FOOD HABITS OF SOME BENTHIC INVERTEBRATES IN A NORTHERN COOL-DESERT STREAM (DEEP CREEK, CURLEW VALLEY, IDAHO-UTAH)[1]

DALE G. KOSLUCHER and G. WAYNE MINSHALL
Department of Biology, Idaho State University, Pocatello, Idaho 83201

KOSLUCHER, D. G. & MINSHALL, G. W. 1973. Food habits of some benthic invertebrates in a northern cool-desert stream (Deep Creek, Curlew Valley, Idaho-Utah). *Trans. Amer. Micros. Soc.*, 92: 441–452. The food habits of several important species of invertebrates inhabiting a northern cool-desert stream were studied on a seasonal basis. The foods eaten were quantified according to frequency of occurrence and were compared with potential foods available in the environment. An assortment of diatoms (Bacillariophyceae) and the filamentous alga *Cladophora glomerata* (Chlorophyta) were the only important living constituents in the diets of the herbivores; no aquatic vascular plant material was found, even when it was abundant in the stream. Plant detritus was the other important food for the herbivores. Of eight invertebrate species studied in detail, five were herbivores, feeding mainly on diatoms and detritus: *Hyalella azteca* (Amphipoda), *Baetis tricaudatus* and *Tricorythodes minutus* (Ephemeroptera), *Hydropsyche occidentalis* (Trichoptera), and *Simulium argus* (Diptera). Three others, *Argia vivida*, *Enallagma anna*, and *Ophiogomphus severus* (Odonata), consistently were carnivorous. Other groups studied less extensively included the herbivores *Gammarus lacustris* (Amphipoda), *Sigara* sp. (Hemiptera), *Optioservus divergens* (Coleoptera), *Limnephilus frijole* (Trichoptera), and Chironomidae (Diptera); and the omnivore *Pacifastacus gambelli* (Decapoda). There were no evident differences between size of the animals and the kinds of foods eaten nor between time of the year and diet. In general, the invertebrate animals in Deep Creek were opportunistic and fed in proportion to the foods present.

The diets of aquatic animals provide valuable clues to an important set of interactions occurring within aquatic ecosystems. Assessment of both the kinds and amounts of foods eaten is necessary for an adequate understanding of the roles of individual species in the biotic community as well as the impact of these species on other members of the community. In addition, such information is of critical importance for proper evaluation of the flow of energy in a given ecosystem. In many aquatic habitats the bottom-dwelling invertebrates comprise an important part in the food conversion processes leading to products of interest to man or necessary for the orderly functioning of the ecosystem. This is especially true in streams, where the benthic invertebrates play key roles in the operation of such ecosystems.

The present study was conducted to determine on a seasonal basis the food relationships of several numerically important invertebrates inhabiting a northern, cool-desert stream. Attempts also were made to discover if the kind of foods eaten changes as the size of the consumer increases and to establish whether the animals select particular foods or eat whatever is available. Data were obtained through examination of gut contents and of materials available as potential food sources.

Widely scattered qualitative records of the food habits of an assortment of benthic invertebrates have appeared in the literature since the turn of the century. However, much work of a quantitative nature, especially in regard to stream-dwelling forms, remains to be done. To date, effort has been concentrated on the Trichoptera (Haage, 1970, 1971; Hanna, 1957; Mecom & Cummins, 1964; Scott, 1958; Slack, 1936; Thut, 1969; Winterbourn, 1971a,b) and to a lesser extent

[1] A contribution of the International Biological Program—Desert Biome Studies.

TRANS. AMER. MICROS. SOC., 92(3): 441–452. 1973.

on the Ephemeroptera (Brown, 1961; Gilpin & Brusven, 1970) and Plecoptera (Hynes, 1941; Mackereth, 1957; Richardson & Gaufin, 1971; Sheldon, 1969). Only a few investigators have undertaken analyses of a representative cross-section of the entire benthic community (Chapman & Demory, 1963; Coffman, Cummins & Wuycheck, 1971; Dunn, 1954; Jones, 1949a,b, 1950; Minckley, 1963; Minshall, 1967; Percival & Whitehead, 1929).

In particular, very few studies have been conducted on food habits of the benthic invertebrates inhabiting streams of the western United States. The most notable are those by Muttkowski & Smith (1929) for a variety of Diptera, Ephemeroptera, Plecoptera, and Trichoptera from four streams in Yellowstone National Park, Wyoming; Sheldon (1969) for *Acroneuria californica* (Plecoptera) in Sagehen Creek, California; Thut (1969) for seven species of *Rhyacophila* (Trichoptera) from an experimental stream in the Cascade Mountains of southwestern Washington; Gilpin & Brusven (1970) for 31 species of Ephemeroptera from the St. Maries River, Idaho; and Richardson & Gaufin (1971) for nine species of Plecoptera from 11 streams along the continental divide in Colorado and Utah. These studies all involved the fauna of mountain ("trout") streams; virtually no previous work has been done on the food habits or trophic relationships of animals inhabiting lowland, desert streams.

This investigation was carried out on bottom-inhabiting invertebrates from Deep Creek, Curlew Valley, Idaho-Utah, as part of a concentrated effort to describe the structure and function of a desert-stream ecosystem. Curlew Valley is a 3,460-km^2 drainage basin astride the Idaho-Utah border and north of the Great Salt Lake. A wide temperature range occurs in the valley (-6 to 20 C mean monthly temperatures), but the climate is semi-arid (less than 40 cm annual precipitation), and the terrestrial vegetation is characteristic of the northern desert biome, with big sage (*Artemesia tridentata*) the most conspicuous native plant.

Description of Study Area

Deep Creek (41° 57′ to 42° 14′ N; 112° 40′ to 112° 46′ W) is a perennial stream which flows toward Great Salt Lake from the north but is reduced by evaporation, is dissipated by irrigation withdrawals, and sinks below ground before reaching the lake. Four physiographic sections of the stream have been distinguished on the basis of climate, terrestrial vegetation, stream-flow characteristics, and type of substratum. Each section is represented by a sampling site which is described below. Additional physical characteristics of each site are given in Table I along with several general indicators of water quality. The locations of the sites correspond in a general way to those used in the comprehensive study referred to, but the specific locations differed slightly to avoid undue disturbance.

Site 1 is situated on the farthest upstream portion of perennial waters lying below the 41-cm (16-in) precipitation isohyeth. It is separated from the remainder of the stream by a 12.7-km-long intermittent section. The surrounding area is sagebrush-grassland, which, in the immediate vicinity of the stream, is periodically heavily used by cattle. The stream bed is deeply incised (up to 4.5 m below the surface) into the valley floor and consists mainly of gravel and silt.

Almost all of the flow at site 2 is provided by Holbrook Springs, which arise 1.3 km upstream. The springfed nature of the stream in this area insures relatively constant flow and temperature (18 C) conditions except for periods of spring floods and irrigation withdrawal. The bankside vegetation is similar to that at site 1 but grazing pressure is lighter and grasses more abundant. Starting at the Springs and extending to Curlew Reservoir (1.9 km) the stream channel

TABLE I

Physical-chemical characteristics for Deep Creek, Curlew Valley, Idaho-Utah based on data for the period September 1970–August 1971[1]

	1	2	3	4
Distance from station 1 (km)	0	18.4	28.6	43.3
Elevation (m)	1517	1406	1387	1357
Mean width (m)	1.3	4.8[2]	2.9	2.1
Mean depth (cm)	14	32[2]	45	44
(at m^3/sec)	(.04)	(1.15)	(.18)	(.32)
Discharge (m^3/sec)	.06	.68	.26	.16
	(.02–.27)	(.02–1.7)	(.09–.99)	(.03–.46)
Substratum	gravel, silt	gravel, sand	muck	silt
Temperatures (°C)				
Maximum	31.9	31.5	26.6	30.0
	(29 June)	(23 August)	(20 July & 10 Aug.)	(20 July)
Minimum	0	2.7	–2.3	–3.5
	(Dec.–Feb.)	(20 March)	(17 Jan. & 7 Feb.)	(13 & 20 Feb.)
Turbidity (J.T.U.)	125	94	71	110
	(10–670)	(4–998)	(10–343)	(31–500)
Specific Conductance	625	640	1342	1715
	(555–769)	(572–703)	(821–1957)	(1147–2431)
Hardness (mg/l as $CaCO_3$)	331	266	486	534
	(243–652)	(242–314)	(290–704)	(398–796)
Total Alkalinity	202	231	251	278
(mg/l as $CaCO_3$)	(147–256)	(167–278)	(226–276)	(233–348)
pH	8.0	7.9	7.9	8.1
	(7.4–8.5)	(7.6–8.2)	(7.5–8.2)	(7.8–8.6)
Nitrate-N	.531	.337	.295	.294
(mg/l)	(.005–1.34)	(.005–1.10)	(.003–2.50)	(.060–.80)
Ortho-P	.372	.140	.392	.218
(mg/l)	(.060–.790)	(.010–.61)	(.090–1.65)	(.040–.35)

[1] Where applicable, the mean is given followed by the range in parentheses.
[2] Does not include periods of reduction due to irrigation withdrawal during which mean depth was 17 cm.

passes through a series of tight meanders and alternates between short riffles and longer reaches. The substratum is predominantly gravel and sand swept clean of accumulations of silt and organic matter. Mats of *Cladophora* and beds of watercress (*Rorippa*) were common during the study period.

Site 3 is located 5 km below Curlew Reservoir dam on a section of Deep Creek which is gently meandering and characterized by non-turbulent flow and a depositing type of substratum. The bottom material consists of a thick layer of silt (up to 1 m deep) intermixed with large amounts of organic matter. Heavy growths of *Potamogeton* and *Cladophora* occur throughout this area during the summer. The water table lies near the surface in this section of the valley, resulting in a distinct shift in the vegetation to low-lying grasses and sedges and the exclusion of sagebrush from the immediate vicinity. Cattle are grazed in the area but cause very little direct disturbance to the banks or to the stream bottom.

The stream in the region of site 4 is used to carry irrigation water to adjacent cropland, and it is regulated and periodically dredged to achieve that end. About 5 km below the location of site 4 permanent flow ceases and Deep Creek again becomes intermittent. Climatic conditions in this region are the most severe of the four sections. Precipitation is marginal for plant growth (annual average 15 cm), and this is reflected in the generally poor cover on the surrounding watershed. However, unlike the situation along most of the remainder of the stream, thickets of wild rose (*Rosa woodsii*) and willow (*Salix* sp.) occur in several stretches and serve both to shade the stream and provide substantial

TABLE II

The number of specimens examined, and the median size classes represented (in parentheses)[1]

	Autumn (Nov.)	Winter (Jan.)	Spring (April)	Summer (Aug.)	Total
A. Examined during most seasons					
Enallagma *anna* Williamson (Odonata)	65 (7,9,11,13,15,17)	25 (3,7,11,15)	15 (11,13,15)	30 (5,9,11,15)	135
Hyalella *azteca* Sars (Amphipoda)	35 (3,5,7)	45 (5,9)	20 (5)	35 (3,5)	135
Baetis *tricaudatus* Dodds (Ephemeroptera)	15 (5)	25 (5)	45 (5,6)	25 (3,9)	110
Hydropsyche *occidentalis* Banks (Trichoptera)	20 (7,9,11)	35 (5,7,9,11,13)	30 (7,9)	15 (5,7,9)	100
Argia *vivida* Hagen (Odonata)	30 (7,9,11,13)	30 (7,9,11,13)	15 (9,11,13)	15 (9,11)	90
Tricorythodes *minutus* Traver (Ephemeroptera)	15 (3)	15 (5)	15 (5)	20 (3)	65
Ophiogomphus *severus* Hagen (Odonata)	15 (5,9)	10 (9)	20 (7,11,15,19)	15 (9,11,13)	60
Simulium argus Will. (Diptera)	15 (5)	20 (5,7,9)	15 (5,7)	0	50
B. Examined during one or two seasons					
Gammarus *lacustris* Sars (Amphipoda)	10 (13)	0	0	15 (9,11)	25
Limnephilus *frijole* Ross (Trichoptera)	0	10 (13)	15 (9,15)	0	25
Sigara sp. (Hemiptera)	10	0	0	0	10
Chironomidae* (Diptera)	0	0	36	0	36
Optioservus *divergens** (Coleoptera)	0	0	36	0	36

[1] An asterisk indicates data provided by members of the Streams & Biotic Production class, Idaho State University.

amounts of organic input. Very little aquatic vegetation occurs in the area, and the mud bottom lacks the high organic content of site 3.

Mean concentrations of total dissolved solids (estimated from specific conductance measurements, Table I) were more than twice as great at the two downstream sites. Additional analyses, not reported in Table I, indicate that most of the differences are due to increases in sodium chloride and calcium-, magnesium-, and sodium-sulfate levels. Mean alkalinity values were high and increased only slightly with progression downstream. In general, concentrations of major plant nutrients (N, P) also were plentiful.

Materials and Methods

Invertebrates were collected from four stations on a seasonal basis starting in autumn (November) 1969 and continuing through winter (January), spring

(April), and summer (August) 1970 (Table II). An effort was made each time to obtain representatives from as many different size classes as possible. During each collecting period samples of algae and macrophytes also were taken and their relative abundance in the stream noted. Invertebrates were collected by stirring up the substratum by kicking and allowing all of the suspended materials to drift into a collecting net (8 threads/cm) held immediately downstream of the area being disturbed.

Preparation of the invertebrate gut contents for examination was performed in the laboratory using a method modified from that of Mecom & Cummins (1964). All specimens were cleaned with a fine brush prior to dissection. The gut contents of five specimens of the same (2-mm increment) size class were pooled to insure sufficient material for examination, as well as to provide a more representative sample. All recognizable animal parts were removed and analyzed separately. The remaining material was then dispersed by agitation with a probe and filtered onto a 0.8 μm membrane filter. The filters were cleared with immersion oil and mounted on glass slides in Permount (Turtox Co.). Enumeration of food items was done in accordance with a combination of methods. First, the contents were examined for the presence of animal remains; if the organism was determined to be a carnivore, the method described by Mecom & Cummins (1964) was followed. If animal remains were not evident, the procedure described by Minshall (1967) was used. A composite food web was constructed on the basis of the percentage of each food in the guts.

The chemical analyses reported here followed standard limnological procedures (Amer. Publ. Health Assoc., 1965). All determinations were made after returning the samples to the laboratory. Hardness was measured by the EDTA titrametric method. Alkalinity was determined by titration with N/50 H_2SO_4 in the presence of phenolphthalein and methyl purple indicators. Analysis for nitrate-nitrogen and phosphate-phosphorus employed the cadmium reduction method and the diazotization method, respectively, using reagents prepared by the Hach Chemical Co. and a Bausch and Lomb "Spectronic 20" colorimeter. Turbidity also was determined with the colorimeter. Specific conductance was measured with an Industrial Instrument Co. Wheatstone bridge (Model RC-1682) and standardized dipping cell.

Temperature records are from maximum-minimum recording thermometers which were read weekly. Discharge also was determined at weekly intervals; current velocity was measured with a small Ott C-1 current meter.

Results and Discussion

Materials potentially available as foods, that is, present in the study area, in addition to detritus, included a variety of diatoms, filamentous green algae, aquatic vascular plants, and aquatic invertebrates (Table III). However, a number of the plants found in the stream apparently were not eaten, and only the diatoms and *Cladophora glomerata* were important constituents in the diet. A similar observation was made by Whitehead (1935) who noted that, contrary to the situation on land, remarkably few invertebrates feed directly on living higher plants. But Gaevskaya (1969) recently has documented the consumption of numerous aquatic macrophytes by benthic invertebrates from other water bodies throughout the world.

Cladophora glomerata was important only during the normal "growing season" except at station 2, where it occurred all year. The diatoms *Diatoma*, *Epithemia*, *Gomphonema*, *Meridion*, *Navicula*, and *Nitzschia* were common at all stations during every season. *Cocconeis* and *Rhoicosphenia* occurred at all stations but at times were absent. *Gyrosigma* was found only at stations 3 and 4 and was

TABLE III

List of the potential plant food materials present in Deep Creek and foods actually eaten by the eight species studied in detail[1]

	Foods eaten								
Foods present	*Hydropsyche occidentalis*	*Baetis tricaudatus*	*Hyalella azteca*	*Simulium argus*	*Tricorythodes minutus*	*Enallagma anna*	*Ophiogomphus severus*	*Argia vivida*	Not eaten
Diatoms									
Achnanthes	+	+	+	0	+	0	+	0	
Caloneis	+	+	+	+	+	+	0	0	
Cocconeis	+	+	+	0	+	+	+	+	
Diatoma	+	+	+	+	+	+	+	+	
Epithemia	+	+	+	+	+	+	+	+	
Gomphonema	+	+	+	+	+	+	+	+	
Gyrosigma	0	0	+	+	+	+	+	0	
Meridion	+	+	+	+	+	+	+	+	
Navicula	+	+	+	+	+	+	+	+	
Nitzschia	+	+	+	+	+	+	+	+	
Rhoicosphenia	+	+	+	+	+	+	+	+	
Rhopalodia	+	+	0	+	0	+	0	0	
Surirella	+	+	+	+	0	0	+	0	
Synedra	+	+	+	+	+	0	+	+	
Green Algae									
Chara	0	0	0	0	0	0	0	0	*
Chlorotylium	0	0	0	0	0	0	0	0	*
Tetraspora	0	0	0	0	0	0	0	0	*
Spirogyra	0	0	0	0	0	0	0	+	
Cladophora	+	+	+	+	0	+	0	+	
Vascular Plants									
Eleocharis	0	0	0	0	0	0	0	0	*
Polypogon	0	0	0	0	0	0	0	0	*
Potamogeton	0	0	0	0	0	0	0	0	*
Ranunculus	0	0	0	0	0	0	0	0	*
Rorippa	0	0	0	0	0	0	0	0	*
Unidentified	0	0	0	0	0	+	0	0	
Invertebrates									
Hydropsyche	0	0	0	0	0	+	+	+	
Baetis	0	0	0	0	0	+	0	0	
Hyalella	0	0	0	0	0	+	+	+	
Simulium	0	0	0	0	0	+	+	+	
Tricorythodes	0	0	0	0	0	+	+	0	
Enallagma	0	0	0	0	0	0	+	+	
Unidentified	0	0	0	0	0	+	+	+	
Detritus	+	+	+	+	+	+	+	+	

[1] + eaten; 0 not eaten; * not eaten by any of the organisms studied.

absent in the autumn. *Synedra*, a prevalent diatom at all stations in the autumn, was found only at station 2 in the winter and at station 4 in the spring. The diatoms consumed most often were (a) autumn —*Navicula*, *Diatoma*, *Cocconeis*; (b) winter —*Diatoma*, *Nitzschia*, *Navicula*; (c) spring —*Navicula*, *Diatoma*; and (d) summer —*Navicula*, *Diatoma*, *Cocconeis* (in order of decreasing importance). *Cocconeis* occurred more frequently as an important component in the diet of *Hydropsyche occidentalis* than in any of the other herbivores examined.

TABLE IV

Percentage of foods consumed by 8 species of benthic invertebrates on a seasonal basis from four collecting stations in Deep Creek, Curlew Valley, Idaho-Utah[1]

Taxa		Autumn				Winter				Spring				Summer			
		a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Herbivores																	
Hydropsyche occidentalis																	
	1	45	45	10		10	85	5		70	30			35	60	5	
Sta.	2	10	85	5		15	85			30	70			40	55	5	
	3					85	10	5		50	50						
	4																
Baetis tricaudatus																	
	1					35	65			75	25			75	25		
Sta.	2	55	45	+		45	55			50	50			50	50		
	3	25	75							50	50			50	50		
	4					90	10			90	10						
Simulium argus																	
	1					35	60	5		60	40						
Sta.	2	40	60			55	45										
	3	45	55			70	30										
	4	60	40			70	30			65	35						
Hyalella azteca																	
	1	70	25	5		45	55							65	30	5	
Sta.	2	80	15	5		55	45							90	10		
	3	85	15			90	10			70	30			70	30		
	4	75	25			85	15			90	10			80	20		
Tricorythodes minutus																	
	1	65	35														
Sta.	2	60	40			42	58			70	30			75	25		
	3																
	4													85	15		
Carnivores																	
Enallagma anna																	
	1	10	5		85	20	15		65					20	10		70
Sta.	2	80	20	+		20	10		70								
	3	40	10		50	35	5		60	20	10		70	30	10		60
	4	10	5	+	85	30	5		65	20	15		65	70	30		
Argia vivida																	
	1	50	15	+	35	20	15	5	60	20	10		70	25	15		60
Sta.	2	10	5		85	30	15		55	20	10		70	30	10		60
	3																
	4																
Ophiogomphus severus																	
	1																
Sta.	2					15	5		80								
	3																
	4	20	15		65	60	10		30					20	10		70

[1] Column a—detritus, b—diatoms, c—filamentous green algae, d—invertebrates. A + indicates that amounts less than 1% were present.

The filamentous green alga *C. glomerata* was consumed in large amounts by *Sigara* and in lesser amounts by *Hyalella azteca*, *Simulium argus*, and *Baetis tricaudatus*. *Chara vulgaris* was present at all stations, but no organisms were found that consumed it.

All of the invertebrates analyzed in this study were mixed feeders and took a wide variety of foods (Table IV). Although it was possible to distinguish those which ate primarily animal matter from those which fed mainly on aquatic plants or detritus, there was no consistent distinction between those feeding

mainly on detritus and those consuming mostly algae. Diatoms and detritus frequently were of equal importance or varied haphazardly in predominance from station to station and season to season. Consequently, any consumers that had substantial amounts of animal remains in their guts were listed as carnivores; the remainder all were considered to be herbivores. In most cases, more than 50% of the food consumed by "carnivores" was of known animal origin.

Of eight invertebrate species considered in detail, five were classified as herbivores and three as carnivores. The food habits of only two of these species appear to have been described previously. However, the results for the others generally agree with those described for closely related species in other parts of the country. Only the more salient points will be mentioned here.

All of the *Hydropsyche occidentalis* larvae examined from Deep Creek were found to contain only plant material. This was confirmed by several of our colleagues following independent examination of other specimens, as well as by growth experiments utilizing plant material as food. However, specimens from Deep Creek held in captivity are known to be cannibalistic (A. R. Gaufin, personal communication), and several other investigators (Coffman et al., 1971; Lloyd, 1921; Muttkowski & Smith, 1929) have observed considerable amounts of animal matter in other species of *Hydropsyche*. Therefore, it is likely that *H. occidentalis* takes animal prey under certain circumstances, but that this generally is not the case under the conditions of abundant plant matter found in Deep Creek. In general *H. occidentalis* was found to ingest more diatoms than detritus; only once was a greater amount of detritus found.

Baetis tricaudatus frequently ate about as much detritus as it did diatoms, but on several occasions the amount of detritus ingested greatly exceeded that of the diatoms. In the St. Maries River, Idaho, *B. tricaudatus* nymphs also fed largely on detritus (52.3%) and diatoms (34.1%) but took some filamentous algae (11%) and higher plants (2.4%) (Gilpin & Brusven, 1970). *Tricorythodes minutus*, another mayfly from Deep Creek, consistently ate more detritus than anything else and as such was similar to *T. minutus* from the St. Maries River, which ate 83% detritus.

Simulium argus larvae in Deep Creek ate both detritus and diatoms more or less indiscriminately; only in about half the samples was more detritus found than diatoms. Some studies (Coffman et al., 1971; Muttkowski & Smith, 1929) have found that *Simulium* consumes mostly algae and only relatively small (15% or less) proportions of detritus. Others (Chapman & Demory, 1963; Minshall, 1967) have found *Simulium* to consume mainly detritus. Considering that *Simulium* is a filter-feeder, such variation is not unexpected and is largely governed by local conditions (Anderson & Dicke, 1960).

Hyalella azteca in lentic waters feeds on the epiphytic growth on rooted aquatic plants, on dead animal and plant matter, and often on live plant material such as filamentous green algae (Cooper, 1965). In Deep Creek, *H. azteca* normally was a detritivore, but it also consumed substantial amounts of diatoms. On three occasions (twice in the autumn and once in the summer) bits of filamentous algae were found in the guts.

Animal remains always were present in the guts of *Argia vivida*, *Enallagma anna*, and *Ophiogomphus severus*. Some detritus and diatoms always were present in their guts also but could have been ingested during feeding or have been in the guts of the prey. *Hyalella azteca*, *Hydropsyche occidentalis*, and *Simulium argus* were the predominant prey, but the remains of several other taxa were found in the guts of the three Odonate carnivores. Somewhat surprisingly, no Chironomidae were found in the gut samples of the carnivores. It also is noteworthy that only *Enallagma anna* was found to eat *Baetis*. Both *Argia vivida* and

Ophiogomphus severus consumed *E. anna*: *A. vivida* in the winter and spring at stations 1 and 2 and *O. severus* at station 4 during the summer and autumn. The only study of the diets of stream-dwelling Odonata available for comparison with the present findings is the observation of predation by *Aeshna umbrosa* and *Agrion maculatum* on blackfly larvae (*Simulium*) (Peterson & Davies, 1960).

Other important consumers which were studied less extensively were Chironomidae (Diptera), *Optioservus divergens* (Coleoptera), *Gammarus lacustris* (Amphipoda), *Sigara* sp. (Hemiptera), *Limnephilus frijole* (Trichoptera), and *Pacifastacus gambelli* (Decapoda). Important species not studied at all included: *Pisidium* sp. (Pelecypoda), *Bithinia* sp. and *Physa* sp. (Gastropoda), *Helobdella elongata* (Hirudinea), and *Dubiraphia guilianii* (Coleoptera).

Gammarus lacustris from station 3 was found to eat 80% detritus in the autumn and 50% during the summer; the remainder of the diet consisted of diatoms. In the summer at station 2, 75% of the diet was detritus. *Limnephilus frijole* was collected only at station 1, where diatoms comprised 90% of its diet in the winter and 45% in the spring; detritus made up the rest. *Sigara* sp. was collected only at stations 3 and 4 in the winter. *Cladophora* made up 40% of the diet and detritus about 50%. The Chironomidae specimens examined contained slightly more detritus (59%) than diatoms (41%). *Optioservus divergens* larvae appeared to eat mainly detritus (83.6%) and fewer diatoms (16.4%). The crayfish *Pacifastacus gambelli* was omnivorous, eating substantial amounts of detritus (32.3%), algae (diatoms, 26.7%; Cladophora, 6.7%), and animals (*Baetis*, 33%; Chironomidae, 0.7%; and *Simulium*, 0.3%).

Some investigators (Brown, 1961; Sheldon, 1969) have noted differences in food habits associated with changes in the size of the consumer, but others (Gilpin & Brusven, 1970) have been unable to detect such a relationship. None of the organisms examined from Deep Creek showed a change in food preference with an increase in size. In most cases, the body-length variations were from 2- to 4-mm increments and may not have been adequate to show any food differences. Also, the limited kinds of food in the stream probably restricted the selection of foods and led to the same general diet for all size classes.

A few investigators have examined the food habits of benthic invertebrates throughout a year's time (Brown, 1961; Chapman & Demory, 1963; Gilpin & Brusven, 1970; Haage, 1970, 1971; Hanna, 1957; Sheldon, 1969; Winterbourn, 1971a). Some (e.g., Chapman & Demory, 1963; Sheldon, 1969) have found relatively clear relationships between the time of the year and the foods eaten; others (e.g., Haage, 1970, 1971; Winterbourn, 1971a) have detected no special differences between seasons. Most agree that the findings reflect local and seasonal conditions of availability and abundance and thus can be expected to vary accordingly. While it was not possible to examine the seasonal relationship of any one species at all stations in Deep Creek, the data do permit comparisons for at least one or two stations. Even so it is difficult to demonstrate any clear, consistent evidence of a seasonal trend. Those that fed extensively on detritus (e.g., *Hyalella azteca*) gave less indication of seasonal variation than did those that took greater proportions of algae. No pattern was evident for the carnivores. There is an indication that diatoms may have been most important during the winter for *Baetis tricaudatus* and *Hydropsyche occidentalis* at station 1. At station 2, where conditions were more stable and growth of algae could occur throughout the year, the proportions of diatoms and detritus taken by these two species generally were more constant from season to season. However, the invertebrate animals in Deep Creek generally appear to be opportunistic in their food habits and to feed in proportion to the foods present.

In any study of the trophic relationships of natural stream ecosystems it soon

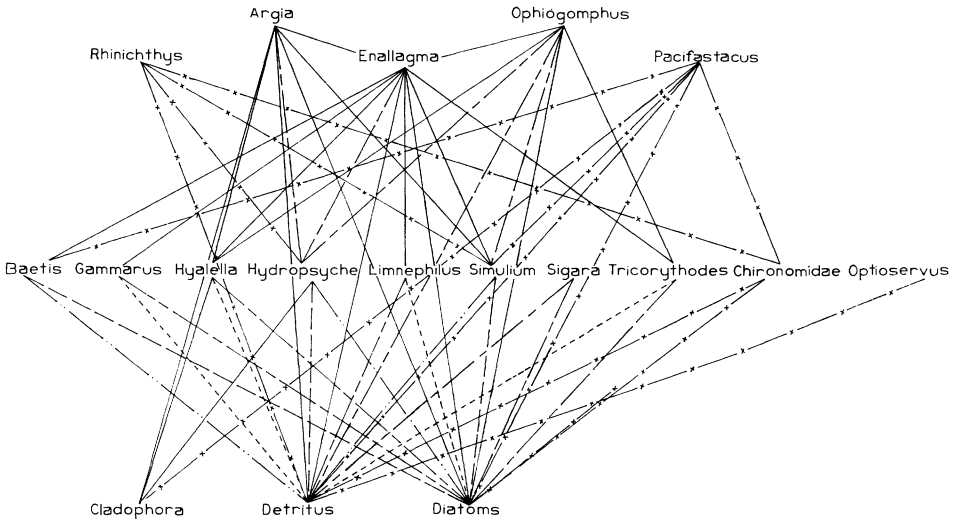

FIG. 1. Trophic relationships of some of the more important groups in Deep Creek based on a composite of data from all stations and seasons. The relative importance of each pathway is indicated by different lines, as follows: ——— = 0–20%; ——— — ——— = 21–35%; — — — = 36–50%; ——— · · ——— = 51–65%; - - - - - = 66–80%; ——— = 81–100%; × —— × = amount unknown.

becomes apparent that the food web is extremely complex (Jones, 1949a; Minckley, 1963; Minshall, 1967; Percival & Whitehead, 1929; Ricker, 1934). This is shown for Deep Creek in Figure 1, which gives only a portion of the food exchange pathways. This food web diagram summarizes conditions of the entire stream for all seasons and was constructed by averaging the data for each station and including every known trophic pathway.

Diatoms and detritus were found to provide the main food base at the primary producer level. In Deep Creek, unlike other streams that have been studied (Minshall, 1967), the detritus appears to be derived largely from autochthonous sources; the contribution from the surrounding watershed (other than from livestock manure) is relatively insignificant. An important terminal role is indicated for the three Odonata (*Argia vivida*, *Enallagma anna*, and *Ophiogomphus severus*), the crayfish (*Pacifastacus gambelli*), and the dace (*Rhinichthys osculus*). The absence of a tertiary consumer level is noteworthy and may be common to small streams (Minshall, 1967). Apparently no previous studies of streams have been done in which Odonata were among the principal predators.

LITERATURE CITED

AMERICAN PUBLIC HEALTH ASSOCIATION. 1965. Standard methods for the examination of water and wastewater. 769 pp.

ANDERSON, J. R. & DICKE, R. J. 1960. Ecology of the immature stages of some Wisconsin black flies (Simuliidae: Diptera). *Ann. Ent. Soc. Amer.*, 53: 386–404.

BROWN, D. S. 1961. The food of the larvae of *Chloeon dipterum* L. and *Baetis rhodani* (Pictet) (Insecta, Ephemeroptera). *J. Anim. Ecol.*, 30: 55–75.

CHAPMAN, D. W. & DEMORY, R. L. 1963. Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. *Ecology*, 44: 140–146.

COFFMAN, W. P., CUMMINS, K. W. & WUYCHECK, J. C. 1971. Energy flow in a woodland

stream ecosystem: I. Tissue support trophic structure of the autumnal community. *Arch. Hydrobiol.*, 68: 232–276.

COOPER, W. E. 1965. Dynamics and production of a natural population of a freshwater amphipod, *Hyalella azteca*. *Ecol. Monogr.*, 35: 377–394.

DUNN, D. R. 1954. The feeding habits of some of the fishes and some members of the bottom fauna of Llyn Tegid (Bala Lake), Merionethshire. *J. Anim. Ecol.*, 23: 224–233.

GAEVSKAYA, N. S. 1969. [The role of higher aquatic plants in the nutrition of the animals of fresh-water basins.] *Nat. Lending Lib. Sci. Technol.*, Boston Spa, England. 629 pp. (in Russian with English translation)

GILPIN, B. R. & BRUSVEN, M. A. 1970. Food habits and ecology of mayflies of the St. Maries River in Idaho. *Melandaria*, 4: 20–40.

HAAGE, P. 1970. On the feeding habits of two Baltic species of caddis larvae (Trichoptera). *Ent. Scand.*, 1: 282–290.

1971. A study of the feeding habits of larvae of *Limnephilus marmoratus* Curtis (Trichoptera) living in the *Fucus* belt of the northern part of the Baltic. *Hydrobiologia*, 37: 253–265.

HANNA, H. M. 1957. A study of the growth and feeding habits of the larvae of four species of caddisflies. *Proc. Roy. Ent. Soc. London* (A), 32: 139–146.

HYNES, H. B. N. 1941. The taxonomy and ecology of the nymphs of British Plecoptera, with notes on the adults and eggs. *Trans. Roy. Ent. Soc. London*, 91: 459–557.

JONES, J. R. E. 1949a. A further ecological study of calcareous streams in the "Black Mountain" district of south Wales. *J. Anim. Ecol.*, 18: 142–159.

1949b. An ecological study of the River Rheidol, North Cardiganshire, Wales. *J. Anim. Ecol.*, 18: 67–88.

1950. A further ecological study of the River Rheidol. The food of the common insects of the mainstream. *J. Anim. Ecol.*, 19: 159–174.

LLOYD, J. T. 1921. The biology of North American caddisfly larvae. *Bull. Lloyd Libr.*, 21: 1–124.

MACKERETH, J. C. 1957. Notes on the Plecoptera from a stony stream. *J. Anim. Ecol.*, 26: 343–351.

MECOM, J. O. & CUMMINS, K. W. 1964. A preliminary study of the trophic relationships of the larvae of *Brachycentrus americanus* (Banks) (Trichoptera: Brachycentridae). *Trans. Amer. Micros. Soc.*, 83: 233–243.

MINCKLEY, W. L. 1963. The ecology of a spring stream, Doe Run, Meade County, Kentucky. *Wildl. Monogr.*, 11: 1–124.

MINSHALL, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. *Ecology*, 48: 139–149.

MUTTKOWSKI, R. A. & SMITH, G. M. 1929. The food of trout stream insects in Yellowstone National Park. *Roosevelt Wildl. Ann.*, 2: 241–263.

PERCIVAL, E. & WHITEHEAD, H. 1929. A quantitative study of the fauna of some types of stream-bed. *J. Ecol.*, 17: 282–314.

PETERSON, B. V. & DAVIES, D. M. 1960. Observations of some insect predators of black flies (Diptera: Simuliidae) of Algonquin Park, Ontario. *Canad. J. Zool.*, 38: 9–18.

RICHARDSON, J. W. & GAUFIN, A. R. 1971. Food habits of some western stonefly nymphs. *Trans. Amer. Ent. Soc.*, 97: 91–121.

RICKER, W. E. 1934. An ecological classification of certain Ontario streams. Univ. Toronto Studies, Biol. Ser. 37, Publ. Ontario Fish. Res. Lab., 49: 7–114.

SCOTT, D. 1958. Ecological studies of the Trichoptera of the River Dean, Cheshire. *Arch. Hydrobiol.*, 54: 340–392.

SHELDON, A. L. 1969. Size relationships of *Acroneuria californica* (Perlidae, Plecoptera) and its prey. *Hydrobiologia*, 34: 85–94.

SLACK, H. D. 1936. The food of caddis fly (Trichoptera) larvae. *J. Anim. Ecol.*, 5: 105–115.

THUT, R. N. 1969. Feeding habits of larvae of seven *Rhyacophila* (Trichoptera: Rhyaco-

philidae) species with notes on other life history features. *Ann. Ent. Soc. Amer.*, 62: 894–898.

WHITEHEAD, H. 1935. An ecological study of the invertebrate fauna of a chalk stream near Great Driffield, Yorkshire. *J. Anim. Ecol.*, 4: 58–78.

WINTERBOURN, M. J. 1971a. An ecological study of *Banksiola crotchi* Banks (Trichoptera: Phryganeidae) in Marion Lake, British Columbia. *Canad. J. Zool.*, 49: 637–645.

1971b. The life histories and trophic relationships of the Trichoptera of Marion Lake, British Columbia. *Canad. J. Zool.*, 49: 623–635.

HISTOCHEMICAL OBSERVATIONS ON PLACENTATION OF THE KANGAROO RAT (*DIPODOMYS*) WITH SPECIAL REFERENCE TO THE TROPHOSPONGIUM AND GIANT CELLS[1]

EUGENE G. FULLER[2] and F. DONALD TIBBITTS
Department of Biology, University of Nevada, Reno, Nevada 89507

FULLER, E. G. & TIBBITTS, F. D. 1972. Histochemical observations on placentation of the kangaroo rat (*Dipodomys*) with special reference to the trophospongium and giant cells. *Trans. Amer. Micros. Soc.*, 92: 452–460. Early in gestation the undifferentiated trophoblast is rich in both alkaline phosphatase and glycogen. However, as the two zones of trophoblast cells differentiate, glycogen becomes localized primarily in the basal zone cells while alkaline phosphatase is detected chiefly in the inner zone cells and maternal blood channels of both zones. The labyrinth exhibited a strong reaction for both glycogen and alkaline phosphatase. The visceral yolk sac was devoid of alkaline phosphatase, but glycogen was present. Alkaline phosphatase was present in the parietal endoderm of the degenerating bilaminar omphalopleure but glycogen was absent. The possible significance of these histochemical findings is discussed in relation to placental function.

A distinctive feature of the chorioallantoic placenta in the Geomyoidea, and apparently unique to this rodent superfamily, is the thick placental hillock formed from hypertrophied trophoblast cells between the maternal decidua and the allantoic mesoderm (Mossman & Straus, 1963). These hillock cells have been compared to the Träger of other rodents (Mossman, 1937) and, similarly, give rise to trophospongium and giant cells during the course of placental development. Unlike the majority of other rodents, however, these trophoblast cells constitute up to two-thirds of the total mass of the definitive placenta in *Dipodomys*.

These hypertrophied trophoblast cells have been called giant cells or large trophoblast cells (Fuller & Tibbitts, 1967; Mossman, 1937; Nielson, 1940) and, if the placental hillock is considered to be homologous with the Träger, then it would seem that the hypertrophied cells derived from it would be comparable to the secondary giant cells derived from the Träger in such rodents as the mouse (Snell, 1941) and hamster (Orsini, 1954). Mossman & Straus (1963) used the

[1] The authors express their appreciation to Dr. Barry F. King for critically reading the manuscript, Dr. Charles Baker for technical assistance, and the Desert Research Institute and the Graduate School of the University of Nevada for continuing financial assistance.

[2] Present address: Department of Biological Sciences, Boise State College, Boise, Idaho 83707.