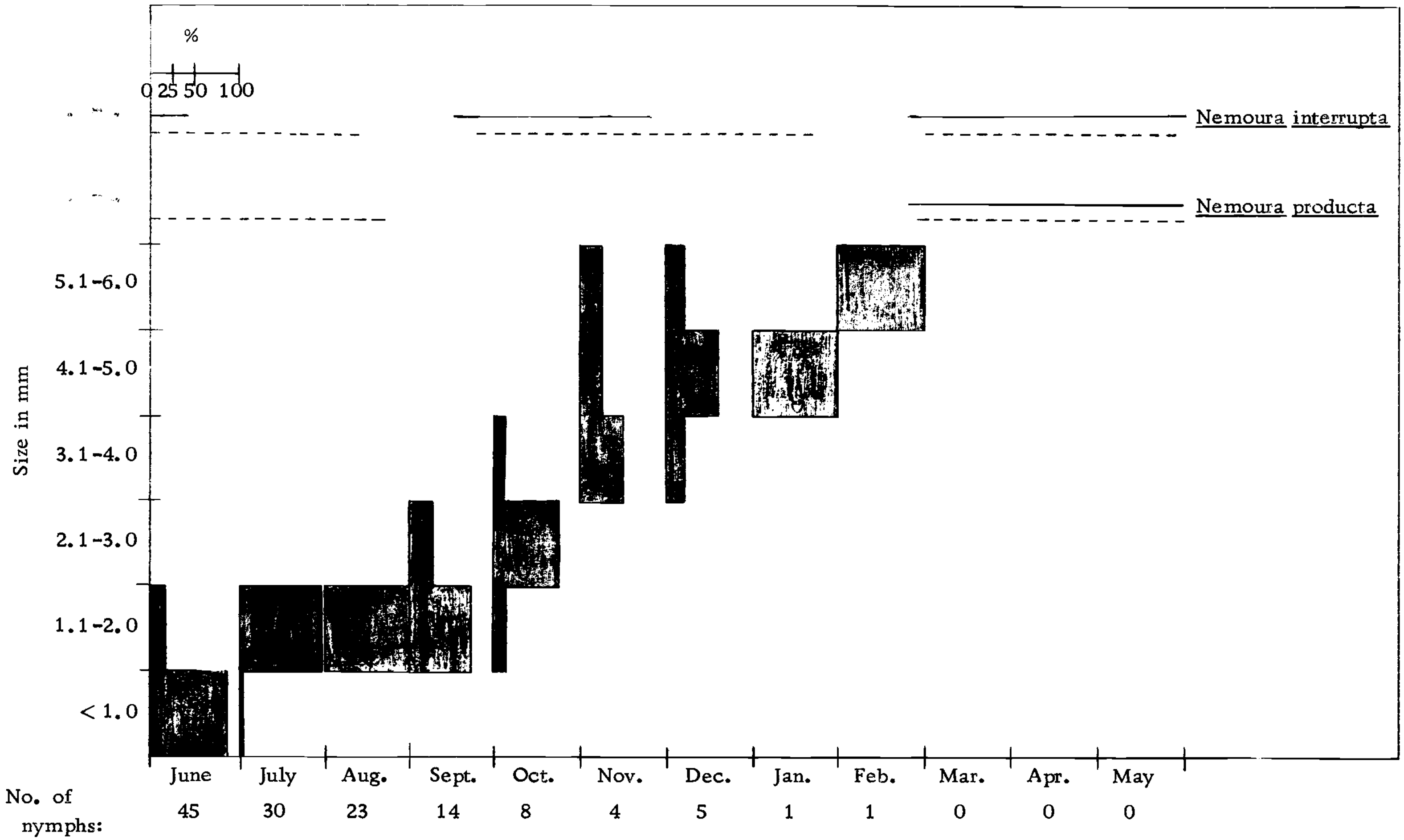


Figure 17. Length frequency of Nemoura interrupta and N. producta nymphs from benthos samples. Frequencies expressed as percentages. ——— Adults present. --- Eggs present.

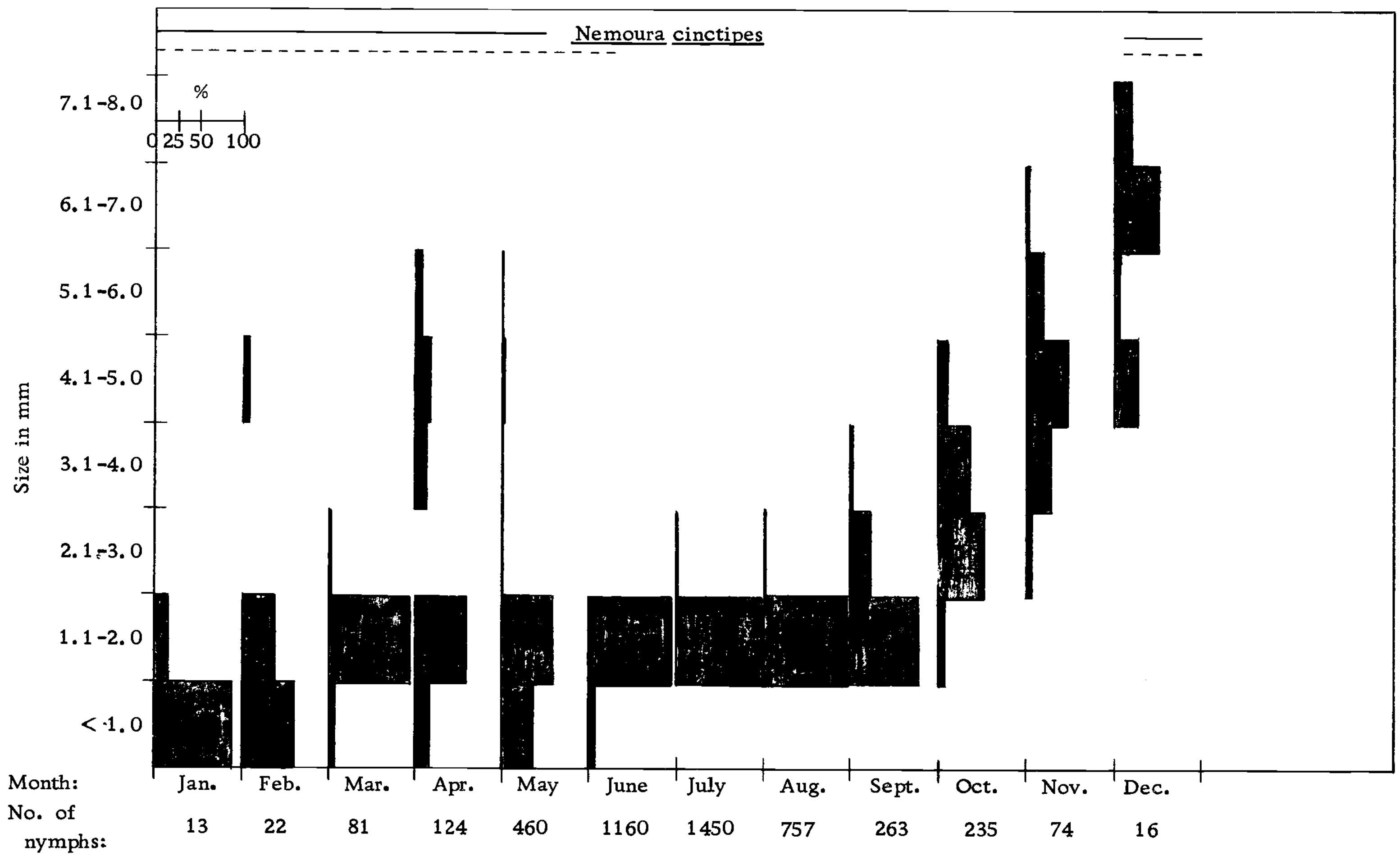


Figure 18. Length frequency of *Nemoura cinctipes* nymphs from benthos samples. Frequencies expressed as percentages.
—— Adults present. --- Eggs present.

seems particularly retarded during the hot summer months. Beginning in September there is a period of very rapid growth correlated with occurrence of leaf fall. This species has a univoltine cycle as do the other species of Nemoura.

Some N. cornuta nymphs may be included here.

Nemoura oregonensis Claassen 1923. This species was uncommon in Oak Creek and the length-frequency data are inadequate for graphical representation. Nymphs were taken from June through November. Nymphs taken from June through August were less than 2 mm in length, but by November all nymphs were 3-5 mm long. Thus, N. oregonensis appears to have a univoltine cycle with rapid growth during the fall. Little growth takes place during the hot summer months. The adults emerge during May and June.

Other Nemoura spp. The following species were collected, with the number in parenthesis being the number taken in emergence traps, but the nymphs were not recognized from benthos samples: N. foersteri Ricker 1943 (3), N. frigida Claassen 1923 (14), and N. obscura Frison 1936 (1).

Genus Leuctra Stephens 1835

Brinck (1949), Hynes (1941, 1962), Minshall (1968, 1969), Svensson (1966), and Ulfstrand (1968) have studied species in this genus and found them to be univoltine. Brinck (1949) discovered that the eggs of two species in Sweden, *L. hippopus* and *L. fusca*, required 21 and 24 days incubation at 18°C while Hynes (1941) relates that the eggs of an English species, *L. inermis*, required 28 days incubation at 15°C.

Claassen (1931) predicted rightly that specific identification of nymphs in this genus would be very difficult. Five of the six species found in the Pacific Northwest have been taken from Oak Creek. The most common species, *Leuctra augusta* Banks 1907, could be identified later in its life cycle due to its larger size. For the remainder of the year, data for all *Leuctra* had to be pooled. The other four species, *L. infuscata* Claassen 1923, *L. forcipata* Frison 1937, *L. occidentalis* Banks 1907, and *L. sara* Claassen 1937 comprised only 36 specimens in the emergence traps, while *L. augusta* was represented by 116 specimens. In addition, if specimens of the closely related genus *Perlomyia* were taken in benthos samples, they were included as *Leuctra*. However, only four adults of *P. collaris* and a single specimen of *P. utahensis* were taken in the emergence traps so populations of *Perlomyia* were undoubtedly small.

The data for the *Leuctra* is given in Figure 19. The eggs of *L. augusta* probably take about two months to hatch as the adults occur in September and October and there is an increase in the 1.1-2.0 mm size class between November and December. *Leuctra* nymphs, being long and slender, are large when they hatch. *L. augusta* has nearly reached mature size by late spring and does little growing during the summer.

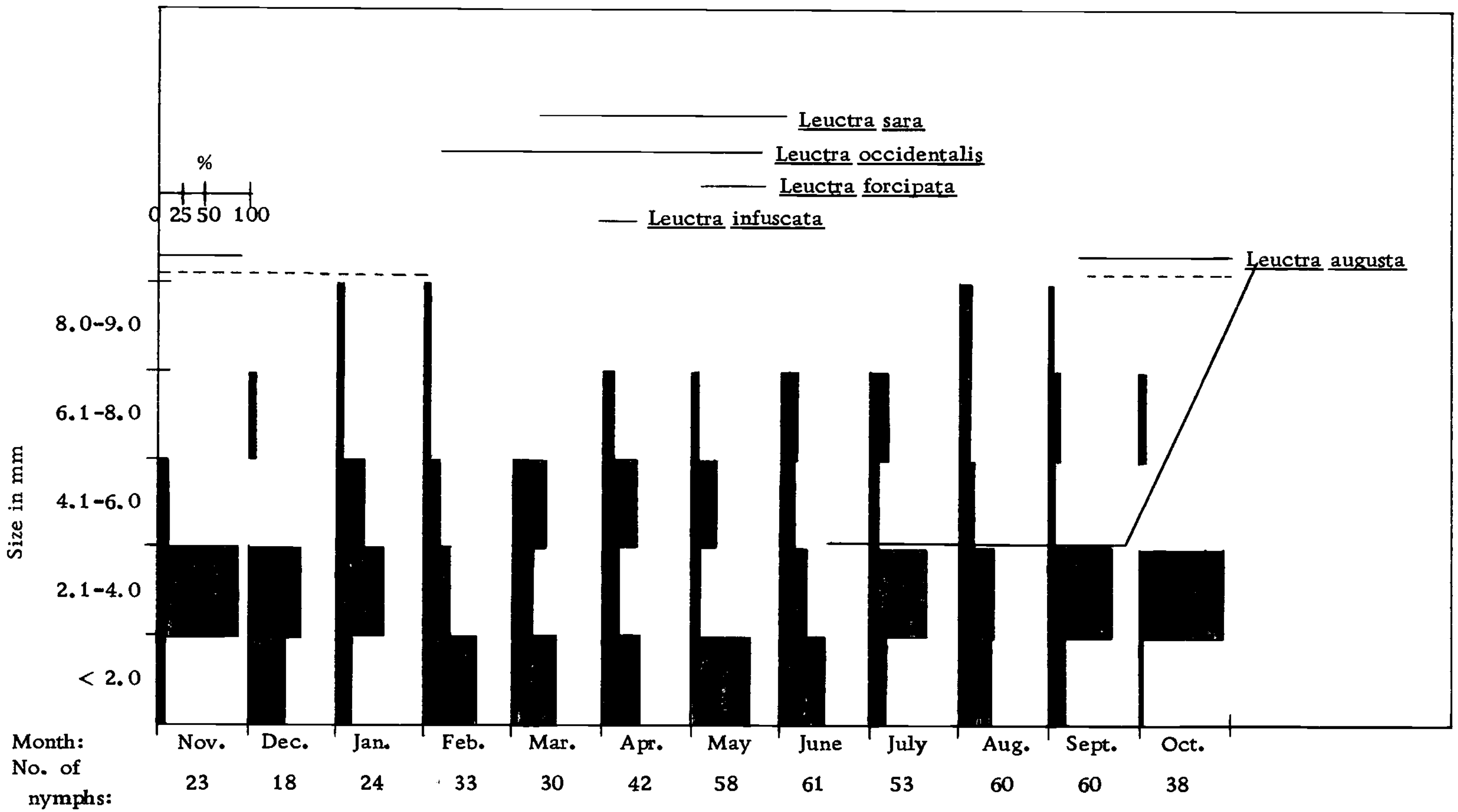


Figure 19. Length frequency of Leuctra spp. nymphs from benthos samples. Frequencies expressed as percentages.
—— Adults present. --- Eggs present.

This species has a one year life cycle.

The remainder of the species in this genus seem to grow in fall and early winter. The eggs seem to hatch quickly in the spring. From what is known of this genus it is likely that life cycles are one year in length.

Genus *Capnia* Pictet 1841 and Other Capniidae

Several authors have found members of the Capniidae to be univoltine (Brinck, 1949; Claassen, 1931; Minshall, 1969). Hynes (1941) states that an incubation period of 17 hours to three days at 15°C is required for *Capnia bifrons*, while Brinck (1949) reported eggs of this species hatching in 0-15 minutes under natural conditions. Another species, *Capnia nigra*, was reported by Brinck (1949) to hatch in 21 days at 15°C.

The following account, liberally drawn from Khoo (1968), is included because the pattern is remarkably similar to the situation in Oak Creek. He studied *Capnia bifrons* in England. Diapausing nymphs are morphologically distinct from non-diapausing nymphs. The former are opaque and white due to an accumulation of fat globules. The head is flexed towards the body. First-instar nymphs are found during May and June. Rising temperatures and increasing day-lengths condition the nymphs to diapause after the first or second instar. Diapause cannot be stopped after initiated. The fourth- or fifth-instar nymphs diapause from June to August. The nymphs are sensitive to both temperature and photoperiod over several instars which means that a diapause stage is insured in cases of a prolonged winter or early occurrence of newly-hatched nymphs.

Falling temperatures and decreasing day-lengths terminate diapause. Nymphal growth is rapid during fall and winter. Emergence of adults occurs from late winter to early spring. An extended emergence period is prevented because increasing photoperiod results in the differentiation of adult characters in immature post-diapause nymphs. Capnia bifrons is strictly univoltine with 14-16 instars and a photoperiodically controlled flight period.

The nymphs in the family Capniidae cannot be identified to species. This made it necessary to work at the Family level with the nymphs. Several species collected by Ball (1946) were not taken in the present study. It is possible that more species of Capnia are to be found on Oak Creek since emergence occurs during a period of high water. I doubt that any species well represented in the stream was missed as collecting was intensive during periods when traps were not functioning. However, during February, for example, an emergence of Capnia promota, a species not taken from Oak Creek, occurred in the Marys River near the mouth of Oak Creek.

The family Capniidae on Oak Creek spend the major portion of the year, about seven months, as quiescent nymphs 1-2 mm in length.

During this period nymphs are found in great numbers (>14, 000 /m^2) in soft, silty substrate with little current. Samples taken September 16, 1968, indicated nymphs were becoming active. The majority were small, white nymphs with the head bent towards the body. Some, however, were darker in color, somewhat transparent, and food could be seen in the digestive tract.

The common species in this family on Oak Creek is Eucapnopsis brevicauda (Claassen) 1924 which was represented by 102 specimens from the emergence traps. The nymphs of C. porrecta, the other species in this family, and E. brevicauda cannot be separated. This necessitated pooling data as illustrated in Figure 20. As there was a marked increase in the small nymphs in April, eggs of E. brevicauda require an incubation time of less than one month.

Growth of E. brevicauda begins at the same time as growth of Capnia porrecta, but is slower. The nymphs of this small species appear to be mature about two months before emergence. This would indicate a quiescent period late in the life cycle. This type of life cycle is very similar to that found by Brinck (1949) for C. bifrons and C. nigra in Sweden. Both of the Oak Creek species have one year life cycles with short growth periods highly adapted for taking advantage of leaf fall. Others (see Minshall, 1967; Elton, 1956) have noted the heavy dependence of primary consumers in streams upon allochthonous leaf materials.

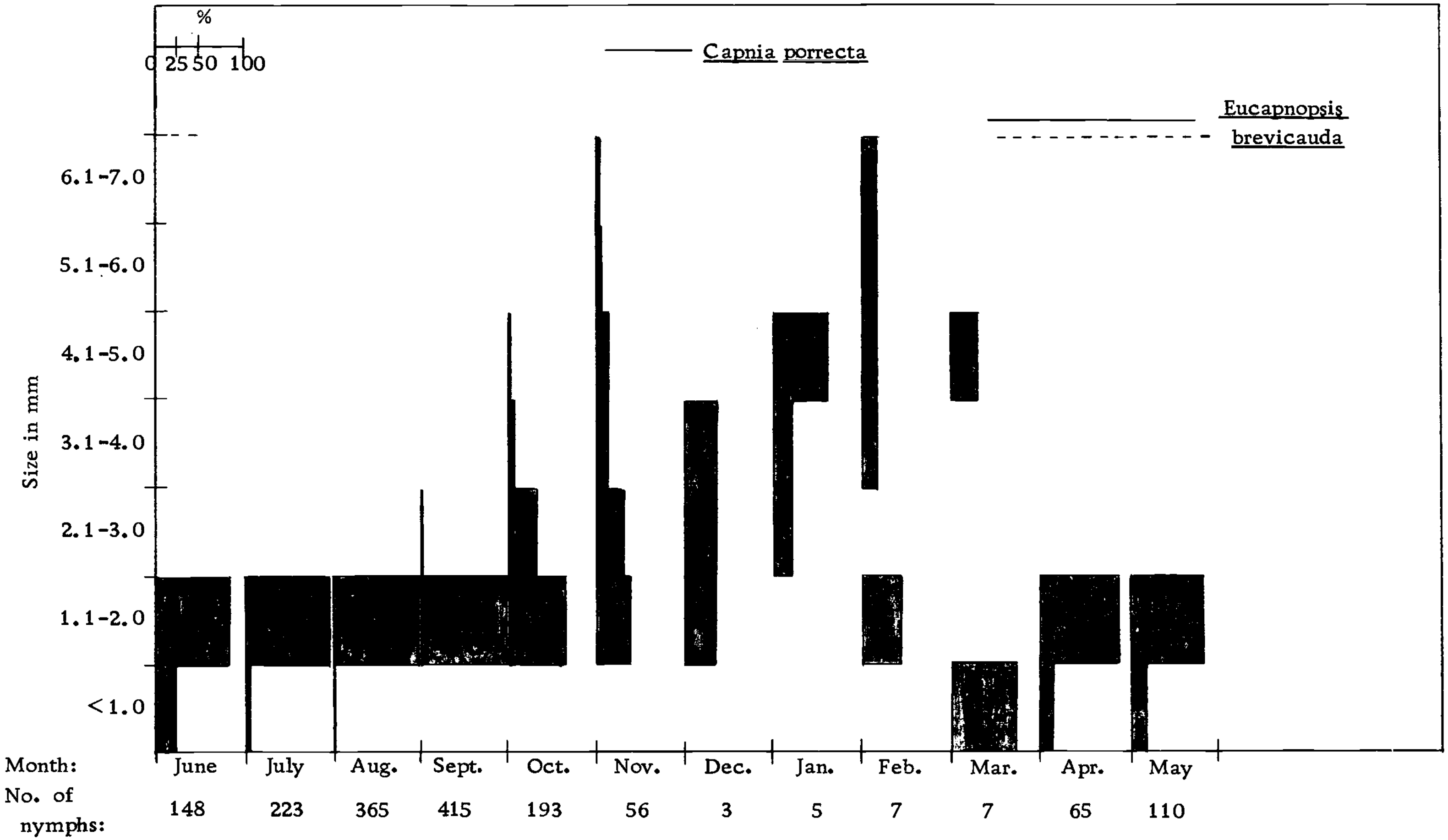


Figure 20. Length frequency of Capniidae nymphs from benthos samples. Frequencies expressed as percentages.
—— Adults present. --- Eggs present.

Capnia porrecta Jewett 1954 was represented in emergence data by only seven specimens. The benthos data for the Capniidae is given in Figure 20. Due to high water during the winter, emergence traps were often washed out. Sweep samples at the time, however, confirm that this species was not very common. *Capnia porrecta* grew rapidly during the fall, reaching adult size in less than two months after cessation of diapause. This species emerges in November.

Several female *Capnia* were taken during the spring. These may be *C. porrecta* but likely represent another species as they are separated from the main emergence period by three months. Jewett (1959) lists the emergence period for *C. porrecta* as October through December. Characters have not been found which will separate the females in this genus.

Genus *Brachyptera* Newport 1851

Thorup (1963) found that *Brachyptera risi* was univoltine in Denmark with a long incubation period and rapid nymphal development. Brinck (1949) reported the same for this species in Sweden. Hynes (1962) found this species to have a univoltine cycle with active growth during the cold winter months in a Welsh mountain stream.

The only species in this genus found in Oak Creek is *Brachyptera nigripennis* (Banks) 1918. This species has a pattern similar to the Capniidae in that the nymphs are inactive the majority of the year.

Nymphs were not taken during much of the year and may be deeper in the substrate. Nymphs taken from November through January were less than 3 mm in length. By February, all nymphs ranged from 3-9 mm. There was considerable variation in the size of the nymphs. Species with rapid growth rates seemed to be subject to more size variation than slower growing species. This pattern, a short rapid period of growth during the cold months, is similar to information found in the literature. Adults are present during March, April, and May. The eggs appear to require between one and two months to hatch as small nymphs were taken in May. Eggs would then be present from March through June, but this is uncertain due to the difficulty in identification of small nymphs.

Genus *Pteronarcella* Banks 1900

Claassen (1931) states that the nymphs of this genus are herbivorous. Ball (1946) believed one year to be required to complete the life cycle of *Pteronarcella regularis*. The nymphs taken by him were nearly the same size except for April and May when very small nymphs were taken with mature ones. He thus felt that the small nymphs hatched from eggs laid by adults which had emerged early in the spring. However, Claassen (1931) believes that not less than two years is required to complete the life cycle in this family, and this is borne out by the present study.

Pteronarcella regularis (Hagen) 1873 was found commonly in the upper portion of Oak Creek. Only 24 nymphs of this species were taken in the benthos samples. Adults emerge during May, June, and July. Small nymphs were not taken until the following November suggesting an incubation period of six months. The eggs can be identified with the aid of descriptions by Knight *et al.* (1965b). Eggs were found in samples as late as August 20, 1968, in large numbers at Site II. At the end of one year nymphs were from 1-4 mm in length. Nymphs taken during July and August were 4-6 mm, while 8-12 mm specimens were found in November. During the second year, growth appeared to be quite rapid particularly during the fall. Since adults are 16-18 mm the largest nymphs were not taken, but it seems reasonable to expect the 8-12 mm nymphs to grow to this size as six months remained until emergence.

Genus *Pteronarcys* Newman 1838

Claassen (1931) relates that the life cycle probably occupies three years. Holdsworth (1941a, 1941b) studied the life history of *Pteronarcys proteus* finding 12 instars for males and 13 for females with both three and four year life cycles possible. Miller (1939) found the eggs of this species to require 305-325 days to hatch under simulated natural conditions.

Pteronarcys princeps Banks 1907 was not common on Oak Creek, being represented by only 13 nymphs. Small nymphs were never taken in benthos samples. Adults emerge during March and April. Eggs were taken in benthos samples as late as August 20, 1968, about five months after emergence of adults. Eight to 14 mm long nymphs were taken during June and must be one, or perhaps two, years old. During October, two other year classes were represented in groups of 20-28 mm and 36-39 mm nymphs. The degree of development of the wing pads was quite different in the two groups. It seems, then, that three or perhaps four years is required for the life cycle, depending upon the length of the incubation period of the eggs (>5 months).

Suborder Setipalpia

Nymphs in this suborder are largely carnivorous (Brinck, 1949; Chapman and Demory, 1963; Claassen, 1931; Frison, 1935; Hynes, 1941; Minshall and Minshall, 1966; Thut, 1969).

Genus *Isogenus* Newman 1833

Species in this genus require one year to complete the life cycle (Brinck, 1949; Minshall and Minshall, 1966). *Isogenus misnomus* (Claassen) 1936 and *I. nonus* (Needham and Claassen) 1925 were taken rarely from the creek. Several nymphs of this genus were taken, but conclusions concerning the life cycles cannot be made.

Genus Calliperla Banks 1947

One specimen of Calliperla luctuosa (Banks) 1906 was taken, but the nymph is unknown.

Genus Isoperla Banks 1906

Minshall and Minshall (1966) found Isoperla clio in Kentucky to be univoltine and require four months incubation for the eggs. Hynes (1962) established that a Welsh species, Isoperla grammatica, had a period of growth retardation during the winter in a mountain stream. This species had a one year life cycle with delayed hatching of eggs. Ulfstrand (1968) found the eggs of I. grammatica and I. obscura hatched shortly after being deposited in Lapland. Both species were univoltine and had long growing periods covering part of two summers and the winter. Svensson (1966) describes a period of reduced growth during the winter with vigorous growth in fall and spring for I. grammatica in Sweden. He also found that this pattern applied to I. difformis in Sweden. Both species were univoltine.

Isoperla ebria (Hagen) 1875, I. marmorata (Needham and Claassen) 1925, I. mormona Banks 1920, I. sordida (Banks) 1906, and I. trictura (Hoppe) 1938 were all present in Oak Creek. I. mormona (36) was the only fairly common species and nearly all nymphs in Figure 21 are of this species from Site IV during April and May. Only 15 specimens of the other four species were collected in the emergence

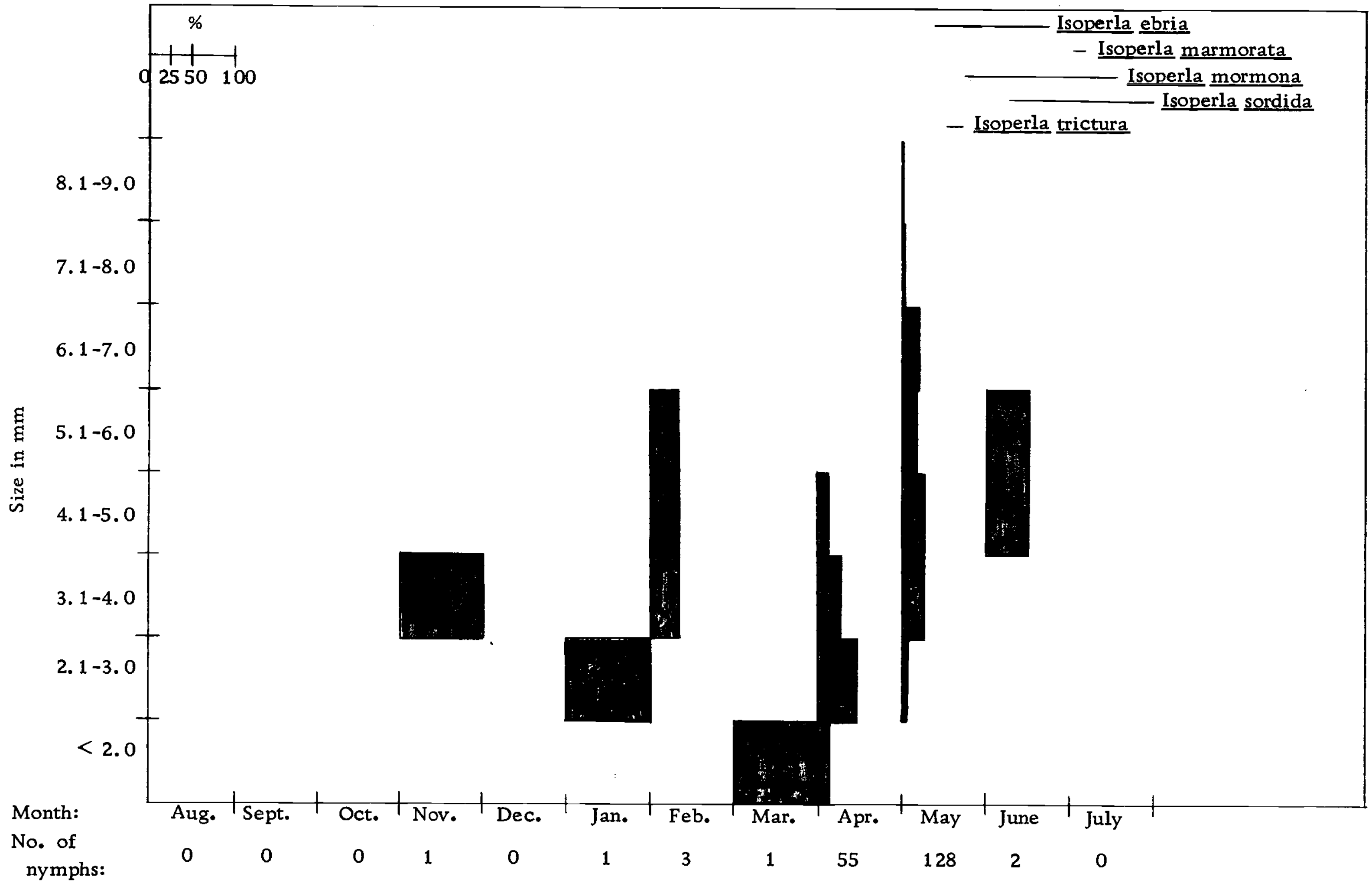


Figure 21. Length frequency of Isoperla spp. nymphs from benthos samples. Frequencies expressed as percentages.
—— Adults present.

traps.

I. mormona grows very rapidly during the spring and begins to emerge in May. This species was largely restricted to Site IV. In May it reached an average density of more than 850 nymphs per square meter at Site IV. Its rapid growth enables it to complete the life cycle during a period of less severe conditions at this site. There is a large amount of food available at this time due to colonization by drift, and the large numbers of chironomid larvae which are active. At Site IV during the winter the water is high, while during the summer, water is quite low, silty, and warm. The small nymphs of *Isoperla* may be represented in a group of unidentifiable small nymphs including *Isoperla* but mainly *Acroneuria*. There were 10-100 of these unidentifiable nymphs 4 mm and under present during all months. Most were 1-2 mm in length. As the nymphs of *Isoperla* grow, they develop a color pattern by which they can be identified. *I. mormona* has a one year life cycle, and it seems likely that the nymphs are relatively inactive for a large portion of the year. No data are available on the nymphs of other species of *Isoperla* in Oak Creek.

Genus *Kathroperla* Banks 1920

Kathroperla perdita Banks 1920 was not uncommon on Oak Creek as 19 specimens were taken during May and June in the emergence traps. Chapman and Demory (1963) describe this species as being herbivorous in Oregon in the nymphal stage. Seventeen nymphs were collected but life history data are inconclusive. Since the adult measures over 20 mm, this species likely requires more than one year to complete the life cycle.

Genus Alloperla Banks 1906

Members of this genus were quite common on the stream. Claassen (1931) believed the life cycle to occupy one year.

Alloperla delicata Frison 1935, A. pallidula (Banks) 1904, A. borealis (Banks) 1895, A. coloradensis (Banks) 1898, A. fidelis Banks 1920, and A. fraterna Frison 1935 were found on Oak Creek. The nymphs, again, cannot be separated as characters have not been found which will suffice. Figure 22 illustrates length-frequency data for this genus.

Since larger nymphs are present after emergence ends and before nymphs would have had time to grow to this size, the larger species, A. borealis and A. fidelis (10-12 mm), apparently require two years to complete their life cycle.

A. fraterna accounted for over 80% of the adult Alloperla in the emergence trap collections. Thus, the great majority of Alloperla nymphs are presumed to be A. fraterna. This species probably requires one year to reach its mature size of 5-7 mm. The other species have a maximum size of 7-9 mm. Much work will be required on this genus

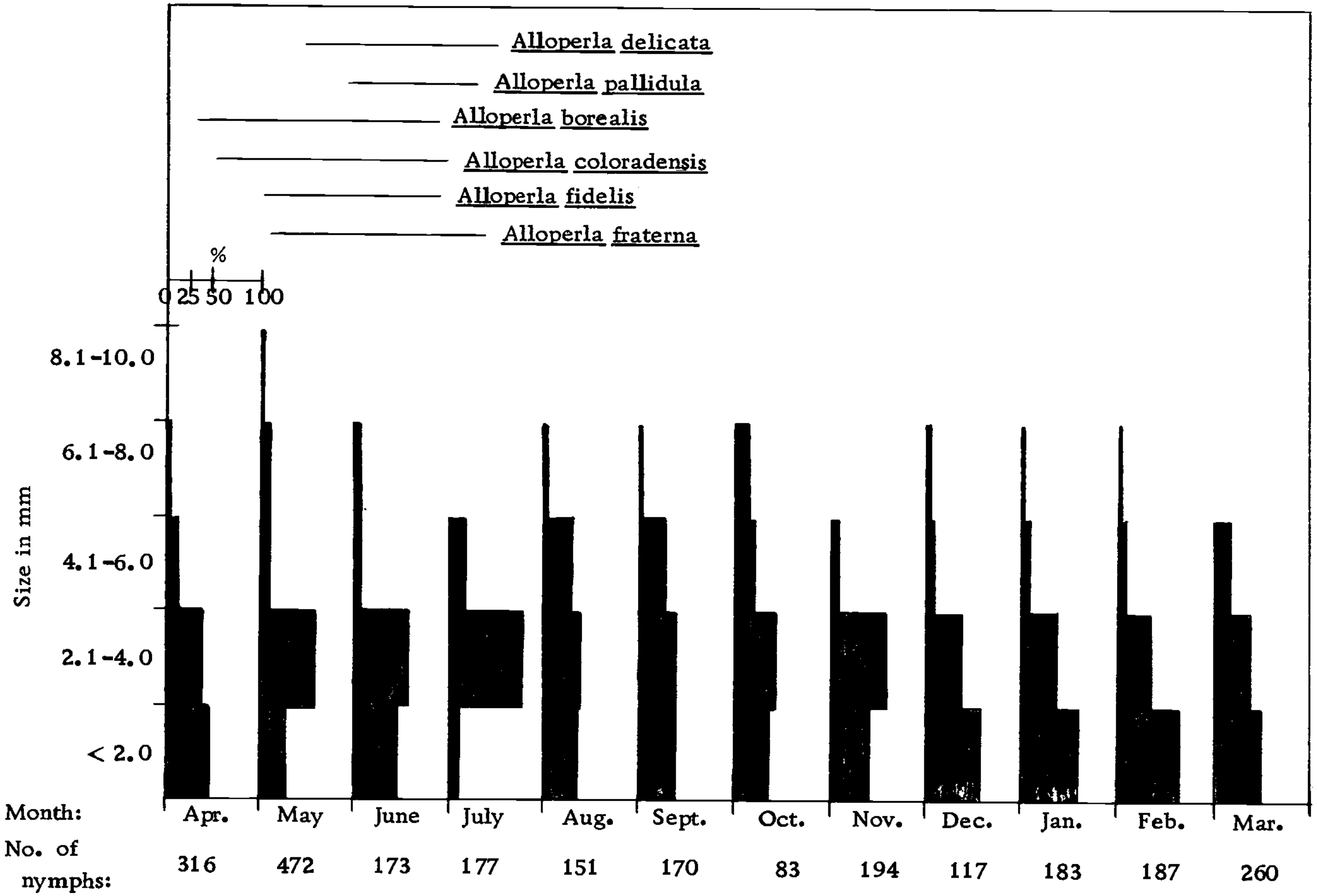


Figure 22. Length frequency of Alloperla spp. nymphs from benthos samples. Frequencies expressed as percentages.
——— Adults present.

taxonomically before insight is gained into the biology as the immatures present a formidable problem. Work also needs to be done with the eggs as there seems to be little growth until the spring following egg deposition, and perhaps there is nearly continuous recruitment from delayed hatching.

Genus *Hastaperla* Ricker 1935

This genus is represented on Oak Creek by a single, rare species, *Hastaperla chilnualna* Ricker 1952. Frison (1935) found that a related species in this genus was herbivorous.

Genus *Acroneuria* Pictet 1841

Claassen (1931) believed the life cycle to occupy three years. Frison (1935) thought two, and perhaps three years, were required.

As was stated previously, 10-100 unidentifiable nymphs believed to be mainly *Acroneuria* were present every month. These small nymphs lack the gills that are characteristic of *Acroneuria*, but some were observed actually in the process of hatching from eggs of *Acroneuria californica* in samples of August 20, 1968. It would seem then that the eggs of *A. californica* require about three months to hatch. Hynes (1941) found the eggs of two other perlid stoneflies required 96 and 97 days at 15°C to hatch. However, since the small nymphs were present throughout the year, a delayed hatching period is likely.

Figure 23 shows data for A. californica (Banks) 1905 which was the most common species in the genus. By spring, small nymphs with gills are appearing. Gills appear when the nymphs are 2-3 mm in length. Evidently cuticular respiration is sufficient until this size is reached. By May, three size classes are visible showing a three year life cycle. Even small nymphs must be one year old since eggs laid in May could not have hatched yet. The medium nymphs must be two years old and the 18-23 mm nymphs three years old. An extended hatching period, I believe, accounts for the size range. One then wonders if a nymph hatching early and having a summer to grow could complete the life cycle in two years rather than three, which may be required by a nymph hatching during the winter. This could complicate the life cycle considerably.

A. pacifica Banks 1900 follows the same pattern as A. californica. Figure 24 shows data for A. pacifica. The nymphs are also without gills when very small. They develop the anal gill first at a smaller size than A. californica develops gills. Three years is probably required for completion of the life cycle.

No nymphs were taken that could be assigned to Acroneuria theodora Needham and Claassen 1922.

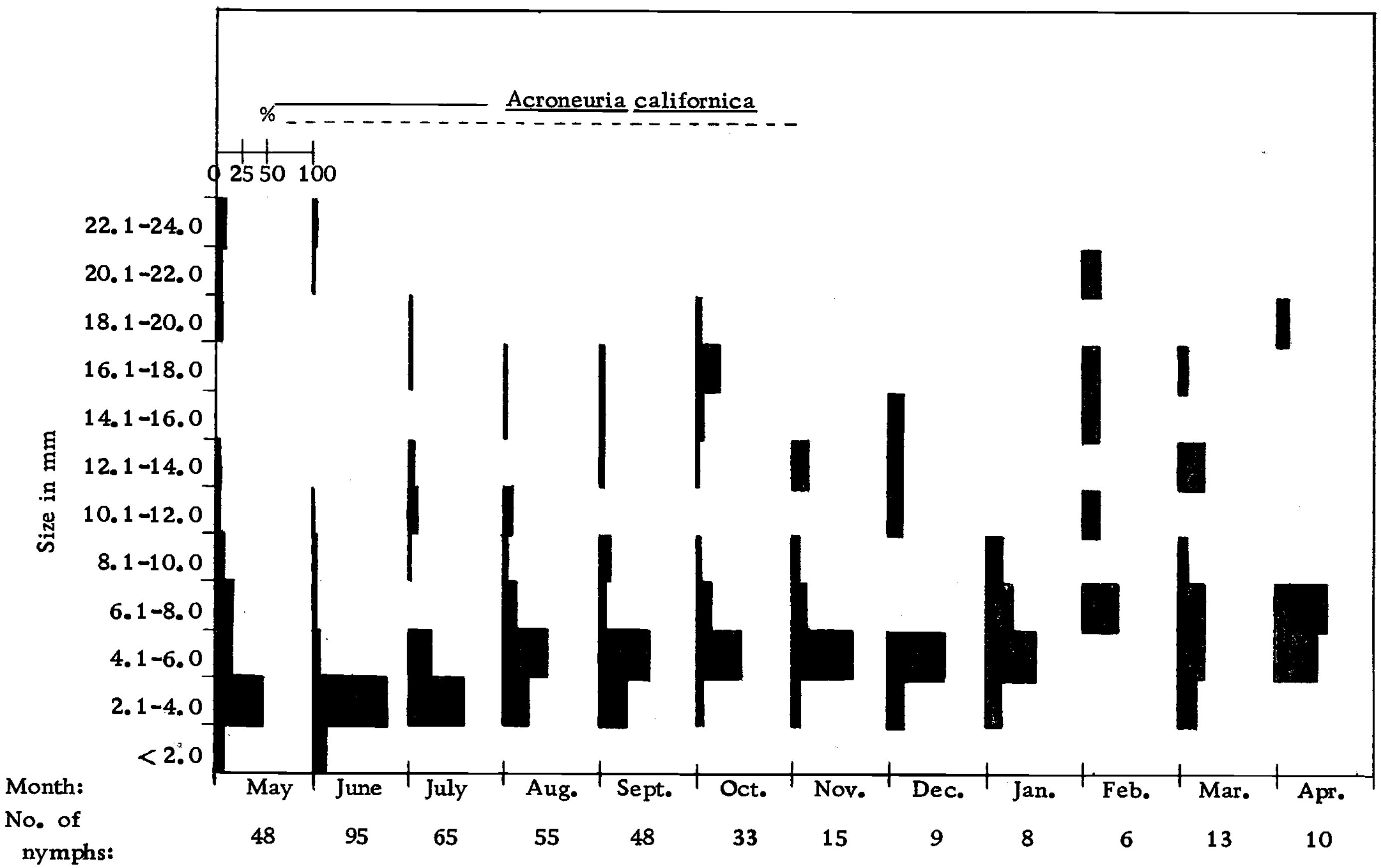


Figure 23. Length frequency of Acroneuria californica nymphs from benthos samples. Frequencies expressed as percentages.
—— Adults present. --- Eggs present.

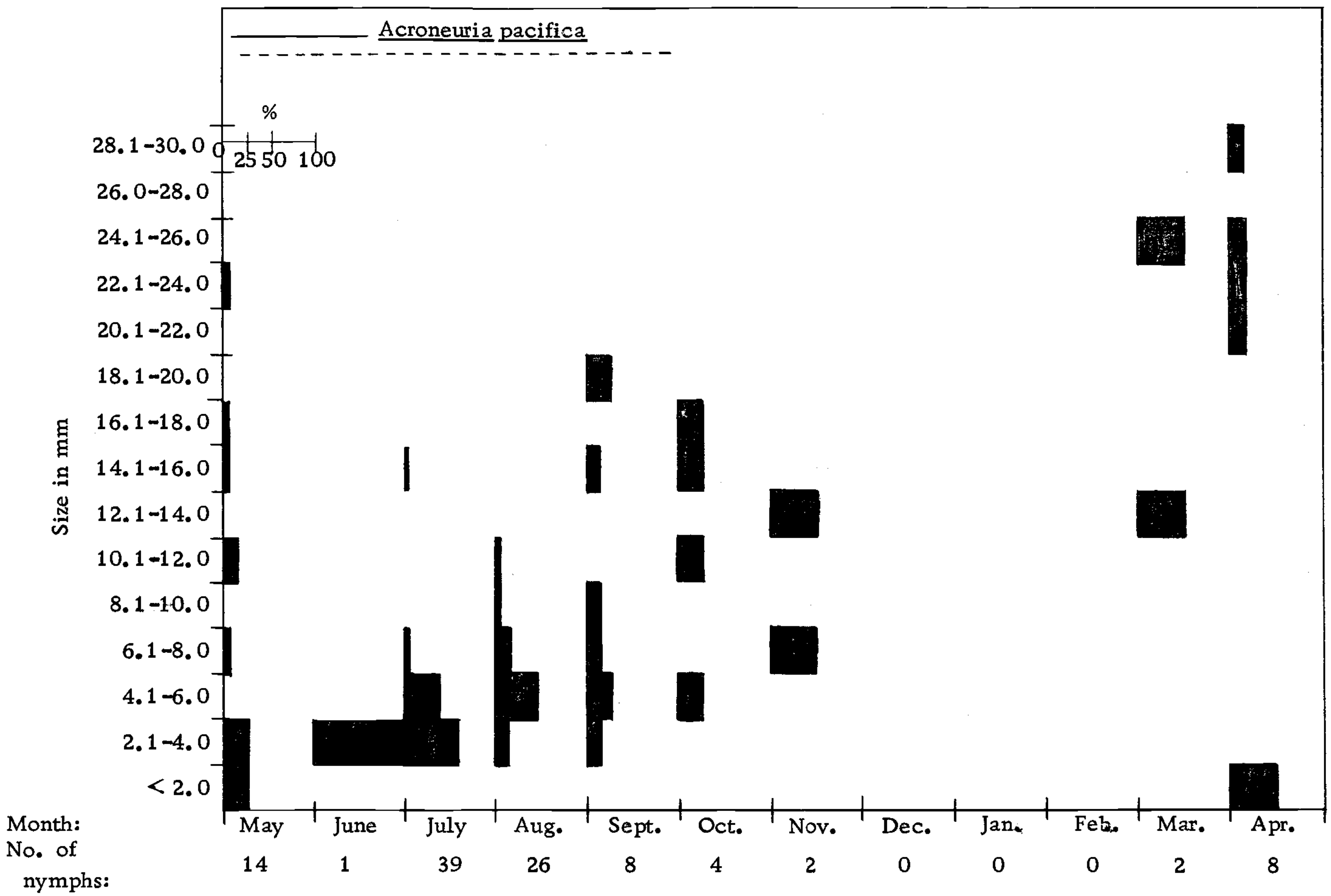


Figure 24. Length frequency of Acroneuria pacifica nymphs from benthos samples. Frequencies expressed as percentages.
—— Adults present. --- Eggs present.

COMPARISON OF PLECOPTERA FAUNA AT FOUR SITES ON OAK CREEK

We have found that Oak Creek supports a great number of species of stoneflies. Table 6 lists the numbers of various species taken at each site over a period of 13 months from the emergence traps. Seasonal succession of adults has been discussed as one method of partitioning the habitat. We return again to the basic problem of habitat partitioning. In this section data from benthos samples and emergence traps are used to compare the stonefly fauna at the four sites. The methods used are a diversity index, a percentage of similarity, longitudinal distribution patterns, and multiple regression analysis.

Diversity

Diversity or information content has been considered a measure of community stability (Southwood, 1966; MacArthur, 1955). Many indices have been used in a number of studies, and the implications of diversity have been discussed at length (Connel and Orias, 1964; Lloyd, Zar and Karr, 1968; MacArthur, Recher and Cody, 1966; Sheldon, 1968; Tilly, 1968). A review of indices is not pertinent as nearly any index will suffice for comparative purposes.

The information content of a community is described by the uncertainty of predicting which species an animal would encounter

Table 6. Numbers of Plecoptera, by species, collected from emergence traps at four sites on Oak Creek from May 14, 1968, to June 23, 1969.

Species	Site			
	I	II	III	IV
Peltoperla quadrispinula	4	1	0	0
Peltoperla brevis	20	3	0	0
Nemoura californica	19	20	4	0
Nemoura cornuta	153	26	39	0
Nemoura foersteri	1	0	2	0
Nemoura obscura	0	0	0	1
Nemoura interrupta	20	10	0	0
Nemoura producta	12	13	0	0
Nemoura cinctipes	39	51	8	5
Nemoura frigida	10	5	1	0
Nemoura oregonensis	1	6	1	0
Leuctra augusta	45	68	5	0
Leuctra infuscata	1	0	0	0
Leuctra forcipata	1	1	0	0
Leuctra occidentalis	6	2	1	0
Leuctra sara	2	20	12	1
Perlomyia collaris	0	0	4	0
Perlomyia utahensis	0	0	1	0
Capnia porrecta	0	1	6	0
Capnia spp.	1	0	2	0
Eucapnopsis brevicauda	24	55	23	0
Brachyptera nigripennis	0	1	7	1
Pteronarcella regularis	1	36	0	0
Pteronarcys princeps	0	3	0	0
Isogenus misnomus	1	0	0	0
Isogenus nonus	0	2	0	0
Calliperla luctuosa	1	0	0	0
Isoperla ebria	3	13	0	0
Isoperla marmorata	0	1	0	0
Isoperla mormona	0	4	7	39
Isoperla sordida	3	4	0	0
Isoperla trictura	0	0	0	1

Table 6. (continued)

Species	Site			
	I	II	III	IV
Kathroperla perdita	7	5	12	0
Alloperla delicata	7	19	61	1
Alloperla pallidula	0	0	32	2
Alloperla borealis	2	8	3	0
Alloperla coloradensis	0	8	1	1
Alloperla fidelis	4	6	3	0
Alloperla fraterna	146	162	397	2
Hastaperla chilnualna	0	0	0	4
Acroneuria californica	18	25	16	1
Acroneuria theodora	1	2	0	0
Acroneuria pacifica	0	0	13	0
Number of species	29	31	25	12

in the next random confrontation (Lloyd et al., 1968). Uncertainty increases as the number of species increases, but also as the individuals are distributed more equally among the species present. An index should measure both aspects to be realistic. One such index is the Shannon-Wiener function from information theory (MacArthur, 1965; Lloyd et al., 1968). This index can be used to summarize a great deal of data. The general form of the equation is:

$$H = -\Sigma p_i \log_e p_i$$

where p_i = the fraction of the total individuals belonging to the i^{th} species.

Emergence trap data were used to calculate species diversity since identification of immatures was questionable. These data represent the stoneflies emerging from one square meter at the four sites over one year. The traps were out at times due to high water, but this period is small in comparison to the total collecting period.

The computing formula for the Shannon-Wiener function is:

$$H = 2.3026 \left(\log_{10} N - \frac{1}{N} [\Sigma n_i \log_{10} n_i]\right)$$

where: N = the total number of individuals of all species.

n_i = the number of individuals of the i^{th} species.

2.3026 = the conversion factor from $\log_{10}$ to $\log_e$.

An index was calculated for each season at each site. Total diversity for all sites was also figured for seasons. Finally, a yearly index was calculated for each site.

Seasonally, diversity is highest in the spring when the great majority of species are emerging (Table 7). Summer would rank second while diversity is lowest during winter and fall. Seasonal trends in diversity at Site III are somewhat different than trends at other sites partly because one species (Alloperla fraterna) accounts for over half of the spring emergence at this site.

Table 7. Seasonal and yearly diversity of stonefly adults at four sites on Oak Creek.

	Spring	Summer	Fall	Winter	Yearly	No. species
Site I	1.9535	1.6445	0.8761	0.8607	2.2959	25
Site II	2.2860	1.3723	0.8558	0.6392	2.5298	28
Site III	1.5128	1.7723	0.5622	1.7352	1.7163	25
Site IV	1.1701	0.0000	0.0000	1.0899	1.6479	8
Total	2.0919	1.8678	1.0783	1.1750	2.4513	39

Site IV is rather unproductive as stonefly habitat and, consequently, has a low diversity index.

It should be emphasized that the critical periods for diversity are probably in the immature stages where competition would possibly occur. This does not create a serious problem as adults can be assumed to represent the successful nymphal population at a site.

The sites rank in the following order on the basis of yearly diversity: II > I > III > IV. Sites I and II are close in diversity, as are sites III and IV. Although Sites I and III both contain 25 species, Site

III is considerably lower in information due to the preponderance of a single species. Thus, one can say generally that there is an inverse relationship between diversity and distance from the headwaters on Oak Creek. MacArthur (1965) believes local differences in diversity can be accounted for by differences in the structural complexity and productivity of the habitat. One must first consider what a structurally complex stonefly habitat might be. If greater diversity of substrate and food supply can be taken as an indication of structural complexity, the two upper sites should be more diverse. Upper areas have more limbs, bedrock, and stone sizes. Site IV is particularly uniform in substrate.

Connel and Orias (1964) think stability of the environment contributes to diversity. There need not be only one reason for all differences in diversity. The downstream areas of the stream have higher temperatures in summer and higher water conditions in winter than upper areas. Thus the environment may be more stable in upper areas where diversity is highest. Site IV offers a particularly unstable environment.

The relationship between diversity and habitat is a particularly interesting one. It is possible that there are simple reasons for the areas of greater diversity. Sheldon (1968), for example, found depth significantly correlated with diversity of stream fishes. Greater depth increased diversity. In the section on factors affecting the distribution of stoneflies, we will see that an important factor in habitat selection by Plecoptera seems to be the depth of the water. However, the relationship is a negative one. Increased depth decreases the numbers of many species taken in a sample. Since Plecoptera show this preference for shallow areas, diversity must decrease over the length of the stream as depth increases.

Percentage of Similarity

This is a method (Southwood, 1966) of comparing two samples which places emphasis upon the dominant species. The computing formula is:

$$\% S = \Sigma \text{Minimum} (a, b, \ldots, x)$$

where: a, b, ..., x are percentages of all individuals represented by each species.

Since % S is calculated by adding the smaller of the two percentages from the two samples being compared, species not found in both samples contribute nothing. The same data were used for this calculation as were used for the section on diversity. This index was used to compare the stonefly fauna at the four sites on a yearly basis only.

As we would expect, Site I is very similar to Site II with a percentage of 77.58. Values are shown in Table 8. More evidence that Sites I and II are very similar is found when these sites are compared to Sites III and IV. The similarity between Sites I and III is very close to the similarity between Sites II and III. Also the value for

Sites I and IV is very close to the value for II and IV.

Table 8. Similarity of four sites on Oak Creek based upon the yearly catch of adult stoneflies.

Site I + Site II	=	77.58%
Site I + Site III	=	49.98
Site II + Site III	=	48.55
Site II + Site IV	=	21.50
Site I + Site IV	=	18.12
Site III + Site IV	=	13.14

Site III is intermediate although closer to the upper sites. Site IV is not at all similar to any of the other sites.

Longitudinal Distribution

In previous sections, the main consideration has been diversity of the Plecoptera fauna, without reference to the particular species. We will now consider the distribution of several species over the length of the stream.

In the studies of stream ecology others have noted a succession or change in species from upper to lower areas (Hynes, 1961; Macan, 1963; Minshall, 1968; Sheldon, 1968; Ulfstrand, 1968). Changes in the stonefly fauna over the length of Oak Creek have been obvious throughout this study. Minshall (1968) provides the following reasoning. The variation between sampling stations on a stream 'provides a measure of a species reaction to conditions at these stations'. Andrewartha and Birch (1954) allow that 'the study of abundance in different parts of the distribution is itself a study of the causes of rareness and commonness in species'. A study of longitudinal distribution patterns is such a study and could also be considered as habitat selection. It should provide insight into partitioning of the habitat.

Of the 43 species (including the unidentified Capnia) taken from Oak Creek, 31 species have been found at Site II, 29 at Site I, 25 at Site III, and 12 species from Site IV (Table 6). As additional evidence of differences in the fauna at the four sites, the Trichoptera collected concurrently in the emergence traps have been identified from May through December. Site II had 18 species, 17 species were taken from Site I, 13 from Site III, and 3 species were found at Site IV. These rank in the same order as do the stonefly data, and the proportions fit quite well.

One should note the gaps in the distribution of species in Table 6. Several of these examples will be further illustrated. Emergence is assumed to reflect the composition of the benthos, but benthos data will be presented where possible. For graphs showing longitudinal distribution, emergence data for one year was used rather than the numbers for the total collection period from Figure 6. This was to make emergence data comparable with benthos densities since otherwise we would be representing emergence to be greater than it is in cases where more than one complete emergence period has been sampled. The benthos densities are average monthly densities. Ninety-two benthos samples were taken from each of the upper three sites while Site IV was represented by 53 samples. The data from Site IV is somewhat questionable as high water prevented stovepipe samples being taken during these times. An attempt was made to determine the equivalent number of stovepipe samples using quasi-quantative samples.

There are several examples of habitat restriction between the sites. Figure 25 shows that both Peltoperla species were restricted to Sites I and II and are more common in headwater areas. Brachyptera nigripennis was very common at Site IV. Emergence of this species was underestimated because the trap was out during parts of the emergence period. As is shown in Figure 26, Nemoura interrupta and N. producta were restricted to Sites I and II; some nymphs, but no adults, were taken at Site III. Pteronarcys princeps and Pteronarcella regularis were also found only at the upper sites.

P. regularis had a very large emergence at Site II. Although this site is only 300 yards below Site I, the difference in abundance of adults is easily noticed on a warm June day. The adults seem attracted by the openness of the area, and can be seen in fairly large numbers. The attractiveness may have to do with oviposition habits. This relatively large species flies along the stream and briefly touches the water surface to wash the eggs from the tip of the abdomen. They

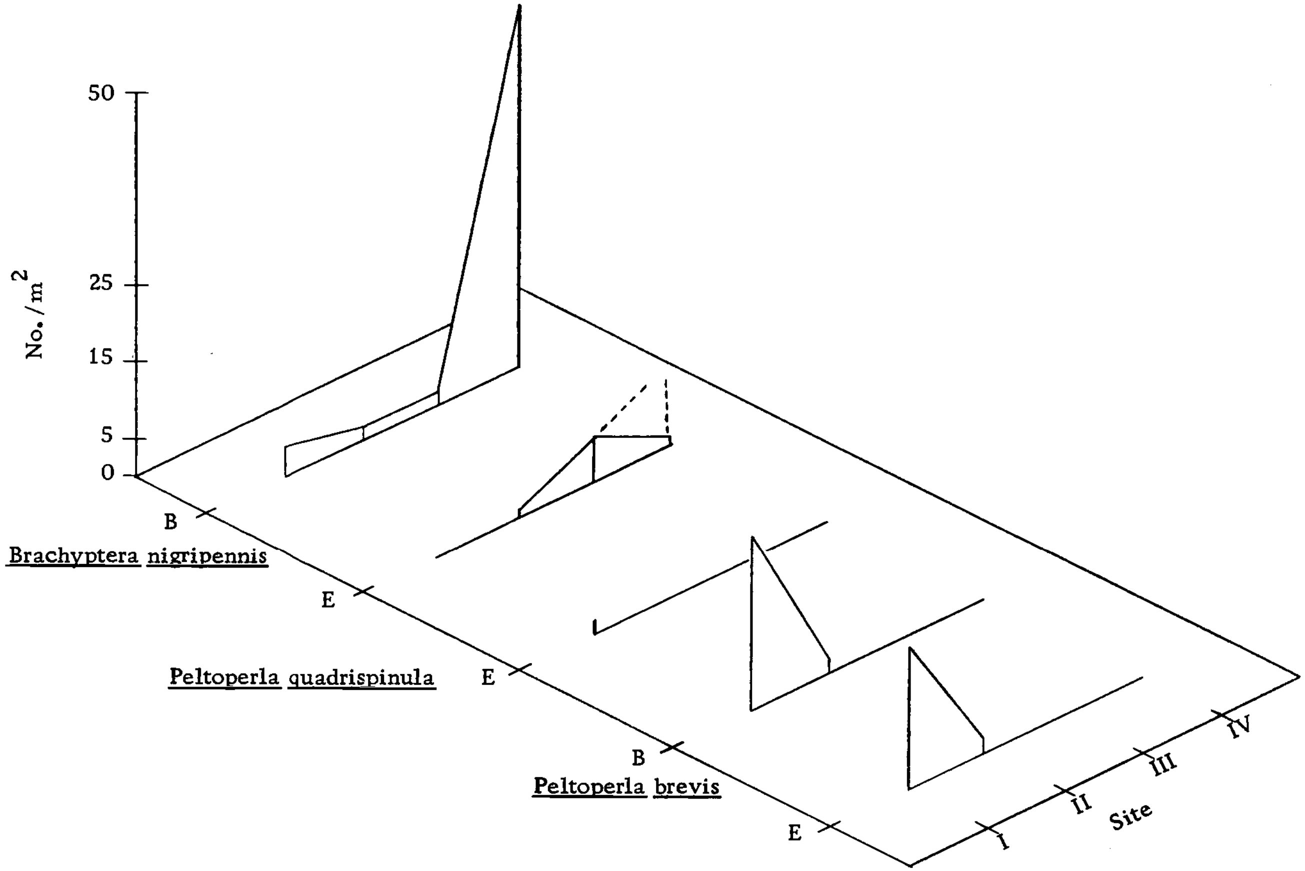


Figure 25. Longitudinal distribution of Brachyptera and Peltoperla on Oak Creek.
E = Emergence data. B = Benthos data. --- Emergence underestimated due to high water conditions.

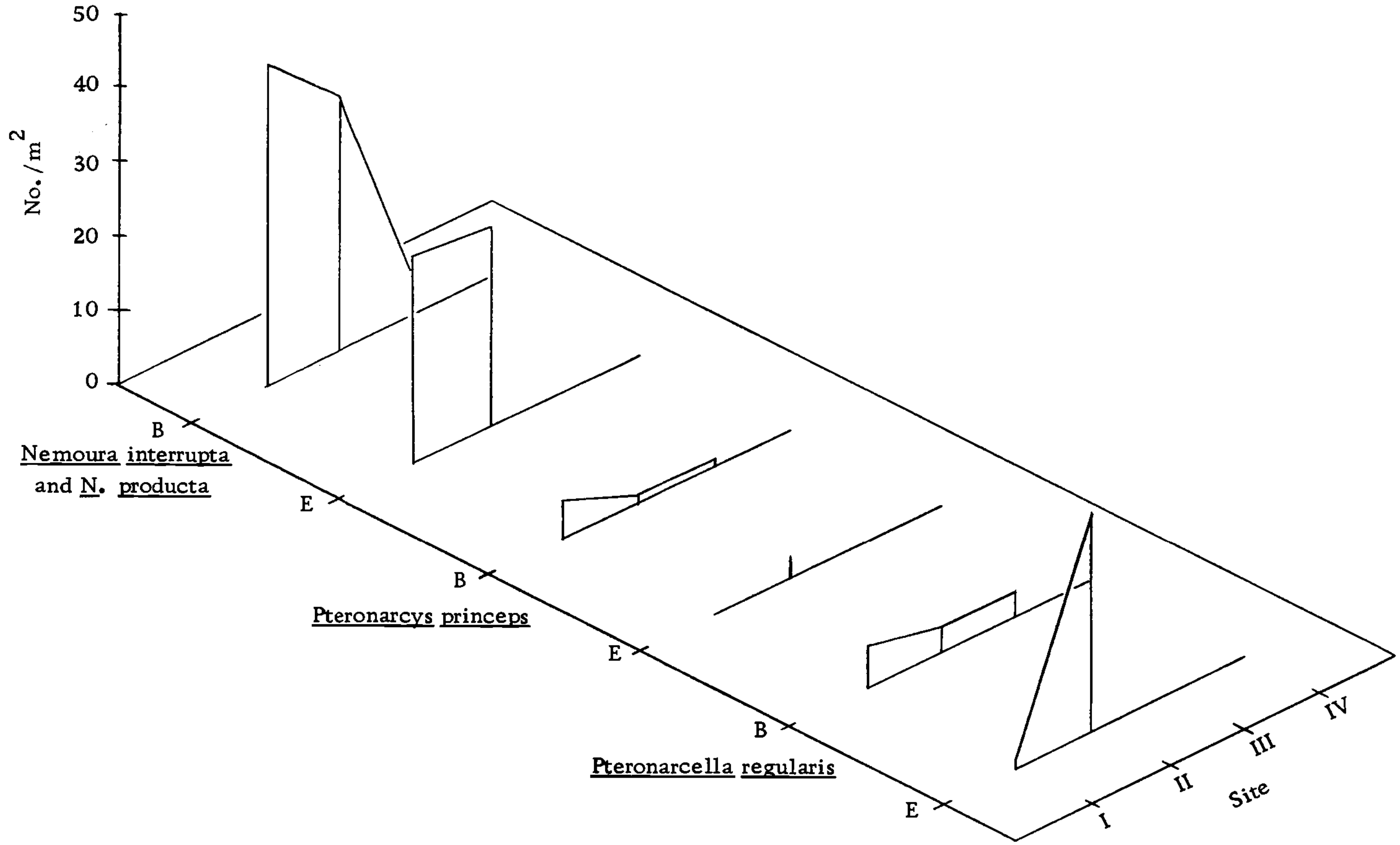


Figure 26. Longitudinal distribution of Nemoura, Pteronarcys and Pteronarcella on Oak Creek. E = Emergence data. B = Benthos data.

probably prefer a straight open reach of stream for oviposition.

Figure 27 illustrates the distribution of several other species. Isoperla mormona is found at the lower sites and may be eliminated from upstream areas by competition. The nymphs at Site IV are probably all I. mormona. Several species of Isoperla are found only at the upper sites. I. mormona has a short, rapid growth period which allows it to explicit a good food resource at Site IV.

Eucapnopsis brevicauda was found at all sites, being more common in upstream areas. Since the trap at Site IV was out very little during the emergence period of this species, the density of Capniidae nymphs suggests that Capnia porrecta (or other Capnia spp.) adults should be more common at Site IV. This would be the case unless the nymphs were very unsuccessful in completing their life cycle at this site. The trap was out during much of the emergence period of Capnia porrecta. Sweep samples indicate that this species was present but not in large numbers. As this species does emerge during the high water season, a great many nymphs must drift downstream from Site IV. It is interesting to note that Minshall (1968) found a species of Allocapnia, a related genus, restricted to lower reaches of a Kentucky stream under similar conditions. This area was subject to flooding from the Ohio River which deposited large amounts of silt.

Figure 28 illustrates the most unexplainable examples of longitudinal distribution. Three species of Acroneuria are found in the

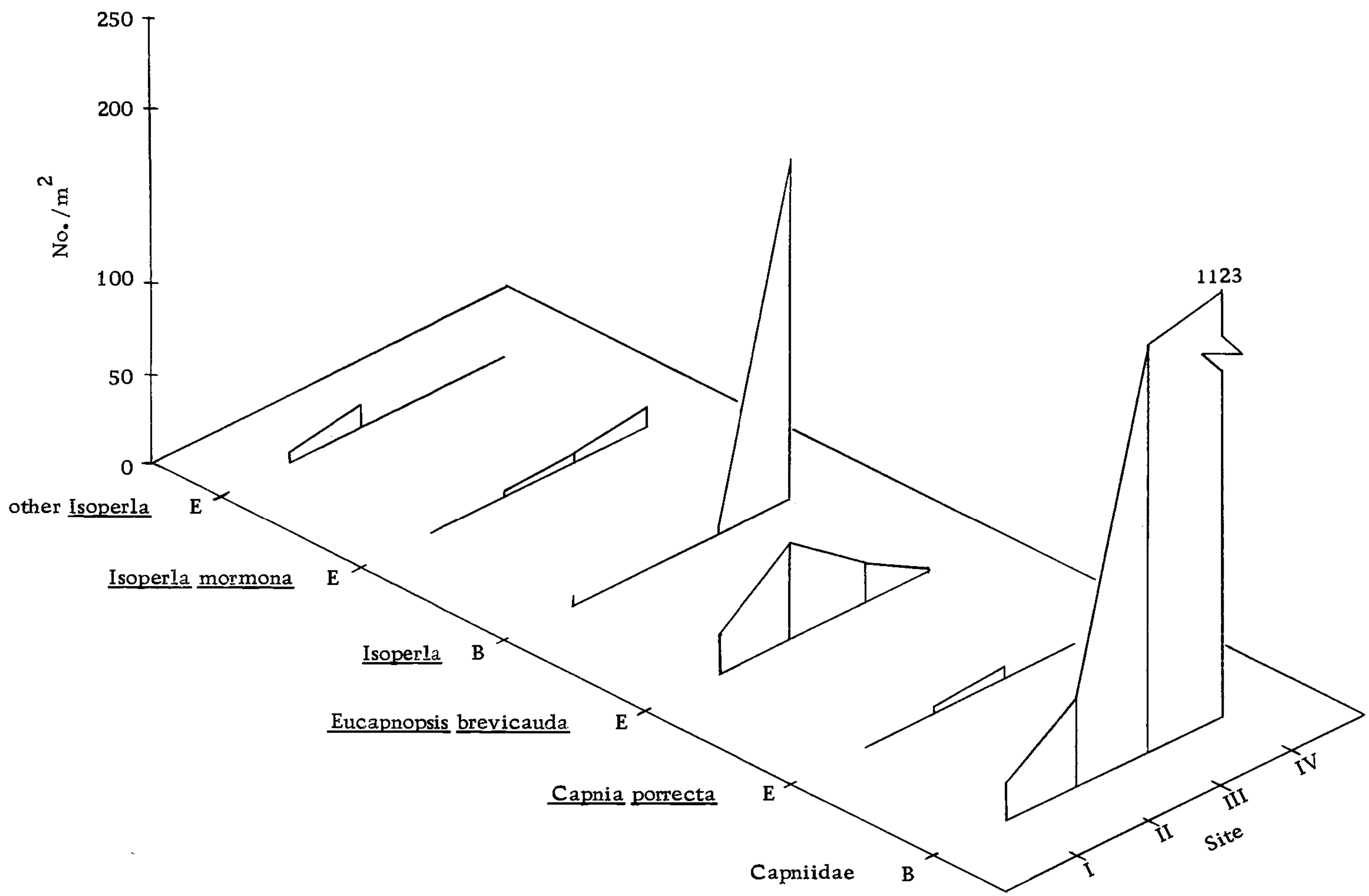


Figure 27. Longitudinal distribution of Isoperla and Capniidae on Oak Creek.
E = Emergence data. B = Benthos data.

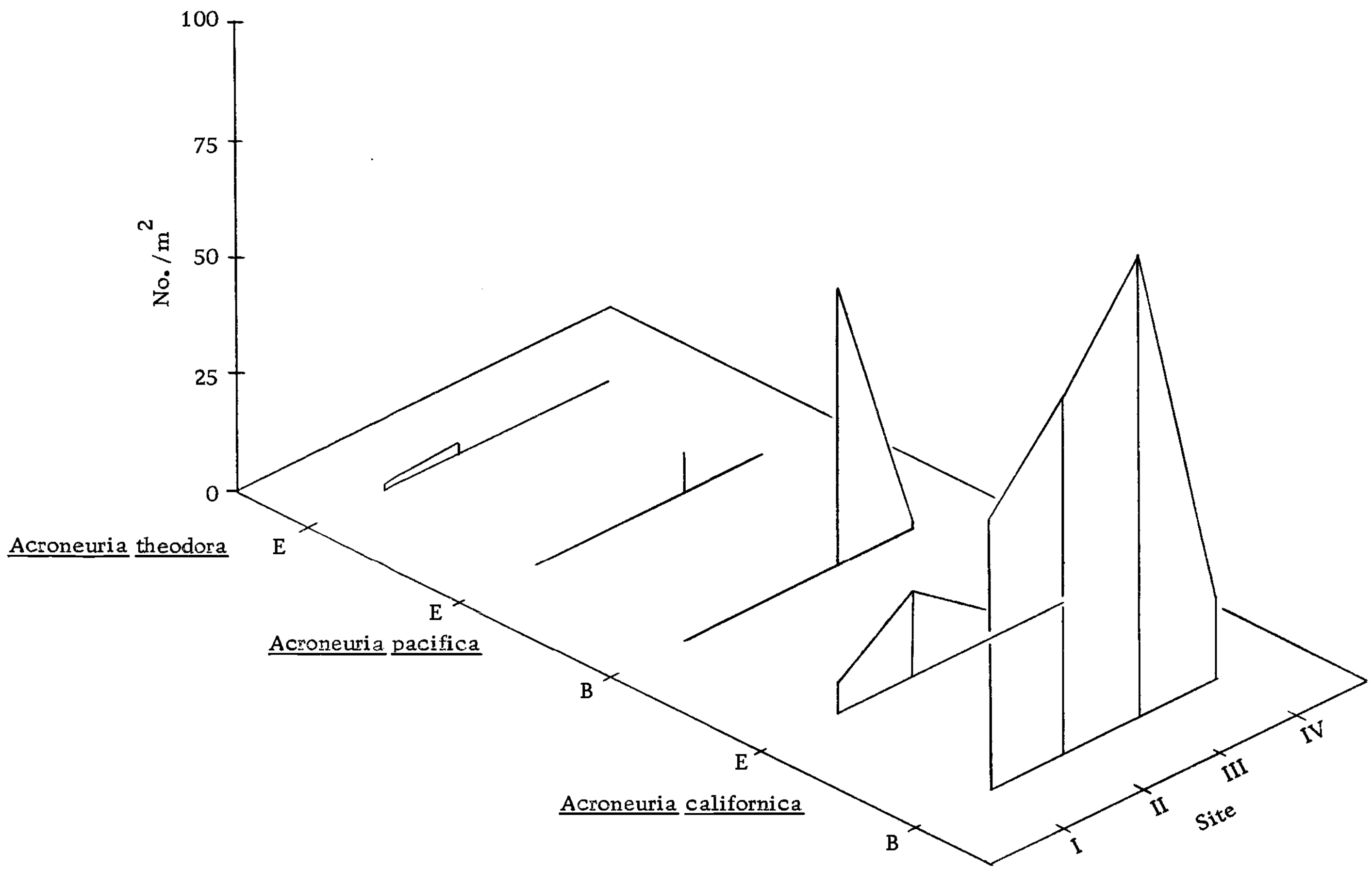


Figure 28. Longitudinal distribution of Acroneuria on Oak Creek.
E = Emergence data. B = Benthos data. Figure does not include small, unidentifiable nymphs that occurred during all months.

stream. _A. californica_ and _A. pacifica_ are the common species. Only three specimens, all adults, of _A. theodora_ have been taken. _A. californica_ and _A. pacifica_ are quite similar morphologically. The major difference is the presence of an anal gill in _A. pacifica_ which is lacking in the other species. _A. californica_ is common at the upper three sites and uncommonly taken in the benthos at Site IV. _A. pacifica_ is limited to Site III although taken very rarely in the benthos at Site IV. The restriction of _A. pacifica_ to Site III may relate to the size of stream preferred as habitat. It may also relate to the amount or type of food available. Table 9 provides evidence that the lower sites support a greater proportion of predaceous stoneflies to emergence.

Table 9. Comparison of herbivorous and carnivorous Plecoptera taken from emergence traps at the four sites.

Site:	I		II		III		IV	
	no.	%	no.	%	no.	%	no.	%
Filipalpia (herb.)	360	61.85	322	52.61	116	16.90	8	11.3
Setipalpia (pred.)	222	38.15	290	47.39	570	83.10	63	88.7
Total	582		612		686		71	

It could be argued that this does not represent benthos since it is based upon adults. Adult emergence, however, is more a measure of success than of the occurrence of immatures. Thus, _A. pacifica_ may be eliminated from upstream areas by competition with _A. californica_ and other predaceous stoneflies. An abundance of food may be available in the lower areas allowing for the existence of an additional species.

Table 9 infers a basic change in the trophic structure of the Plecoptera community over the length of the stream. The majority of the Plecoptera from Site I were herbivorous. This value decreases with a corresponding increase in carnivores until over 80% of the stoneflies are carnivores at Sites III and IV. The predominance of herbivores in the upper sections of the stream may be related to the type of food available. There are more mosses at Site I. Leaf material seems abundant at the upper three sites. It seems that this change would be food related.

Factors Influencing Distribution of Plecoptera

A stepwise multiple linear regression analysis was run for ten of the common groups recognized in the benthos. Ten months' data from the upper three sites was pooled for the analysis. Site IV was excluded because of incomplete samples and also because of its uniqueness. The independent variables for which accurate measurements were available were: date, current speed, water depth, and distance from the shore. Substrate diameter, amount of leaves, detritus, and silt were ranked on a scale of increasing size or amount. Detritus included any finely divided leaves and other material such as bark, lichens, sticks, etc. Stone size was the most difficult measurement because a given sample may contain a certain amount of all stone sizes up to six inches in diameter.

R^2, the multiple correlation coefficient, varied from .06 to .27 for the ten cases. This indicates that the fit of the regression model to the data is not good. Reasons other than lack of fit, I feel, are possible for these low values. Identification of immatures must be improved, better methods for measuring some variables need to be found, and more variables may need to be added. The relationship may not be straight line. This would seem reasonable for current speed and stone size where organisms may be selecting for a certain range out of those available.

Table 10 will be used to indicate factors which seem to be important in the distribution of Plecoptera. Date is often significant because the numbers one finds depends upon the stage of the life cycle which, in turn, depends upon the season.

The current speed is not significant in any case. As was previously stated this may be due to the selection of a particular current speed. After graphing some data this possibility seems unlikely. The variation is quite large, but generally Plecoptera seem to be found at current speeds between .25 and 1.25 feet per second. This would, of course, not give a straight-line relationship.

The depth of the water is an important factor. The relationship is a negative one. For most groups the numbers found in a sample decrease with increasing water depth, but the Capniidae increase in

Table 10. Summary of t values for coefficients of independent variables from final regression equations. Corresponds to a two-tailed test of the hypothesis that a given coefficient equals zero.

Nymphal group	Date	Current	H_2O depth	Distance	Stones	Leaves	Detritus	Silt
Nemoura cinctipes + N. cornuta	-4.671*	-0.990	-2.065*	-0.262	1.290	5.298*	1.965*	-3.060*
Nemoura producta + N. interrupta	-4.128*	-1.070	-3.547*	0.135	-0.216	4.118*	0.559	-1.609
Nemoura californica	5.552*	-0.628	-2.639*	-0.311	-0.019	3.140*	2.107*	-1.263
Capniidae	-1.620	0.638	2.641*	3.090*	-1.348	3.441*	-1.462	2.180*
Leuctra augusta	3.536*	-0.674	-1.479	-1.344	1.127	0.306	0.780	1.029
Other Leuctra	-1.233	0.886	-3.666*	-0.776	-0.378	0.828	1.354	1.280
Alloperla spp.	4.409*	-1.202	-2.533*	-1.248	0.675	-2.098*	-1.723*	-1.109
Acroneuria californica	-5.660*	-0.156	-4.273*	-0.353	0.228	1.617	0.058	-2.945*
Acroneuria pacifica	-0.154	0.196	0.445	0.207	0.748	6.050*	1.410	-1.205
Small Acroneuria + Isoperla	2.966*	-0.604	-0.190	-0.914	1.841*	-0.325	-0.704	0.390

*Reject when $|t| > 1.645$ at 10% significance level.

number with increasing water depth. This may in part be due to the nymphs being found in deeper water during diapause. They would seem to be found in shallow water, particularly leaf drifts, when active. This relationship is interesting since the Capniidae nymphs are found so commonly at Site IV. *Acroneuria californica* seems to prefer shallow water while *A. pacifica* shows little or no relationship. This could be one factor separating these species.

The distance the sample was taken from the shore seems unimportant. It was significant in the Capniidae and may be correlated with water depth.

The data on stone size is not considered meaningful for reasons already stated.

The amount of leaves was very important. Increasing the amount of leaves in a sample increases the numbers of most groups particularly the *Nemoura* and Capniidae. Leaves seem very important in the distribution of *Acroneuria pacifica* but less so in the distribution of *A. californica*. This could be another factor separating these species.

The amount of detritus has a negative effect in the case of *Alloperla* and positive effects upon *Nemoura cinctipes*-*N. cornuta* and *N. californica*.

Increasing amounts of silt adversely effect the numbers of *Nemoura cinctipes*-*N. cornuta*, and *Acroneuria californica*. The numbers of Capniidae nymphs increase with the amount of silt in a sample. This relates to the inactive period when nymphs are found in large numbers in heavy silt.

Of the group not included in the regression analysis, the following can be deduced based upon the benthos samples. Of the areas sampled the best place to take Peltoperla brevis, Nemoura oregonensis, Pteronarcys princeps, and Pteronarcella regularis nymphs is also in leaf drifts at sites where these species occur.

It becomes apparent that if one wishes to collect any stonefly present at a site, leaf drifts are a very good place to do so. This is not surprising after the discussion of feeding habits of the nymphs. They would be expected to be found where large amounts of food exist. As has been stated, allochthonous material has been found to be important to benthic organisms in streams. Minshall (1967) found that leaf material supplied the main source of energy for the entire benthic community in a Kentucky stream. Whether organisms are feeding upon the leaves or the bacteria and fungi that decompose the leaves is problematical. Predaceous Plecoptera are found in leaf drifts feeding upon the large numbers of animals that either directly or indirectly utilize the leaves as food. Leaves probably also provide excellent shelter.

Habitat selection does not appear to be very rigorous. Leaf drifts appear to be 'superhabitats' for stoneflies. Grant and MacKay (1969) found that "congeneric species of stream insects live in much the same habitat." They believe natural selection to favor a difference in time when each species has a maximum impact upon the resources. Even though emergence times do not differ, it is possible that growth periods are staggered. I have been very impressed with how quickly nymphs can grow. It is also interesting how short this period of growth can be in relation to the total time spent in the nymphal stage.

SUMMARY AND CONCLUSIONS

Forty-two species of Plecoptera in 15 genera were collected on Oak Creek. The species composition is similar to what it was in Ball's (1946) study 35 years ago. When the number of species in Oak Creek is compared to studies in small stream rithron biotopes, it is concluded that Oak Creek is a stream very productive in species.

Adult Plecoptera can be collected during every month of the year, but 37 of the 42 species complete their emergence during the spring. Little seasonal succession in emergence periods occurs in the suborder Setipalpia. In the suborder Filipalpia, the *Nemoura* and *Leuctra* species show temporal separation in emergence periods that could aid in lessening competition. Two species, *Nemoura californica* and *N. interrupta*, have split emergence periods. This would be advantageous in cases where severe weather occurred during one of the periods, as well as providing opportunities for speciation. Early emergence of males occurs in some species, but generalizations do not hold.

Species diversity of emerging adults by season ranks in the following order: Spring > Summer > Winter > Fall. Using a yearly diversity index the sites rank as: II > I > III > IV. Diversity tends to decrease from the upper areas of the stream to lower areas. Diversity may be related to the structural complexity of the habitat and stability of the environment. Stoneflies select shallow water as their habitat. Thus, diversity decreases down the stream as the depth of the water increases.

The faunas at Sites I and II are quite similar based upon a percentage of similarity. Site III is intermediate, while Site IV is quite different.

Differences in longitudinal distribution were found to be important on the creek. Many species are restricted in distribution. This can be an important method of ecological segregation. Herbivorous Plecoptera are more common in the upper sections of the stream while predaceous forms predominate in lower areas. This may be related to the type of food available.

Depth of water and amounts of leaves and silt are important factors in the distribution of stoneflies in Oak Creek. Most species are found in greatest abundance in leaf drifts. It appears that longitudinal and seasonal succession are more important in ecological segregation than microhabitat differences.

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