

to influence drift except perhaps between 1700 and 2100 hours (Table 2). This is evidently a correlative rather than a causative relationship. The absence or presence of light was the dominant factor controlling the magnitude of aquatic drift organisms.

Acknowledgments

The authors wish to thank Mr. Norman Reimers, Director of the Sierra Nevada Aquatic Research Laboratory, for guidance, Mr. Sandy Dole for technical assistance, and Dr. Thomas Jenkins for helpful criticisms.

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Received November 22, 1971.

Accepted for publication April 4, 1972.

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Comparative Food Habits of Four Species of Stream-Dwelling Vertebrates (*Dicamptodon ensatus*, *D. copei*, *Cottus tenuis*, *Salmo gairdneri*)

When two or more species occupy the same habitat and have the same requirements for food and space, supposedly limited in supply, then these species are in direct competition. Ultimately, the least adapted species may be excluded from the competitive arena. This is a simplification of Gause's Principle (1934) or Hard "competitive exclusion principle" which states that complete competitors cannot occupy the same niche (Smith, 1966). If the niches (niche is defined here as the residence and nutritional requirements of an organism) only partially overlap, then the organisms involved may coexist, and often behavior mechanisms serve to establish partial exclusion. For example, MacArthur (1958) found that several species of warblers with similar food habits were able to coexist in the same wood by a combination of adaptations including partitioning of the forest canopy and selective feeding by at least one species.

Four species of cold-blooded vertebrates often occur together in northwest streams. These are: *Dicamptodon ensatus* (Pacific giant salamander), *Dicamptodon copei* (Cope's salamander), *Cottus tenuis* (slender sculpin), and *Salmo gairdneri* (rainbow trout). Only the branchiate, larval forms of the two salamanders are of interest in this study.

Casual observations suggested that the habitats of these four species were similar especially among smaller individuals. Individuals of all species take cover under rocks and logs and in crevices, and often individuals of two or more of the species can be found sharing the same hiding place. In light of these observations, it was thought that a comparative study of the food habits of these four species within a single section of a stream would help to reveal the role that each of the species has in the stream community, and that possible exclusion mechanisms might be found.

The food of *S. gairdneri* is generally known through a widely scattered literature. Bailey's (1952) study of the food of *Cottus bairdi* suggests that freshwater cottids are largely opportunistic feeders, although he gave no information on availability

Dineen (1951) studied the comparative food habits of *C. bairdi* and sympatric species of trout. His study included information on food availability and stomach contents and indicated that major food items were similar but that competition may be relaxed by differential feeding behavior at certain times of the year. Dineen also noted that cottids are mainly bottom feeders whereas salmonids feed at all levels.

Metter (1963) studied the food of larval *D. ensatus* in a small stream in Latah County, Idaho. He found that 52 percent of the stomachs contained trichopteran larvae and 14 percent tadpoles of the tailed frog, *Ascaphus truei*. Both of these items were abundant in the stream studied. Johnson and Schreck (1969) examined the stomach contents of 51 larval *D. ensatus* from Fern Lake, Humboldt County, California. They found that 70.5 percent of the larvae had eaten Odonata nymphs, and that 39.2 percent had eaten larvae of the northwestern salamander, *Ambystoma gracile*. Odonata nymphs and larvae of *A. gracile* are known to be common in ponds and lakes and rare or absent in streams. Warren *et al.* (1969) examined stomachs of *D. ensatus* larvae from Berry Creek, Benton County, Oregon. The snail, *Oxytrema* sp., was the most common food item and parts of crayfish were found in several stomachs. *Oxytrema* is exceedingly abundant and crayfish common in Berry Creek. Franz (1970) reported that larval *D. ensatus* regurgitated caddisfly cases of a species common in the small pond from which the larvae were collected. These and numerous other observations (Nussbaum, unpubl.) indicate that larval *D. ensatus* can easily adapt to different kinds of food in different environments and that, in general, they feed on whatever is most abundant.

The purpose of this study was to determine which aspects of "partial exclusion" might be responsible for the coexistence of the four species in a mountain stream in southwestern Washington.

At the time of this study only one species of *Dicamptodon* (*D. ensatus*) was known, and therefore only one salamander was considered in the analysis. Nussbaum (1970), since then, has determined that the *Dicamptodon* complex contains two species, *D. copei* and *D. ensatus*, and that the two occur at the study site. Therefore, all gut analyses are for *D. ensatus* and *D. copei*, collectively, and any reference to food items shall refer to *Dicamptodon* spp.

Methods and Materials

The Study Site

A 500-ft section of Maratta Creek was chosen as the study site. Maratta Creek is a tributary of the Toutle River located on the western slopes of the Cascade Mountains in Cowlitz County, Washington (T9N, R4E, Sec. 3). The stream is about 1.5 mi long, heading at 2740 ft and ending at 2100 ft with an 8 percent gradient. Vegetation at the study site is largely old growth Douglas-fir with some western red cedar. Undergrowth is sparse. Precipitation is about 80 in per year. The stream is clear and rocky-bottomed with abundant cover provided by fallen logs. Discharge during the 12-month study period (April, 1968 to March, 1969) varied from 6 cfs in July to 188 cfs in March. Stream temperatures ranged from 1°C in April, December, and February to 15°C in July. Diel temperature fluctuations ranged from 0.5°C in April and December to 5°C in October. Dissolved oxygen varied from 9.9 ppm in July to 12.7 ppm in February. The range of pH was 7.0 to 7.3, with the low readings in the summer months and the high readings in the winter months.

Sampling Methods

Ten random samples, five in mid-stream and five near the sides, were taken each month with a square-foot Surber bottom sampler within the 500-ft study section. The sample sites were selected using a random numbers table system. Samples were placed in jars containing 70 percent alcohol and taken back to the lab where both organisms were separated from the rubble and debris. The organisms were then sorted according to order and identified to family. All individuals were labeled and preserved, and are housed at Central Washington State College. Salamanders and fish were normally collected at night, although some were collected during daylight hours. Sample sizes are listed in Table 1.

TABLE 1. Numbers of stream-dwelling vertebrates taken at study site.

Name	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Feb.	M.
<i>Dicamptodon</i> spp.	19	20	27	34	9	19	3	0	0	1	
<i>Cottus</i> <i>tenuis</i>	12	5	9	20	3	6	5	2	0	0	
<i>Salmo</i> <i>gairdneri</i>	14	17	14	9	27	22	27	15	1	6	

Three techniques were used to collect vertebrates. A standard fish shocker was employed at the beginning of the project. A seine net gave good results in trapping trout and was generally employed for catching these animals. Salamanders and sculpin could not be caught in this manner and the best method used for trapping them could best be described as a "chase and corral" technique whereby an individual was forced by hand into a dipnet.

As soon as possible after animals were captured they were anesthetized. Trout were injected with 2-3 cc of 10 percent formalin, put in formalin for several hours and then preserved in 70 percent alcohol. The fish were put directly into 10 percent formalin. However, they were placed in separate containers because formalin often caused regurgitation of stomach contents and care had to be taken to prevent mixing of stomach contents in a common container. The stomachs were removed and preserved in labeled vials containing 70 percent alcohol.

Results and Discussion

Bottom Fauna

Bottom sample data are summarized in Table 2. The frequency and density of each type of bottom organism are listed by month from April, 1968 to March, 1969. Frequency is the percent of samples in which a particular type of organism occurred and density is the mean number of individuals per sample.

Food items were categorized as sparse ($.00 > \text{freq.} < .10$), moderately abundant ($.10 \geq \text{freq.} \leq .40$), and abundant ($.40 > \text{freq.} \leq 1.00$). Those families in the abundant category are referred to as "stream staples."

Mayflies, caddisflies, stoneflies, two families of dipterans, one family of beetle and a small white oligochaete comprise the most abundant food organisms in the stream. In general this was true for the duration of the study. Of the mayfly baetids, heptageniids, and ephemeroptera were abundant. Siphonurids and leptophlebiids

TABLE 2. Average frequency/density of stream organisms taken in bottom samples.

Food Item	Apr.	May	June	July	Sept.	Oct.	Nov.	Dec.	Feb.	Mar.
<i>INSECTS</i>										
<i>EPHEMEROPTERA</i>										
Siphonuridae	30/ 0.5	20/ 1.2	70/ 6.1	70/ 3.8	10/ 0.1	20/ 0.6	30/ 1.3
Baetidae	70/18.8	70/10.0	70/ 4.6	70/ 6.2	60/ 3.7	40/ 0.7	80/ 3.1	50/ 2.3	40/ 4.4	60/ 2.8
Ephemerellidae	70/ 2.7	80/ 2.4	70/ 4.7	60/ 2.7	40/ 5.1	70/ 3.7	80/ 4.6	70/10.3	40/ 7.8	50/ 2.9
Heptageniidae	60/ 8.6	70/ 8.7	60/ 4.8	70/ 1.6	70/ 1.6	70/14.3	60/14.6	80/18.3	40/19.9	50/11.8
Leptophlebiidae	20/ 0.3	40/ 1.5	40/ 2.0	50/ 3.2	30/ 0.3	10/ 0.1	10/ 0.6	40/ 0.9	30/ 2.6
<i>PLECOPTERA</i>										
Perlodidae	10/ 0.1	30/ 0.6	50/ 1.1	70/ 1.4	70/ 2.1	30/ 0.4	70/ 1.2	50/ 1.2	40/ 0.5	40/ 1.1
Chloroperlidae	10/ 0.4	60/ 1.5	50/ 1.0	20/ 0.4	30/ 0.6	40/ 0.9	50/ 2.5	60/ 1.6	30/ 1.4	40/ 1.8
Perlidae	20/ 0.2	10/ 0.1	10/ 0.1	60/ 0.2	70/ 2.4	60/ 2.0	50/ 1.9	60/ 2.2	30/ 0.5	20/ 0.3
Nemouridae	60/ 1.8	20/ 0.5	30/ 0.4	60/ 4.4	40/34.3	40/ 5.6
Peltoperlidae	10/ 0.1
<i>TRICHOPTERA</i>										
Rhyacophilidae	10/ 0.2	30/ 0.6	40/ 0.6	40/ 0.5	50/ 0.6	30/ 0.9	10/ 0.1
Limnephilidae	10/ 0.1	90/ 6.6	40/ 1.7	50/ 2.7	10/ 0.2	10/ 0.1	20/ 0.4	40/ 1.5
Lepidostomidae	40/ 0.5	40/ 2.9	30/ 1.2	70/ 3.8	50/ 1.4	70/ 1.2	30/ 1.3	40/ 1.0	20/ 0.5	50/ 1.4
Hydropsychidae	50/ 0.6	40/ 0.5	20/ 0.2	40/ 6.7	60/ 6.9	50/ 1.0	60/ 2.3	30/ 1.0	30/ 3.0
Glossomatidae	10/ 0.1	40/ 0.4	20/ 0.3	50/ 0.7	50/ 5.7	70/15.7	80/ 2.6	80/ 5.8	30/ 0.8	30/ 1.0
Philopotamidae	20/ 0.3
Psychomyiidae	10/ 0.1	10/ 0.1
Brachycentridae	10/ 0.1	10/ 0.6	10/ 0.1
<i>DIPTERA</i>										
Chironomidae	10/ 0.1	30/ 0.5	60/ 1.6	20/ 0.6	40/ 0.6	20/ 0.2
Tipulidae	20/ 0.2	40/ 1.0	60/ 1.3	90/ 7.1	50/ 1.5	70/ 1.4	40/ 0.6	30/ 0.6	30/ 2.3	10/ 0.2
Simuliidae	10/ 0.2	10/ 0.1	10/ 0.1	40/ 1.6	50/10.9	40/ 0.6	20/ 0.3
Blepharoceridae	10/ 0.1	10/ 0.3
Sciariidae	10/ 0.1
Rhagionidae	20/ 0.2	10/ 0.1	20/ 0.2
<i>COLEOPTERA</i>										
Elmidae	30/ 0.4	10/ 0.5	40/ 0.8	70/ 5.6	70/12.2	70/10.1	60/ 1.2	50/ 0.9	40/ 7.0	10/ 0.1
Haliplidae	10/ 0.2
Dytiscidae	10/ 0.1
Ptilodactylidae	20/ 0.2

TABLE 2 (Continued)

Food Item	Apr.	May	June	July	Sept.	Oct.	Nov.	Dec.	Feb.	Mar.
<i>INSECTS</i>										
<i>COLLEMBOLA</i>										
Sminthuridae	10/ 0.1
Entomobryidae	10/ 0.1	10/ 0.1
<i>OTHER</i>										
Oligochaetes	20/ 0.2	20/ 0.7	20/ 0.8	60/ 3.6	40/ 6.2	70/24.9	80/26.9	90/17.3	40/ 3.8	40/ 4.7
Nematomorpha	10/ 0.1	20/ 0.2	20/ 0.3	10/ 0.1
Nematodes	10/ 0.1	10/ 0.1
Turbellarians	30/ 0.5	30/ 0.8	10/ 0.3	20/ 0.3	20/ 0.2
Spider	10/ 0.1
Eggs	20/ 0.2	20/ 0.2
<i>A. truei</i>	10/ 0.1	10/ 0.1	10/ 0.1
<i>S. gairdneri</i>	20/ 0.3	10/ 0.1
<i>C. tenuis</i>	20/ 0.3	10/ 0.1

were abundant to moderately abundant depending upon the time of year. Of the caddisflies, limnephileids, lepidostomids, and glossosomatids were abundant with a few exceptions. The other families of trichopterans were sparse to moderately abundant with a few cases of abundant, depending upon time of year. The stoneflies listed were abundant to moderately abundant with Perlodidae being the most common family. One exception was evident in the family Peltoperlidae. This group occurred only once in July, 1968 with one representative individual. Chironomidae and Tipulidae were the most commonly occurring families of Diptera. Tipulids were moderately abundant to abundant. Chironomids were never more than moderately abundant and not taken at all in some months. Elmidae was the only family of coleopterans that occurred significantly in the samples. They were abundant during the summer months and sparse at the beginning and end of the study. Except at the beginning of the study, oligochaetes were always at least moderately abundant. Many other families occurred in the samples but in general they were sparse or infrequent.

Gut Analyses

Records for gut analyses can be found in Tables 3-5. In general, the common stream organisms, with the exception of oligochaetes, were eaten in proportion to their availability. The sculpins appear to be an exception to this in that they seem to prefer siphonurids, limnephilids, and chironomids. Chironomids occurred in the stomachs of sculpins at all times, but did not appear in bottom samples in April, September, October, or November of 1968. Siphonurids did not occur in bottom samples during September, November, or December of 1968 but were found in sculpins in September and November. Siphonurids were in limited numbers in the stomachs of *Dicamptodon* spp. and *S. gairdneri* in September but not when they did not occur in stream samples during November and December. Chironomids were frequent in both *Salmo* and *Dicamptodon* spp., even in months when they were not found in stream samples. The other staples occurred in sculpins, but in extremely low numbers relative to the three families already mentioned. Many of the families found in *Salmo* and *Dicamptodon* did not occur in sculpins. Two sculpins were collected which had eaten small trout. Nematodes were nearly always found in *Cottus* but these organisms may well be parasites.

Dicamptodon spp. appeared to be extremely opportunistic, feeding on what was available at the time. The stream staples comprised the bulk of their diet. Emergent adults and allochthonous or foreign organisms added variety to their diets, but were sparse relative to their major food items. Young salmonids and sculpins frequent their diets during summer low water periods when the concentration of fish is greatest.

Salmo, as in the case of *Dicamptodon* spp., appears to be extremely opportunistic and feeds on all the staples of the stream. But in addition to the stream staples, a great variety of nonaquatic families and emergent aquatic adults were also eaten. This was true throughout the year, but especially so during the months of maximum emergence and activity over the stream. Adult tipulids, adult nemourids, leafhoppers, tree hoppers, spiders, centipedes, and a variety of terrestrial beetles are some examples of these allochthonous types. These items occur rarely in *Dicamptodon* spp. and scarcely at all in *Cottus* (Fig. 1). Dineen (1951) did not indicate this difference of autochthonous and allochthonous material in his comparison of trout and sculpin diets.

TABLE 3. Average frequency/density of food organisms found in *Dicamptodon* spp. by month¹

Food Item	Apr.	May	June	July	Aug.	Sept.	Oct.
INSECTS							
EPHEMEROPTERA							
Siphonuridae	40/ 1.0	55/ 1.6	18/ 0.4	35/ 0.8	22/ 0.6	16/0.16	30/ 0.6
Baetidae	11/0.11	35/0.35	11/0.11	56/ 2.3	33/ 0.6		
Ephemerellidae	31/ 0.5	23/ 0.6	15/ 0.5	44/ 1.0	22/ 1.0	10/ 0.1	
Hepageniidae	21/ 0.6	55/ 1.3	11/ 0.3	24/ 0.6	22/ 0.2	10/ 0.1	30/ 0.3
Leptophlebiidae	25/ 0.5	55/ 1.7	26/ 3.3	29/ 1.1	11/0.11	53/ 1.8	30/ 0.3
PLECOPTERA							
Perlodidae	11/0.11	10/ 0.1		29/ 0.4		21/ 0.2	
Chloroperlidae	25/ 0.3	30/ 0.7	4/0.03	18/0.21		10/ 0.1	
Perlidae				6/0.06			
Nemouridae	25/ 0.5			23/ 0.3	22/ 0.2		
TRICHOPTERA							
Rhyacophilidae	5/0.05	10/ 0.4		12/ 0.2		10/ 0.1	
Limnephilidae		5/0.05	4/0.03	44/ 1.6	66/ 1.6	32/ 0.5	
Lepidostomidae	5/0.05	5/ 0.1		6/ 0.2	22/ 0.5	21/ 0.2	
Hydropsychidae	5/0.05			6/0.06			
Glossosomatidae				6/0.09			
Philopotamidae				6/0.12			
DIPTERA							
Chironomidae	21/ 0.2	25/ 0.4	19/0.22	38/ 0.6	22/ 0.3	26/ 0.3	
Tipulidae		25/ 0.4	11/0.19	8/0.08	22/ 0.2	10/ 0.2	
Tabanidae					11/ 0.1		
Simuliidae		5/0.05		18/0.24			
COLEOPTERA							
Carabidae*		10/ 0.2		3/0.03	11/ 0.1		
Cerambycidae*					22/ 0.2	5/0.05	
Elmidae*			4/0.03	12/ 0.1		10/ 0.2	
Elmidae			4/0.03	3/0.03			
Dytiscidae*	5/0.05						
HOMOPTERA							
Membracidae*							
Cercopidae*							
HYMENOPTERA							
Tenthredinidae*							
LEPIDOPTERA			37/0.04		11/ 0.1		
ORTHOPTERA					11/ 0.1	5/0.05	

TABLE 3 (Continued)

OTHER							
Pelycepoa	---	15/0.15	---	---	---	---	---
Gastropoda	---	5/0.05	---	---	3/0.12	---	---
Spider*	---	5/0.05	---	---	---	---	5/0.05
Mite	5/0.05	---	---	---	---	---	---
Nematode	---	---	---	---	3/0.03	---	---
Detritus	16/ 0.3	5/0.15	11/0.11	12/ 0.2	11/ 0.1	21/ 0.2	---
Salmo	5/0.05	---	11/0.33	9/ 0.2	11/ 0.1	5/0.05	---
Cottus	---	---	4/0.03	3/0.03	---	---	---

¹ No organisms were found in stomachs from November to March. *Adult.

TABLE 4. Average frequency/density of food organisms found in *Cottus tenuis* by month.¹

Food Item	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Mar.
INSECT									
EPHEMEROPTERA									
Siphonuridae	42/ 0.7	20/ 0.2	22/ 0.2	50/ 1.0	66/ 0.6	33/ 0.5	20/ 0.2	50/ 0.5	---
Baetidae	50/ 0.6	40/ 0.6	---	15/0.35	---	17/ 0.2	---	---	---
Ephemerellidae	50/ 1.3	40/ 0.6	---	20/0.25	---	---	---	---	---
Heptageniidae	17/ 0.3	---	---	5/0.05	---	17/ 0.2	20/ 0.2	---	---
Leptophlebiidae	---	40/ 1.4	---	20/ 0.2	---	17/ 0.2	---	---	---
PLECOPTERA									
Perlodidae	17/0.17	---	---	20/ 0.4	---	---	---	---	---
Nemouridae	17/ 0.3	---	---	5/0.05	---	17/ 0.2	---	50/ 0.5	---
Chloroperlidae	17/ 0.3	---	---	---	---	---	---	50/ 0.5	---
TRICHOPTERA									
Rhyacophilidae	---	20/ 0.2	11/ 0.1	5/0.05	---	---	---	---	---
Limnephilidae	---	---	22/ 0.2	40/ 1.2	33/ 0.3	33/ 0.3	60/ 3.2	---	---
Lepidostomidae	8/0.25	20/ 0.2	---	---	---	---	---	---	---
Hydropsychidae	8/0.08	---	---	---	---	---	---	50/ 0.5	---
Glossosomatidae	---	---	---	---	---	---	40/ 0.4	---	---
DIPTERA									
Chironomidae	42/ 1.6	60/ 0.6	56/ 1.7	50/ 1.2	66/ 0.6	83/ 7.8	20/ 0.6	50/ 0.5	100/ 2.0
Tipulidae	---	---	---	5/0.05	---	---	20/ 0.2	50/ 0.5	100/ 1.0
COLEOPTERA									
Elmidae*	---	---	---	---	33/ 1.3	---	---	---	---
Elmidae	---	---	---	20/ 0.3	---	---	40/ 0.4	---	100/ 1.0
Dytiscidae*	---	---	---	5/0.05	---	---	---	---	---
OTHER									
Pelycepoa	8/0.8	40/ 0.4	---	---	---	---	---	50/ 0.5	---
Mites	---	---	---	5/0.05	33/ 0.3	---	---	---	---
Nematode	42/ 0.8	20/ 0.4	22/ 0.3	5/0.05	33/ 0.3	---	20/ 0.2	---	---
Detritus	8/0.08	20/ 0.2	11/ 0.1	5/0.05	---	---	---	---	---
Salmo	---	---	11/ 0.2	---	33/ 0.3	---	---	---	---

¹ No organisms were found in stomachs during December and February. *Adult.

TABLE 5. Average frequency/density of food organisms found in *Salmo gairdneri* by month.¹

Food Item	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Feb.	Mar.
INSECTS										
EPHEMEROPTERA										
Siphonuridae	7/0.07	12/0.12	21/ 0.2	66/ 1.0	11/0.15	14/0.18	---	---	17/0.17	13/0.25
Baetidae	7/0.07	18/0.18	36/ 0.6	100/ 8.8	22/ 0.4	14/0.36	---	13/0.13	---	13/0.13
Ephemereillidae	---	12/0.12	14/0.14	33/ 0.6	---	14/0.18	---	---	---	38/ 0.4
Heptageniidae	7/0.07	12/0.12	14/ 0.2	22/ 0.6	4/0.04	9/0.09	3/0.07	7/0.07	---	13/0.25
Leptophlebiidae	---	---	---	22/ 0.6	7/0.07	14/0.18	---	---	---	13/0.13
PLECOPTERA										
Perlodidae	---	---	14/0.14	45/ 1.3	11/0.15	5/0.05	7/0.07	---	---	---
Peltoperlidae	---	---	---	---	---	---	---	---	---	13/0.13
Chloroperlidae	---	12/0.18	---	22/ 0.2	7/0.07	9/0.09	3/0.03	---	17/0.17	---
Perlidae	---	---	---	---	---	---	---	7/0.07	---	---
Nemouridae	7/0.07	24/0.35	---	56/ 0.9	11/ 0.1	---	---	7/0.13	---	25/ 0.4
Nemouridae*	---	---	---	---	---	14/0.14	3/0.03	---	---	38/ 0.5
Rhyacophilidae	7/0.07	---	---	11/0.45	7/ 0.1	14/0.14	11/ 0.1	7/0.07	---	---
Limnephilidae	14/0.14	12/0.12	---	---	4/0.04	27/ 0.3	3/0.03	---	---	---
Lepidostomidae	---	---	14/ 0.9	33/ 0.3	11/0.11	9/0.27	7/0.07	7/0.07	17/0.17	---
Hydropsychidae	---	---	---	---	4/0.07	14/0.14	7/0.15	7/0.07	---	---
Glossosomatidae	---	---	---	---	11/0.15	5/0.05	3/0.03	7/0.07	---	---
Trichoptera*	---	---	14/ 0.3	---	15/0.15	---	---	---	---	13/0.13
DIPTERA										
Chironomidae	14/ 0.4	41/ 2.5	71/ 4.9	100/13.0	90/ 7.0	68/ 2.6	22/ 0.2	20/ 0.2	50/ 0.8	50/ 3.1
Tipulidae	---	---	---	22/ 0.2	11/ 0.1	9/0.18	11/ 0.1	---	---	---
Tipulidae*	36/ 1.1	59/ 1.4	43/0.86	33/ 0.6	15/0.15	32/ 0.6	48/ 1.2	7/0.07	66/ 0.8	63/ 2.1
Ceratopogonidae	---	---	---	---	---	9/0.09	---	7/0.07	---	13/0.13
Simuliidae	---	12/0.12	14/0.14	33/ 0.6	22/ 0.5	14/0.14	---	---	17/0.17	---
Simuliidae*	---	---	14/0.14	---	---	---	11/0.18	---	---	38/ 0.4
COLEOPTERA										
Scolytidae*	---	---	---	---	4/0.04	---	---	---	---	---
Staphylinidae*	---	---	---	11/ 0.1	7/ 0.2	---	---	---	---	---
Lagriidae*	---	---	7/0.07	---	---	---	---	---	---	---
Mordellidae*	---	---	---	---	4/0.04	---	---	---	---	---
Carabidae*	---	---	---	---	---	---	3/0.03	---	---	---
Hydrophilidae*	---	---	---	---	---	---	3/0.03	---	---	---

TABLE 5. (Continued).

Food Item	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Feb.	Mar.
INSECTS										
COLEOPTERA (cont.)										
Scarabaeidae*	---	---	---	---	7/0.07	---	3/0.03	---	---	---
Elmidae*	---	---	21/ 0.2	11/ 0.1	7/0.07	9/0.09	15/0.15	7/0.07	---	---
Elmidae	---	---	---	11/ 0.1	---	5/0.05	15/ 0.9	---	---	---
Pselaphidae*	---	6/0.06	14/0.14	---	7/0.07	---	3/0.03	---	---	13/0.13
Dytiscidae*	---	---	---	---	---	---	3/0.03	---	---	---
Chrysomelidae*	---	---	---	---	---	---	3/0.03	---	17/0.17	---
Tenebrionidae*	---	---	---	---	11/0.18	5/0.05	7/0.07	---	---	---
	---	---	---	---	7/ 0.1	---	---	---	---	---
HOMOPTERA										
Cicadellidae*	---	18/ 0.2	---	11/ 0.1	33/ 0.2	5/0.05	---	7/0.07	---	---
Membracidae*	---	---	---	---	15/ 0.2	---	3/0.03	---	---	---
HEMIPTERA										
Gerridae*	---	---	---	---	4/0.04	---	---	---	---	---
Scutelleridae*	---	---	7/0.07	---	4/0.04	---	---	---	---	---
HYMENOPTERA										
Braconidae*	---	---	---	---	4/0.04	5/0.05	---	---	---	---
Formicidae*	---	6/0.06	---	---	4/0.04	9/0.09	---	---	---	---
Cynipoidea*	---	---	---	---	7/0.07	---	---	---	---	---
Chalcidoidea*	---	---	7/0.07	---	---	---	---	---	---	---
COLLEMBOLA										
Sminthuridae*	---	29/0.35	---	11/ 0.1	29/ 0.8	14/0.27	19/0.45	27/ 0.3	17/0.17	38/ 1.9
Entomobryidae*	---	29/ 0.5	14/ 0.4	---	15/0.18	---	3/0.03	---	---	50/ 1.1
OTHER										
Millipede*	---	---	---	---	---	5/0.05	---	---	---	---
Centipede*	---	---	---	---	---	5/0.05	---	---	---	---
Pelycepoda	---	12/0.12	---	---	---	5/0.05	---	---	---	---
Gastropoda	---	---	---	---	7/ 0.1	---	---	---	17/ 0.3	13/0.13
Oligochaete	---	---	---	---	---	---	---	7/0.07	35/ 1.3	---
Spider*	---	6/0.06	---	---	---	---	---	7/0.07	---	---
Mite	---	12/ 0.9	36/ 0.7	11/ 0.1	18/0.18	14/0.14	26/0.26	---	17/0.17	---
Nematode	---	---	57/ 0.4	22/ 0.2	7/0.07	---	3/0.03	---	---	13/0.13
Detritus	---	---	---	---	7/0.07	---	---	---	17/0.17	---
	---	---	---	---	4/0.04	---	---	---	---	---

¹No organisms were found in stomachs during December.

* Adult.

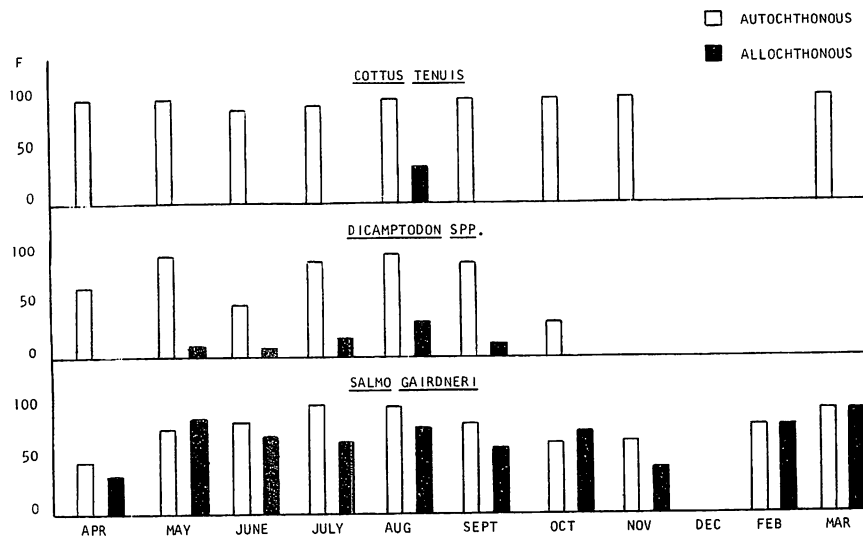


Figure 1. Frequency of occurrence of truly aquatic food items (autochthonous) versus that of emergent adults and nonaquatic organisms (allochthonous).

The data indicate that there is considerable overlap in the diets of the four animals studied. With the exception of *Cottus*, stream organisms are consumed relative to their availability. The overlap is not absolute. *Dicamptodon* spp. and *Cottus* are restricted largely to autochthonous organisms, while *Salmo* includes many allochthonous families. The fact that *Salmo* feeds on allochthonous organisms as well as stream staples suggests that *Salmo* has a relatively broad food niche. The seemingly selectiveness of the sculpin narrows its food niche considerably in comparison with the other two vertebrates. From these observations it seems that complete competition, at least in relation to food, is not occurring except perhaps in the case of *Cottus* whose selectivity may put it in the realm of complete competition with the other two vertebrates. *Salmo* and *Dicamptodon* show sufficient diversity in feeding habits to describe them as partial competitors. There were fewer sculpins collected than trout, and rareness may be an indication that they are having difficulty coexisting with the other species. However, at any time or place, disease, water temperature, lack of breeding sites, accidents, or any number of other variables could affect the density of the sculpins independent of the presence or absence of the other species. Since it is impossible to control all of these variables, except in very artificial circumstances, positive proof is probably unattainable. During the winter months, *Dicamptodon* spp. seemed to disappear from the stream. Assuming some kind of subterranean overwintering, this may be another manner in which complete competition is avoided by *Dicamptodon* spp.

Summary

Dicamptodon spp., *Salmo gairdneri*, and *Cottus tenuis* were collected from Maratta Creek at monthly intervals for one year. Examination of their stomach contents relative to availability of stream organisms indicates that feeding is, for the most part,

opportunistic. *C. tenuis* exhibits a degree of selectivity which may impose so competitive stress upon it. *Dicamptodon* spp. appears to feed almost entirely benthos while *S. gairdneri* feed on organisms throughout the stream. The relative rarity of sculpins may suggest that competition with the other two vertebrates is approaching completion. Competition between *Salmo* and *Dicamptodon* spp. is related somewhat by diversity of feeding habits and the probably subterranean habits *Dicamptodon* spp. during part of the year. The feeding habits of the salmonid and salamanders suggest only "partial exclusion."

Acknowledgments

Sincerest thanks go to Dr. P. Dumas and Mr. C. Wiberg of Central Washington State College for their numerous suggestions during the course of this study. We are grateful to S. G. Jewett for identifying several individuals of plecopterans. Special thanks are given to J. Burton Laukhart, Chief, Game Management Division for cooperation during the project.

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Received October 22, 1971.

Accepted for publication April 3, 1972.