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Amphipod-substrate relationships in a warmspring slough

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Amphipod-Substrate Relationships

In A Warmspring Slough

by

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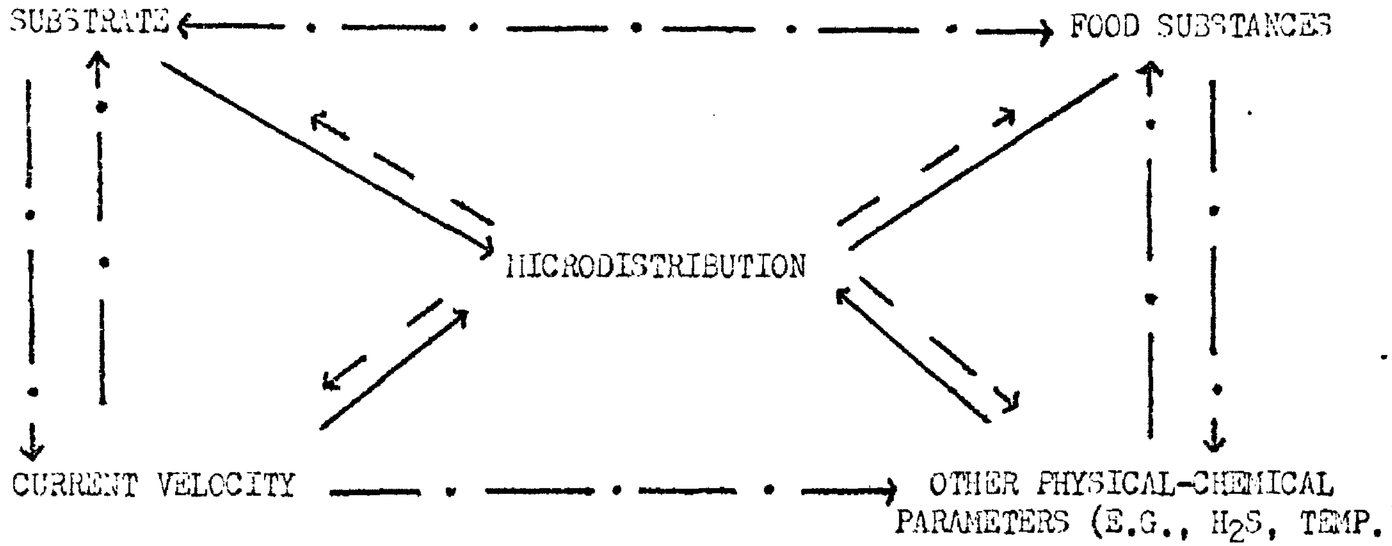
CHAPTER I

INTRODUCTION

The substrates in aquatic ecosystems have been shown directly to influence the microdistributional pattern of benthic invertebrates (Cummins, 1964). Whereas currents, temperatures, or concentrations of chemicals may limit the general ranges of habitat tolerance (macrodistribution), it appears that substrates or food supply probably cause primary differences in the distribution of a species within a community (microdistribution) (See Figure 1). Microdistributional studies have significantly sharpened the ecologist's approach to the study of individual organisms as well as communities of organisms (Odum, 1959). The data are valuable in calculating energy flow through various populations within a community, also, given the geographical range of any species, an established relationship between substrate-type and microdistribution pattern can be of critical importance in establishing index species in water quality studies (Cummins and Lauff, 1969).

The majority of research conducted on organism-substrate relationships has been on marine organisms, and few similar types of studies have been conducted using freshwater organisms. Most of the freshwater work, in turn, has involved aquatic insects. Brinkhurst (1967) related chemical and textural characteristics of bottom sediments to invertebrate distributions in Lake Huron. Milne (1943) discovered a relationship between



——→ Influence of environment on a benthic species which results in recognition of microhabitat

—·—→ Interactions between components of the environment to which a given benthic species interacts

— — → Influence of a given benthic species on the microhabitat

Figure 1. -- General relationships between environmental parameters and the microdistribution of a species of benthic macroinvertebrate. Lengths of lines are proportional to importance of each parameter (Modified after Cummins and Lauff, 1969).

the nature of the sediments on which caddisflies were found in Saskatchewan lakes and their case building requirements. Numerous other papers have correlated the distribution of aquatic insects with the occurrence of particle sizes of the substrates inhabited by insects (Linduska, 1942; Pennak and VanGerpen, 1947; Cummins, 1964; etc.). Few papers have considered amphipod-substrate relationships. The investigation of Marzolf (1965) on the deepwater amphipod *Pontoporeia* is important, because it correlates field and laboratory studies and includes sediment analysis with special emphasis on the role of bacteria within the benthos. The *Pontoporeia* were able to discriminate between various particle sizes of bottom substrates. Hargrave (1970a) demonstrated the ability of *Hyalella azteca* to select sediments containing viable microflora in laboratory substrate-choice experiments. When the concentration of diatoms in sediment was altered, *Hyalella* chose substrates with the highest concentrations of the algae.

The studies of Marzolf (1965) and Hargrave (1970a) stress the role of subsurface sediment as an influence on microdistribution, because the freshwater amphipods, particularly *Hyalella azteca*, are negatively photactic, rarely planktonic, and usually inhabit benthic sediment (Phipps, 1915; Pennak, 1953). *Hyalella* is widely distributed throughout the lakes, streams and ponds of North America, where it is often a dominant organism (Smith, 1952; Cooper, 1965; Hargrave, 1970a). In western Montana its distribution is usually concentrated in the benthic zone of permanent ponds and sloughs. A unique habitat for *Hyalella*, however, occurs at Shandy Slough, the area chosen for the present study. The slough is a warmspring located about two miles east of Bearmouth, Montana. The slough is approximately two acres in extent and empties into the Clark Fork of the Columbia River. The water temperature at the spring outlet fluctuates only slightly from 17.5°C and provides a nearly constant environment in this temperate climate, since testing in subzero weather showed that temperature varied no more than two degrees (Weisel, 1961). Because some areas of the slough, further from the source, vary considerably in temperature during the coldest weather, the study was conducted in the area near the spring outlets. As described by Weisel and Newall (1970), the slough has a relatively high calcium hardness of 215 ppm and a total alkalinity of 190 ppm. The pH is 8.2, carbon dioxide concentration is 30 ppm and the dissolved oxygen concentration is 5 ppm. Sulfur compounds, however, provide the most severe physicochemical limiting factor in the pond. Although the sulfate concentration is only 140 ppm, the high concentration of hydrogen sulfide in the soft silt bottom makes the benthic zone too noxious for macroinvertebrates with the exception of a few chironomid larvae.

With the bottom of the slough eliminated as a habitat for *Hyalella*, the amphipods must form associations with other substrates. Associations between higher plants and amphipods have been reported by other investigators. Keiner and Ollier (1970) noted an association between *Gammarus fossarium* and *Chara fragilis* in the Capeau River, France. The distribution of *Hyalella azteca* showed an association with aquatic plants such as *Chara*, *Elodea* and *Myriophyllum* in Sugarloaf Lake, Michigan (Cooper, 1965). The distribution of *Hyalella* over three species of aquatic plants was also noted by Rosine (1955). He found that considerable variation existed in the extent to which the animals were found on equal areas of plants. *Chara delicatula* was found to harbor from 1.5 to 5 times as many amphipods as the other plants, which factor he considers to indicate a substrate preference.

An extension of such studies, stressing the importance of cover in determining the microdistribution of *Hyalella*, seems warranted at Shandy Slough. Since the benthic portion of the slough is not inhabited by the amphipods, relationships with different plant species are the only substrate-choices for *Hyalella*. In my study, the higher plant species are considered only as substrates and not as actual food for *Hyalella*. Although early studies (Embody, 1912; Pennak, 1953) considered *Hyalella* to be an omnivore, more recent investigations (Kaushik and Hynes, 1968; Hargrave, 1970a) strongly suggest that the diet of the species consists of periphyton, rather than tissues of higher organisms. My own studies agree with the latter investigations. In my laboratory observations of feeding, *Hyalella* left the roots of *Lemna* and stalks of *Chara* untouched while grazing the periphyton.

The purpose of the present study is to investigate how amphipod-substrate relationships are pertinent to the distribution of *Hyalella* at Shandy Slough, and more specifically:

1. to undertake preliminary investigations of the community composition of the slough, with emphasis on the macroinvertebrate populations and probable predators of *Hyalella azteca*

2. to attempt to determine whether there be demonstrable associations between *Hyalella* and specific plant species (substrates)

3. to investigate how other animal populations, particularly the predators, might influence the selection of any substrate by *Hyalella*.

CHAPTER II

METHODS AND MATERIALS

FIELD SAMPLING

Field data were collected at Shandy Slough from October, 1970 through June, 1971; although the majority of the sampling was from March through June. The data were collected not only to determine if specific associations existed between *Hyalella azteca* and the higher plants, but also to survey the slough community. For the community composition investigations, emphasis was placed on the ecological dominants, those species at each trophic level which largely control the energy flow by virtue of their numbers, size or activities (Odum, 1959). Concentrating on these dominants provides a significant amount of information about communities, as well as specific populations. Trophic levels refer to positions in the links of food chains. Within the sequences of a food chain, animals that produce or convert the same food energy are considered to be in the same trophic level. Numbers of links in such chains are variable but three to five trophic levels are common (Whittaker, 1970). In my study reference is made to four levels.

The samples were collected using a small hand sieve with an outside diameter of 25 cm and mesh openings of 0.5 mm. With such a small sample, the macroinvertebrates were measured only in terms of relative abundance, rather than true density. For reasons that will be stated later, only two species of plants, *Lemna minor* (duckweed) and *Chara vulgaris*, a large green alga with a life form resembling that of higher plants, were collected. Care was taken to collect random samples of both substrates on three different dates. This ensured that the best possible values within the study area were being measured. Samples were taken every four hours on each date; and on April 10, the substrates were sampled every four hours for a twenty-four hour period. The samples were all collected from near the surface of the water by placing the sieve under the plant, raising the resulting sample above the water level, and removing all plant material outside of the sieve by pounding around the edge with a small piece of wood. The samples, consisting of the plant and associated macroinvertebrates, were emptied into plastic containers and returned to the laboratory at the University of Montana. The invertebrates were separated from the plants, identified, placed in size classes and enumerated. The biomass of substrate and animal species in each sample was recorded as dry weight after placing the samples in a drying oven for twelve hours at 60°C and weighing them to the nearest 0.1 mg on a Mettler single pan balance.

LABORATORY SUBSTRATE SELECTION

As a follow-up to the field study of substrate-choice, *Hyalella azteca* was allowed in the laboratory to select the common substrates collected from the slough. For the determinations, a 60 X 40 X 10 cm enameled pan was sealed off into four equal sections by glass partitions. Each of the four sections could be furthur divided into quarter-sections by removable plexiglass plates. Four substrate-choice experiments could thus be conducted simultaneously; and in each of the four sections, four different substrates or combinations of substrates could be tested.

The bottoms of each quarter-section were covered with autoclaved sediment, except for one quarter-section in each section which was covered with untreated sediment. The untreated sediment had been aerated for twenty-four hours to remove most of the hydrogen sulfide. Hyalella could therefore choose a subsurface sediment with organic material in the same proportions as it is found at Shandy Slough, without the noxious gas being present. All sediments were uniformly 2 cm in depth. Each section was then filled with water from the slough to a depth of 8 cm by slowly adding the water from one end so that the sediment was undisturbed. In each section fresh samples of Lemna and Chara were added in sufficient quantity to each fill a quarter-section. The remaining quarter-sections containing only autoclaved sediment served as controls. The pan was placed in an environmental chamber at 16°C in constant darkness, and thirty-two adult Hyalella were evenly distributed along the surface of each section. After twenty-four hours the plexiglass plates were added and the number of amphipods within a quarter-section were enumerated.

PREDATION

Predation or other population and community relationships often affect the occurrence and survival of organisms in nature as much as do the direct action of chemical or physical factors. Samples of adult fish were collected. Individuals were seined from three different groups, all near the spring outlets. Stomach contents were examined, and the prey identified and placed in size classes. Other potential predators such as damselfly naiads were found in all substrates at Shandy Slough where amphipods were abundant. Predation was difficult to observe and evaluate because of the nature of the substrates at the slough, dense *Chara* and *Lemna* mats. Therefore, laboratory experiments were set up to attempt to measure the influence of the odonates on the amphipod population. Various densities of amphipods were placed in containers with individual naiads that had been starved for twenty-four hours. *Daphnia sp.*, another invertebrate from the slough and potential prey for the Odonata, was also tested.

GROWTH RATES

Laboratory experiments were conducted to determine the effect of diet on the growth of *Hyalella*. By comparing growth rate differences, inferences can be made as to whether substrate selection is dependent upon abundance. Plants with attached periphyton were brought from the slough. After removing all macroinvertebrates and larvae, duplicate cultures, using *Chara* and *Lemna*, were each established in 2000 ml erlenmeyer flasks, filled with 1000 ml of autoclaved water from the slough. Composite cultures, containing both plant species and aerated sediment, were also maintained in duplicate. After determining average dry weight values for early instar amphipods of approximately 2.5 mm total length, twenty *Hyalella* in this size class were added to each culture. The flasks were then covered, aerated and held at 20°C (±2°) on a twelve hour light-dark cycle. A large General Electric "Gro Lux" aquarium lamp was used for illumination. Equal amounts of fresh substrate were added every three to five days. Amounts of substrate were measured as damp-dry weight, which is a standardized measure established by pressing the samples between Whatman No. 1 filter paper under a petri dish for one minute before weighing (Hargrave, 1970b). After a predetermined time period, amphipods from all cultures were removed, oven dried and weighed. Growth rates were calculated by comparing amphipod mean dry weight at the beginning and end of the time period.

Chara and Lemna were both analyzed for organic content, using the technique of Conover (1966). The plants were heated for twelve hours at 45°C to obtain dry weights and then ashed in a muffle furnace at 450°C for one hour. Ash-free dry weights were determined by subtracting the amount of ash from the dry weight. Percentage of organic content for each substrate was derived by dividing the ash-free weight by the dry weight and multiplying by 100.

Several assimilation experiments using both substrates were conducted to establish that the diet of Hyalella consists of periphyton rather than the tissues of Lemna and Chara. For each experiment, fifteen adult Hyalella were placed in cultures containing fresh Lemna or Chara and 300 ml of autoclaved water. After twelve hours, fecal pellets from both cultures were collected and also analyzed for percentage of organic content.

Hyalella assimilates most organic matter (except blue-green algae) with nearly the same efficiency (Hargrave, 1970b). If fecal pellets from both the Lemna and Chara cultures contain nearly the same percentage of organic matter, the Hyalella must be ingesting foods in both cultures that are very similar in percentage of organic content. The percentage organic content of many species of algae is similar (Parsons, Stephens and Strickland, 1961).

Lemna and Chara, however, differ significantly in percentage of organic content because of large amounts of calcium in the tissues of Chara. Consistant values in the percentage organic content of fecal pellets from both cultures would therefore suggest that Hyalella ingests periphyton rather than the tissues of the substrates.

CHAPTER III

RESULTS

COMMUNITY COMPOSITION

Preliminary sampling in the late fall and early winter of 1970-71 indicated that the animal community at Shandy Slough contained few species. Observations and sampling in the spring and early summer months confirmed that the number of species at the slough during this time of year is also lower than in similar cold water communities. Constant temperature in aquatic communities often minimizes the number of species within a community (Odum, 1959). The temperature at the spring outlets fluctuated little from 17.5°C. However, most of the macroinvertebrates were concentrated near the water surface, where they may be nearly a meter above or several meters away from a spring outlet. Also the surface temperatures may vary considerably with extremes in air temperature. Therefore, temperatures were taken one centimeter below the surface over a twenty-four hour period during subfreezing weather. The results, illustrated in Figure 2, show that although the air temperature dropped considerably during the night, the surface temperature changed very slightly. Average temperatures and the average depth above which measurements were taken are also shown. All points on the graph are means of at least three values.

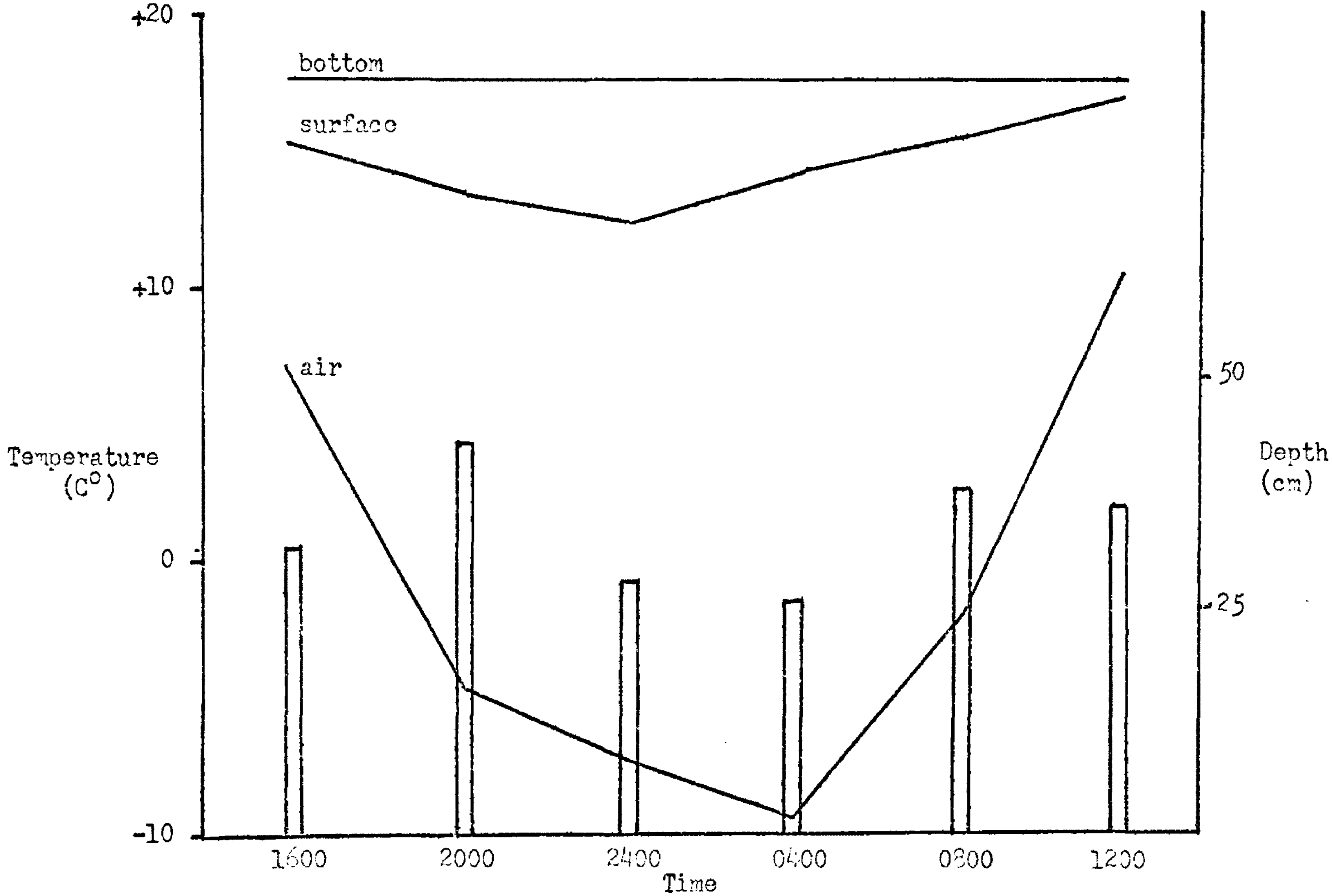


Figure 2. -- Water and air temperatures at Shandy Slough on April 10 and 11, 1971. Lines illustrate temperature variations, and bars depict average depth above which surface temperatures were taken.

Several macroinvertebrate taxa, common in most aquatic communities in western Montana, were not found at Shandy Slough. The most obvious missing populations are those of the Ephemeroptera and Plecoptera larvae. The exclusion of these populations is to be expected, however, because these organisms are for the most part benthic and usually inhabit lotic areas. Aquatic Coleoptera are also rarely present. Larvae and adults from the Dytiscidae and Gyrinidae families are very abundant in other ponds and sloughs of this region even in summer months when water temperatures may be equal or above those characteristic of Shandy Slough. The only beetles inhabiting the slough in significant numbers are small semi-aquatic species. A predatory hemipteran, Ambrysus mormon (Naucoridae), was rarely collected at Shandy Slough, although the species is quite common at Nimrod Warmsprings, which is only a few miles west of the slough. Several populations, which are present during warm weather, were also missing during the months when most of the present study was conducted. Copepods and Daphnia sp. were present in the plankton and algal patches only after late April. The nektonic hemipteran families, Notonectidae, Corixidae and Gerridae, began appearing in samples at the same time, when subfreezing air temperatures were less common. The only macroinvertebrates known to be present in appreciable numbers and collected the year-round were Hyalella azteca, damselfly larvae and snails. The snails were distributed evenly across all plants at the slough and were considered unimportant in influencing substrate selection by Hyalella. Because of this, I designated the Hyalella and damselfly populations as the ecological dominants of the herbivore and primary carnivore trophic levels, respectively, during my study. They were so assigned, not only because of their large standing crop during my study period, but also because of their influence on the transfer of energy through the aquatic community throughout the year. _Hyalella_ specimens brooding eggs were collected as late as November and again in February samples, suggesting that juveniles are being added to the population throughout most of the year. Such a prolonged growing season is unusual, because _Hyalella_ normally carries broods only from spring until late fall (Cooper, 1965). The life cycle of the damselflies was also modified, with early instar animals being collected in February samples and adults appearing in the spring at an earlier date than was noted in cold water communities near the slough.

Naiads of the other suborder of Odonata, Anisoptera (dragonflies) were also collected, but in numbers far less than the damselflies. Over a thousand damselflies were collected, but only thirteen of the Anisoptera were ever collected, and these were all taken with the _Chara_ samples. Another amphipod species, _Gammarus lacustrus_, was also collected, but specimens were taken in only seven of forty-one samples and never in numbers comparable to those of _Hyalella_. Because of this, I did not consider _Gammarus_ to be an influence on the substrate relationships of _Hyalella_.

Several species of fish inhabit the slough. Squawfish (_Ptychocheilus oregonensis_), suckers, (_Catostomus catostomus_), and brown trout (_Salmo trutta_) are concentrated in areas near the slough's entrance into the Clark Fork River. The only species that inhabits the area near the spring outlets in any significant numbers is the redside shiner, _Richardsonius balteatus_ (Weisel, 1951). Since the majority of my field data was collected at a time which coincided with the shiner's spawning, the fish were often present in schools of thirty to fifty individuals in pools near the springs and my observations indicate that they were the dominant secondary carnivores.

A similar "simple" situation existed in the plant portion of the community during the months of cold temperature. In summer months, with longer photoperiod length, the slough may be filled with Myriophyllum (water milfoil), Radicula (water cress), and Spirogyra, a filamentous green algae. Lemna minor and Chara vulgaris are present but are not nearly as obvious. During the winter and early spring, however, when field sampling was concentrated, these latter two plants were, without question, the dominant substrates in the spring region of the slough. For this reason, these two plants, along with treated subsurface sediment, were selected to be the substrates used in all subsequent studies of substrate selection.

Samples of Lemna or Chara together with associated macroinvertebrates were collected on the three major sample dates. Samples of each substrate were taken from two distinct habitat-types. For Chara, samples were taken within mats which were shaded by Lemna and also from uncovered areas. Similarly, Lemna samples were taken from aggregations that had Chara patches directly below and from areas without the algae. The results, illustrating numbers of Hyalella and damselfly naiads collected on the specified dates, are compiled in Tables 1 and 2. The numbers of larvae of Chironomidae collected with the April 10 and 11 samples were also enumerated, since these Diptera larvae were the only other macroinvertebrate population collected in numbers great enough to be considered. Chironomid larvae have feeding preferences similar to Hyalella, so they would also be included within the second trophic level of the slough's food web. Each of the populations were separated into three basic size classes, according to total length. The basic categories outlined by Cooper (1965) were used to classify

Table 1.-- Number of selected macroinvertebrates associated with *Lemna*, based upon equal-area samples.

Substrate	Date	Time	Hyalella 0.0-2.5 mm	Hyalella 2.5-5.0 mm	Hyalella 5.0 mm +	Hyalella Total	Odonata naiads 0.0-10.0 mm	Odonata naiads 10.0-20.0 mm	Odonata naiads 20.0 mm +	Odonata naiads Total	Chironomid larvae 0.0-5.0 mm	Chironomid larvae 5.0-10.0 mm	Chironomid larvae 10.0 mm +	Chironomid larvae Total
	3/28	1300	1	15	4	20	3	2	0	5				
	3/28	1700	3	10	11	24	2	4	2	8				
Lemna	4/10	1600	0	9	9	18	4	12	1	17	1	9	1	11
with no	4/10	2000	5	24	12	41	35	35	3	73	0	8	0	8
inter-	4/10	2400	51	103	30	184	53	34	5	92	6	31	5	42
mediate	4/11	0400	10	31	14	55	18	13	2	33	2	15	3	20
Chara	4/11	0800	10	37	26	73	28	13	2	43	7	45	5	57
	4/11	1200	14	49	23	86	21	12	3	36	8	0	0	8
	5/3	1500	34	47	27	108	15	12	4	31				
	3/28	1300	7	17	9	33	14	9	2	25				
	3/28	1700	2	15	12	29	6	10	1	17				
	4/10	1600	2	7	6	15	34	28	2	64	0	8	0	8
Lemna	4/10	2000	23	31	17	71	29	10	3	42	0	6	2	8
with	4/10	2400	5	26	21	52	25	13	6	49	0	0	7	7
inter-	4/11	0400	3	14	11	28	34	43	1	78	0	8	0	8
mediate	4/11	0800	3	15	10	28	13	26	4	43	0	0	0	0
Chara	4/11	1200	16	45	24	85	10	4	1	15	0	14	2	16
	5/3	1600	15	19	7	41	25	14	3	42				
	5/3	1600	15	20	13	43	24	8	2	34				
	5/3	1600	19	22	16	57	12	12	1	25				
Totals			238	556	302	1096	425	319	48	772	24	144	25	193

Table 2.-- Number of selected macroinvertebrates associated with <u>Chara</u>, based upon equal-area samples.

Substrate	Date	Time	Hyalella 0.0-2.5 mm	Hyalella 2.5-5.0 mm	Hyalella 5.0 mm +	Hyalella Total	Odonata naiads 0.0-10.0 mm	Odonata naiads 10.0-20.0 mm	Odonata naiads 20.0 mm +	Odonata naiads Total	Chironomid larvae 0.0-5.0 mm	Chironomid larvae 5.0-10.0 mm	Chironomid larvae 10.0 mm +	Chironomid larvae Total
	3/28	1300	4	2	3	9	10	5	3	18				
	3/28	1700	2	1	1	4	5	7	1	13				
	4/10	1600	1	2	1	4	7	13	2	22	0	0	0	0
Chara	4/10	2000	1	4	5	10	3	5	2	10	0	2	2	4
with	4/10	2400	2	0	1	3	9	6	2	17	0	4	1	5
no	4/11	0400	3	8	17	28	11	12	1	24	0	0	0	0
Lemna	4/11	0800	4	3	0	7	11	19	9	39	11	34	0	45
above	4/11	1200	2	5	4	11	14	11	9	34	0	11	0	11
	5/3	1600	2	1	4	7	18	25	1	44				
	5/3	1530	1	0	0	1	17	9	1	27				
	5/3	1500	0	2	3	5	6	6	1	13				
	3/28	1300	0	1	0	1	9	7	2	18				
	3/28	1700	2	3	1	6	6	8	0	14				
	4/10	1600	0	1	0	1	20	6	0	26	0	6	7	13
Chara	4/10	2000	3	5	5	13	4	2	2	8	0	6	7	13
with	4/10	2400	5	7	10	22	3	4	0	7	2	4	0	6
Lemna	4/11	0400	1	1	2	4	7	7	0	14	7	3	0	10
above	4/11	0800	0	0	1	1	5	4	1	10	4	10	4	18
	4/11	1200	2	9	4	15	5	4	4	13	11	2	0	13
	5/3	1600	0	0	4	4	20	20	2	42				
	5/3	1600	0	2	2	4	17	9	0	26				
Totals			35	57	68	160	207	189	43	439	35	82	21	138

Hyalella. The 0.0-2.5 mm size class encompasses an "all juvenile" category. The 2.5-5.0 mm group roughly represents the young adult category, and animals 5.0 mm and larger are adults from the previous summer or fall. The developmental stages of the damselflies were also categorized. Damselflies in the 0.0-10.0 mm size class were the young, recently hatched group. The 10.0-20.0 mm individuals were roughly intermediate instars not likely to emerge in the near future, and those 20.0 mm and larger were considered the late instar stages, preparing to emerge. Chironomid larvae were also separated into three size classes. The totals in Tables 1 and 2 indicate that higher numbers of both *Hyalella* and damselflies were associated with the *Lemna* substrate.

PREDATION

The higher number of animals associated with the *Lemna* substrate is summarized in Table 3, which also depicts a higher ratio of damselflies to *Hyalella* in associations with *Chara* samples. Generally speaking, there were three *Hyalella* for every two damselfly naiads taken with the *Lemna*, versus one *Hyalella* for every three damselflies in *Chara*. A proportionally greater number of predators, then, were found in *Chara*. However, these numbers represent the standing crop for all sizes of both prey and predator populations. As was found in later predation experiments in the laboratory, the majority of predation was by damselflies larger than 10.0 mm upon amphipods smaller than 2.5 mm in length. (See below). If animals only within these size classes are considered, a measure of "effective predation" can be derived for both substrates. The ratio of damselflies to amphipods then becomes 1.5 in *Lemna* and 6.6 in *Chara*, showing an even higher proportion of

Table 3.-- Hyalella/Odonata naiad ratios occurring in substrates brought from Shandy Slough. Numbers are totals of all size classes collected within the samples.

Date	Time	Lemna: No. of animals / sample: Hyalella	Lemna: No. of animals / sample: Naiads	Lemna: Ratio	Date	Time	Chara: No. of animals / sample: Hyalella	Chara: No. of animals / sample: Naiads	Chara: Ratio
3/28	1300	20	5	4.00	3/28	1300	9	18	0.50
3/28	1300	33	25	1.32	3/28	1300	1	13	0.08
3/28	1700	24	8	3.00	3/28	1700	4	13	0.33
3/28	1700	29	17	1.71	3/28	1700	6	14	0.43
4/10	1600	18	17	1.06	4/10	1600	4	22	0.18
4/10	1600	15	64	0.23	4/10	1600	1	26	0.04
4/10	2000	41	73	0.56	4/10	2000	10	10	1.00
4/10	2000	71	42	1.69	4/10	2000	13	8	1.63
4/10	2400	184	92	2.00	4/10	2400	3	17	0.18
4/10	2400	52	49	1.06	4/10	2400	22	7	3.14
4/11	0400	55	33	1.67	4/11	0400	28	24	1.17
4/11	0400	28	78	0.36	4/11	0400	4	14	0.29
4/11	0800	73	43	1.69	4/11	0800	7	39	0.18
4/11	0800	28	43	0.65	4/11	0800	1	10	0.10
4/11	1200	86	36	2.38	4/11	1200	11	34	0.32
4/11	1200	85	15	5.66	4/11	1200	15	13	1.15
5/3	1500	108	31	3.48	5/3	1600	7	44	0.16
5/3	1600	41	42	0.98	5/3	1600	4	42	0.10
5/3	1600	48	34	1.41	5/3	1600	4	26	0.15
5/3	1600	57	25	2.28	5/3	1530	1	27	0.04
					5/3	1530	5	13	0.33
Totals		1096	772	1.420			160	439	0.364

predators in *Chara* than what was brought out by data in Table 3.

A direct effect of damselfly naiads upon the amphipod population was estimated by laboratory experiments. Preliminarily, different numbers and sizes of amphipods were placed in beakers with various sizes of naiads (*Enallagma sp.*) that had been starved for at least twenty-four hours. These investigations showed 1) that damselflies smaller than 10.0 mm in length rarely attempted to capture amphipods, and 2) that the larger damselflies could rarely capture amphipods that were over 2.5 mm in length. Therefore, subsequent experiments were conducted only with *Enallagma* naiads larger than 10.0 mm and with the smallest size class of *Hyalella*.

The first predation trials were conducted in 500 ml beakers, each containing one damselfly and 300 ml of pond water. Various numbers of *Hyalella* were used; results are in the first half of Table 4. The table shows, not only how many successful captures were made by each naiad, but also how many times they attempted to capture an amphipod. "Attempts" were recorded whenever a naiad's labium was extended and made contact with an amphipod, without a successful capture resulting. Prey individuals were replaced whenever one was captured, so their numbers remained constant. After trials with different densities of *Hyalella*, it was noticed that the general activity of the *Enallagma* naiads often increased and less direct food capturing moves were made when amphipods began to cling to the predator's appendages or dorsal surface. As often as not, naiads seemed to strike in an effort to remove the amphipods rather than in an effort to capture prey. This appeared to cause the percentage of successful captures to decrease. To alleviate the situation as much as possible, trials were conducted in shallow petri dishes (11 cm diameter) with stalks of *Chara* added. The stalks

Table 4.-- Results of laboratory predation by damselfly naiads upon juvenile *Hyalella azteca*. Trials were conducted for thirty minutes, using naiads that had been isolated for twenty-four hours.

Trial	Number of Hyalella	Attempted captures	Successful captures	Percentage success
		300 ml beaker with no *Chara* stalks		
1	10	4	1	25.0
2	10	5	1	20.0
3	10	3	2	66.7
4	20	11	5	45.5
5	20	17	8	47.0
6	20	9	1	11.1
7	20	7	2	22.2
8	30	0	0	00.0
9	30	1	0	00.0
10	30	33	7	22.2
11	30	3	0	00.0
Totals		93	27	29.0
		100 ml petri dish with *Chara* stalks		
1	20	8	5	62.5
2	20	10	6	60.0
3	40	10	5	50.0
4	40	2	1	50.0
Totals		30	17	56.7

not only gave the amphipods an object for attachment, but also gave the naiads a surface along which to align themselves. Such alignment is characteristic of the food capturing behaviour of many odonates (Usinger, 1956). The results of these trials, showing an apparent increase in the percentage of successful captures, are contained in the second half of Table 4.

In samples collected after mid April, Daphnia sp. began to appear in Chara samples. Since these cladocerans could be a logical alternate prey for the naiads, samples of Daphnia and Hyalella were mixed. Ten individuals of each prey species were placed in the petri dishes, along with stalks of Chara and 100 ml of pond water. Only large Daphnia, approximately 2.5 mm in length, were used in the combinations. The prey organisms were again replaced whenever an individual was captured. Daphnia were apparently captured, not only at a higher frequency, but also with a higher percentage of successful captures (Table 5).

To measure the possible effects of the secondary predators on substrate selection by Hyalella, adult redside shiners were collected. Individuals were taken from three different schools, and their stomach contents examined. These examinations revealed that the shiners were feeding predominantly on chironomid larvae and damselfly naiads (Table 6). In total numbers, chironomid larvae were more significant in the diet of the fish; however, in terms of biomass, the damselflies were equal to the chironomid larvae or slightly more important. No evidence of predation on Hyalella was found. Prey animals were not counted unless definite evidence of an organism was present. Chironomid larvae were most often identified by their head capsule which appeared comparatively resistant to digestion, but in

Table 5.-- Results of laboratory predation by damselfly naiads upon combinations of juvenile *Hyalella azteca* and adult *Daphnia sp.* Trials were conducted for thirty minutes using one naiad that had been isolated for twenty-four hours. Ten individuals of both species were in each trial.

	Daphnia			Hyalella		
Trial	Attempted Captures	Successful Captures	Percent Success	Attempted Captures	Successful Captures	Percent Success
1	8	7	87.5	7	0	00.0
2	2	2	100.0	8	2	25.0
3	1	1	100.0	0	0	00.0
4	0	0	00.0	1	0	00.0
5	5	3	60.0	3	0	00.0
6	5	4	80.0	7	1	14.3
7	1	0	00.0	3	0	00.0
Totals	22	17	77.3	17	3	17.6

Table 6.-- Stomach content analysis of adult Redside Shiners, <u>Richardsonius balteatus</u>, collected from Chandy Slough on May 25, 1971

Length of fish in mm.	Stomach contents					
	Odonata				Chironomidae	Plant material
	0.0-10.0 mm.	10.0-20.0 mm.	20.0 mm. +	Unknown size		
84				anal gill		filamentous algae
78			1			
77	1	1			2	filamentous algae
76	2					
71	4					
70		1			29	
68						
64	3	1			7	filamentous algae
63	2				2	
62	1	1		appendages	3	green debris
61	3				4	
59						
58						dark debris
57					15	filamentous algae
55						
53	2	2			5	
52	1		1		5	dark debris
51					5	filamentous algae
51			1		3	
49					10	
48					2	dark debris
44	2	2			3	
Totals	21	8	3		95	

some instances whole animals were found. Estimation of damselfly numbers, on the other hand, were usually based on the presence of appendages or anal gills. If there was ever any doubt as to how many were present, the smaller number was chosen as an estimate. The plant debris and filaments found within the stomachs may have been ingested only incidentally along with the invertebrates.

SUBSTRATE SELECTION

The data in Tables 1 through 3 show that a higher proportion of both Hyalella and damselflies were collected with samples of Lemna. These data compare the two substrates on the basis of 600 cm^2 samples (the total area of the sieve used in the sampling). However, since aggregations of Chara are much more compact than the duckweed, one attempt to compare the substrates equitably is to reduce the samples to apportionments of one gram each. To make these reductions, the number of animals in each sample was divided by the dry weight of substrate in the sample. This data is compiled in Tables 7 and 8, which again show totals by size classes, comparing individuals taken with the two substrates. These figures strongly suggest a substrate preference of Lemna by Hyalella, since over eleven times as many amphipods were associated with an equal biomass of this substrate, compared to Chara. Probably this difference is, if anything, conservative, since nearly half of the weight and surface area of Lemna is above water, and thus is not available as a substrate for amphipods. Since all organisms were collected only a few centimeters below the water surface, sample depth did not contribute to this difference. Also, changes in the weather have little influence on substrate associations, since the differences prevailed

Table 7.-- Number of selected macroinvertebrates associated with *Lemna*, after conversion of data to number of animals/gram dry weight of substrate.

			Number of animals by size class											
			Hyalella				Odonata naiads				Chironomid larvae			
Substrate	Date	Time	0.0-2.5 mm	2.5-5.0 mm	5.0 mm +	Total	0.0-10.0 mm	10.0-20.0 mm	20.0 mm +	Total	0.0-5.0 mm	5.0-10.0 mm	10.0 mm +	Total
	3/28	1300	0.4	5.4	1.4	7.2	1.1	0.7	0.0	1.8				
	3/28	1700	1.3	4.3	4.7	10.3	0.9	1.7	0.9	3.5				
Lemna	4/10	1600	0.0	3.5	3.5	7.0	1.5	4.6	0.4	6.5	0.4	3.1	0.4	3.9
with no	4/10	2000	1.9	9.2	4.6	15.7	13.4	13.4	1.1	27.9	0.0	3.1	0.0	3.1
inter-	4/10	2400	6.9	13.9	4.0	24.8	7.1	4.6	0.7	12.4	0.3	4.2	0.7	5.2
mediate	4/11	0400	3.5	10.7	4.8	19.0	6.2	4.5	0.7	11.4	0.7	5.2	1.0	6.9
Chara	4/11	0800	3.6	13.3	9.3	26.2	10.0	4.7	0.7	15.4	2.5	16.1	1.8	20.4
	4/11	1200	3.9	13.7	6.4	24.0	5.9	3.4	0.8	10.1	2.2	0.0	0.0	2.2
	5/3	1500	15.4	21.4	12.3	49.1	6.8	5.5	1.8	14.1				
	3/28	1300	4.8	11.8	6.2	22.8	9.7	6.2	1.4	17.3				
	3/28	1700	0.8	5.7	4.6	11.1	2.3	3.8	0.4	6.5				
	4/10	1600	0.7	2.4	2.0	5.1	11.6	9.6	0.7	21.9	0.0	2.7	0.0	2.7
Lemna	4/10	2000	5.5	7.4	4.0	16.9	6.9	2.4	0.7	10.0	0.0	1.4	0.5	1.9
with	4/10	2400	1.1	5.6	4.5	11.2	5.4	3.9	1.3	10.6	0.0	0.0	1.5	1.5
inter-	4/11	0400	0.8	3.7	2.9	7.4	8.9	11.3	0.3	20.5	0.0	2.1	0.0	2.1
mediate	4/11	0800	2.0	9.9	6.6	18.5	8.6	17.1	2.6	28.3	0.0	0.0	0.0	0.0
Chara	4/11	1200	3.3	9.3	4.6	17.2	2.1	0.8	0.2	3.1	0.0	2.9	0.4	3.3
	5/3	1600	4.5	5.8	2.4	12.7	7.6	4.2	0.9	12.7				
	5/3	1600	7.1	9.5	6.2	22.8	11.4	3.8	0.9	16.1				
	5/3	1600	7.6	8.8	6.4	22.8	4.8	4.3	0.5	10.1				
Totals			75.1	175.3	101.4	351.8	132.2	111.9	17.0	260.2	6.6	40.3	6.3	53.7

Table 8.-- Number of selected macroinvertebrates associated with Chara, after conversion of data to number of animals/gram dry weight of substrate.

Substrate	Date	Time	Hyalella 0.0-2.5 mm	Hyalella 2.5-5.0 mm	Hyalella 5.0 mm +	Hyalella Total	Odonata naiads 0.0-10.0 mm	Odonata naiads 10.0-20.0 mm	Odonata naiads 20.0 mm +	Odonata naiads Total	Chironomid larvae 0.0-5.0 mm	Chironomid larvae 5.0-10.0 mm	Chironomid larvae 10.0 mm +	Chironomid larvae Total
Chara with no Lemna above	3/28	1300	0.3	0.4	0.6	1.3	1.9	0.9	0.6	3.4				
	3/28	1700	0.5	0.3	0.3	1.1	1.3	1.9	0.3	3.5				
	4/10	1600	0.2	0.3	0.2	0.7	1.1	2.0	0.3	3.4	0.0	0.0	0.0	0.0
	4/10	2000	0.2	0.6	0.8	1.6	0.5	0.8	0.3	1.6	0.0	0.3	0.3	0.6
	4/10	2400	0.3	0.0	0.1	0.4	1.2	0.8	0.3	2.3	0.0	0.5	0.1	0.6
	4/11	0400	0.4	1.2	2.5	4.1	1.6	1.8	0.1	3.5	0.0	0.0	0.0	0.0
	4/11	0800	0.2	0.2	0.0	0.4	0.6	1.1	0.5	2.2	0.6	1.9	0.0	2.5
	4/11	1200	0.2	0.5	0.4	1.1	1.4	1.1	0.9	3.4	0.0	1.1	0.0	1.1
	5/3	1600	0.2	0.1	0.4	0.7	1.9	2.7	0.1	4.7				
	5/3	1530	0.1	0.0	0.0	0.1	2.2	1.1	0.1	3.4				
	5/3	1500	0.0	0.2	0.3	0.5	0.7	0.7	0.1	1.5				
Chara with Lemna above	3/28	1300	0.0	0.6	0.0	0.6	5.3	4.1	1.2	10.6				
	3/28	1700	0.9	1.3	0.4	2.6	2.6	3.4	0.0	6.0				
	4/10	1600	0.0	0.2	0.0	0.2	3.9	1.2	0.0	5.1	0.0	1.2	1.4	2.6
	4/10	2000	0.7	1.1	1.1	2.9	0.9	0.4	0.4	1.7	0.0	1.3	1.5	2.8
	4/10	2400	1.4	1.9	2.8	6.1	0.8	1.1	0.0	1.9	0.6	1.1	0.0	1.7
	4/11	0400	0.1	0.1	0.2	0.4	0.8	0.8	0.0	1.6	0.8	0.4	0.0	1.2
	4/11	0800	0.0	0.3	0.0	0.3	1.7	1.3	0.3	3.3	1.3	3.3	1.3	5.9
	4/11	1200	0.4	1.6	0.7	2.7	0.9	0.7	0.7	2.3	2.0	0.4	0.0	2.4
	5/3	1600	0.0	0.7	0.0	0.7	3.3	3.3	0.3	6.9				
	5/3	1600	0.0	0.8	0.8	1.6	6.5	3.5	0.0	10.0				
Totals			6.6	12.4	11.6	30.6	41.1	34.7	6.5	82.3	5.3	11.5	4.6	21.4

under all observed conditions.

Laboratory substrate-selection also strongly demonstrated (P<.001) a substrate preference for Lemna by Hyalella. Laboratory results are given in Figure 3, which shows how the substrates were arranged within the four sections of the enameled pan. (Only twenty-nine amphipods were placed in the third section, three individuals being lost during their transfer to the section.)

Figure 3.-- Results of laboratory substrate-choice experiments. The arrangement of the substrates within the four sections is shown, as well as the number of Hyalella in each quarter-section after a twenty-four hour period. Vertical lines show the partitioning of the pan into sections, and the dashed lines represent the positions of the plexiglass plates.

CONTROL 0	LEMNA 23	SEDIMENT 1	CHARA 14
SEDIMENT 1	CONTROL 1	CHARA 1	SEDIMENT 3
LEMNA 26	SEDIMENT 2	CONTROL 0	LEMNA 14
CHARA 5	CHARA 6	LEMNA 22	CONTROL 1

GROWTH RATES

Laboratory trials on growth rate were conducted in two different sets, spanning two time periods. The first set covered a thirty-one day period from January 21st until February 21st. Amphipods averaging 2.5 mm in total length were used in each of the eight cultures. In the cultures containing plants as substrates, equal amounts (damp dry weights) were added at intervals of three to five days. A cumulative total of five grams was in each flask at the end of the period. In sediment cultures, enough aerated substrate was initially added to cover the bottom of both flasks to a depth of one centimeter. Additional sediment was then added at similar intervals until a total of 70 grams was in the flasks. Composite cultures had five grams of mixed Chara and Lemna and 30 grams of sediment at the end of the time period. After thirty-one days, the Hyalella were removed and their dry weights determined. Growth rates were obtained by comparing these weights with average values of groups containing twenty amphipods, approximately 2.5 mm in length.

The best growth rates were obtained from the Chara. Lemna and the composite cultures produced individuals with nearly the same average weight. The subsurface sediment contained the smallest Hyalella. These results are shown in Figure 4.

Mortality rates under these laboratory conditions were relatively high, averaging roughly 25 percent in all cultures. The increased mortality of Hyalella was possibly influenced by handling specimens with an eyedropper during their initial transfer into the flasks. Also, the thirty-one day culturing period proved to be long enough for some individuals over 2.5 mm in length to develop a brood. All of the cultures, except those maintained on sediment, contained recently hatched individuals.

The second set of growth rates was conducted to confirm the above growth rate differences. The trials were maintained over a shorter twenty-four day period. Only juvenile animals, less than 2.5 mm in length were used. An eyedropper with a larger aperture, less likely to injure the

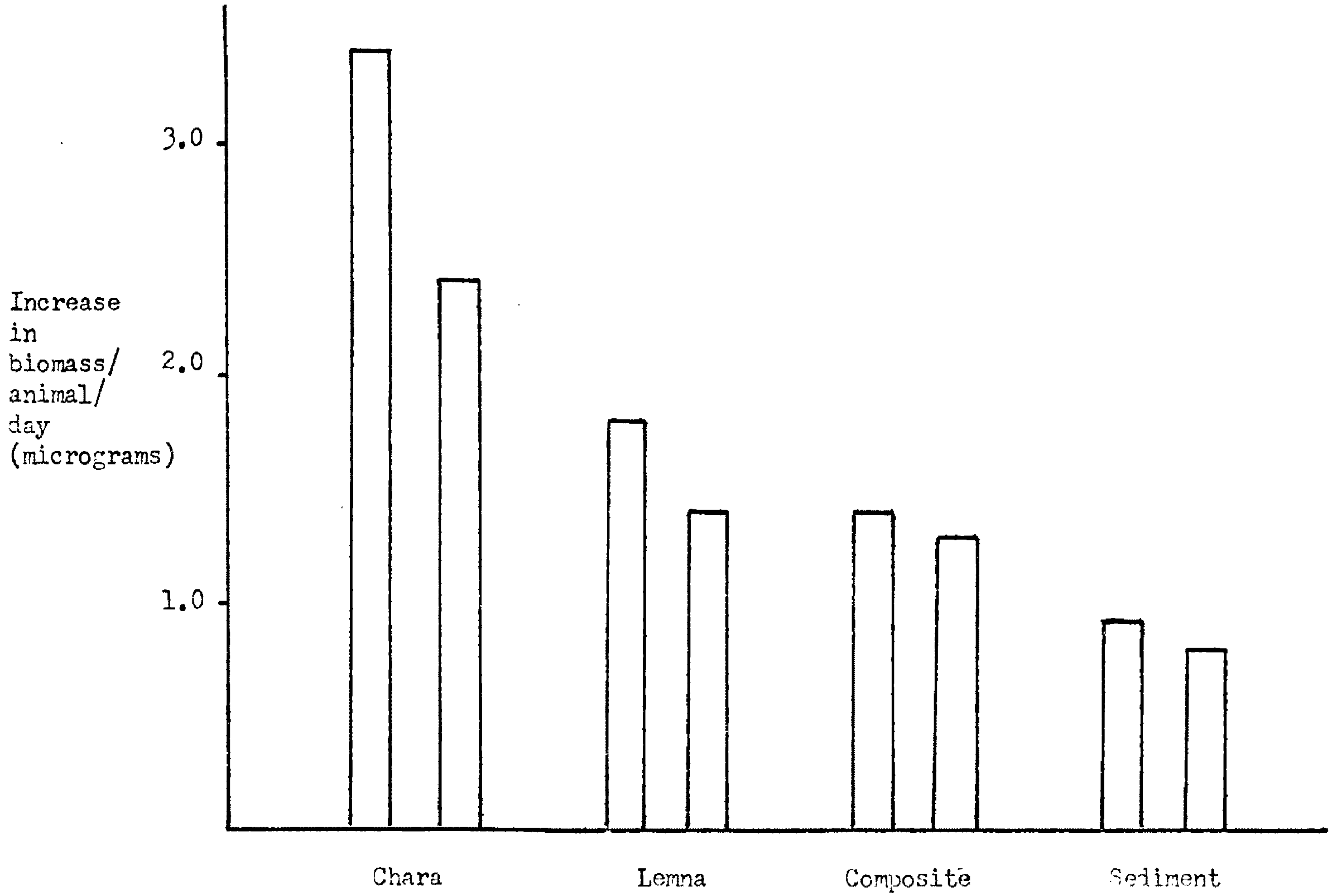


Figure 4. -- Laboratory growth rates for *Hyalella azteca*. (See text for further explanation.)

animals, was used in handling specimens. The same periodic feeding schedule was maintained, except this time one flask for each substrate was given twice the amount of plant plus periphyton, so that a total of ten grams (damp dry weight) was added. Flasks to which the normal five grams of substrate was added were designated "Group A", and those to which ten grams were added, "Group B". The obtained growth rates, along with the cumulative feeding schedules for each group are illustrated in Figure 5. Again animals held on Chara demonstrated the best growth rates. There was little difference in growth rate between the two Chara groups, and the growth rates of the second set were slightly higher, but comparable to those of the first set, approximately 3.2 micrograms/animal/day. The composite in Group A had a better growth rate than the Group A Lemna culture. However, in Group B, as in the first set, the growth rates for Lemna and the composite were nearly equal. These trials were conducted over a short enough time period, and with small enough animals at the start, so that no broods developed. Also, mortality was less than five percent overall with a total of only two deaths, both occurring in the Chara Group A flask.

The percentage organic content of Chara from nine replicates averaged 25.5 with a standard error of 1.1. The percentage organic content of Lemna from five replicates averaged 70.0 with a standard error of 2.4. The fecal pellets produced by Hyalella in Chara were found to have an average organic content of 14.7 (standard error 0.5), while the corresponding figures for Lemna were 14.9 (standard error 3.0). These results suggest that the amphipods were feeding upon the same food material, periphyton, in both cases. The most plausible alternative explanation for the similar figures of organic content in the feces would be that Hyalella assimilates

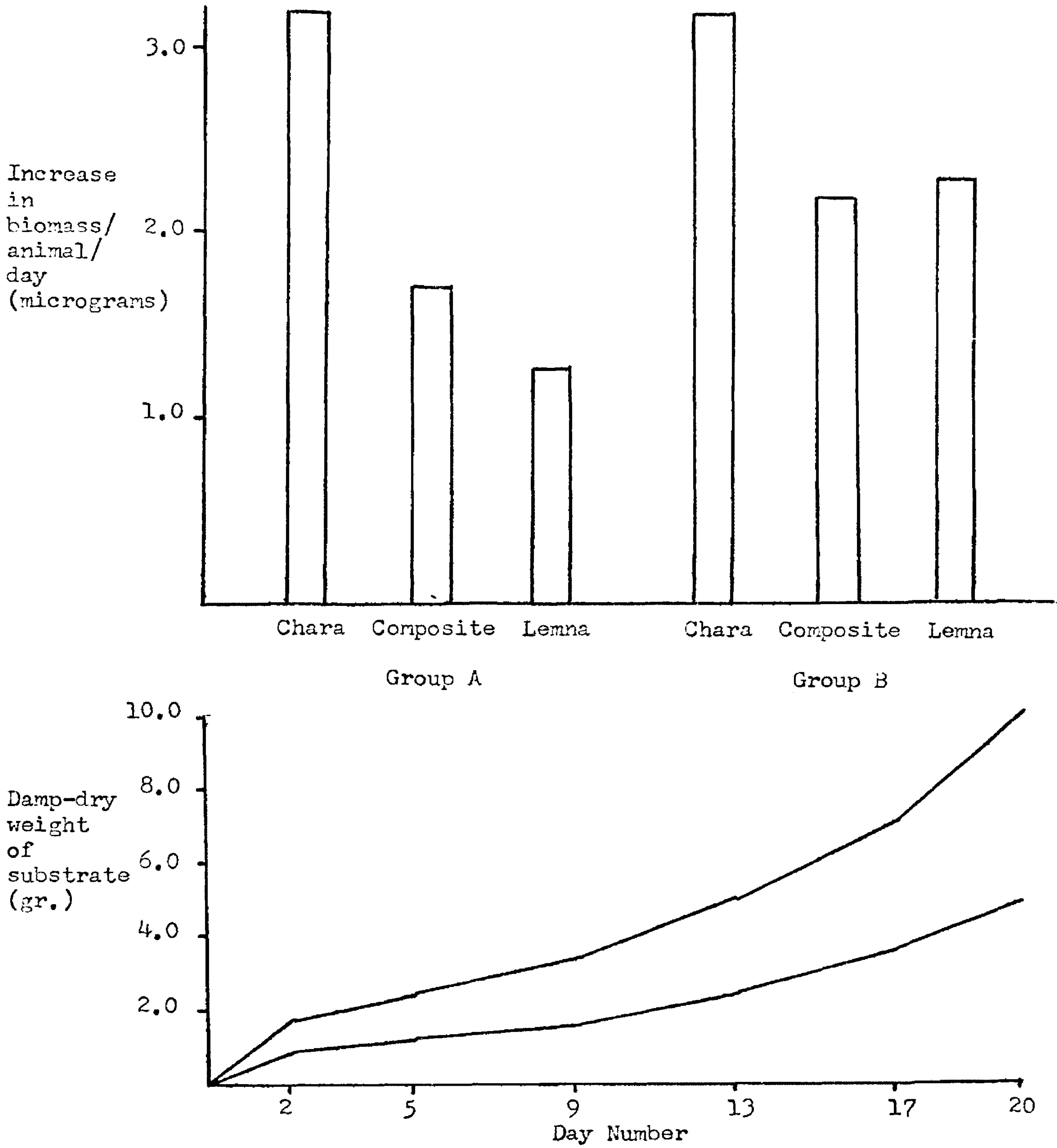


Figure 5. -- Laboratory growth rates for Hyalella azteca and cumulative feeding schedules maintained for a twenty-four day period.

Chara plus periphyton at a much higher efficiency than it does the _Lemna_ plus periphyton.

CHAPTER IV

DISCUSSION AND CONCLUSIONS

COMMUNITY COMPOSITION

A reduced standing crop of higher plants is present at Shandy Slough during the winter months. A similar condition concerning the periphyton (first trophic level) can also be inferred if winter and spring growth rate data of Hyalella azteca are compared. Such data reflect the amount of nutrition received from the periphyton. In the main, the higher the amphipod growth rate, the more periphyton must be available for consumption. Other factors, such as changes in the species diversity of microflora, occur throughout the year. However, such factors, compared to periphyton density, would probably have little influence on growth rates, because the organic content of many species of the algae, at least, is similar. Although no growth rate experiments were conducted later in the year with substrates from Shandy Slough, the spring and early summer data compiled by Hargrave (1970a) can be used as a probable substitute for production in these months. Laboratory conditions for both experiments were very similar. Animals and plants for the latter were taken from Marion Lake, British Columbia, a temperate, freshwater community. For Marion Lake in May, growth on Chara as a substrate was 6.9 micrograms/animal/day, and on bottom sediment it was 1.2 micrograms/animal/day. For a similar period in June results were 8.8 micrograms/animal/day on Chara and 2.1 micrograms/animal/day on sediment.

With *Chara* taken from Shandy Slough in February, growth averaged 2.9 micrograms/animal/day and in March, 3.2 micrograms/animal/day. The aerated sediment from the slough averaged 0.8 micrograms/animal/day during both months. These results suggest that during the winter, production within the first trophic level is reduced, even though water temperature remains favorable for periphyton growth. A similar reduction in algal standing crop, indicating a dependence on long photoperiod length for maximum production, was found by Stockner (1967) in Mount Rainier and Yellowstone Park warmsprings. With loss of production within the first trophic level, corresponding reductions in the fauna must occur. Many animals respond with dormant stages. The *Daphnia* and copepods possibly deposit their resting eggs within the *Chara* aggregations. Necktonic Hemiptera overwinter as adults in protected areas on or near the water surface. Again we see that the hydrogen sulfide in the benthic zone may limit diversity, because aquatic Coleoptera, which are present at the slough only in low numbers, require a mud habitat for hibernation. Physical factors other than the hydrogen sulfide prevent the occurrence of Ephemeroptera and Plecoptera populations, since the stoneflies, at least, are low temperature stenotherms and apparently need temperature changes greater than are found at Shandy Slough, to help trigger their emergence (Sheldon and Jewett, 1967).

Hyalella azteca has no known resting stage; its population persists throughout the year even when primary production at the slough becomes relatively low. Since the *Daphnia* and copepod populations are, for the most part, inactive throughout much of the winter, *Hyalella* is clearly the dominant population of the second trophic level.

SUBSTRATE SELECTION

In both laboratory and field studies, Hyalella indicated a definite preference for Lemna as a substrate. Previous studies have shown that Hyalella discriminates between substrates containing various concentrations of diatoms. Early studies on macroinvertebrate distributions similarly linked associations between animals and plants to surface area for periphyton growth (Krecker, 1939; Rosine, 1955). The latter two studies relate the leaf dissection of submerged aquatic plants to the density and diversity of associated animal populations. However, my studies at Shandy Slough demonstrated that the substrate providing the best growth rate (Chara) was not selected. Similarly, the study by Hargrave (1970a) also found that relationships between periphyton production (surface area) and amphipod growth and distribution are not clear cut. As stated earlier, he found that periphyton associated with Chara was a better source of food for growth than was sediment microflora. Yet at Marion Lake, where Chara and Potomogeton beds with abundant periphyton occur around springs, Hyalella is neither more numerous nor larger in size than amphipods found on adjacent open sediment. In fact, 80 percent of the amphipods are found on the open sediment, and nothing approaching a clumped distribution occurs in areas of highest periphyton density.

Reasons other than food supply, then must contribute to the selection of Lemna by Hyalella at Shandy Slough. Bryden (1952) found that a species of hydra occurred on some plant species and not on others. An apparent biochemical influence on the emergence of mosquito larvae was also suggested by Abdel-Malek (1948). These facts strongly suggest a direct influence by plants on the development of periphyton on their surfaces and possibly on the animals in the water around them. The nature of similar chemical regulators of algae has been studied by Proctor (1956, 1957), but further studies will have to be made to clarify any such antibiotic action exerted on the fauna by these extracellular compounds.

Another possible explanation for the field selection results would be the shading effect of Lemna. The negative phototaxis of Hyalella, when combined with increasing effects of hydrogen sulfide near the bottom of the slough, would make the substrate that allowed the least light penetration and, at the same time had most of its biomass near the water surface the most favorable for Hyalella. In order to find an amount of shade equal to that of duckweed within the Chara aggregations, Hyalella must go to a considerable depth below the water surface.

Finally, the influence of predation on the field results can not be overlooked. Damselflies are the main predators upon the Hyalella population at Shandy Slough. The predation, by Enallagma sp. at least, is upon specific size classes of amphipods (individuals less than 2.5 mm in length). Although Chara was not selected as a substrate by the damselflies, the effective number of predators was higher in this substrate. This, in turn, made existence for early instar Hyalella slightly more precarious when within Chara than when within Lemna. Chara beds were also the only place where the large Anisoptera naiads were found. Unfortunately, by the time the laboratory predation experiments were conducted, all of these predators had emerged. The Anisoptera very likely prey on the amphipods as well as early instar damselflies, and are probably an important factor in population regulation within Chara. Odonata naiads are likely to be more successful predators in the *Chara*; the mats of this substrate are much more compact, making the distance to prey much less, and thus very likely increasing the percentage of successful captures. *Chara* stalks are also thicker and more compact than those of *Lemna*. This situation contributes to the protective coloration of the naiads. Further, Odonota within *Chara* aggregations are generally safe from predators, since the aggregations are too concentrated to allow fish of any size to enter. All of these factors make the *Chara* an unstable place for *Hyalella's* survival, and make the predation influence more clear than is brought out in standing crop figures.

Reasons for laboratory substrate selection are less clear. Since the experiments were conducted in total darkness, the shade factor would be eliminated. Predators were not present to influence the selection, and food concentration has been essentially eliminated as an influence. Horizontal arrangement of substrates made little difference. Further studies on the biochemical influence of plants upon macroinvertebrate development, or perhaps on the specific periphyton associated with each substrate would aid in the clarification.

CHAPTER V

SUMMARY

The diversity of animal populations at Shandy Slough is relatively low, when compared to other aquatic communities in western Montana. Physicochemical limiting factors such as high alkalinity and, in the benthos, hydrogen sulfide eliminate many populations characteristic of cold-water counterparts of the slough. Other physical factors, such as moderate dissolved oxygen concentration and little seasonal temperature variation, are also factors which contribute to the low diversity.

Hyalella azteca, normally a benthic macroinvertebrate, was found to have definite substrate preferences in an ecosystem without a habitable benthos. Laboratory and field studies indicated that these amphipods had a definite preference for *Lemna* over other available substrates. In addition, substrate, rather than food supply, appears to have the most influence on microdistribution of *Hyalella* at Shandy Slough.

Predation is a strong factor influencing numbers of amphipods associated with substrates in the field. Another likely influence upon the field results would be the abundant shade provided by *Lemna*.

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