

FEEDING OVERLAP BETWEEN ROACH
AND JUVENILE STEELHEAD
IN THE EEL RIVER

by

Kenneth Ray Fite

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AND JUVENILE STEELHEAD
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Kenneth Ray Fite

Approved by the Master's Thesis Committee

Roger A. Barnhart Chairman

Richard L. ...

Jerry D. Roelofs

James B. Kaplan

Approved by Graduate Dean

Alma M. Gillespie

i

ABSTRACT

The extent of feeding overlap between roach (Hesperoleucus symmetricus) and juvenile steelhead (Salmo gairdneri) was studied in the South Fork, Eel River 3/72 to 10/72. Feeding behavior and feeding overlap were shown to be closely associated with habitat and aquatic insect population changes. Roach and trout inhabited two different feeding zones. However some overlap of these zones did occur. Occasional interspecific aggression by trout toward roach helped maintain or increase this spacial segregation. Increased segregation in feeding time and location was observed during the more critical period of low flow and high temperature. Segregation may have been limited by the simplicity of the habitat. The major food of the roach was attached algae, 73 percent by volume. Some feeding overlap for insects occurred. The general feeding overlap for insects was 40 percent, and the species overlap was 41 percent. However, the two most important insects did not overlap in the diet of roach and steelhead. The community composition and biology of the individual species of insects played a significant role in determining fish interaction. Competition for food by roach and juvenile steelhead in the riffle study section of the South Fork, Eel River was of a limited nature. Theory concerning feeding overlap and competition is discussed.

TABLE OF CONTENTS

	Page
ABSTRACT	i
LIST OF TABLES	iii
LIST OF FIGURES	iv
INTRODUCTION	1
METHODS	3
RESULTS	8
The Study Area	8
Fish Distribution	15
Food & Feeding	18
Time and Location of Feeding	18
Availability & Food Consumption	18
Feeding Overlap	22
DISCUSSION	29
SUMMARY	33
BIBLIOGRAPHY	34
APPENDIX	35

LIST OF TABLES

Table	Page
1. Species list & relative abundance of fish & insects, South Fork, Eel River, 1972	10
2. Seasonal abundance of food species as indicated by percentage of the twelve most abundant benthic insects in riffles, South Fork, Eel River, March to October, 1972	12
3. The twelve most numerous insects in order of abundance, found in the benthos, drift, roach stomachs, & trout stomachs from the South Fork, Eel River, February to October, 1972	19
4. Percent volume of algae in roach and the average number of insects per roach and steelhead taken March to October, 1972, South Fork, Eel River	21
5. Amount of food type overlap, general-percentage-feeding-overlap, and corresponding roach and trout sample sizes from March to October, 1972, in the South Fork, Eel River	24

LIST OF FIGURES

Figure	Page
1. Example calculation of a high and low general-percentage-feeding-overlap between two species of fish	6
2. Numbers of insects per hour per drift net taken at dawn, February to October, 1972, South Fork, Eel River	9
3. Flow & temperatures of the South Fork, Eel River, two miles south of Garberville, California, 1971-1972	14
4. Juvenile steelhead, roach & juvenile sucker feeding zones in the South Fork, Eel River, summer 1972	17
5. Relative fish sizes and ages of roach & steelhead based on length frequency data of samples, South Fork, Eel River, September, 1971 to September, 1972	23
6. Utilization of the more important food items by juvenile steelhead & roach February to October, 1972, South Fork, Eel River	26
7. Competition phase diagram illustrating the outcome of placing two species of fish with similar diets into the same habitat	31

INTRODUCTION

Sportsmen and biologists are concerned about the decrease in runs of steelhead (Salmo gairdneri Richardson) and salmon (Oncorhynchus kisutch Walbaum and Oncorhynchus tshawytscha Walbaum) in the Eel River during the past two decades. Virtually undetected in the past, populations of the California roach (Hesperoleucus symmetricus Baird and Girard), a small minnow, seem to be increasing in abundance and spreading in distribution in the Eel. This fact coupled with the knowledge obtained by Fry (1936) that the roach has feeding habits similar to juvenile steelhead and salmon, indicates possible interspecific competition.

The roach occurs in many other California drainages (Fry 1936). Because of its wide distribution and its possible competition with salmonids, the biology of the roach needs clarification. This investigation should help in understanding the significance of the roach in California waters.

The only work done on the California roach was a general life history (Fry 1936). However, little was learned about the feeding habits of roach. Fry reports the following two observations concerning feeding: (1) Roach under 40 mm are mostly carnivorous, feeding on crustaceans and aquatic insects, and (2) Roach over 40 mm also

include filamentous algae in their diet. No quantitative feeding data were collected.

Interspecific competition is defined by Larkin (1956) as the demand by more than one organism for the same resource in excess of immediate supply. When two species with similar food habits come together in the same habitat, a change in diet ususally occurs to minimize feeding similarities (Maitland 1965, Johannes and Larkin 1961). The amount of overlap in feeding is a measure of feeding competition. Maitland (1965) used this approach to study competition in a five-species community. The purpose of my study is to report the extent of feeding overlap measured between the roach and juvenile steelhead in riffles in the South Fork, Eel River during the summer of 1972.

METHODS

Initial investigations started in August 1971. A general survey of river conditions and habitat was made of the Eel and Van Duzen Rivers. Length frequency data were collected for both trout and roach at various locations.

The site selected for the major study area was two miles above Garberville on the South Fork, Eel River. Data were collected over a half mile stretch of river. Data used in comparisons were taken from one riffle section each month throughout the study period.

Monthly samples of juvenile steelhead, roach, western suckers, insect drift, bottom samples, and physical conditions were collected from February 1972 to October 1972. All samples were taken in the same riffle. The exact collection site was dependent upon river conditions and fish distribution at that time.

As part of a survey to find what food items were available to the fish, insect drift was sampled just prior to collection of fish. Drift samples were taken at dawn when drift numbers were found to be near their peak. Two to six drift nets were set for 20 to 40 minutes each time. The nets were placed in approximately the same location each time at the downstream end of the riffle section.

The bottom fauna was sampled by taking random kick samples and surber samples from the selected riffle section.

Fish were collected in early morning, (just after dawn) for the first four months. The sampling time was later changed to approximately an hour later because the roach started feeding later in the day. Roach, steelhead and suckers were collected by electroshocking. Sampled fish were killed immediately and put into ten percent formalin. Larger fish were cut open to allow rapid preservation. Little regurgitation of stomach contents occurred. Fish were placed in 70 percent ethanol the following day to facilitate handling. Only data pertaining to steelhead and roach are presented in this paper. Data on suckers are being analyzed in a separate masters study by Phil Ashley at California State University, Humboldt.

The juvenile steelhead stomachs were analyzed individually. Only insects in the stomach were analyzed. Insects usually were identified to species, but some were categorized to higher taxonomic levels because they were impossible to identify further. Sometimes an insect group was categorized under two headings if different life stages were normally found in different habitats. For example, midges were not identified beyond family, but were divided into an adult and larval stage which represented two different food types available to the fish.

Roach samples were divided into 10 mm size classes. Ten fish in each size class were set as the goal for stomach analysis each month. This goal was not always achieved, especially for the very small fish (0 to 20 mm) and the very large fish (over 50 mm) because

of the limited numbers in the habitat at various times. Each size class was analyzed as a pooled sample. The roach has an intestinal tract resembling that of a sucker; that is there is no true stomach, just a slight expansion of the foregut. The contents of the foregut from the stomach to the first bend were removed with forceps. Because of the grinding action of the pharyngeal teeth most insects were in pieces. Identification was based on hard parts such as the head, thorax, and legs. Parts were compared with whole insects in a reference collection for identification. Because of the low diversity of the insect community this method resulted in accurate identifications.

Algae and insects were measured volumetrically by displacement. Because of the small volumes and retention of water by the algae and insect parts, this method provided only an approximation.

The method of calculating the general-percentage-feeding-overlap is shown in Figure 1. If the diets of each fish species were presented as bar graphs as in Figure 1, and then superimposed, the general-percentage-feeding-overlap would be the summation of the overlapping bars. If two species of fish ate the same food types and in the same proportions then the general-percentage-feeding-overlap would be large (80 to 100 percent). If two species of fish ate dissimilar food types or ate disproportionate amounts of each food type, then the general-percentage-feeding-overlap would be low (0 to 20 percent), indicating very dissimilar diets.

Example of two species of fish having similar diets; resulting in a large general-percentage-feeding-overlap.

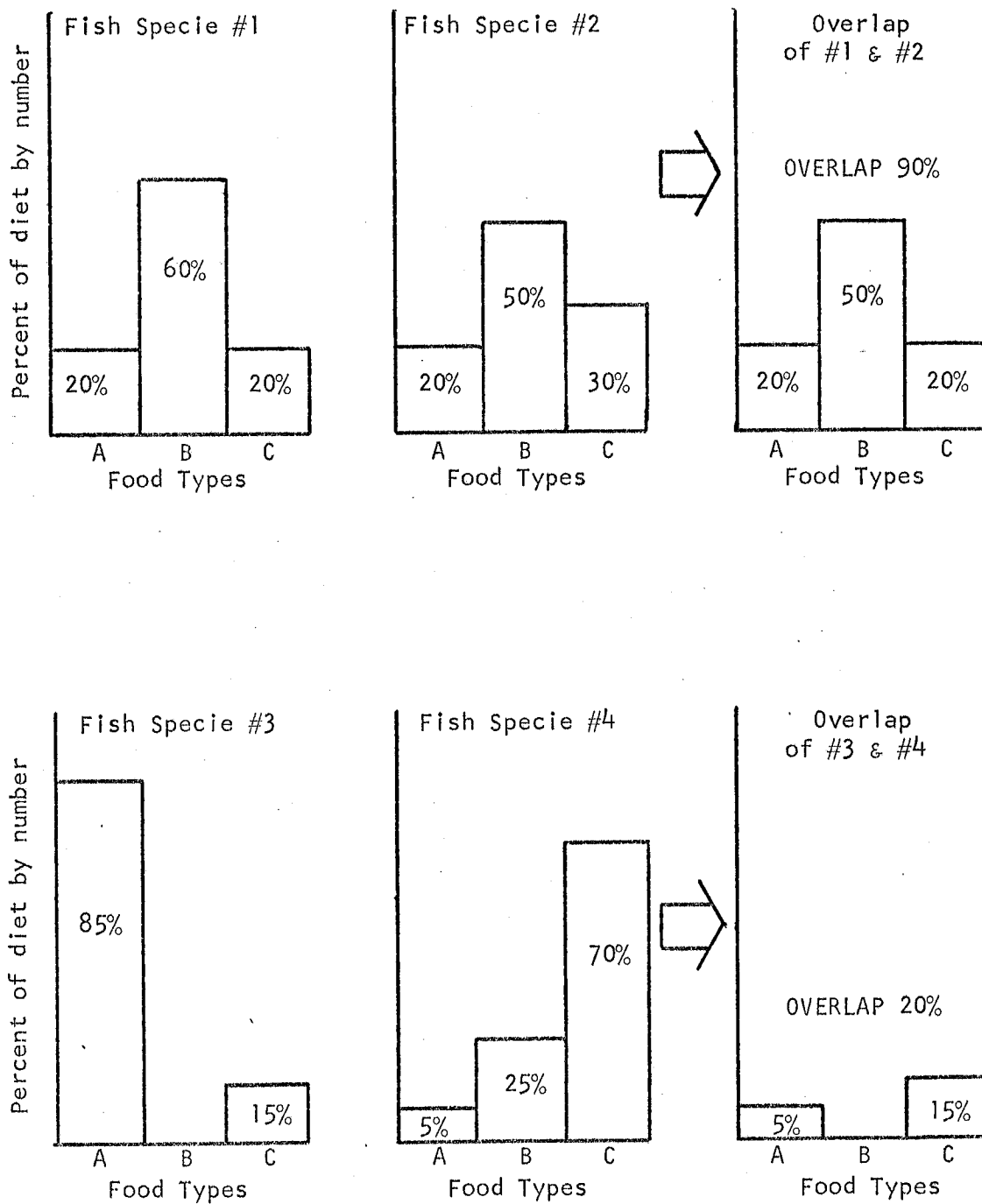


Figure 1. Example calculation of a high and low general-percentage-feeding-overlap between two species of fish.

Behavioral observations were made in several ways. During most of the summer, above-water observations of fish in the backwaters and pools were possible because of the shallow and clear water. Behavior in riffles was observed by skin diving and by the use of a periscope. To observe individuals a little closer, a 100 gallon laboratory stream with two small observation windows was set up outdoors in a shaded area. A current was maintained with two small submersible pumps. Water near the pump outlets moved very fast, but other areas in the tank exhibited only a mild current. Thus fish were able to select preferred currents. Foods and substrate, presumably suitable to roach and steelhead, were brought in from the Eel River.

RESULTS

The Study Area

The study area was exposed to direct sunlight most of the day. There was little streamside vegetation for shelter or shade. Algae, filamentous green and diatoms, formed the base of the food web. In late summer and fall filamentous algae formed streamers up to a meter in length; these provided shelter for small fish.

There were no algae on the rocks in early spring because high winter flows and an extremely high silt load scoured the river. It was also difficult to find insect life in early spring. Once the high flows ceased and the water cleared, the algae began to appear on the rocks, and became abundant as summer progressed. Rocks became encrusted with diatoms which provided favorable habitat for small insects. This periphyton was the major food item of roach and suckers. The increase in benthic production as summer progressed is suggested by Figure 2 which indicates the increase in numbers of drift organisms during this time.

Table 1 lists the fish and insects found in the study area. Out of forty-seven different organisms twenty-eight were characterized as common or abundant. These constituted a relatively simple community.

The composition of the bottom fauna throughout the study period is given in Table 2. However, three abundant insects; tendipedids,

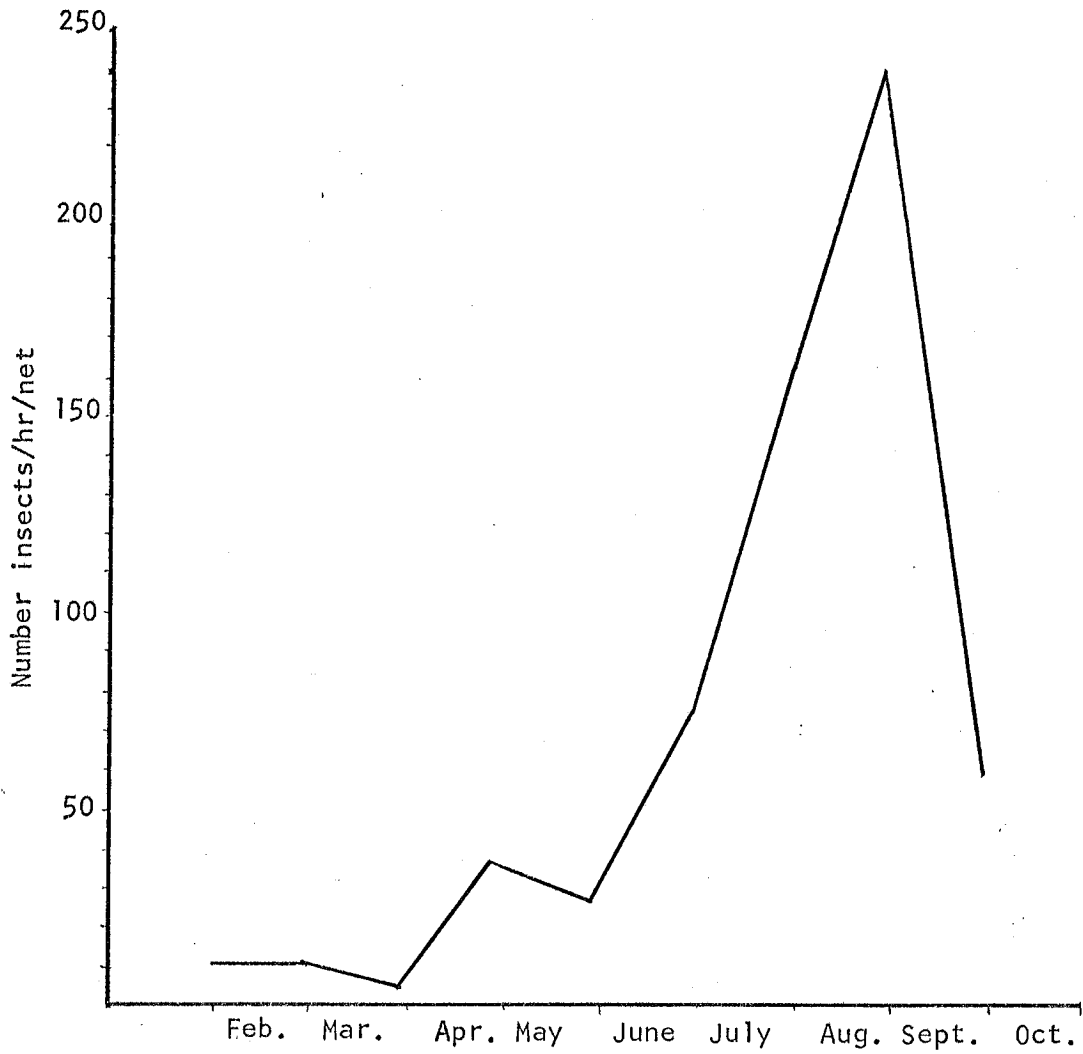


Figure 2. Numbers of insects per hour per drift net taken at dawn, February to October, 1972, South Fork, Eel River.

Table 1. Species list and relative abundance of fish and insects,
South Fork, Eel River, 1972.

Species List	Relative Abundance*
<u>I FISH</u>	
<u>Salmo gairdneri</u>	A
<u>Oncorhynchus kisutch</u>	F
<u>Oncorhynchus tshawytscha</u>	R
<u>Hesperoleucas symmetricus</u>	A
<u>Catostomus occidentalis humboldtianus</u>	A
<u>Lepomis cyanellus</u>	F
<u>II INSECTS</u> Usinger's classification, (Usinger 1968)	
Plecoptera	
Perlidae <u>Acroneuria californica</u>	A
Chloroperlidae <u>Alloperla</u> sp.	R
Pteronarcidae <u>Pteronarcys</u> sp.	R
Ephemeroptera	
Heptagenidae <u>Rithrogena decora</u>	A
Baetidae <u>Isonychia velma</u>	A
Baetidae <u>Baetis</u> sp.	A
Baetidae <u>Ephemerella walkeri</u>	A
Baetidae <u>Trichorthodes fallax</u>	C
Baetidae <u>Paraleptophlebia helena</u>	F
Baetidae <u>Choroterpes terratoma</u>	R
Trichoptera	
Odontoceridae <u>Marila flexuosa</u>	A
Hydropsychidae <u>Hydropsyche</u> sp.	A
Hydropsychidae <u>Cheumatopsyche</u> sp.	A
Helicopsychidae <u>Helicopsyche borealis</u>	A
Hydroptilidae <u>Neotrichia</u> sp.	C
Hydroptilidae <u>Ochrotrichia</u> sp.	R
Leptoceridae <u>Leptocella</u> sp.	F
Sericostomatidae <u>Sericostoma</u> sp.	F
Odonata	
Gomphidae <u>Ophiogomphus occidentis</u>	F
Gomphidae <u>Gomphus confraternus</u>	F
Libellulidae <u>Leucorrhinia ferruginea</u>	F
Hemiptera	
Naucoridae <u>Ambrysus mormon</u>	A
Nepidae <u>Ranatra brevicollis</u>	C
Veliidae <u>Microvelia californiensis</u>	C

Continued

Table 1. Continued

Species List	Relative Abundance*
Coleoptera	
Psephinidae <u>Psephnus</u> sp.	C
Elmidae <u>Zaitzevia</u> sp.	C
Elmidae <u>Optioservus canus</u>	C
Dytiscidae <u>Oreodytes</u> sp.	R
Hydrophilidae	R
Diptera	
Tendipedidae (Chironomidae) <u>Pseudochironomus</u> sp.	A
Tendipedidae <u>Micropsectra</u> sp.	A
Tendipedidae <u>Chironomus</u> sp.	A
Tendipedidae <u>Pentaneura</u> (<u>Monilis</u>)	A
Simuliidae	A
Tipulidae <u>Hexatoma</u> sp.	C
Stratiomyidae	R
Ephydriidae	R
Tabanidae	R
Lepidoptera	
Pyralidae <u>Parargyractis</u> sp.	A
← Megaloptera	
Sialidae <u>Sialis californiensis</u>	C
<u>III OTHER</u>	
Hydracarina	A
Physa	F

* A: Abundant C: Common F: Few R: Rare

Table 2. Seasonal abundance of food species as indicated by percentage of the twelve most abundant benthic insects in riffles, South Fork, Eel River, March to October, 1972.

	M	A	M	J	J	A	S	O
<u>Tendipedidae</u> *	-	-	0.4	0.1	2.8	1.2	3.0	6.5
<u>Marila flexuosa</u>	1.1	-	21.6	51.0	41.7	-	46.7	70.3
<u>Baetis</u> sp.	2.2	-	59.6	1.4	-	0.3	-	-
<u>Isonychia velma</u>	-	-	-	2.7	-	67.6	2.9	0.2
<u>Acroneuria californica</u>	57.6	65.5	2.6	1.7	4.8	10.7	1.5	-
<u>Rithrogena decora</u>	37.0	27.0	-	1.1	1.2	-	0.4	-
<u>Ephemerella walkeri</u>	-	-	-	22.5	17.3	-	0.3	-
<u>Hydropsychidae</u>	-	2.1	0.9	0.3	0.4	0.3	9.1	3.2
<u>Parargyractis</u> sp.*	-	-	-	-	-	-	3.3	5.2
<u>Elmidae</u>	-	-	1.7	6.5	9.6	4.7	5.3	3.9
<u>Ambrysus mormon</u>	-	1.6	7.8	1.1	4.4	4.8	1.1	0.5
<u>Helicopsyche borealis</u>	-	-	-	0.5	-	-	0.5	-
# Insects in monthly sample	92	94	230	724	249	318	766	1037

* Under-sampled, see text for details.

naucourids, and pyralids are under-represented. Midges were under-sampled because they were small and entangled in the periphyton. Naucorids were under-sampled because they inhabited the slower water of pools and backwaters. Pyralids became very abundant in later summer and early fall but were under-sampled earlier since they forage on periphyton under a silken canopy which protected them from being dislodged by the sampling technique. Psephenids also were underestimated since they were very difficult to dislodge from rocks. Table 2 shows the seasonal abundance of benthic insects, and demonstrates the changing nature of the benthic community with time. Peaks in population of different insects occur at various times. The fish exhibited enough flexibility in feeding to utilize food available at any particular time.

Figure 3 shows the flow and temperature regime over one year. These data are modified from unpublished Geological Survey data taken at Leggett, California. Competition for food or space should occur to the greatest degree during periods of low stream flow because of reduced living space and increased food demand due to higher temperatures. July and August would thus represent such a critical period. If isolating segregation mechanisms were operating to reduce competition they should have been more evident at this time. The increases in segregation observed were concerned with feeding times and locations. This is discussed later.

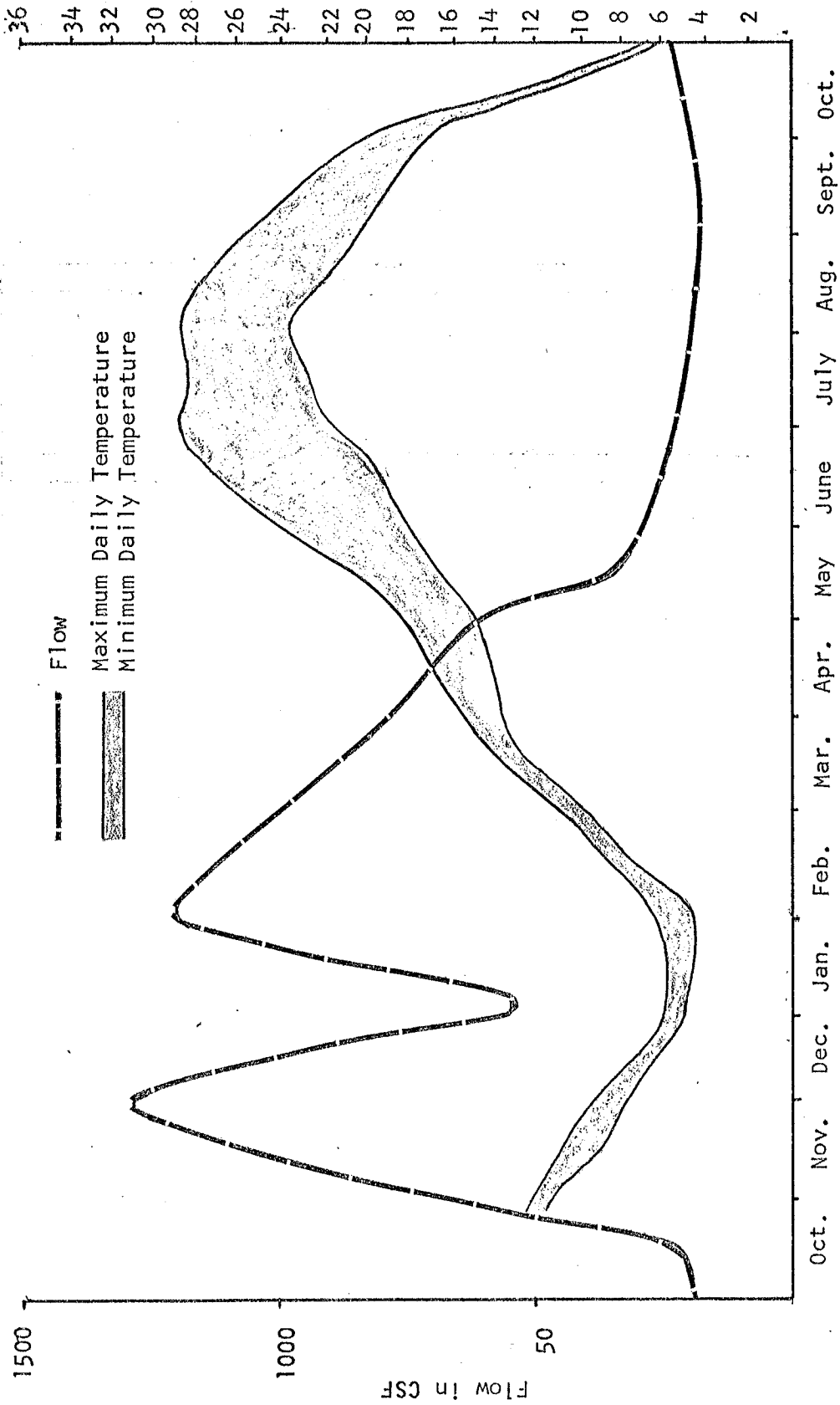


Figure 3. Flow and temperatures of the South Fork, Eel River, two miles south of Garberville, California, 1971-1972.

Fish Distribution

During periods of moderate flow, trout were found almost exclusively in riffles and headwaters of pools where there was considerable current. The low gradient of the river is responsible for the lack of extensive reaches of riffles and fast water. Therefore a great deal of the river was uninhabited by steelhead. Further restriction of trout habitat occurred in late summer when low stream flows reduced the riffle area. This restriction usually was complicated by increased stream temperatures which reached 29°C. At this time large schools of trout could be found wherever subterranean cold water welled up or springs occurred. A few juvenile silver salmon were found in pools.

Schools of downstream migrant salmonids congregated in the headwaters of pools from May to July. These schools were not sampled because they were just passing through.

Roach were found in all areas, but medium-sized roach inhabited the shallow riffles and pool headwaters. Large roach and very small roach were found in large pools. The large roach inhabited deep open water or areas around large rocks and boulders. They fed on insects trapped at the surface and periphyton. Mating swarms of mayflies were observed twice. The spent insects tended to accumulate on the surface of pools where the large roach consumed them.

Roach fry were numerous in shallow water of both pools and riffles. Counts up to 160 ten millimeter fry per square meter were

made in some areas. As the fry grew, they moved into deeper open water and into riffles. Near the end of summer there were still many small fry in the shallows. These small fish were not observed during winter. They probably were washed downstream during high flows.

A tag-and-recovery sample conducted in late summer indicated there were about ten roach to every trout. The community structure of a selected riffle 62.1 meters long with a 5.2 meter average width and 0.4 meter average depth was estimated to contain 1,461 roach, 152 juvenile steelhead, 28 suckers, and 17 green sunfish. On a weight basis there was approximately 0.5 gram of roach per gram of trout.

Figure 4 represents the feeding zones occupied by trout, roach and suckers in the study area. Overlap of the roach zone with both the trout and sucker zones occurred; the roach behavior resembled, to some extent, the behavior of both trout and suckers. When in a riffle, the roach spent most of their time just above the bottom in a stationary location eating periphyton and occasionally seizing near-by drift. The juvenile suckers remained on the bottom obtaining periphyton from rocks.

Skin-diving observations in the field and observations of trout, roach and suckers in the laboratory stream showed an occasional aggressive act of nipping by steelhead toward roach. This may keep the roach more toward the bottom at times. Generally the roach were ignored by steelhead, even though there were at times twenty roach

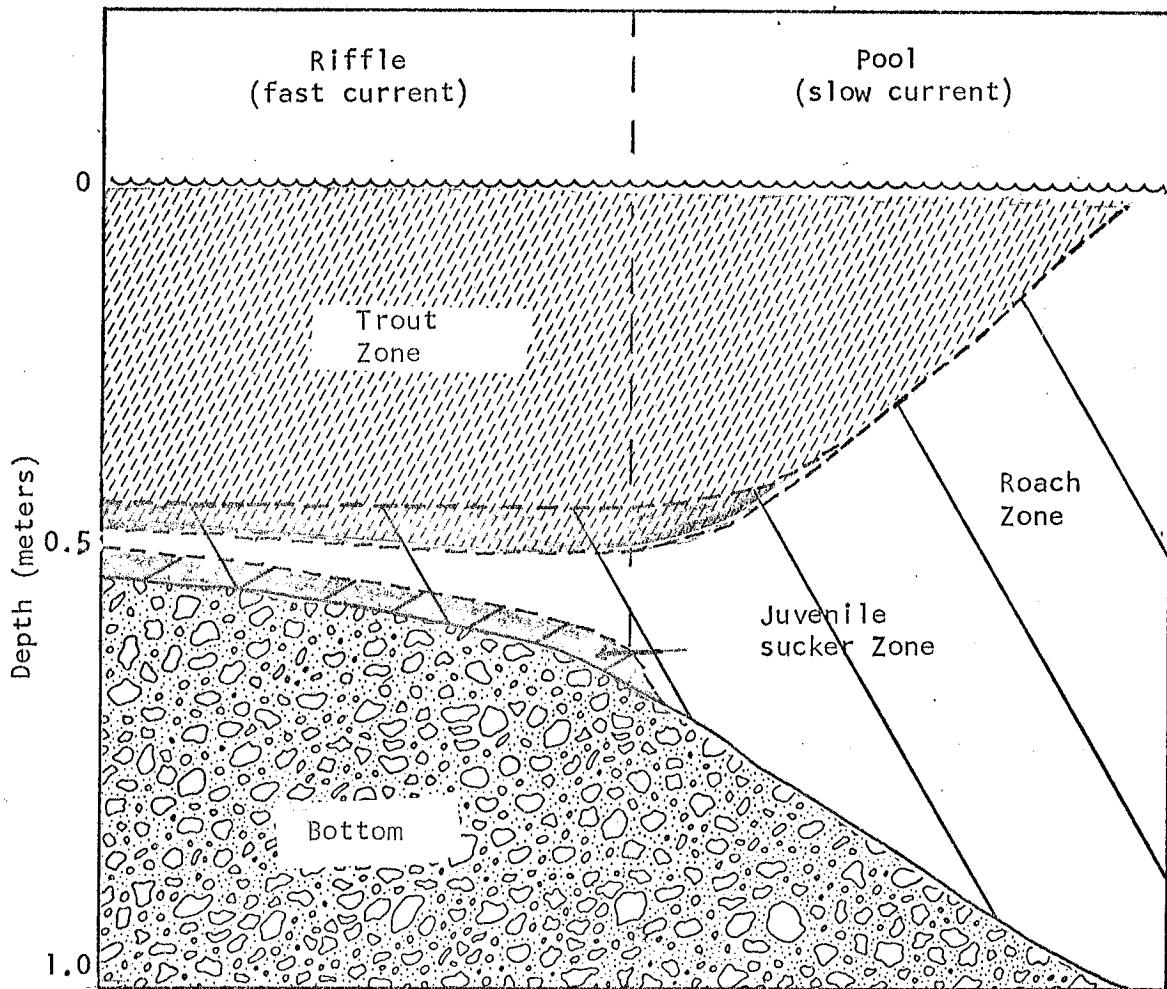


Figure 4. Juvenile steelhead, roach and juvenile sucker feeding zones in the South Fork, Eel River, summer 1972 (shaded area represents areas of species overlap).

in their feeding zone below them.

No aggressive action by roach toward other fish was observed, but some intraspecific aggression did occur. This behavior was exhibited by large roach toward small roach in the early spring. The larger roach were in schools around rock out-croppings. This schooling behavior was probably concerned in some way with spawning. The larger roach would nip and chase off any small roach that came too close. At this time small roach were widely dispersed.

Food and Feeding

Time and location of feeding. During spring and early summer roach fed in early morning. As summer progressed more empty stomachs were found in early morning samples. Samples taken later in the morning showed an increase in stomach contents. In mid-July an all day activity study was made. It showed fullness of roach stomachs increased as the day progressed. I also observed that riffle sections where many roach occurred during the day were not occupied by roach in the very early morning. This behavior could segregate roach and trout feeding periods. The juvenile steelhead were found feeding throughout the riffles. Juvenile silver salmon were only found in the pools.

Availability and food consumption. Data on monthly insect food types and their corresponding percent in the diet of trout and roach are summarized in the appendix.

Table 3 lists the twelve most numerous insects found in the

Table 3. The twelve most numerous insects in order of abundance, found in the benthos, drift, roach stomachs, and trout stomachs from the South Fork, Eel River, February to October 1972.

BENTHIC INSECTS		DRIFT INSECTS		ROACH STOMACHS		TROUT STOMACHS	
(No. Insects Sampled: 3510)		(No. Insects Sampled: 368)		(No. Stomachs Sampled: 224)		(No. Stomachs Sampled: 100)	
Tendipedidae	s*	<u>Marila flexuosa</u>	s	Tendipedidae	s	Baetis sp.	s
<u>Marila flexuosa</u>	s	Terrestrial	m	<u>Marila flexuosa</u>	s	<u>Ephemereilla walkeri</u>	m
Baetis sp.	s	<u>Acroneuria californica</u>	m	<u>Ephemereilla walkeri</u>	m	<u>Trichorthodes fallax</u>	s
<u>Isonychia velma</u>	l	Tendipedidae	s	Baetis sp.	s	Tendipedidae	s
<u>Acroneuria californica</u>	m	<u>Helicopsyche borealis</u>	s	Hydropsychidae	l	<u>Marila flexuosa</u>	s
<u>Rithrogena decora</u>	l	Hydropsychidae	l	<u>Isonychia velma</u>	l	Hydropsychidae	l
<u>Ephemereilla walkeri</u>	m	Baetis sp.	s	<u>Acroneuria californica</u>	m	<u>Paragyractis sp.</u>	m
Hydropsychidae	l	Elmidae	s	Terrestrial	m	<u>Isonychia velma</u>	l
<u>Paragyractis sp.</u>	m	<u>Isonychia velma</u>	l	<u>Rithrogena decora</u>	l	<u>Acroneuria californica</u>	m
Elmidae	s	<u>Ephemereilla walkeri</u>	m	<u>Ambrysus mormon</u>	m	Elmidae	s
<u>Ambrysus mormon</u>	m	Simuliidae	s	Elmidae	s	<u>Rithrogena decora</u>	l
<u>Helicopsyche borealis</u>	s	<u>Rithrogena decora</u>	m	<u>Trichorthodes fallax</u>	s	Simuliidae	s

* Relative size of insect: l = large, m = medium, s = small.

benthos, drift, roach diet, and trout diet. These summary data for nine months indicate that when an insect was numerous in the benthos, it usually appeared as an important part of the roach diet. However, these same insects did not show a similar relationship to the trout diet, probably because of differences in feeding zones. The available food in the feeding zone of the trout was comprised mostly of drift items.

Throughout the year the main food of roach was algae. Table 4 gives the percent volume of algae for roach stomachs and the mean number of insects per roach and trout stomach for each month of the study. For roach the average stomach contents consisted of 73 percent algae and 27 percent insect material by volume. This is only an approximation because of wide daily fluctuations in the proportions of algae and insects and because of the inexact method of measurement. The monthly data suggested that more insects and less algae were eaten by roach as the summer progressed. This coincided with a greater abundance of available insects due to increased production and increased number of insect hatches. The number of insects per roach and steelhead stomach examined also increased during mid-summer. During July, each steelhead stomach averaged eighteen insects while each roach averaged two. This suggests that the roach ate few insects, but it must be remembered that the roach greatly out-numbered the steelhead.

Table 4. Percent volume of algae and insects in roach and the average number of insects per roach and steelhead taken March to October, 1972, South Fork, Eel River.

	M	A	M	J	J	A	S	O
<u>ROACH</u>								
Percent Vol. of Algae	55	98	82	72	48	52	88	89
Percent Vol. of Insects	45	2	18	28	52	48	22	11
Av. No. Insects Per Roach	0.2	0.4	1.0	2.0	2.3	2.4	1.3	0.4
Total No. of Roach Sampled	47	35	32	34	25	18	33	20
<u>STEELHEAD</u>								
Av. No. Insects Per Steelhead	2.4	4.3	18.3	8.3	17.9	10.6	11.9	9.6
Total No. of Trout Sampled	10	10	17	13	10	12	10	11

No predation on roach by trout occurred in the study area, but a small amount was observed on the Van Duzen River in early fall. This river had a greater proportion of large trout. These were either 2+ and 3+ steelhead or resident fish. In winter when adult spawning steelhead were running the river, the water was very turbid. If these fish were feeding at this time, the roach would be difficult to locate since they were congregated in vegetation in the back-waters. The roach might be more vulnerable during summer steelhead runs.

Feeding overlap. The ability to consume insects is in part based on mouth size. Larger fish have an advantage since they can consume both small and large insects. The 0+ steelhead hatched earlier than the roach and maintained a size advantage over the 0+ roach (Figure 5). The 0+ steelhead grew rapidly and overlapped the 1+ age roach in size for only a short time in spring when the habitat was less restricted. These 1+ roach made up a large portion of the roach population both in number and in biomass.

The extent to which trout and roach fed on the same food type is indicated in Table 5. On the average, out of a possible 28 common or abundant insect types available in the habitat (Table 1), each fish utilized only ten to twelve types at a time. Altogether, this accounted for sixteen different food types. Only six of these food types were the same for both fish. The degree to which the fish utilized these six overlapping food types is indicated by the average general-percentage feeding-overlap of 40 percent (Table 5). No general trends,

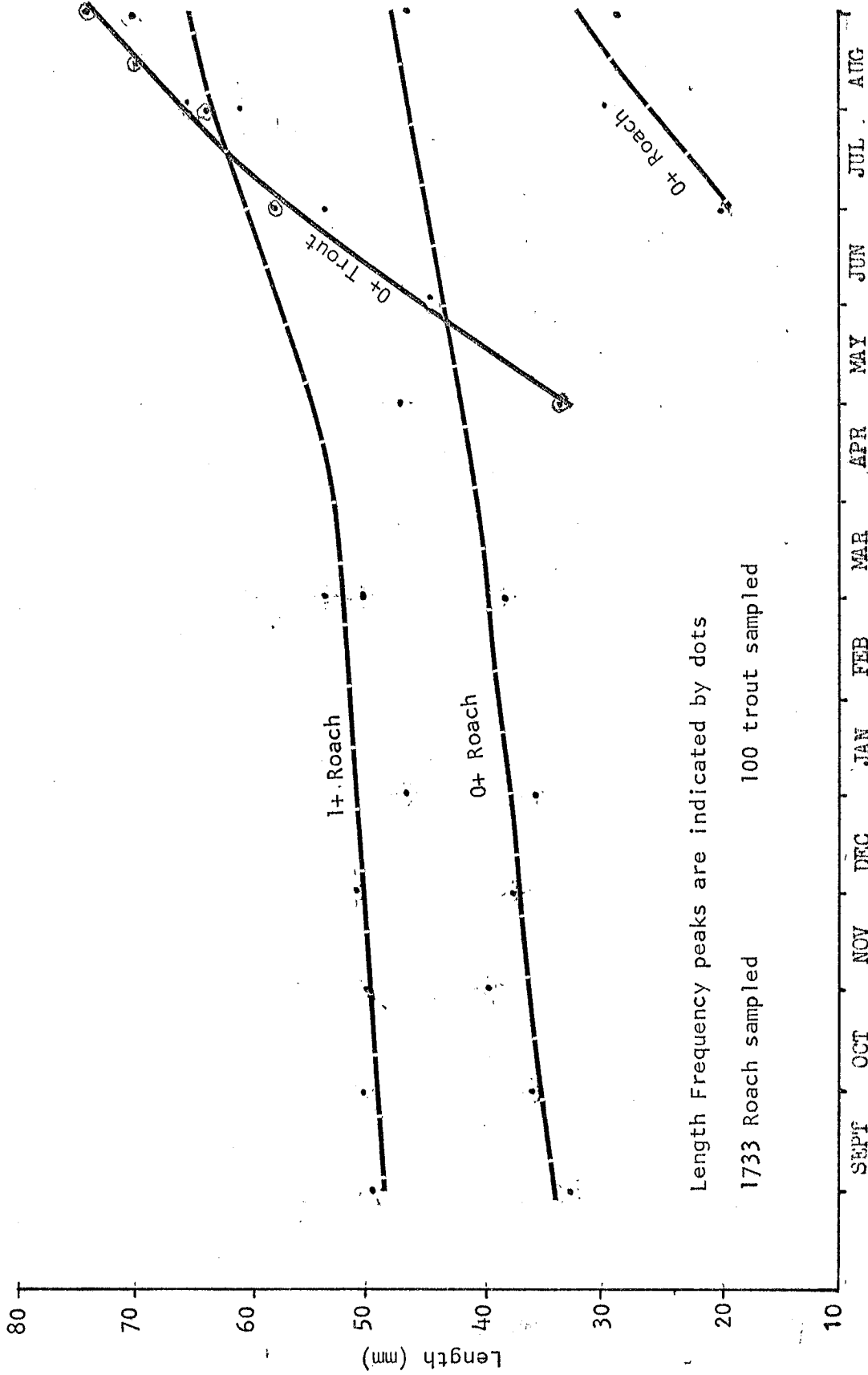


Figure 5. Relative fish sizes and ages of roach and steelhead based on length frequency data of samples, South Fork, Eel River, September 1971 to September 1972.

Table 5. Amount of food type overlap, general-percentage-feeding-overlap, and corresponding roach and trout sample sizes from March to October 1972, in the South Fork, Eel River.

	M	A	M	J	J	A	S	O	MEAN
No. of Food Types Trout Consumed	11	14	18	5	17	12	9	11	12
No. of Food Types Roach Consumed	11	5	10	16	12	12	10	5	10
Total No. of Food Types Eaten by Trout and Roach	15	14	20	16	17	19	13	11	16
No. of Food Types Alike	7	5	8	5	12	4	6	5	6
Percent of Food Types Alike	47	36	33	31	70	21	46	45	41

Percent General Feeding Overlap	47	52	25	39	56	33	26	43	40

<u>SAMPLE SIZE</u>									
No. of Roach	47	35	32	34	25	18	33	20	31
No. of Insects Examined in Roach Stomach Analysis	9	14	32	68	58	50	43	8	35
No. of Trout	10	10	17	13	10	12	10	11	12
No. of Insects Examined in Trout Stomach Analysis	24	43	311	108	179	127	119	106	127

over time, in either the food type overlap or the general-percentage feeding-overlap occurred.

Figure 6 illustrates the utilization of the different food items throughout the study period. It shows that four of the major food items were utilized to a large extent by both fish at the same time. These included Baetis sp., Tendipedidae larvae, Hydropsychidae, and Acroneuria californica. Of these only Hydropsychidae was of any importance to the diets of both fish because of its fairly large size, and availability in both the benthos and drift.

Four groups (Isonychia velma, Ephemerella walkeri, Parargyrectis sp., and Ambrysus mormon) were utilized at different times with little or no overlap because these insects were available to only one species of fish at a time. For example, Isonychia velma was utilized in the spring by roach when it was plentiful in the benthos and was small enough for roach to consume. Because of its small size and inability to free-swim like the larger nymph of this species it was not as likely to be found in the feeding zone of trout. However, in summer and fall the situation was reversed and the steelhead heavily utilized Isonychia velma as it became abundant in the trout feeding zone. It had become free-swimming, larger and thus more susceptible to drifting. At this stage the nymph became too large for the roach to consume. This insect contributed greatly to the growth of the juvenile steelhead because of its large size and abundance. It is probable that if this major food item was shared, serious

competition could have existed. Here segregation seems to be a function of insect size, insect behavior, relative fish sizes, and a difference in feeding zones.

The second most abundant benthic insect in summer and fall was Marila flexuosa. This small caddisfly was the most numerous insect food item of the roach. It was used heavily by the roach throughout the entire study period (Figure 5). It could have been cropped incidentally in the consumption of algae. This insect also occurred in the steelhead's diet sporadically but was of dubious importance to the trout because of the insect's small size and the trout's inability to break up the case to facilitate digestion of this insect. Since the population of Marila flexuosa was so large, hatches and swarms of this species provided more insects than the trout could have consumed. Thus roach were not affecting the availability of adults by harvesting the larvae. Therefore the major insect food item of the roach apparently was of little importance to the steelhead.

Figure 6 points out another interesting facet. The trout utilized terrestrial drift at a low continuous level throughout the study period. Roach normally did not use this food source. Only when large hatches or mating swarms occurred did the roach feed heavily on them. This occasional phenomenon left large numbers of insects trapped in the surface film. These insects were concentrated in certain areas by back eddies or by slow moving surface water in pools

where roach were numerous. Few trout were normally present in this type of water. Thus, only the roach took full advantage of these large numbers of trapped insects.

DISCUSSION

The feeding plasticity of freshwater fish is well known (Hartley 1948, Larkin 1956). The data presented in this paper suggest this. For example, neither trout nor roach were obligated to feed on only certain insects, but were able to utilize almost any insect in their feeding zone. The only restriction was size of the insect in relation to size of mouth of the fish. Larkin (1956) feels that the freshwater environment offers little opportunity for feeding specialization thus causing many species to have considerable flexibility of feeding habits. This leads to a general sharing of food resources among different species depending on the limitations imposed by the habitat. When a forced diet change occurs in one fish, most of the other species in the community will in some way be affected (Hartley 1948, Johannes et al. 1961; 1948, Nilsson 1967).

Many factors effect the seriousness of feeding overlap (Colwell 1971). Concerning my data, it should be remembered that only feeding overlap for insects occurred; not for the entire diet. The main question is whether the overlapping food items are in short supply and are needed by the different species. When two species having somewhat similar diets (even if just for insects as in the case of roach and trout) come together in the same habitat, changes in their diets should occur to reduce competition and to allow for better exploitation of the

available food resources by each species (Mann 1967). This process should take only a short time if their feeding behavior is flexible as is the case of most freshwater species. However, the degree to which their diets become dissimilar may be limited by the available foods (i. e., benthic species composition and the biology of these organisms). The more simple and harsh a habitat is, as in the Eel River, the more the opportunity for diet specialization is restricted.

To help establish the extent and seasonal severity of competition between two species, one can follow feeding similarity over a period of time to establish trends. Figure 7 is a competition phase diagram to help illustrate the outcome of putting two different species of fish with similar diets together in the same habitat. After a period the diets should become more dissimilar. This may be caused by (1) decreased consumption of certain food items due to altered food preference (Mann 1967); (2) segregation or displacement of the competing species in space (Hartman 1965, Nilsson 1967); or (3) segregation or displacement of food habits (Hartman 1965). After a time the diets should stop changing except for seasonal changes as indicated by the waviness in the bands of Figure 7; Hartman (1965) discusses seasonal segregation. The process of the diets becoming more dissimilar should now have been completed in the case of the roach and steelhead in the Eel River because of their now longtime association of ten or fifteen years. The data collected should represent the third phase depicted in Figure 7.

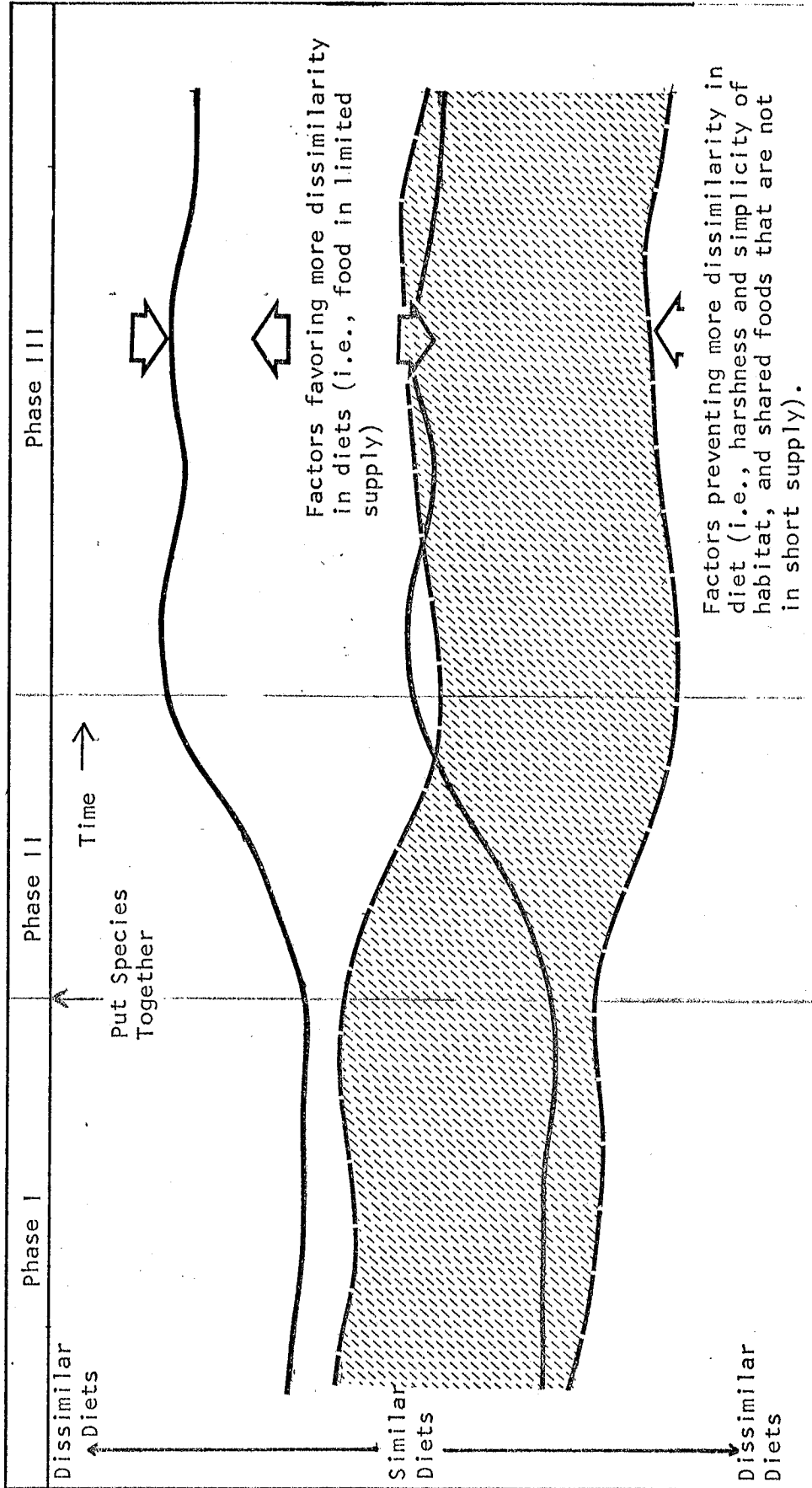


Figure 7. Competition phase diagram illustrating the outcome of placing two species of fish with similar diets into the same habitat. (Band width indicates diversity of diet).

The resultant amount of general feeding-overlap (40 percent) for insects in the case of roach and trout, could indicate some competition for insects in the riffle areas. The next step would be to determine if the overlapping food items existed in limited amounts. This study was not designed to determine this. The measured overlap in this study seems to be a result of the limited habitat. However, the most important insect food items (Isonychia velma and Marilia flexuosa) did not overlap in the diets of roach and trout, and those insects that do occur in the diet of both fish species are of lesser importance.

Because most of the roach diet was composed of algae, and the important insect food species did not overlap in the diets of roach and trout, I conclude that in the South Fork, Eel River competition for food by roach and juvenile steelhead in riffles is of limited nature. However, one should be careful not to apply these results to other drainages where trout and roach occur. It cannot be over-emphasized that the biology and composition of insects in the fauna are the key factors in determining feeding conflict, and these vary greatly from one area to another.

SUMMARY

1. Roach and trout inhabited two different feeding zones. However some overlap of these zones did occur. Occasional interspecific aggression by trout toward roach helped maintain or increase this spatial segregation.
2. Increased segregation in feeding time and location was observed during the critical period of low flow and high temperature. Segregation may have been limited by the simplicity of the habitat.
3. The major food of the roach was attached algae, 73 percent by volume.
4. Some feeding overlap for insects occurred. The general feeding overlap for insects was 40 percent and the species overlap was 41 percent. However the two most important insects did not overlap in the diets of roach and steelhead.
5. The community composition and biology of the individual species of insects played a significant role in determining fish interaction.
6. Competition for food by roach and juvenile steelhead in the study section of the South Fork, Eel River was of limited nature.
7. Theory concerning feeding overlap and competition is discussed.

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APPENDIX

Monthly insect food types and their corresponding percent makeup of the diet of trout and roach from the riffle study section, South Fork, Eel River, March to October, 1971.

MARCH

<u>TROUT</u>		<u>ROACH</u>	
<u>Acroneuria californica</u>	21.0%	<u>Acroneuria californica</u>	12.5%
<u>Pteronarcys</u> sp.	13.1%		
<u>Rithrogena decora</u>	8.7%	<u>Rithrogena decora</u>	13.0%
<u>Isonychia velma</u>	4.3%	<u>Isonychia velma</u>	8.7%
<u>Hydropsychidae</u>	8.7%	<u>Hydropsychidae</u>	17.4%
		<u>Hydroptilidae</u>	4.3%
		<u>Gomphidae</u>	17.4%
<u>Psphenus</u> sp.	8.7%		
<u>Elmidae</u> (L)	13.1%	<u>Elmidae</u> (L)	4.3%
<u>Elmidae</u> (A)	4.3%		
<u>Dytiscidae</u>	4.3%	<u>Hydrophilidae</u>	4.3%
<u>Tendipedidae</u> (L)	4.3%	<u>Tendipedidae</u> (L)	8.7%
<u>Tipulidae</u>	8.7%	<u>Tipulidae</u>	4.3%
		<u>Paragyraetis</u> sp.	4.3%

APRIL

<u>Acroneuria californica</u>	11.7%	<u>Acroneuria californica</u>	12.5%
<u>Rithrogena decora</u>	4.8%		
<u>Isonychia velma</u>	4.8%	<u>Isonychia velma</u>	12.5%
<u>Marila flexuosa</u>	2.4%		
<u>Hydropsychidae</u>	16.4%	<u>Hydropsychidae</u>	12.5%
<u>Helicopsyche borealis</u>	2.4%		
<u>Microvillia californiensis</u>	2.4%		
<u>Psephenus</u> sp.	2.4%		
<u>Elmidae</u> (L)	9.2%		
<u>Elmidae</u> (A)	4.8%	<u>Tendipedidae</u> (L)	50.0%
<u>Tendipedidae</u> (L)	21.0%		
<u>Tendipedidae</u> (P)	11.7%		
<u>Paragyraetis</u> sp.	2.4%	<u>Paragyraetis</u> sp.	12.5%
<u>Terrestrial Homoptera</u>	2.4%		

MAY

<u>TROUT</u>		<u>ROACH</u>	
<u>Acroneuria californica</u>	4.8%	<u>Rithrogena decora</u>	12.5%
<u>Rithrogena decora</u>	1.0%	<u>Isonychia velma</u>	6.2%
<u>Isonychia velma</u>	2.9%		
<u>Baetis sp.</u>	2.9%		
<u>Ephemerella walkeri</u>	61.8%		
<u>Trichorthodes fallax</u>	0.6%		
<u>Paraleptophlebia helena</u>	0.3%		
<u>Hydropsychidae</u>	5.2%	<u>Hydropsychidae</u>	6.2%
<u>Marila flexuosa</u>	11.6%	<u>Marila flexuosa</u>	56.2%
		<u>Ambrysus mormon</u>	3.1%
<u>Psephenus sp.</u>	1.0%		
<u>Elmidae (L)</u>	0.3%	<u>Elmidae (L)</u>	3.1%
<u>Elmidae (A)</u>	0.3%	<u>Elmidae (A)</u>	3.1%
<u>Dytiscidae</u>	0.3%		
<u>Tendipedidae (L)</u>	3.6%	<u>Tendipedidae (L)</u>	3.1%
<u>Tipulidae</u>	0.3%	<u>Tipulidae</u>	3.1%
<u>Paragyractis sp.</u>	1.3%		
<u>Terrestrial Coleoptera</u>	0.6%		
<u>Unidentified</u>	1.0%	<u>Hydraorina</u>	3.1%

JUNE

<u>Acroneuria californica</u>	1.0%	<u>Acroneuria californica</u>	2.9%
<u>Rithrogena decora</u>	9.2%	<u>Rithrogena decora</u>	8.7%
<u>Isonychia velma</u>	10.0%	<u>Isonychia velma</u>	2.9%
		<u>Baetis sp.</u>	5.7%
		<u>Ephemerella walkeri</u>	8.7%
<u>Trichorthodes fallax</u>	63.0%	<u>Trichorthodes fallax</u>	2.9%
<u>Marila flexuosa</u>	16.5%	<u>Marila flexuosa</u>	24.6%
		<u>Hydropsychidae</u>	1.4%
		<u>Terrestrial Trichoptera</u>	
		(A)	4.3%
		<u>Elmidae (L)</u>	1.4%
		<u>Elmidae (A)</u>	1.4%
		<u>Tendipedidae (L)</u>	27.5%
		<u>Tipulidae</u>	1.4%
		<u>Terrestrial Coleoptera</u>	2.9%
		<u>Unidentified</u>	1.4%
		<u>Hydracarina</u>	1.4%

JULY

<u>TROUT</u>		<u>ROACH</u>	
<u>Acroneuria californica</u>	0.6%	<u>Acroneuria californica</u>	5.1%
<u>Rithiogenia decora</u>	3.4%	<u>Rithiogenia decora</u>	1.7%
<u>Isonychia velma</u>	3.9%	<u>Isonychia velma</u>	3.4%
<u>Baetis sp.</u>	54.3%	<u>Baetis sp.</u>	25.6%
<u>Ephemerella walkeri</u>	3.4%	<u>Ephemerella walkeri</u>	17.3%
<u>Trichorthodes fallax</u>	5.0%	<u>Trichorthodes fallax</u>	3.4%
<u>Paraleptophlebia helena</u>	1.1%	<u>Paraleptophlebia helena</u>	1.7%
<u>Marila flexuosa</u>	3.4%	<u>Marila flexuosa</u>	12.0%
<u>Hydropsychidae</u>	9.5%	<u>Hydropsychidae</u>	3.4%
<u>Trichoptera (A)</u>	3.4%		
<u>Elmidae (L)</u>	0.6%		
<u>Tendipedidae (L)</u>	7.3%	<u>Tendipedidae (L)</u>	22.2%
<u>Tendipedidae (P)</u>	0.6%	<u>Tendipedidae (P)</u>	1.7%
<u>Tipulidae</u>	0.6%		
<u>Simuliidae</u>	2.2%	<u>Simuliidae</u>	1.7%
<u>Sialis californiensis</u>	0.6%		
<u>Unidentified</u>	0.6%		

AUGUST

		<u>Acroneuria californica</u>	2.3%
<u>Rithrogena decora</u>	2.4%		
<u>Isonychia velma</u>	10.2%	<u>Isonychia velma</u>	4.5%
<u>Baetis sp.</u>	65.0%	<u>Baetis sp.</u>	22.4%
<u>Paraleptophlebia helena</u>	0.8%	<u>Ephemeroptera (A)</u>	3.5%
		<u>Marila flexuosa</u>	4.5%
<u>Marila flexuosa</u>	0.8%	<u>Hydropsychidae</u>	4.5%
<u>Hydropsychidae</u>	2.4%	<u>Hydroptilidae</u>	31.4%
<u>Terrestrial Trichoptera (A)</u>	4.7%		
<u>Ambrysus mormon</u>	2.4%	<u>Tendipedidae (L)</u>	2.3%
<u>Elmidae (L)</u>	0.8%	<u>Tendipedidae (A)</u>	6.7%
		<u>Simuliidae</u>	2.3%
		<u>Tabanidae</u>	2.3%
<u>Paragyraetis sp.</u>	3.9		
<u>Sialis californiensis</u>	6.8%		
<u>Unidentified</u>	0.8%	<u>Unidentified</u>	2.3%

SEPTEMBER

<u>TROUT</u>		<u>ROACH</u>	
<u>Rithrogena decora</u>	2.5%		
<u>Isonychia velma</u>	3.4%		
<u>Baetis sp.</u>	48.8%	<u>Baetis sp.</u>	4.8%
<u>Ephemerella walkeri</u>	9.3%	<u>Ephemerella walkeri</u>	28.6%
		<u>Paraleptophlebia helena</u>	2.4%
<u>Marila flexuosa</u>	0.8%	<u>Marila flexuosa</u>	21.5%
<u>Hydropsychidae</u>	4.2%	<u>Hydropsychidae</u>	9.5%
		<u>Ambrysus mormon</u>	2.4%
<u>Psephenus sp.</u>	0.8%		
<u>Tendipedidae (L)</u>	4.2%	<u>Tendipedidae (L)</u>	21.5%
		<u>Tendipedidae (A)</u>	2.4%
<u>Paragyraetis sp.</u>	26.1%	<u>Paragyraetis sp.</u>	2.4%
		<u>Unidentified</u>	2.4%

OCTOBER

<u>Acroneuria californica</u>	1.0%		
<u>Isonychia velma</u>	8.7%		
<u>Baetis sp.</u>	24.0%	<u>Baetis sp.</u>	14.3%
<u>Ephemerella walkeri</u>	1.0%	<u>Ephemerella walkeri</u>	14.3%
<u>Paraleptophlebia helena</u>	5.8%		
<u>Marila flexuosa</u>	11.5%	<u>Marila flexuosa</u>	14.3%
<u>Hydropsychidae</u>	3.8%		
<u>Tendipedidae</u>	14.4%	<u>Tendipedidae</u>	28.6%
<u>Paragyraetis sp.</u>	25.0%		
<u>Terrestrial Diptera</u>	1.9%	<u>Terrestrial Diptera</u>	28.6%
<u>Unidentified</u>	1.9%		