SEASONAL CHANGES IN THE FOOD INGESTED BY AQUATIC INSECT LARVAE AND NYMPHS IN TWO OREGON STREAMS

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Introduction

Knowledge of the major components of the food web in aquatic ecosystems is essential if efficiency of energy transfer and production statistics of the several trophic levels are to be fully developed and understood. This study is an initial effort to learn the food components for aquatic insect larvae and nymphs in 2 small Oregon coast range streams.

Food habits of some common insect larvae and nymphs present in the streams were investigated from November, 1959 to April, 1961, to determine whether immature insects important in the diet of the dominant carnivore, juvenile coho salmon (*Oncorhynchus kisutch* (Walbaum) obtained their energy primarily from aquatic autotrophic producers or from terrestrial plant debris, and whether the energy source utilized changed seasonally. The diet of coho salmon was studied by Demory (1961) and the insects investigated in the present work were chosen on the basis of his analysis.

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Description of Study Streams

The streams are about 2.5 miles apart, and their seasonal changes in biota and physical characteristics are similar. Figure 1 shows streamflow and demonstrates the great variability occurring during this study period. Figure 2 shows water temperature records, and demonstrates the relatively small variability resulting from influence of marine air and heavy vegetative cover over the streams. Deer Creek drainage area is 815 acres; Needle Branch drains 230 acres.

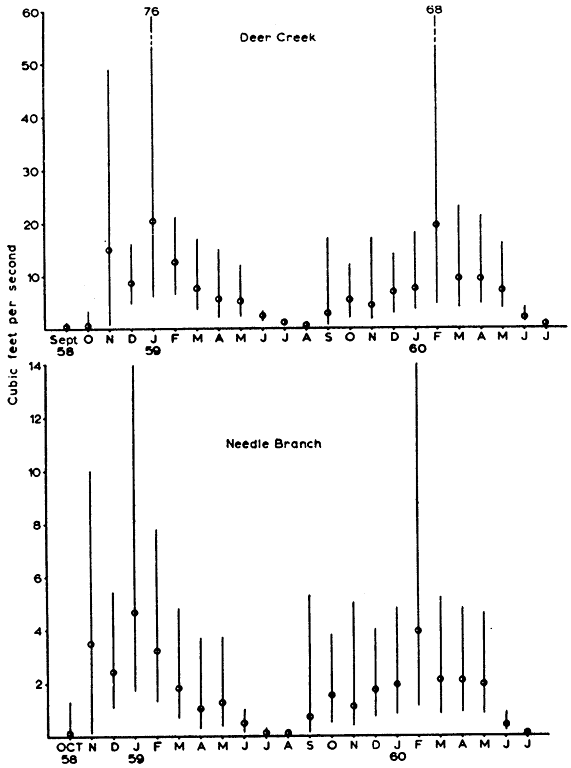

Fig. 1. Streamflow monthly mean and range.

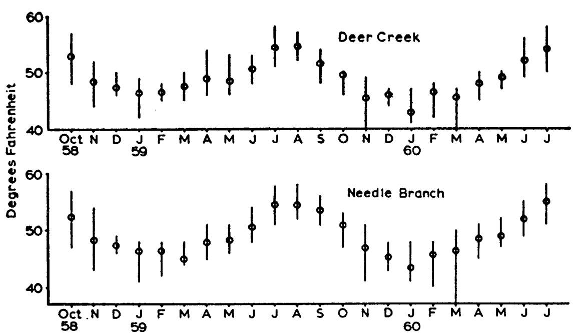

Fig. 2. Stream temperature monthly mean and range.

Both watersheds are covered by a dense growth of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, about 110 years old. Deer Creek is heavily shaded by red alder, *Alnus rubra* Bong., and some salmonberry, *Rubus spectabilis* (Pursh.) Needle Branch is shaded largely by salmonberry. Both streams receive some shading from the Douglas-fir forest canopy in addition to that provided by moist-habitat species such as red berry elder, *Sambucus callicarpa* (Greene), skunk cabbage *Lysichitum americanum* Hulten and St. John, and thimble berry, *Rubus parviflorus* (Nutt).

The heavy low growth of deciduous vegetation along the streams makes it impossible for one to walk upright in much of the stream beds; the dense shading profoundly influencing algal distribution and variety. The only green alga found frequently in the streams is *Protoderma viride* Kutz, and this appears only in better lighted areas. The diatoms constitute the most abundant algal groups, the most frequently observed genera being *Navicula, Gomphonema, Amphora, Cocconeis,* and *Pinnularia.* Bluegreen algae most often found are *Chamaesiphon, Oscillatoria,* and *Entophysalis rivularis* Kutz. A red alga, *Batrachospermum,* is found occasionally, as is a yellow green, *Vaucheria.* Under very dense shade, nothing but scattered diatoms are to be found.

Aquatic liverworts and mosses are found frequently on stable substrata, usually in areas holding large gravel or rubble particles. Genera identified are *Chiloscyphus, Riccardia, Scapania,* and *Eurhynchium.*

The density and deciduous nature of the streamside vegetation have some interesting effects upon incident light. Mean daily light energy, calculated for each month, ranged from a low of about .062 B.t.u. per square inch in December to about .359 B.t.u. per square inch in July. These data indicate seasonal fluctuations in light availability in the open, but conditions beneath the forest canopy along the streams were greatly different. Table I shows relationships among light meter readings in the

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open and under the canopy (at the same time of day and the same area on the stream for each sample), and cloud cover. All data are for Needle Branch, but conditions on Deer Creek would be similar.

TABLE I. Light incidence in foot candles as recorded at midday in an open meadow and under the forest canopy at Needle Branch. Levels indicated were obtained from one reading in an open meadow and mean of readings at 4 stations under forest canopy

Date	Light Intensity (fc)		Ratio of light along stream under canopy to light in open meadow	Weather	
	Open meadow	Under canopy		Cloud cover	Light type
1959					
Nov. 6	2660	280	.11	cloudy	diffuse
Nov. 13	3375	79	.02	none	direct
Dec. 21	475	125	.26	cloudy	diffuse
Dec. 23	375	131	.35	cloudy	diffuse
1960					
Apr. 30	1950	345	.18	cloudy	diffuse
Jun. 17	700	90	.13	cloudy	diffuse
Jul. 20	3950	47	.01	none	direct

As Park (1931) has shown for sub-canopy light incidence in hardwood stands near Chicago, light availability under the forest canopy is greater (at midday under given cloud condition) in winter and spring than in summer because the deciduous trees are barren of leaves at these times. Algal production in the streams is higher at midday on cloudy days than on clear ones (Chapman 1961) because light availability is greater under diffuse lighting produced by cloud cover.

The dense overstory of streamside vegetation leads to a heavy fall of plant parts into the streams, especially in autumn. The accumulation of leaf material is heavy in the streams until freshets begin flushing the material downstream in late October.

METHODS

Aquatic insect larvae and nymphs taken for stomach analysis were collected at 20 stations on Deer Creek and 10 on Needle Branch. Both streams had numbered markers at 100 foot intervals, and sampling stations were chosen by use of random number tables and the marker numbers. It was also necessary to randomize the cross-stream location of each sample by means of random number tables. At the sampling point, about one ft^2 of bottom was disturbed and a fine-mesh net was swept upstream along the bottom. The net held immature insects as small as one mm in length. Three immatures of each form available in the sample were examined. This number was set by time limitations. Samples were usually taken approximately monthly. Where sampling was more frequent, the data for each month were lumped for graphing. Insects taken from sampled areas were placed in plastic vials and cooled in ice water to reduce metabolic rates. Some insect samples were preserved in 70% ethanol immediately after sampling. Stomachs were examined within 6 hours of collection if cooled, and within 72 hours if preserved. The latter procedure minimized leaching of chlorophyll from plant material within the insect guts.

The insect to be examined was usually measured to the nearest mm from base of cerci to tip of snout, then decapitated on a microscope slide and the thoracic gut contents forced out on the slide. Further dissection was necessary to reach the gut in some of the larger insects. Stomach contents were mounted in water beneath a cover slip and examined under a compound microscope.

Stomach contents were recorded in the following manner: The presence or absence of algae (including fragments of aquatic mosses and liverworts) was determined. An arbitrary estimate was made of the percentage of volume of the sample made up by algal cells. This estimate was subject to errors such that a reported value of 25 might actually be as low as 10 or as high as 50%. Identification of algal genera was made in some cases.

All data are shown in 2 forms: as an arbitrary volume estimate and as a percentage of insects containing algae. The former method was used by Wissmeyer (1926), the latter by Jones (1950).

There were essentially 4 kinds of material present in the samples; algal cells, recognizable leaf fragments, detritus (usually amorphous), and animal matter. Small amounts of grit were mixed with algae; stomachs containing detritus had considerable grit present, and stomachs containing leaf fragments held grit only rarely. The "detritus" classification was considered to include terrestrial detritus only. This classification is open to question since dead algal material could be an important component. However, if much dead algal material were present in the detritus, diatom frustules should have been evident. Diatoms are usually abundant in any live benthic algal population, and should have been recognizable in dead algal material because the frustules retain their form for long periods after the protoplasm is dead (Smith 1950). Frustules were scarce in what was classified as "detritus" in this study.

Some error was possible when detritus or algae was found in the gut of an insect known to be carnivorous. This plant material could have come from the stomachs of prey organisms not observed in the smear or could have been ingested directly.

OBSERVATIONS

The stomach contents of 24 different insect groups from Deer Creek are summarized in Table II, and the analyses of the food of 23 taxonomic groups from Needle Branch are shown in Table III. Sample size is very small in some groups because of relative scarcity in the stream. In groups for which adequate samples were obtained, results are shown graphically. The tables show results of the 2 types of stomach analyses, the sample size, and the range in lengths of insects examined in each sample where body measurements were made. Where data on mean percentage of larvae or nymphs containing algae are given, the figures are a mean of the sample means for all available samples for one year. Estimated mean algal content of all larvae, the mean of all sample means, was rounded to the nearest 5%. The mean of sample means was used in order to give a more reasonable picture of the probable food composition of a given insect group over the year. For ease of comparison, percentages are used even where sample size is very small.

Ephemeroptera

All mayfly nymphs examined fed on both algae and detritus. *Baetis, Ephemerella,* and *Epeorus* were largely algal feeders, and *Paraleptophlebia* took mostly detritus. Figures 3-5 indicate that food of all mayfly groups changed seasonally, with greatest use of algal forms in spring.

Baetis fed upon algae, chiefly diatoms, in spring but detritus in other seasons. Jones (1949), working on open, calcareous streams in South Wales, found *Baetis* to feed on moss, detritus, green algae and diatoms. Jones (1950) found *B. rhodani* to feed on detritus and *Batracho-*

TABLE II. Mean thoracic gut contents and percentage of aquatic insects containing algae, November, 1959–April, 1961, Deer Creek. Means were obtained by averaging results of samples taken approximately monthly for one full year

Group	Mean % algae in gut; complement is % detritus	Mean % of insects containing algae	Insects examined	Size range of individuals (mm)
Baetis sp.	70	97	290	—
Paraleptophlebia sp.	5	30	444	—
Ephemerella sp.	60	80	7	3-6
Cynigmula sp.	40	57	229	1-11
Epeorus sp.	60	63	30	1-12
Peltoperla brevis	90	90	4	2-3
Nemoura sp.	0	0	14	2-7
Kathroperla perdita	50	72	6	1-9
Alloperla sp.	Carn.	Carn.	26	2-6
Acroneuria californica	Carn.	Carn.	17	3-15
A. pacifica	Carn.	Carn.	5	2-8
Rhyacophila sp.	Carn.	Carn.	10	3-11
Glossosoma sp.	95	100	16	3-7
Psychomyiidae	Carn.	Carn.	2	4-5
Hydropsychidae	50	50	2	5-6
Limnephilidae, wood case.	25	25	9	3-19
Limnephilidae, stone case.	80	86	40	1-15
Lepidostoma sp.	5	25	62	1-11
Micrasema sp.	90	100	36	1-6
Optioservus quadrimaculatus (adults)	65	88	6	2-8
Elmidae (larvae)	90	95	10	2-7
Dixa sp.	5	25	4	4-6
Simulium sp.	5	19	33	2-7
Hydrobaeninae	10	39	316	—

TABLE III. Mean thoracic gut contents and % of aquatic insects containing algae, November, 1959–April, 1961, Needle Branch. Means were obtained by averaging results of samples taken approximately monthly for one full year

Group	Mean % algae in gut; complement is % detritus	Mean % of insects containing algae	Insects examined	Size range of individuals (mm)
Baetis sp.	55	90	220	—
Paraleptophlebia sp.	5	36	371	—
Cynigmula sp.	35	63	98	1-7
Epeorus sp.	25	38	8	3-8
Peltoperla brevis	0	0	2	3
Nemoura sp.	0	0	9	3-6
Pteronarcys sp.	0	0	2	17-22
Kathroperla perdita	5	3	20	3-8
Alloperla sp.	Carn.	Carn.	26	1-9
Acroneuria californica	Carn.	Carn.	18	2-16
Rhyacophila sp.	Carn.	Carn.	6	5-6
Glossosoma sp.	95	100	10	4-8
Philopotamidae	75	100	1	6
Psychomyiidae	35	50	2	3-5
Hydropsychidae	0	0	1	12
Limnephilidae, wood case.	50	50	4	4-15
Limnephilidae, stone case.	60	69	34	2-13
Lepidostoma sp.	5	3	31	2-7
Micrasema sp.	75	78	10	2-5
Optioservus quadrimaculatus (adult)	0	0	1	2
Elmidae (larvae)	100	100	1	6
Simulium sp.	5	13	9	3-6
Hydrobaeninae	15	45	255	—

spermum, and felt that this species would take any vegetable food.

Paraleptophlebia nymphs showed a strong dependence upon detritus. Experimental work with the behavior of this form showed it to be negatively phototactic. Nymphs were found to occupy the dark areas beneath rocks during daylight hours and to move onto the upper surface of the substrate only in darkness. This habitat preference would help explain the dominance of detritus in nymphal stomachs.

The mean estimated percentage of algae in stomachs of 44 *Paraleptophlebia* nymphs collected in Needle Branch before daylight on September 7, 1960 was 22%, a much

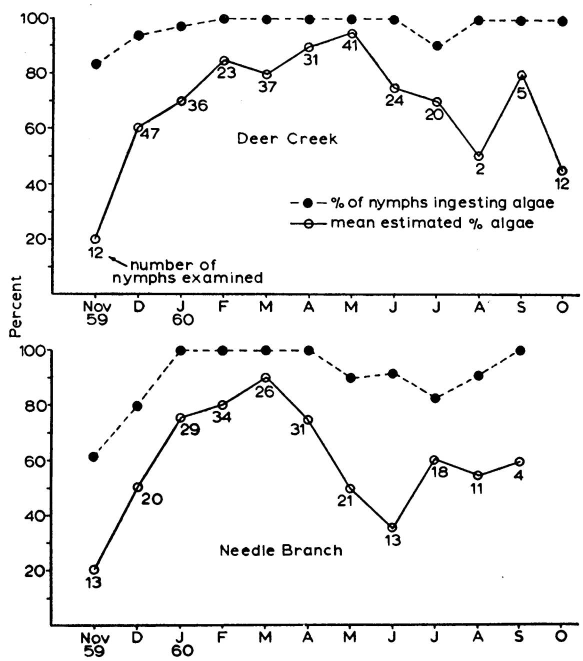

FIG. 3. The percentage of *Baetis* nymphs ingesting algae and the mean percentage of algae in guts of nymphs. Insects collected Nocember '59 to October '60.

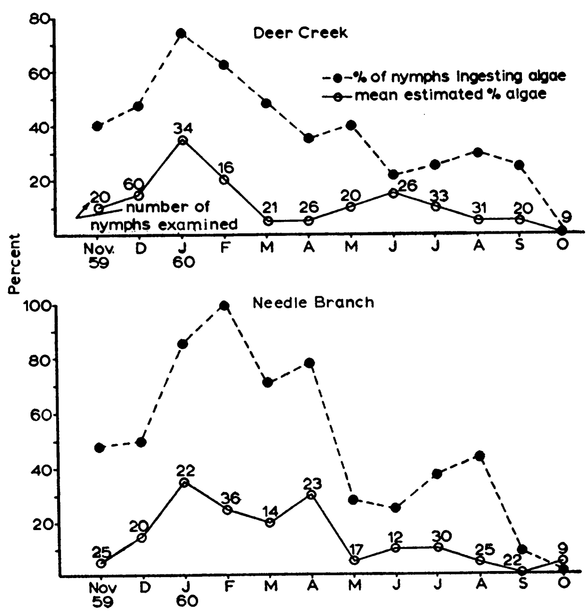

FIG. 4. The percentage of *Paraleptophlebia* nymphs ingesting algae and the mean percentage of algae in guts of nymphs. Insects collected November '59 to October '60.

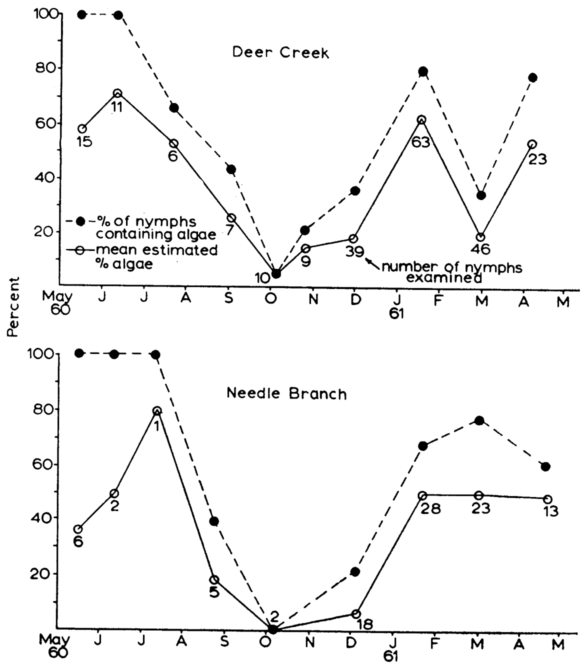

FIG. 5. The percentage of *Cynigmula* nymphs containing algae and the mean percentage of algae in guts of nymphs. Insects collected May '60 to April '61.

higher average than that observed in any sample taken during September in daylight, and 4 times the mean estimated percentage for September. Mean estimated percentage of algae in stomachs of 19 nymphs collected before dawn in Deer Creek on January 27, 1961, was 4%. Stomachs of 16 nymphs collected in daylight the previous day contained no algae.

Fig. 5 shows that *Cynigmula* nymphs fed heavily on algae in spring and early summer, but turned to detritus in late summer and continued to feed heavily on detritus until mid-winter. Diatoms were the dominant algae, with *Chamaesiphon, Entophysalis,* and *Protoderma* also appearing occasionally.

Larvae of *Stenonema,* a genus in the same family as *Cynigmula,* were found by Morgan (1913) to take diatoms and fragments of higher plants.

Epeorus feeding patterns were similar to those of *Cynigmula. Epeorus* fed on algae, chiefly diatoms, in spring and early summer but appeared to feed mostly on detritus from summer to December.

Plecoptera

Stonefly nymphs varied greatly in their diet. *Peltoperla, Nemoura, Pteronarcys,* and *Kathroperla* were herbivores while *Acroneuria* and *Alloperla* were carnivores.

Peltoperla brevis (Banks) nymphs held mostly algae, while *Nemoura* contained recognizable leaf fragments only. The cell structure of the leaf material appeared to be that of *Sambucus callicarpa,* the redberry elder. *Nemoura* was taken from relatively quiet water areas where detritus and leaves accumulated.

Nemoura has been found by other workers to be entirely herbivorous, feeding largely on decaying leaf material. Wu (1923) reported that *N. vallicularia* fed primarily on decaying leaves with diatoms and desmids minor dietary components. Hynes (1941) worked with 6 species of Nemouridae, including *N. variegata,* and found dead leaves and incidental algae in their stomachs. *Leuctra,* a closely related genus, was found by Jones (1949, 1950) and Hynes (1941) to be entirely herbivorous. Brinck (1949) found 11 species of *Nemoura* to be entirely herbivorous, with most nymphs feeding heavily on detritus.

Trichoptera

Like the stonefly nymphs, some caddis larvae were carnivores, including *Rhyacophila* and Psychomyiidae, while others were herbivores, such as *Glossosoma,* Philopotamidae, Limnephilidae, *Lepidostoma,* and *Micrasema. Glossosoma* larvae were taken only in February and April, possibly because the collecting procedures used before this missed them. In prior sampling, no effort was made to pick stone-cased Trichoptera larvae off tops of rocks before the bottom was disturbed. When the sample was taken, the heavy cases dropped between rocks and were not picked up in the net. Diatoms, especially *Navicula,* were the dominant food found in *Glossosoma, Entophysalis, Chamaesiphon,* and *Protoderma* also were seen.

Wood-cased Limnephilidae larvae contained mostly detritus. Lloyd (1921) mentions that members of the family Limnephilidae take vascular plants, living or dead, and some diatoms. Ross (1944) states that limnephilid larvae take plankton and sessile diatoms, and that some will take animals.

Stone-cased limnephilid larvae fed mostly on algae in spring and early summer but took detritus from late summer to December (Figure 6). The chief staple food was diatoms but *Chamaesiphon, Entophysalis, Protoderma* and *Batrachospermum* were also taken, sometimes in quantity.

Micrasema, a smooth-cased caddis, was found only in association with mosses and liverworts. Only rarely was any other plant material found in stomachs of the larvae. The most frequent food of *Micrasema* was *Eurhynchium.* Diatoms appeared also, but these may have been ingested while attached to mosses or liverworts.

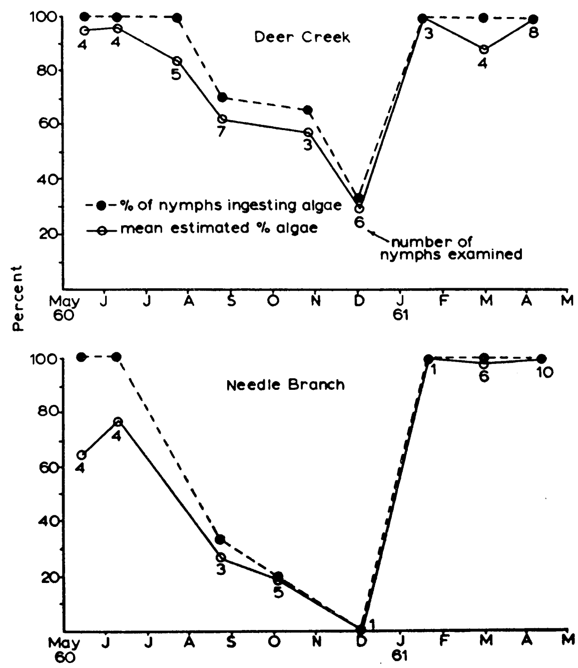

FIG. 6. The percentage of stone-cased Limnephilidae nymphs ingesting algae and mean percentage of algae in guts of nymphs. Insects collected from May '60 to April '61.

Hynes (1941) states that *Brachyptera risi,* a form closely related to *Micrasema,* fed on plant material, mostly algae, and these larvae appeared to scrape rocks for encrusted sessile algae. Brinck (1949) found *Brachyptera braueri* and *B. risi* to be herbivores.

Coleoptera

Optioservus quadrimaculatus (Horn), an adult riffle beetle, and Elmidae larvae appeared to be heavily dependent on algae, chiefly diatoms.

Diptera

Dixa larvae contained virtually no algae, probably because of their residence at the water surface. *Cocconeis* and *Pinnularia* were found in one *Dixa.* Wirth and Stone (1956) mention that *Dixa* feeds on organisms in the surface film.

Most of the food of *Simulium* was detritus, but diatoms were taken on occasion. Puri (1925) reviewed the food data in the literature on Simuliidae, and concluded that the variety of food (mentioned by several authors) including minute crustacea, diatoms, green algae, and *Chironomus* larvae, was due to collections from a variety of habitats. Puri collected *Simulium* from the River Cam, near Cambridge, and found that they fed solely on diatoms. Jones (1949) found *Simulium* to contain fragments of moss, leaves, and assorted algal cells. The same author (1950) found *Simulium* from River Rheidol to contain grit, leaf fragments, and various algal cells.

The sub-family Hydrobaeninae fed mostly upon detritus, with diatoms also appearing in the diet. Figure 7 shows that early spring is apparently the peak period for algal ingestion by Hydrobaeninae larvae.

Discussion

The evidence presented shows that different insect groups from the same stream varied greatly in the type of food taken. Some ingested mostly algae, some fed largely on detritus, others were carnivorous and some

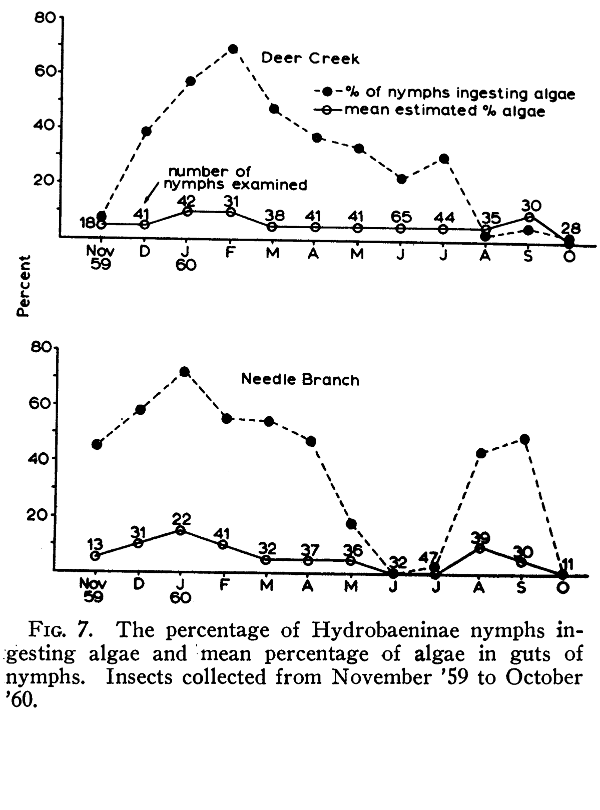

FIG. 7. The percentage of Hydrobaeninae nymphs ingesting algae and mean percentage of algae in guts of nymphs. Insects collected from November '59 to October '60.

changed food habits seasonally. Among the algal feeders were the stonefly nymph *Peltoperla brevis,* the caddis larvae *Glossosoma* and *Micrasema,* and stone-cased Limnephilidae, the riffle beetles, Elmidae, and the adult beetle *Optioservus quadrimaculatus.* Detritus feeders included the mayfly, *Paraleptophlebia, Nemoura* a stonefly, wood-cased Limnephilidae and another caddis, *Lepidostoma,* and the Diptera groups *Dixa, Simulium* and Hydrobaeninae. All of the insect groups listed as dominantly algal feeders took small amounts of detritus, and the dominantly detritus feeders usually took some algal forms. Carnivorous forms were the stonefly nymphs *Alloperla, Acroneuria californica,* and *A. pacifica,* and the caddis larvae *Rhyacophila* and Psychomyiidae.

Habitat can be invoked to explain the algal feeding of *Glossosoma* and *Micrasema.* The former was found only on upper surfaces of gravel or rubble particles where no detritus was present. *Micrasema* was taken only in conjunction with patches of mosses and liverworts where little or no detritus was found.

Of the detritus feeders, *Nemoura, Lepidostoma,* and wood-cased Limnephilidae were found only in slowly-moving water where accumulations of detritus and leaf material occurred and algae was scarce. *Dixa* was found only in the surface waters of the streams often along the downstream edges of twigs and small branches. In this habitat only drifting food particles were available, most of which probably was detritus fragments. Puri (1925) describes the feeding of *Simulium,* mentioning that larvae strain passing water, ingesting what is taken by the fans, but occasionally taking particles scraped from the substrate with the mandibles. In streams richer in algae than Deer Creek and Needle Branch, *Dixa* and *Simulium* might utilize greater amounts of algae available in the passing water.

The apparent dominantly-detritus feeding habits of *Paraleptophlebia* partly are due to the negative phototaxis of this form and the fact that samples for stomach analysis were secured largely near midday. Had samples been taken in the hours of darkness, it is likely that greater amounts of algae would have been found. *Paraleptophlebia* nymphs were found in many different types of habitat, including areas where algal forms as well as detritus were abundant.

It is possible that some of the apparently seasonal differences in food of insect groups identified only to genus or family were due to undetermined specific differences.

Only casual observation is necessary to see that there is a change in relative abundance of algae, detritus, and recognizable leaf material on the stream bed at different times of year. It was obvious, for example, that abundance of leaf material was greatest in October and early November, the period of greatest leaf fall, and that the greatest visible standing crop of algal forms was present in spring before trees had their complete foliage and when a maximum amount and intensity of light was available.

In preliminary studies of algal production in Needle Branch, oxygen production of unit areas of substrate was measured by means of light-dark tests in stirred aquaria placed in the stream bed. Tests were conducted on 2 ft^2 of gravel and rubble having visible growth of *Chamaesiphon* and diatoms. This growth was the most abundant seen anywhere in the study streams and the strata chosen probably constituted maximum production areas. Tests were conducted in November, December, April, June, and July in the same areas. Highest oxygen production (mean of 3.1 mg O_2 per ft^2 per hour) and hence greatest photosynthetic activity, was measured in winter and spring. Butcher (1946) found seasonal changes in algal abundance in calcareous streams in England with summer the period of maximum production. The English streams were relatively exposed to light.

If the food habits of a given insect change with season as, for example, for *Cynigmula,* this may be due to several possible causes: change in food preference, change in food availability or abundance, or change in relative abundance of different species of *Cynigmula* with different food habits.

The tendency for *Paraleptophlebia* to feed on algae at night and detritus in daylight shows that at least this form is facultative in its feeding. It could be reasoned with some justification that live algal cells constitute more nutritious food than do particles of detritus or leaf material, since the latter must undergo gradual loss of nutritive value from leaching and activity of bacteria.

The seasonal peaks in estimated proportion of algae in stomachs of aquatic insects coincide with peaks in percentage of aquatic insects found in coho salmon stomachs (Demory 1961) as spring is the period of maximum utilization of aquatic insects by coho. Late spring is also the period of maximum coho production, in terms of tissue elaborated (Chapman 1961).

It is probable that the following network of events is involved in the seasonal changes in utilization of algae by insects with facultative feeding behavior: wetted area, light incidence, water temperature, and bottom stability are together typically most favorable to algal production and high standing crop of insects in late spring. Streamflow, though relatively high, does not fluctuate greatly; light incidence is high while the deciduous canopy is incomplete, and water temperatures are increasing. Either earlier in the spring or in the summer one or more of the stream variables would be much less favorable to optimum algal or insect production.

Low utilization of algae in late summer and early fall takes place when wetted areas are small, the bottom areas available for insect populations and algal production are at their lowest level, light availability at stream surface is decreased and leaf fall has begun.

Utilization of algae increases in late winter when total light availability at stream surface is increasing, allowing increased algal production, and much of the leaf material has been flushed downstream so that detritus is quite scarce.

The changes in quantities of terrestrial detritus and algae observed in the streams were so striking that they appeared sufficient to explain the seasonal changes in food habits of insects. Jones (1949) mentions that *Ephemerella* feeds on *Ulothrix* when this is plentiful and turns to *Fontinalis* when *Ulothrix* is scarce. Jones thought it possible that other forms might feed on green algae when this was available and turn to some standby food when algae was scarce.

Wissmeyer (1926) shows a suggestion of a seasonal change in the food of *Cloeön* in cold European brooks of latitude similar to that of Oregon: 10 *Cloeön* nymphs contained 8-30% detritus on August 11, 1922, and 6 nymphs taken October 22, 1922 contained 45-92% detritus.

Factors other than food availability or preference might cause seasonal or even diel changes in insect food habits. Behavior is one of these, as has been mentioned for *Paraleptophlebia.* Diel changes in food habits which could have influenced data were checked in Needle Branch insect sampling on one occasion. Samples (without *Paraleptophlebia*) were secured at midday and midnight in the same 24-hour period. No difference in algal content could be detected in the 2 sets of samples.

Consideration of energy sources for coho salmon production led to some interesting relationships. Demory (1961) found that 34% of the annual diet of Deer Creek coho (based on dry weight of stomach contents) was made up by terrestrial insect forms. About 62% was made up by aquatic insects, and about 4% could not be identified. In the present analysis of aquatic insect food habits about 52% of the food ingested by the insect prey of coho salmon was detritus of allochthonous origin, 12% was autochthonous algae, and 36% could not be assigned to allochthonous or autochthonous energy sources.

Application of aquatic insect food habit data to coho food habits indicated (Chapman 1961) that 66% of the total energy intake leading to coho production was derived from allochthonous sources, either directly as terrestrial insects or indirectly as aquatic insects that fed on terrestrial detritus. Seven % of the coho total energy intake was attributed to autochthonous sources, and the origin of about 26% of the energy intake could not be established. Although these calculations of energy sources had many inherent assumptions and limitations, they indicate the great importance of terrestrial plant energy to the stream ecosystem in these small, shaded streams.

Demory (1961) reported the feeding habits of coho from May through September on 3 streams. Coho from Deer Creek, the largest and least shaded of the streams, contained 21% terrestrial organisms; coho from Flynn Creek, a slightly smaller stream, contained 29% terrestrial animals; and coho from Needle Branch, the smallest and most densely-shaded stream, contained 40% terrestrial organisms. There is no reason to think that this relative relationship would change greatly if a full year of data were available on all 3 streams. A year's data from Flynn Creek show a terrestrial insect contribution to the coho diet about equal to that occurring in Deer Creek. The limited data available for a full year on the Needle Branch coho diet indicate that terrestrial forms were more important to coho in this stream than in the others.

Figs. 3, 5 and 6 suggest that Needle Branch insects in the groups *Baetis, Cynigmula* and stone-cased Limnephilidae ingested a slightly greater proportion of detritus than did similar Deer Creek forms. This indication and the limited data showing a greater proportion of terrestrial insects in the Needle Branch coho stomachs suggest that dependence upon the terrestrial environment may be even greater than is the case for coho in Deer Creek. Heavy overhead cover and summer pooling conditions would tend to limit algal and aquatic insect production in low flow periods so that the contribution of terrestrial energy may have been a result of low aquatic production.

Comparison of the insect food studies of Jones (1949, 1950) with the present data indicates that the 2 open streams of Wales supported a much richer growth of aquatic autotrophs which were taken by the herbivorous aquatic insects. Jones found detritus to be important insect food in the 2 streams, but this detritus appeared to be of aquatic origin in one and terrestrial origin in the other. The latter origin was due to the less stable stream bed being less conducive to production of sessile algae.

Inductively, one comes to the conclusion that the wider a coastal stream becomes as it flows seaward, the less dense will be overhead cover and the less important will be terrestrial insects in the diet of coho, and probably of other salmonids as well. It is likely that the importance of terrestrial detritus to the diet of aquatic insects will also decrease as the stream becomes larger.

Summary

1. From November, 1959 to April, 1961, the food habits of some common aquatic insects were studied in 2 small Oregon Coast Range streams, tributaries of Drift Creek, an Alsea River tributary. The objectives were to determine whether insects important in the diet of juvenile coho

salmon obtain their energy primarily from aquatic autotrophs or terrestrial plant debris, and whether the energy sources change seasonally.

2. Some physical characteristics of Deer Creek and Needle Branch, respectively, were as follows: drainage area—815 and 230 acres; annual streamflow range—0.5-76 and 0.1-14 cfs; annual stream temperature range—40-58 and 37-58°F.

3. Both drainages were covered with dense stands of coniferous timber, and the stream bottoms were heavily shaded by hardwoods. Deer Creek had a stream cover less dense than that on Needle Branch.

4. Insects found to feed primarily on algae included the nymphs of *Peltoperla brevis,* and larvae of *Glossosoma, Micrasema* (mosses and liverworts), Elmidae, and adult *Optioservus quadrimaculatus.*

5. Insects found to feed largely on detritus included *Paraleptophlebia, Nemoura,* wood-cased Limnephilidae, *Lepidostoma, Dixa, Simulium,* and Hydrobaeninae.

6. Carnivorous forms were *Alloperla, Acroneuria californica, A. pacifica, Rhyacophila,* and Psychomyiidae.

7. Groups showing seasonal changes in utilization of algae and detritus included *Baetis, Paraleptophlebia, Cynigmula, Epeorus,* stone-cased Limnephilidae, and Hydrobaeninae.

8. Reasons for food habits of particular groups are fairly evident in some cases; for example *Glossosoma* was found only on upper surfaces of rocks, where algae was the only available food. *Micrasema* occurred only in patches of mosses and liverworts. *Nemoura, Lepidostoma,* and wood-cased Limnephilidae were found only in slow-moving water where detritus accumulated. *Paraleptophlebia* was found to be negatively phototactic and to take more algae at night when foraging on top of the bottom particles. In daylight this form remained under bottom particles, where detritus was taken.

9. Seasonal changes in food of herbivorous aquatic insects appeared to be associated with changes in availability of algae and detritus. Utilization by facultative feeders of algae was greatest in late winter and spring, and least in late fall.

10. Consideration of relationships of coho salmon, as predators, to insect prey indicated that well over half the energy reaching the coho was obtained from terrestrial sources, either directly as terrestrial insects or indirectly as aquatic insects that had fed on terrestrial detritus.

11. It appeared that the animal population of Needle Branch, the smallest and most densely shaded stream, was more heavily dependent upon the terrestrial environment than was the case in Deer Creek, the larger, less heavily shaded stream.

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ARTIFICIAL FROST APPARATUS

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This paper reports two attempts to simulate natural frost in a temporary insulated enclosure out-of-doors, one using, around the plant, a refrigerating coil through which was passed carbon dioxide gas newly vaporized from its original liquid state in a pressure cylinder, the other using solid carbon dioxide (dry ice) on a steel disc above the plant. The frosting was done at the University of Minnesota Cedar Creek Natural History Area in northern Anoka County, Minnesota, on May 25, 1960, and on May 29, 1962. An artificial frost apparatus had been devised earlier by Studhalter (1942) for injuring cambium tissue of individual tree branches; the effects have