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Stream Resource Utilization of Sympatric and Allopatric Juvenile Brown *(Salmo trutta)* and Steelhead Trout *(Salmo gairdneri)*

Robin Lynn Ziegler

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STREAM RESOURCE UTILIZATION OF SYMPATRIC AND ALLOPATRIC JUVENILE BROWN (*SALMO TRUTTA*) AND STEELHEAD TROUT (*SALMO GAIRDNERI*)[1]

Robin Lynn Ziegler

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By

Robin Lynn Ziegler

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ABSTRACT

STREAM RESOURCE UTILIZATION OF SYMPATRIC AND ALLOPATRIC JUVENILE BROWN (*Salmo trutta*) AND STEELHEAD TROUT (*Salmo gairdneri*)

By

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The dietary and habitat preferences of sympatric and allopatric juvenile brown (*Salmo trutta*) and steelhead trout (*Salmo gairdneri*) were measured in order to assess potential areas of interaction between the two species.

Juvenile brown and steelhead trout in the Little Manistee, Pere Marquette, and Boardman Rivers were found to utilize the same food and space resources. Both species ate primarily chironomid and simuliid larvae of approximately the same size.

Analysis of habitat utilization indicated that both brown and steelhead trout are commonly associated with instream structure, particularly down timber. No major differences in utilization were observed for sympatic versus allopatric populations of these trout. However, differences in physical parameters such as depth and velocity did allow distinction to be made between trout populations from different rivers.

INTRODUCTION

The introduction of anadromous steelhead (rainbow) trout and salmon into the Great Lakes has provided midwest sportsmen a magnificent fishery. Annual stocking of these anadromous species into tributaries of Lakes Michigan, Huron, and Superior has led to the utilization of many quality trout streams for spawning and nursery purposes by these fish (Latta 1974). As a result, there has been mounting concern regarding the impact of salmon and steelhead trout on the resident stream brook (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) populations (Taube 1975, Stauffer 1977, Cunjak and Green 1983, and Fausch 1986). Many anglers feel that salmon and steelhead trout seriously impact the trout resources in coastal Great Lakes streams and are the cause of the perceived decline in the resident stream trout populations. Both anadromous and resident salmonid species are popular, highly prized game fish for Michigan sportsmen. Therefore, angler interest in these fisheries necessitates further research to determine proper management practices.

Salmonid species are usually territorial in stream environments, maintaining relatively fixed positions within their territories and feeding primarily on drifting benthic invertebrates (Kalleberg 1958, Chapman 1966). In addition to similarities in behavior, previous research has also indicated a similarity in the utilization of food and space resources by sympatric populations of salmonids (Fausch 1981, Bowlby and Roff 1986). Therefore, development of interspecific competitive relationships between these fishes is a likely possibility.

Researchers have examined competitive interactions between coho salmon (Oncorhynchus kisutch) and brown trout (Taube 1975, Stauffer 1977, Fausch 1986), coho salmon and rainbow trout (Salmo gairdneri) (Hartman 1965), steelhead trout and chinook salmon (O. tshawytscha) (Everst and Chapman 1972), rainbow and brook trout (Cunjak and Green 1983), and brook and brown trout (Nyman 1970, Fausch and White 1981, Cunjak and Power 1986). However, with the exception of diet studies (Wagner 1975, Johnson 1981, Bolwby and Roff 1986), no studies have dealt specifically with the interactions of juvenile steelhead and brown trout in the stream environment.

A study conducted on the fishery of the Pere Marquette River has indicated a significant decline in the brown trout population over the past fifteen years whereas the numbers of juvenile steelhead trout have increased (Kruger 1985). In addition, brown trout in this river system exhibit growth rates below the Michigan state average for fish measuring less than ten inches. The mechanisms responsible for this decline in abundance and growth have not been determined. However, the marked increase in steelhead trout abundance and the fact that growth of brown trout is above the state average after ten inches in length (the time at which steelhead trout smolt) suggests there may be some association between these two species.

Interaction between ecologically similar stream fishes has been shown to cause displacement and/or declines of individuals from one of the interacting fish populations (Burton and Odum 1945, Gibson 1981, Hearn and Kynard 1986). Displacement of subordinate species to marginal habitats may negatively effect the fitness and subsequently the growth of these displaced individuals (Werner and Hall 1976, Itzkowitz 1979). In order to determine if the observations made on the Pere Marquette fishery are the product of interactive mechanisms between brown and steelhead trout, the degree of similarity for stream resource utilization needs to be established for both species.

The goal of this research was to observe the resource preferences of juvenile brown and steelhead trout in the stream environment to determine if interaction between these species may act as a population regulating mechanism. When closely related species occur in the same environment certain aspects of their behavior or resource requirements must differ sufficiently to allow their coexistence. Observing niche shifts on allopatric versus sympatric populations of closely related species may provide insight into the mechanisms which operate to permit their coexistence. Therefore, in order to assess potential areas of interaction the specific objectives of this study were 1) to determine the dietary preferences in terms of taxon and size for both sympatric and allopatric juvenile steelhead and brown trout 2) to determine the habitat preferences for these same populations and 3) to determine the amount of overlap between these preferences with an emphasis on its implications for management practices.

MATERIALS AND METHODS

Site Selection

Stream survey data provided by Michigan Department of Natural Resources, Fisheries Division was reviewed in order to evaluate long term trends in brown and steelhead trout abundance in Lake Michigan tributaries and to collect information on the current status of several designated trout steams. The purpose of this review was to locate tributaries containing reproducing populations of brown and steelhead trout. With this accomplished, we began walking stretches of streams in order to locate study areas that could be electrofished effectively with backpack or stream shocking units, were easily accessible and contained similar substrate and cover to facilitate between stream comparisons. At the conclusion of the walking surveys, nine Lake Michigan tributaries were selected for assessment of their current trout populations. The size distribution and relative abundance of brown and steelhead trout were evaluated by electroshocking a 100 meter section on each tributary. All trout collected were placed in a holding tank, measured to the nearest millimeter, weighed on an Ohaus portable balance (D-500), and released.

Mapping Available Habitat

Following Instream Flow Methodology guidelines (Bovee 1982) depth, velocity, substrate, and cover were measured to define available habitat in the 100 meter study sections on each tributary. In order to standardize measurements, codes and criteria to define cover (Table 1) and substrate (Table 2) were established prior to collecting data in the field. A metric wading rod and a Marsh-McBirney model 201D microflow meter were utilized to measure depth and velocity. Mapping of aquatic habitat was accomplished by running bank to bank transects every three meters from the downstream to the upstream boundaries of the study section. Measurements were made at one meter intervals along each transect. Depth, velocity, and codes for substrate and cover were recorded at each location. In addition, macrohabitat measurements (length and width) of all riparian and instream structure were recorded.

The stream channel was mapped utilizing a modified Deflection-Angle Traverse Method (Orth, 1983). Station one

Table 1. Stream habitat numeric codes and descriptions of cover types at study sites.

Cover Code	Description
1	No cover
2	Undercut bank < 30 cm
3	Undercut bank > 30 cm
4	Overhanging vegetation > 30 cm above surface
5	Overhanging vegetation < 30 cm above surface
6	Emergent or submergent aquatic vegetation
7	Down timber
8	Half-log improvement structure
9	Large rock or boulder

Table 2. Substrate numeric codes and descriptions of substrate types at study sites.

Substrate Code	Description
1	Rooted aquatic vegetation
2	Fines (sand, silt)
3	Pebble (up to 3 cm)
4	Gravel (3 to 8 cm)
5	Cobble (8 to 30 cm)
6	Boulder (greater than 30 cm)
7	Bedrock
8	Detritus
9	Down timber embedded in substrate

was located at the downstream boundary of the study section. Consecutive stations were located at three meter intervals until the upstream boundary of the study section was reached. At each station, a transect was run across the stream channel to the opposite bank, a metric measuring tape was used to determine the width of the channel at the transects location. A stand pole compass was utilized to measure the deflection angle from the present station to the following station and the traverse angle from the station to the point across the stream that the transect had been located.

Utilizing the channel morphology and habitat measurements collected in the field, scale drawings of the stream study sections were constructed. The abundance of each habitat type and total area of the stream study section was measured utilizing a digitizing program which calculates the area of irregular polygons (Arnold and Van Nort 1987, Eves 1975).

Underwater Observation

The utilization of available habitat by juvenile brown and steelhead trout was observed by diving with mask and snorkel. Samples were collected at monthly intervals from June through November on each tributary except during occasional times of poor visibility. As visibility was essential for proper identification and length estimation of juvenile trout, diving was usually done between 1000 and 1400 hours when direct sunlight hit the stream surface and light intensity was the greatest.

The study sections were divided lengthwise into right and left sides. Two divers, each working a side of the channel, crawled upstream from the downstream boundary investigating the main channel and all structures that might have contained trout. Due to the rheotaxic nature of trout, divers approached from the downstream direction reducing the chances of disturbing the trout and allowing observations of their natural positions to be made.

Upon visual location of a trout its behavior was observed to determine if it had been disturbed. Actions such as darting from one spot to another or digging into the substrate were assumed to be a reaction to the divers presence and no data were collected from these fish. If a fish did not appear to be disturbed, divers identified the species, estimated its total length and distance from the substrate with a centimeter scale, marked its position with a numbered lead weight, and recorded this information on an underwater slate.

At the conclusion of the dive, the lead weights were collected and measurements of depth, velocity, substrate, and cover were made at each location. A Marsh-McBirney model 201D microflow meter and metric wading rod were used to measure depth and velocity. The same codes and criteria established for cover and substrate in the mapping procedure were used to evaluate cover and substrate at each fish position (Tables 1 and 2).

Electrofishing Procedure

The relative abundance of trout in each study section was estimated monthly from June through November 1986 using electrofishing. The electrofishing unit consisted of a small wooden barge carrying a 250-v, 1.75-KW DC generator. The electrofishing crew proceeded from the downstream to the upstream boundary of the study section. A single pass was made up each bank and another up the center of the stream.

All trout collected were placed in a holding tank, measured to the nearest millimeter and weighed on a Ohaus portable balance (D-500). Scale samples were taken from all size classes of trout for age and growth determination. The trout were then released at the downstream boundary of the section to allow olfactory orientation to their previous positions in the stream.

Diet Analysis

A backpack and/or stream electrofishing unit was utilized to collect trout for stomach content analysis monthly from June through November. Trout were collected from areas adjacent (above and below) to the study section to avoid removing fish from the section. It was assumed that prey availability above and below the study section would be comparable to that available within the section. All trout captured were measured to the nearest millimeter and weighed on a Ohaus portable balance (D-500). A subsample of up to 5 trout from each 10 mm size class collected were preserved in a buffered 10% formalin solution and analyzed for stomach contents. Food items were identified to family and counted in the laboratory. In addition, head capsules of all insects were measured for size analysis of the diet.

Stomach contents were evaluated for intra- and interspecific similarities in terms of prey size and taxon. Intraspecific diet comparisons were made between species from different river systems and for each trout species within a river system between sampling dates. Interspecific diet comparisons were made between species within a river system.

Statistical Analysis

All statistical procedures and comparisons in this study were performed using Statistical Analysis System (SAS Institute Inc. 1985) on the Michigan State University Computer Network. Statements of statistical significance indicate p-values less than or equal to 0.05 unless stated otherwise.

Habitat utilization was evaluated in terms of availability and for species or population specific preferences. Utilization of instream structures as cover was compared to structure availability using a Chi-square test (Steel and Torrie 1980). Structure availability was measured in terms of the percent of the total study site area each type of structure comprised.

A logistic regression procedure was run to determine the physical and biological attributes of brown and steelhead trout that were helpful in classifying fish into a specific population or species. The logistic regression model is formulated mathematically by relating the probability of some event, E, occurring conditional on a vector of explanatory variables (Press and Wilson 1978). In this case, E, is the probability that a fish belongs to a particular species or population and the explanatory variables are the physical and biological measurements made in the field. The variables measured were total fish length, distance from the substrate, depth and velocity at the fish's position, and the type of structure and substrate with which the fish was associated.

Diet preferences were evaluated both qualitatively and quantitatively. Qualitative analysis was based on size and taxon of prey items. Similarities in prey taxon were evaluated through calculation of Schoener's (1970) index:

$$\text{Overlap} = 1 - 0.5 \left| Px_i - Py_i \right|$$

where:

Px_i= proportion of food i in the diet of species X

Py_i= proportion of food i in the diet of species Y

Overlap values of 0.6 or greater are considered significant (Smith 1985).

Differences in mean headcapsule width of prey items for each trout species between river systems and within river systems were tested using F-test and t-test comparisons (Steel and Torrie 1980). Differences in mean headcapsule width of prey items for each trout species within a river system between sampling dates was tested using a two-way analysis of variance and Student-Newman-Kuels' multiple comparison test (Steel and Torrie 1980).

A quantitative description of diet was developed by calculating percent occurrence, mean number per stomach, and number of stomachs containing an item for each insect taxon found in the stomach contents. These data were utilized to determine the predominate prey items for all trout species found in each river system throughout the sampling season.

Growth was evaluated by calculating the average daily increase in length for each trout population. A z-statistic was calculated for each paired comparison using the following formula: (Kendall and Stuart 1977)

$$z = \text{mean1} - \text{mean2} / \text{variance 1} + \text{variance 2}$$

In addition, the length and weight of each individual fish captured in the electrofishing surveys were plotted to graphically depict the length-weight relationship for brown and steelhead trout in the river systems examined.

RESULTS

Study Site Selection

Preliminary electrofishing surveys conducted on nine Lake Michigan tributaries (Table 3) indicated that several of the streams supported populations of brown and steelhead trout. Utilizing this information, three streams, the Little South Branch of the Pere Marquette River, the Little Manistee River, and the South Branch of the Boardman River, were selected for research purposes. This selection was based upon physical properties, the abundance of young of the year trout captured within the survey section, and the ratio of brown to steelhead trout. The Pere Marquette contained primarily steelhead trout, the Boardman exclusively brown trout, and the Little Manistee a mixed population of both species. Therefore, these streams could be used to evaluate changes in resource utilization by both species of trout in sympatry versus allopatry.

Population Parameters

Relative abundance and growth data were collected from each river in order to make comparisons between study sections. Trout populations in the Little Manistee River

Table 3. Relative abundance of brown and steelhead trout in nine Lake Michigan tributaries surveyed as potential study streams, 1985.

Stream	Abundance		
	Brown Trout	Steelhead Trout	Total
Williamsburgh Creek	29	0	29
Boardman (S. Branch)	124	0	124
Bear Creek	1	5	6
L. Manistee	3	13	16
Platte	6	40	46
Pere Marquette (Little S. Branch)	7	80	87
Pine Creek	14	22	36
White River	2	0	2
Filer Creek	0	0	0

were the most abundant with an average of 118 fish in the 100 meter study section (Table 4). The Boardman and Pere Marquette Rivers had an average of 56 and 50 fish in their study sections respectively. The ratio of brown to steelhead trout in the Little Manistee River was approximately 1:2. On all sampling dates brown trout had a larger mean length than steelhead trout (Table 4). However, this difference in length between species diminished across the sampling season. For example, steelhead collected in July were 28 mm shorter than brown trout but in September they were only 17 mm shorter than the brown trout collected on the same date.

Growth was compared between all three rivers for both species of trout. Brown trout from the Little Manistee and Boardman Rivers had an average daily increase in length of 0.32 mm and 0.34 mm respectively. These values were not statistically different from one another (z-test). Steelhead trout from the Little Manistee and Pere Marquette Rivers had a daily average increase in length of 0.56 mm and 0.58 mm respectively. These values were also not significantly different from one another (z-test). Comparison of brown trout growth to steelhead growth indicated that the average daily increase of these species were significantly different from one another. All species regardless of the river system in which they were found exhibited similar length-weight relationships. In other

Table 4. Estimates of relative abundance and mean length of trout species from shocking runs.

River	Date	Species	Length ± Standard Error (mm)	Number of Fish
Boardman (S. Branch)	Jun 25, 1986	Brown	61.6 ± 2.7	69
	Aug 23, 1986		81.7 ± 1.7	43
Pere Marquette (Little S. Branch)	Jul 31, 1986	Steel-head	56.1 ± 2.1	44
	Aug 27, 1986		72.3 ± 2.3	56
Little Manistee	Jul 24, 1986	Brown	75.0 ± 1.6	47
	Aug 11, 1986		83.1 ± 1.8	38
	Sep 9, 1986		90.5 ± 2.1	30
	Jul 24, 1986	Steel-head	46.5 ± 0.9	118
	Aug 11, 1986		59.6 ± 1.6	58
	Sep 9, 1986		73.4 ± 2.0	63

words, the weight of a fish at a particular length was the same for both brown and steelhead trout.

Available Habitat

The quality and quantity of available habitat was found to be very similar in each river's study section (Table 5). Open areas with no structures comprised the majority of the total study area for all three rivers. The second most abundant habitat type available in the sections was a combination of down timber and overhanging vegetation such as tag alder or cedar. However, each section did contain structures that were unique to their river's system. The Little Manistee river has had man-made habitat improvement structures constructed in its waters and the Pere Marquette river contains many large boulders and rock structures that were not found in the other sections. Despite these and other inherent differences that occur between river systems, I assumed that the study sections were similar enough to allow between stream comparisons to be made. This assumption was based on the fact that all three sections contained the same predominate instream structures and were capable of supporting trout populations.

Underwater Observations

Brown and steelhead trout appear to be selective for

Table 5. Area of habitat types (m^2) measured in all three study sections.

Habitat	River					
	Boardman South Branch		Pere Marquette Little S. Branch		Little Manistee	
	Area	%	Area	%	Area	%
None	529.4	59.3	547.8	59.1	731.8	64.3
Overhanging Vegetation-Timber Complex	208.2	23.3	221.1	23.9	156.9	13.8
Down Timber	109.8	12.3	69.2	7.5	39.3	5.8
Overhanging Vegetation	14.4	1.6	23.5	2.5	130.7	11.5
Boulder	0.0	0.0	35.7	3.9	0.0	0.0
Habitat Improvement Structure	0.0	0.0	0.0	0.0	65.6	5.8
Aquatic Vegetation	0.0	0.0	11.1	1.2	0.0	0.0
Island	20.7	2.3	0.0	0.0	0.0	0.0
Root Wad	0.0	0.0	9.9	1.1	0.0	0.0
Other	10.0	1.1	8.3	0.9	14.4	1.3

particular types of structure regardless of their availability. Utilization of habitat was significantly different from that expected based on habitat availability (Table 6). Both species whether allopatric or sympatric with one another, were most frequently found under logs or holding positions in close proximity (within a meter) to down timber, even though other types of structure were more abundant.

<u>Logistic Regression</u>

<u>Brown Trout</u>

Difference in total body length was found to be the most significant (X^2= 23.92) variable in classifying brown trout from the Boardman and Little Manistee Rivers. Brown trout observed in the Boardman river were on the average 8.57 centimeters long which was significantly larger ($p < 0.0623$) than the 5.68 centimeter average length of brown trout observed in the Little Manistee River (Table 7 and 8). The linear model developed by the logistic regression procedure contained several cover and substrate variables which pertained to microhabitat measurements taken at the fish's position. The significance of these variables is difficult to evaluate because their chi-square values are minimal and differences in availability of microhabitat between river systems is unknown.

The model correctly classified brown trout in the Boardman River 99.4% of the time. This indicates that

Table 6. Chi-square analysis for habitat utilization versus habitat availability.

Site	Species	Date	Calculated Chi-square	Critical Chi-square
Boardman River (South Branch)	Brown Trout	June-Nov.	158.01*	7.82
L. Manistee River	Brown Trout	June-Nov.	19.24*	7.82
L. Manistee River	Steelhead Trout	June 18	135.77*	9.49
		July 21	438.63*	11.07
		Aug. 18	82.93*	9.49
		Sept. 9	147.77*	11.07
		Nov. 7	95.50*	9.49
Pere Marquette River (Little S. Branch)	Steelhead Trout	July 7	188.64*	11.07
		July 29	73.22*	11.07
		Aug. 29	361.21*	11.07
		Oct. 30	341.94*	11.07
		Nov. 22	61.38*	11.07

* Significant values which indicate that habitat is not used in proportion to availability.

Table 7. Mean, range, and standard error of significant variables from logistic regression procedure for the South Branch of the Boardman River.

Species	Variable	Mean	Range: Minimum Value	Range: Maximum Value	Standard Error of Mean
Brown Trout	Length	8.57	2.0	16.0	0.18
	Average Velocity	0.94	0.0	3.08	0.03
	Depth (cm)	48.4	14	100	0.96
	Distance from Substrate	2.61	0	30	0.15

Table 8. Mean, range, and standard error of significant variables from logistic regression procedure for the Little Manistee River.

Species	Variable	Mean	Range		Standard Error of Mean
			Minimum Value	Maximum Value	
Steelhead Trout	Length	6.94	2.0	16.0	0.22
	Average Velocity	0.94	0.0	2.82	0.04
	Depth (cm)	39.6	11	105	1.31
	Distance from Substrate	3.09	0	23	0.23
Brown Trout	Length	5.68	3.0	12.0	0.42
	Average Velocity	0.66	0.0	2.49	0.08
	Depth (cm)	29.2	12	56	1.87
	Distance from Substrate	0.71	0	4	0.20

trout in this river have extremely consistent values for the length, cover, and substrate variables found in the model. Brown trout observed in the Little Manistee River were more variable in length and utilization of microhabitat than brown trout in the Boardman River. Therefore, they were more difficult to classify and the model was only correct 65.6% of the time.

Steelhead Trout

Steelhead trout in the Pere Marquette and Little Manistee Rivers utilized different water velocities and depths depending on the river system in which they were located. Steelhead trout in the Little Manistee utilized a wider range of water depths (11 to 105 cm) but on the average were found in shallower waters than Pere Marquette rainbow trout (Table 8 and 9). However, the mean depths utilized by both trout populations were not statistically different based on a t-test analysis. The range of velocities utilized by both trout populations were very similar. Pere Marquette River steelhead trout were found in velocities ranging from 0.06 to 2.38 meters per second and Little Manistee River steelhead trout were found in velocities ranging from 0.0 to 2.82 meters per second. A t-test comparison of mean velocity values for these populations determined that steelhead trout in the Little Manistee River utilize significantly faster velocities than Pere Marquette River steelhead trout. Trout from both

Table 9. Mean, range, and standard error of significant variables from logistic regression procedure for the Little South Branch of the Pere Marquette River.

Species	Variable	Mean	Range Minimum Value	Range Maximum Value	Standard Error of Mean
Steelhead Trout	Length	8.69	2.0	16.0	0.23
	Average Velocity	0.85	0.06	2.38	0.03
	Depth (cm)	53.0	14	100	1.25
	Distance from Substrate	3.88	0	30	0.20

river systems were found most frequently in water velocities less than 1.5 meters per second. Little Manistee River steelhead trout were equally distributed in velocities ranging from 0 to 1.5 meters per second whereas steelhead trout in the Pere Marquette River were found concentrated in 0.5 meters per second and 1.3 to 1.4 meters per second water velocities.

The linear model developed by the logistic regression procedure found water depth and velocity to be the most significant variables in classifying steelhead trout in the Little Manistee and Pere Marquette Rivers. As with the logistic regression model developed to classify brown trout populations, the steelhead trout model also contains several cover and substrate variables whose chi-square values are insignificant. The model had a correct classification rate of 76.3% for steelhead trout observed in the Pere Marquette River and 84.9% for those in the Little Manistee River. Therefore, it appears that both populations vary to some extent in their utilization of cover and substrate as well as water depth and velocity.

Sympatric Brown and Steelhead Trout

Brown and steelhead trout in the Little Manistee River were found to differ most significantly in the distance above the substrate that they held positions. Brown trout were more closely associated with the substrate than steelhead trout. They held positions that were on the average 0.71 cm above the stream bottom and were never found in positions greater than 4 cm from the substrate. Rainbow trout positions ranged from 0 to 23 cm above the substrate and had a mean value of 3.09 cm. The mean values for distance from the substrate (Table 8) were found to be statistically different between species by a t-test comparison.

The logistic regression procedure developed a model that contained several cover and substrate variables as well as distance from the substrate measurements. However, the chi-square values for the cover and substrate variables were insignificant. The model correctly classified steelhead trout 95.6% of the time. This high percentage suggests relatively consistent values for the variables contained in the model. Brown trout, on the other hand, appeared to be extremely inconsistent in their utilization of these variables and were only classified correctly 38.8% of the time.

Food Habits

Brown Trout

Brown trout in the Boardman and Little Manistee rivers did not exhibit major differences in preference of prey items. Larval insects belonging to the families Chironomidae and Simuliidae were the most commonly occurring food items in the stomach contents of both brown trout populations (Tables 10 and 11). Diets were also

Table 10. Stomach contents of young of the year brown trout collected in the Little Manistee River, 1986.

Food Item	Number Stomachs Containing Item	Mean Number Per Stomach	Frequency of Occurrence
TRICHOPTERA	10	1.6	0.20
Hydropsychidae	15	1.8	0.31
Glossomatidae	21	2.7	0.43
Limnephilidae	3	2.0	0.06
Brachycentridae	4	1.0	0.08
DIPTERA	2	2.0	0.04
Tipulidae	6	3.0	0.12
Ceratopogonidae	6	2.2	0.12
Simuliidae	28	6.1	0.57
Chironomidae	30	6.3	0.61
Pupae	4	3.5	0.08
EPHEMEROPTERA	11	1.8	0.22
Baetidae	14	3.2	0.29
Ephemerellidae	8	2.5	0.16
PLECOPTERA			
Perlodidae	3	1.7	0.06
TERRESTRIAL INSECTS	8	3.5	0.16
GASTROPODA	14	1.6	0.29
ISOPODA	7	1.3	0.14
COLEOPTERA	4	2.5	0.08
OTHER	19	1.1	0.39

Table 11. Stomach contents for young of the year brown trout collected in the South Branch of the Boardman River, 1986.

Food Item	Number Stomachs Containing Item	Mean Number Per Stomach	Frequency of Occurrence
TRICHOPTERA	8	1.6	0.10
Hydropsychidae	5	1.0	0.06
Glossomatidae	9	1.3	0.11
Limnephilidae	9	4.6	0.11
Brachycentridae	17	3.5	0.21
DIPTERA			
Tipulidae	4	1.3	0.05
Ceratopogonidae	7	4.4	0.09
Simuliidae	31	4.0	0.39
Chironmidae	42	4.4	0.53
Pupae	7	2.3	0.09
EPHEMEROPTERA	17	1.4	0.21
Siphlonuridae	6	1.2	0.08
Baetidae	27	3.7	0.34
Heptageniidae	5	1.0	0.06
Ephemerellidae	10	1.8	0.13
Tricorythidae	3	1.3	0.04
TERRESTRIAL INSECT	7	1.9	0.09
GASTROPODA	10	1.7	0.13
COLEOPTERA	4	1.0	0.05
ISOPODA	3	2.0	0.04
OTHER	13	2.0	0.16

compared by calculating the overlap value for the stomach contents. The calculated Schoener's index had a value of 0.758 which indicated that brown trout in the Little Manistee and Boardman Rivers overlap significantly in terms of prey taxon present in the diet.

Size analysis of the diet produced results similar to that of prey taxon. The mean headcapsule width of prey was calculated for the entire season (Table 12). The average headcapsule width for brown trout in both the Boardman and Little Manistee Rivers was 0.588 mm. Therefore, despite the probable differences in prey availability between river systems brown trout appear to eat the same taxon and size class of prey regardless of their geographic location.

Steelhead Trout

Steelhead trout in the Pere Marquette and Little Manistee rivers exhibited a preference for the same prey taxa. Larval Chironomidae and Simuliidae were the predominate prey of both populations (Tables 13 and 14). Overlap of prey taxon in the diet was found to be significant between these populations with a calculated Schoener's index of 0.647.

Size analysis of the diet produced results which indicated that despite the similarity in preference of prey taxon steelhead trout in the Pere Marquette and Little Manistee Rivers eat different size classes of prey. Mean

Table 12. Diet data for each site and species over the entire sampling season.

Site	Species	Number Fish Examined	Number Of Prey Items	Mean Head Capsule (mm)	Standard Error
Boardman River (South Branch)	Brown Trout	80	721	0.588	0.014
Little Manistee River	Brown Trout	49	701	0.588	0.015
Little Manistee River	Steelhead Trout	92	2275	0.653	0.031
Pere Marquette River (Little S. Branch)	Steelhead Trout	14	313	0.485	0.016

Table 13. Stomach contents for young of the year steelhead trout collected in the Little Manistee River, 1986.

Food Item	Number Stomachs Containing Item	Mean Number Per Stomach	Frequency of Occurrence
TRICHOPTERA	15	1.6	0.16
Hydropsychidae	25	2.2	0.27
Glossomatidae	20	2.8	0.22
Limnephilidae	5	1.4	0.05
Brachycentridae	7	3.1	0.08
DIPTERA	5	3.2	0.05
Tipulidae	8	2.1	0.09
Ceratopogonidae	21	2.7	0.23
Simuliidae	53	8.1	0.58
Chironomidae	73	12.1	0.79
Pupae	32	10.1	0.35
Adult	12	2.8	0.13
EPHEMEROPTERA	24	2.1	0.26
Siphlonuridae	11	1.6	0.12
Baetidae	26	2.7	0.28
Ephemerellidae	8	1.8	0.09
Tricorythidae	6	4.0	0.07
PLECOPTERA			
Perlodidae	9	2.1	0.10
TERRESTRIAL INSECT	20	4.7	0.22
ISOPODA	12	1.4	0.13
OTHER	59	1.6	0.64

Table 14. Stomach contents for young of the year steelhead trout collected in the Little South Branch of the Pere Marquette River, 1986.

Food Item	Number Stomachs Containing Item	Mean Number Per Stomach	Frequency of Occurrence
TRICHOPTERA	6	1.5	0.43
Hydropsychidae	5	2.8	0.36
Glossomatidae	3	1.0	0.21
DIPTERA			
Tipulidae	4	2.0	0.29
Simuliidae	10	2.3	0.71
Chironomidae	11	17.6	0.79
Pupae	4	2.8	0.29
Adult	1	8.0	0.07
EPHEMEROPTERA	2	4.5	0.14
Baetidae	4	2.5	0.29
Tricorythidae	6	1.5	0.43
OTHER	10	1.4	0.71

headcapsule widths of prey items found in the Little Manistee River steelhead trout was 0.653 mm and 0.485 mm for Pere Marquette River steelhead trout (Table 12). These mean values were found to be significantly different based on a t-test analysis. Therefore, steelhead trout in both river systems eat the same taxon of prey but appear to choose different size classes of prey.

Sympatric Brown and Steelhead Trout

Brown and steelhead trout in the Little Manistee River exhibit very little difference in food habits in terms of both size and taxon of prey. Both species ate predominately Chironomidae and Simuliidae larvae (Tables 10 and 13) and overlap of all prey taxon in the diet was significant for the entire season with an index value of 0.705. Date-by-date comparisons indicated that overlap was significant on all sampling dates except November (Table 15).

Size analysis of the diet produced the same results. Seasonal mean headcapsule width of prey for brown trout was 0.588 mm and 0.653 mm for steelhead trout. These values were not found to be significantly different based on a t-test analysis. Date-by-date mean headcapsule widths were also not significantly different between species (Table 15). Prey with headcapsules less than 1.0 mm were ingested more frequently than other size classes (Figures 1 and 2).

Table 15. Schoener's diet overlap and comparison of mean headcapsule width for sympatric brown and steelhead trout in the Little Manistee River, 1986.

Date	Interacting Species	Overlap	T-Test Comparison of Mean Head Capsule
July	Brown-Steehead Trout	0.764	NS
Aug.	Brown-Steelhead Trout	0.704	NS
Sept.	Brown-Steelhead Trout	0.652	NS
Nov.	Brown-Steelhead Trout	0.447	NS

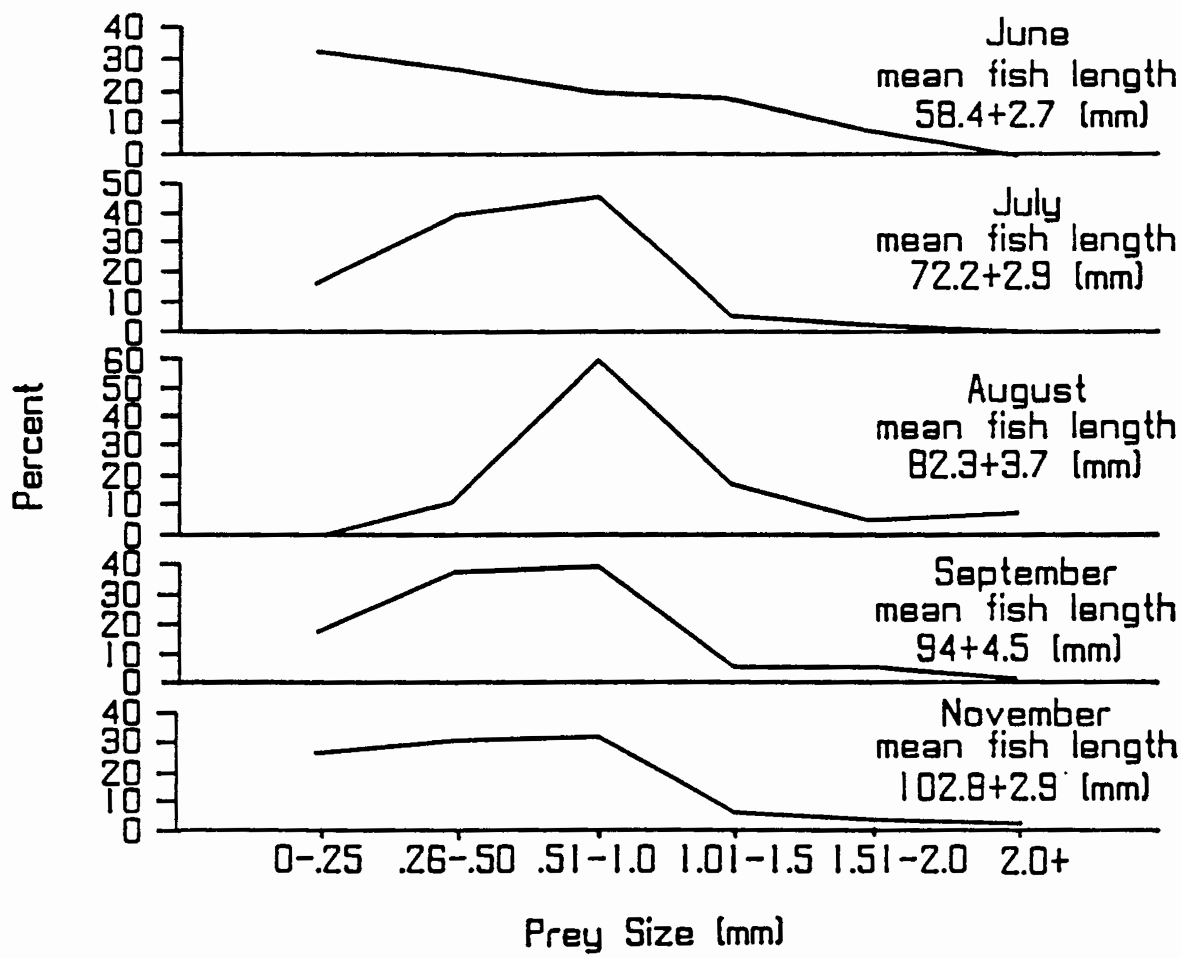

Figure 1. Percent composition of diet by prey size for Little Manistee River brown trout collected on each sampling date.

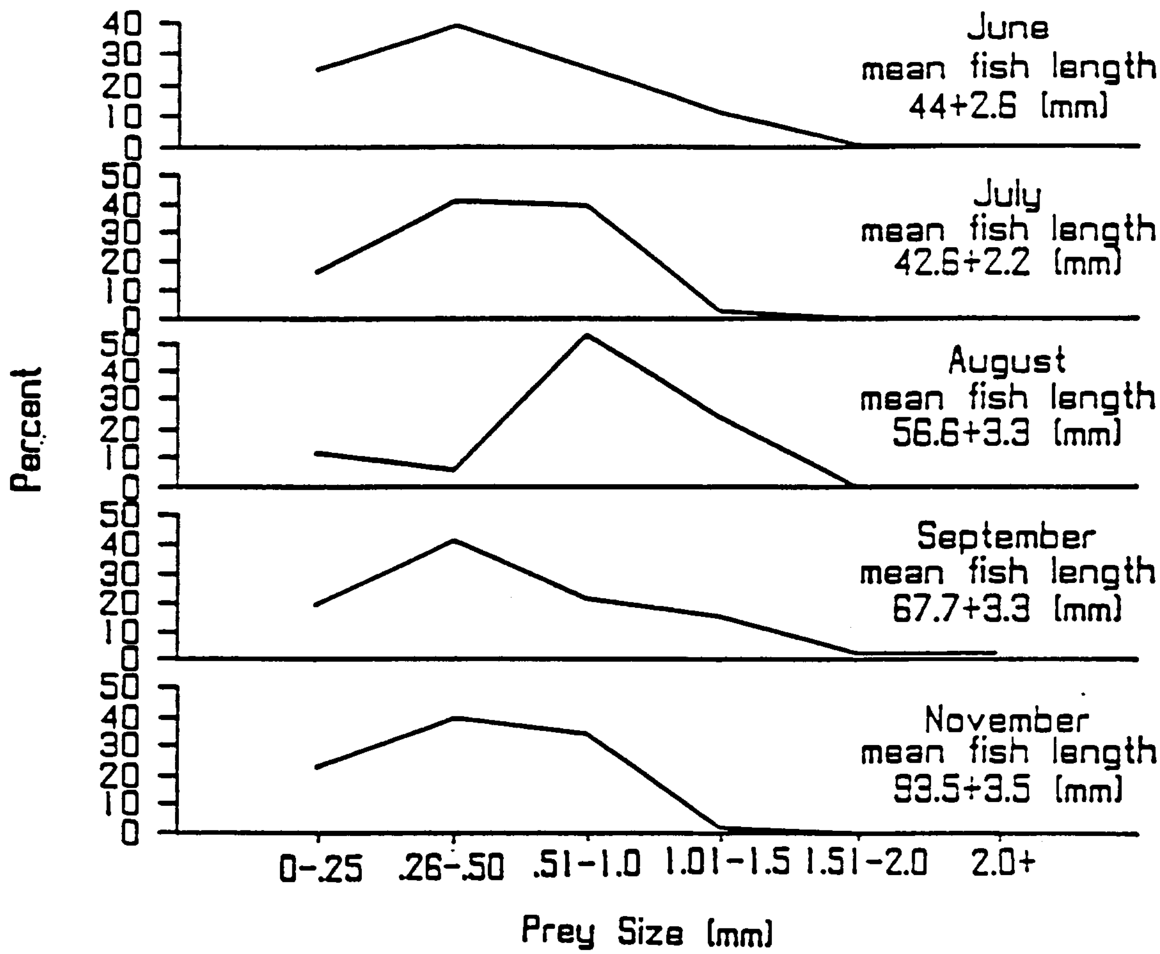

Figure 2. Percent composition of diet by prey size for Little Manistee River steelhead trout collected on each sampling date.

Therefore, it appears that both brown and steelhead trout eat the same taxon and size class of prey in the Little Manistee River where they co-occur.

Monthly Diet Analysis

Within each river system diet overlap and mean headcapsule width of prey items for each trout species were compared between sampling dates to observe changes that may occur from June to November.

Boardman River Brown Trout

Brown trout in the Boardman River did not exhibit the same food habits across the sampling season. Date to date comparisons indicated that overlap of prey taxon was not significant from June through November (Table 16). Prey size also changed between sampling dates. Mean headcapsule width of prey items (Table 17) were found to be significantly different for different dates based on a 1-way analysis of variance. A Student-Newman-Kuels' multiple comparison test found the mean headcapsule width of prey items from each of the sampling dates to be significantly different from one another except for the months of June and November (Table 18). Prey with headcapsules ranging from 0.51 to 1.0 mm were eaten most frequently in all months except June (Figure 3). Therefore, prey in the diets of brown trout in the Boardman River appears to be dependent on the time of season when samples were

Table 16. Diet overlap as indicated by Schoener's index for between month comparisons for each trout species.

Site	Species	Interacting Months	Index
Boardman River (South Branch)	Brown Trout	June-July	0.435
		July-Aug.	0.492
		Aug.-Nov.	0.228
Pere Marquette (Little S. Branch)	Steelhead Trout	July-Aug.	0.628*
Little Manistee River	Brown Trout	July-Aug.	0.686*
		Aug.-Sept.	0.561
		Sept.-Nov.	0.217
Little Manistee River	Steelhead Trout	June-July	0.304
		July-Aug.	0.693*
		Aug.-Sept.	0.680*
		Sept.-Nov.	0.201

* indicates significant values

Table 17. Diet data for each site and species for each sampling date, 1986.

River	Species	Month	No. Fish	No. Prey	Mean Head Capsule (mm)	Standard Error
Boardman River (South Branch)	Brown Trout	June	30	116	0.788	0.043
		July	14	109	0.639	0.034
		Aug.	20	433	0.474	0.048
		Nov.	16	63	0.785	0.051
Little Manistee River	Brown Trout	June	1	5	0.213	0.031
		July	17	256	0.532	0.015
		Aug.	13	147	0.575	0.039
		Sept.	5	249	0.583	0.027
		Nov.	13	44	0.985	0.105
Little Manistee River	Steel-head Trout	June	18	163	0.512	0.028
		July	21	193	1.052	0.720
		Aug.	13	318	0.457	0.014
		Sept.	3	1580	0.581	0.058
		Nov.	10	21	1.739	0.957
Pere Marquette River (Little S. Branch)	Steel-head Trout	July	12	151	0.512	0.026
		Aug.	2	162	0.458	0.019

Table 18. Student-Newman-Kuel's test results for between month comparison of mean prey headcapsule. Months with the same letters are not significantly different.

Site	Species	June	July	Aug.	Sept.	Nov.
Boardman River (South Branch)	Brown Trout	A	B	C	-	A
L. Manistee River	Brown Trout	B	B	B	B	A
L. Manistee River	Steelhead Trout	B	B	B	B	A
Pere Marquete River (Little S. Branch)	Steelhead Trout	-	A	A	-	-

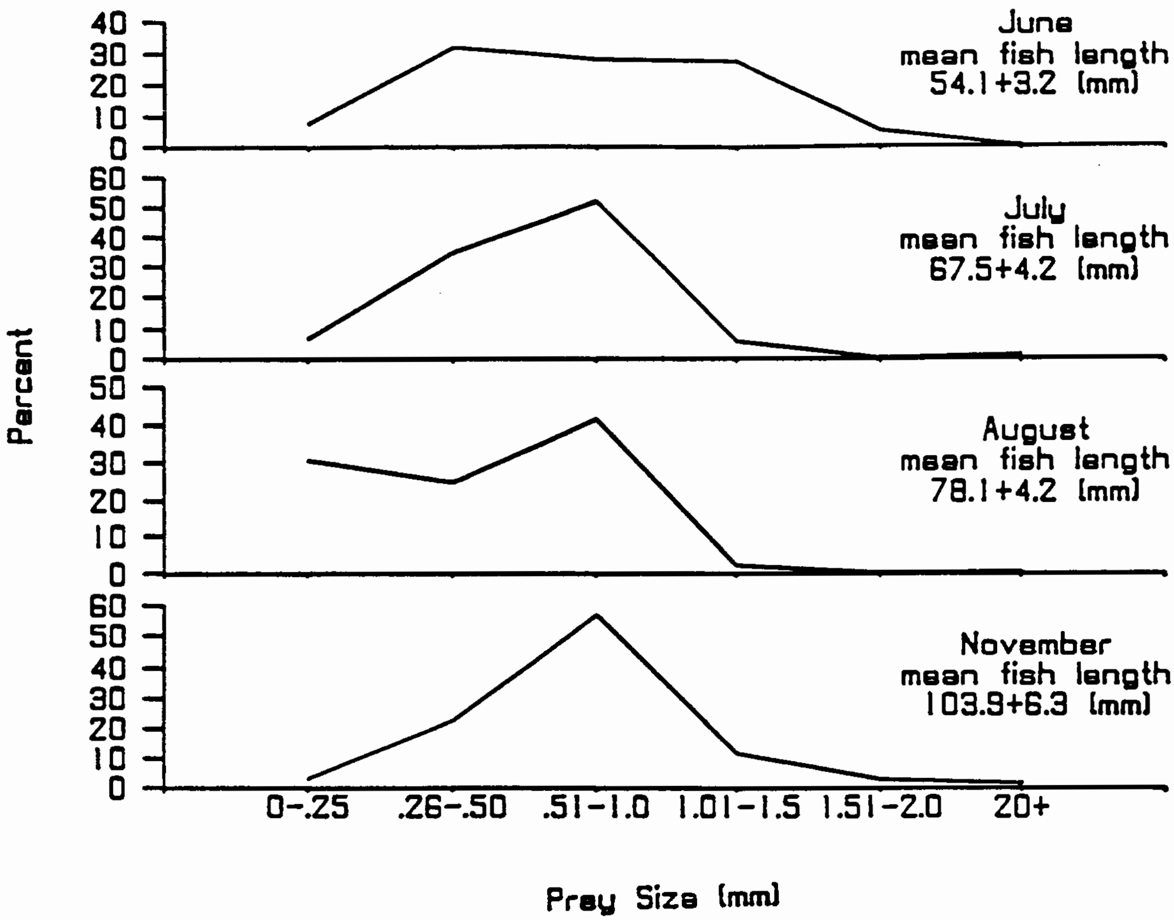

Figure 3. Percent composition of diet by prey size for Boardman River brown trout collected on each sampling date.

collected.

Little Manistee River Brown Trout

Brown trout in the Little Manistee River exhibited relatively consistent food habits across the season. Prey taxon overlapped significantly between the July-August and August-September sampling dates (Table 16). Prey size was found to differ from June to November based on a 1-way analysis of variance procedure. Mean headcapsule width was calculated for each date sampled (Table 17). A Student-Newman-Kuels' multiple comparison test found the mean headcapsule width of prey from the July, August, and September sampling dates to not be significantly different from one another (Table 18). However, headcapsule width of prey from the July sampling date were significantly different from samples collected on the other dates. The majority of prey in the diets had headcapsules less than 1.0 mm in width (Figure 1). There did not appear to be a preference for a particular size class of prey except for during the month of August when prey with headcapsules ranging from 0.51 to 1.0 mm were eaten approximately 60% of the time. Therefore, brown trout in the Little Manistee River eat different taxa of prey items but eat the same size class of prey from July to September.

Little Manistee River Steelhead Trout

Steelhead trout in the Little Manistee River ate a wide variety of taxon and size classes of prey from June to November. Overlap values for comparison of prey taxa from trout collected in June-July and September-November were not significant (Table 16). However, prey taxa did overlap significantly from July to September.

A 1-way analysis of variance on stomach contents indicted that prey size differed across the sampling season. Mean headcapsule widths were calculated for each sampling date (Table 17) and compared with a Student-Newman-Kuels' multiple comparison test. The results of this test found the mean headcapsule width of prey items from the November sampling date to be significantly different from the June, July, August, and September sampling dates (Table 18). The majority of prey found in the diets had headcapsules less than 1.0 mm in width with no particular size class preferentially selected Therefore, steelhead trout in the Little Manistee River exhibit some consistency in food habits between sampling dates but do not preferentially eat particular taxa and size classes of prey.

Pere Marquette River Steelhead Trout

Food habits of steelhead trout were based on a limited sample size (n=14). The size and taxa of prey were consistent between the two dates sampled. Overlap of prey taxa had a value of 0.628 (Table 16) which is significant.

Mean headcapsule widths calculated for each month (Table 17) were not statistically different based on a 1-way analysis of variance procedure. Prey with headcapsules less than 1.0 mm in width were eaten most frequently (Figure 4). Samples from other points in the season may have allowed a more complete analysis of food habits for these trout.

DISCUSSION

Although juvenile brown and steelhead trout commonly co-habit coastal Lake Michigan tributaries little work has been done to measure relations between these species in terms of food, space and growth. Results from this study have been presented in an attempt to describe some aspects of interactions between juvenile brown and steelhead trout in the stream environment.

Habitat Utilization

Brown and steelhead trout have been shown to prefer the same types of stream positions with similar depths, water velocity, and cover (Jenkins 1969, Slaney and Northcote 1974, Shirvell and Dungey 1983). The habitat preferences of juvenile brown and steelhead trout in my study appeared to support this premise. Both species whether allopatric or sympatric were most often found holding positions associated with instream cover,

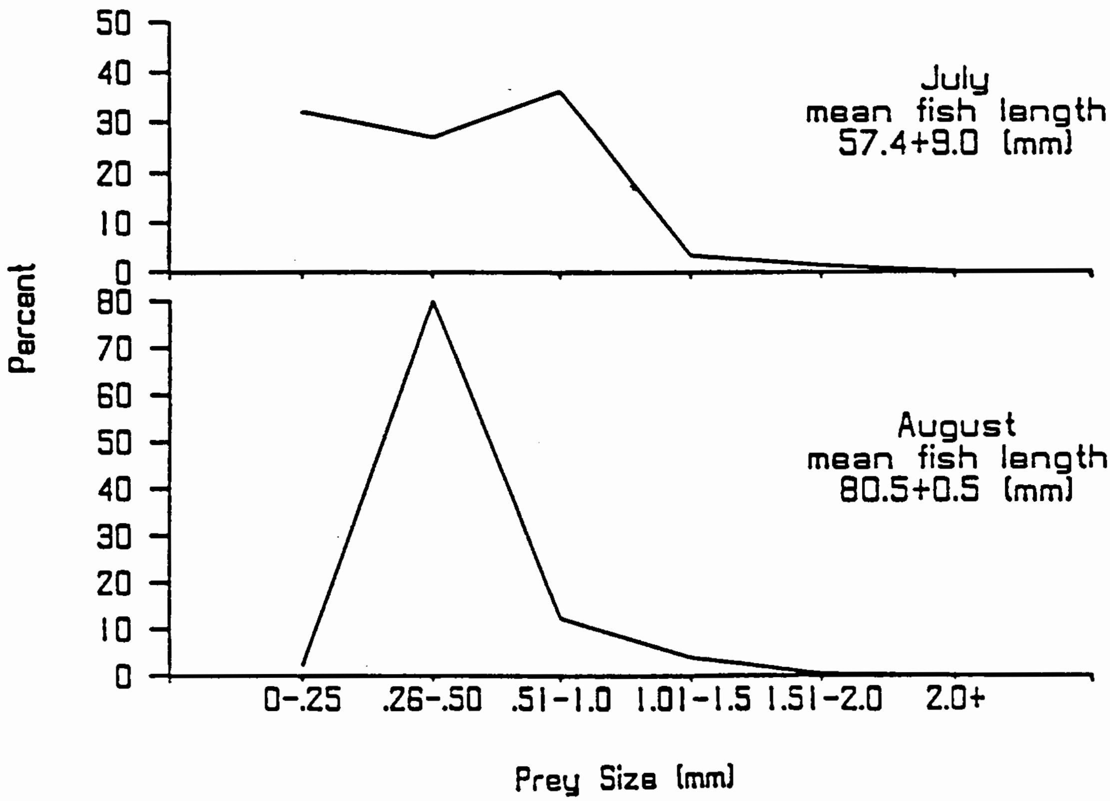

Figure 4. Percent composition of diet by prey size for Pere Marquette River steelhead trout collected on each sampling date.

particularly down timber.

Previous studies investigating habitat use of brown and steelhead trout have produced the same results. Fausch and White (1981) found brown trout associated with cover more often than in open positions of the Au Sable River. Their results indicated a particular preference for undercut banks, natural log jams, and half log habitat improvement structures. Similarly, Hartman (1965) found densities of young steelhead trout to be highest in the upstream reaches of the Salmon River where much of the shoreline was overgrown and covered with fallen trees. Of the instream cover available in these stretches, large log jams were found to have the largest number of steelhead trout associated with them.

Instream cover is of particular importance to trout because it conceals them from predators and shelters them from current (Devore and White 1978, Hartzler 1983). Mortensen (1977) further demonstrated the importance of cover when he found the natural mortality of age 0 brown trout to be higher in streams where cover was removed than in control streams which were not manipulated. In addition, the association with cover has been shown to become more pronounced when the amount of available cover is limited (Cunjak and Power 1986).

Both brown and steelhead trout have been shown in this and previous studies to have similar habitat preferences.

This similarity has created the potential for interaction and competitive relationships to develop between these two species. If the amount of available habitat is limited changes may occur in habitat utilization when brown and steelhead trout are allopatric versus sympatric with one another. This possibility was investigated by statistically comparing the data collected on stream positions of the trout populations in all three study sections.

The results from the logistic regression were used to evaluate the effect of instream cover and other physical parameters on the spatial distribution of brown and steelhead trout when allopatric and sympatric with one another. Intraspecific comparisons of brown trout from the Little Manistee and Boardman Rivers and steelhead trout from the Little Manistee and Pere Marquette Rivers demonstrated that utilization of instream cover and other physical parameters did not differ significantly between river systems for the majority of variables included in the logistic model. Many times the utilization of a particular type of cover or substrate was so infrequent that its significance is difficult to evaluate. Cover and substrate types included in the model very seldom had r^2 values of 0.25 or greater. Therefore, their contribution to the overall explanation of variance was minimal.

Water depth and velocity were important factors in differentiating steelhead trout population habitat preferences in the study sections. Field observations showed that Little Manistee steelhead trout utilized a wider range of depths but were on the average observed in shallower water locations than steelhead trout in the Pere Marquette River. Stream positions held by individual trout from both populations were found to have significantly different average velocity values when the two river systems were compared. Little Manistee steelhead trout were found in faster water than steelhead trout in the Pere Marquette River. However, it is unlikely that depth or velocity alone are the major limiting factors in habitat choice for salmonid species. Kennedy and Strange (1982) found differences in water depth and stream gradient preferences by sympatric Atlantic salmon and brown trout but concluded that neither depth or gradient by themselves could account for the habitat choices exhibited by these species. It is more likely that the combination of depth and velocity effects stream position choice. The differences in depth and velocity measured at the fish's position in this study may have been a function of availability which was different between river systems. The Little Manistee had a higher percentage of open areas which did not provide shelter from the current and a steeper gradient than the Pere Marquette study section.

Brown trout in the Boardman and Little Manistee Rivers did not exhibit habitat preferences which could be utilized to differentiate between their populations. The most important distinguishing factor for these fish was total body length of the individuals. Juvenile brown trout in the Boardman River were significantly larger than those in the Little Manistee River. Werner and Hall (1977) have shown that when two ecologically similar species, bluegill sunfish (Lepomis macrochirus) and green sunfish (Lepomis cyanellus), occur in sympatry, bluegill sunfish growth rate is depressed compared to its growth in allopatry. Brown trout are sympatric with steelhead trout in the Little Manistee River. Due to the similarity in ecological requirements of these two salmonids, the presence of steelhead trout may be the cause of the smaller body size observed in the Little Manistee River brown trout. However, analysis of growth did not show a significant difference between river systems. Brown trout in the Little Manistee and Boardman Rivers exhibited average daily growth rates that were not statistically different form one another. Therefore, the observed differences in total body length for these populations is probably due to the time of fry emergence or some other system specific parameter rather than interaction between brown and steelhead trout.

Interspecific comparisons of sympatric brown and steelhead trout in the Little Manistee River demonstrated that utilization of available habitat and other physical attributes of the trout did not differ significantly between species for all variables included in the logistic model, except for distance from the substrate. Brown trout were only identified correctly 38.8% of the time which indicates that the variables measured in this study have the same values for both brown and steelhead trout. In other words, they appear to have the same habitat preferences when they co-occur in a river system.

Distance from the substrate was the only environmental factor that appeared to be helpful in differentiating between trout species. Steelhead trout occupied positions with a wider range and higher mean value for distance from the substrate than brown trout. However, it is unlikely that this factor alone is essential in determining habitat choice between these species. This is evident by the fact that even when utilizing distance from the substrate in the logistic model brown trout were only correctly classified approximately 38.8% of the time.

Diet Analysis

Brown and steelhead (rainbow) trout exhibit many similar dietary habits. Both species feed on drifting and epibenthic invertebrates and appear to be selective for particular size classes and taxa of prey (Bryan and Larkin 1972, Tippets and Moyle 1977, Ringler 1979, Nilsson and

Northcote 1981). The food habits of juvenile brown and steelhead trout in my study were similar. Larval aquatic insects belonging to the taxonomic families of Chironomidae and Simuliidae were the most abundant items ingested by juvenile trout in the Pere Marquette, Little Manistee, and Boardman River systems. Both sympatric and allopatric brown and steelhead trout selected and ate the same taxonomic groups of insects.

Similarities in dietary taxon have been reported previously for brown and steelhead trout by Wagner (1975). He found significant correlations between diets of yearling rainbow (steelhead) and brown trout in the Platte River of Michigan. Idyll (1942) also presented results which indicated that for brown and steelhead fry and fingerlings (up to 100 mm) there was no difference in food items found in the stomach contents of both species. In contrast, Johnson (1981) showed that dietary overlap between coexisting yearling brown and rainbow (steelhead) trout was not significant for prey taxon in the stomach contents of these fishes. These results, as well as the results of my study, suggest that similarity in dietary behavior does occur between brown and steelhead trout but it may only be evident at particular life stages or size classes of these species.

Size analysis of diet indicated that mean headcapsule width of prey were not significantly different for brown and steelhead trout in the Little Manistee and Boardman Rivers. However, prey ingested by steelhead trout in the Pere Marquette River were on the average smaller than prey ingested by trout in the other study streams. The mechanism behind this difference is unknown as the size range of available prey was not established through forage base sampling in the study sections.

Previous studies investigating size selective predation by brown and steelhead trout have indicated that the preferences of both species are similar. Bisson (1978) found that body size was the most important factor affecting vulnerability of prey to predation by both small (3 g) and large (45 g) hatchery reared rainbow trout. Larger individuals within the prey taxa were found to constitute a greater proportion of the diet than their proportion in the drift. Invertebrates less than 2 mm in size were rarely consumed despite the fact that these smaller size classes constituted the majority of the total drift. Ware (1972) reported similar results in a laboratory study where the density and size of prey were controlled. Four rainbow trout ranging from 134 mm to 170 mm in length were obtained from Marion Lake, B.C. and observed for feeding behavior in his study. The trout selected large prey items over small prey items regardless of the density of each size class in the drift. In addition, his results demonstrated that rainbow trout were capable of locating large prey from greater distances than small prey. Ware suggested that visual location of prey was the controlling factor determining the dietary preferences of these fish.

Size selective predation by brown trout has been investigated by Ringler (1979). He designed a laboratory study to determine the effect of prey size, density, and distribution on the feeding behavior of wild brown trout. His results indicated that selective predation by brown trout was most directly related to prey size. Large food items were preferentially ingested over small prey items regardless of the abundance or distribution of the smaller items. Therefore, body size appears to be the most important factor in determining the vulnerability of prey to predation by both brown and steelhead (rainbow) trout.

It is evident from data presented in this study and previous studies that juvenile brown and steelhead trout utilize the same size and taxon of prey resources. This similarity has created the potential for interaction and competitive relationships to develop between these two species. One species may limit the amount or type of prey available to another species and subsequently cause changes in the resource utilization of the subordinate species. Shifts in resource use by species when similar forms are present provide evidence for the action of competition in structuring communities.

Data in this study did not indicate changes in food habits when brown and steelhead trout were allopatric versus sympatric. Therefore, interaction or competition for food resources does not appear to occur.

Temporal segregation of food utilization was investigated by observing seasonal variation in dietary habits. This was accomplished by comparing gut contents of individuals collected from the same populations between sampling dates. Taxonomic dietary overlap was not found to be significant for the majority of between sample comparisons for both allopatric and sympatric brown and steelhead trout (Table 16). However, mean headcapsule width of ingested prey items were not found to be significantly different between sampling dates for all trout populations except Boardman River brown trout. This suggests that size, rather than taxonomy, is the more important factor in the food selection of both brown and steelhead trout in this study. Differences in taxon utilization between sampling dates may be a mechanism which allows coexistence of brown and steelhead trout. However, it is more likely the result of differences in prey availability due to emergence of various aquatic and terrestrial insects. Changes in taxon utilization would only need to occur when these species are sympatric for it to act as mechanism for coexistence. In this study, taxon utilization changed from date to date for both allopatric and sympatric brown and steelhead trout which indicates these changes were probably due to prey availability.

Conclusions and Future Research

The potential of interaction or competition for stream resources between juvenile brown and steelhead trout exists. Both species ingest the same types and sizes of prey and have similar space requirements. This overlap of resource utilization did not appear to substantially effect the growth and survival of the young-of-the-year trout examined. However, in aquatic systems where resources are limited it is likely that interaction between brown and steelhead trout may affect the population dynamics of one another.

Evidence of a population level response to interaction between brown and steelhead trout was not documented in this study. However, there was a difference in population size structure observed between brown trout in the Boardman and Little Manistee Rivers. Trout measuring 203 mm to 254 mm in length were much more abundant in the Boardman River than in the Little Manistee River. Previous researchers have also observed the same distribution of sizes in the Little Manistee River during the course of their studies (Paul Seelbach, Mich. Dept. Nat. Res.).

Further research needs to be conducted to investigate the possible mechanisms that influence size structure of trout populations. The results of this study do not indicate a specific population controlling mechanism which influences juvenile trout during their first summer of life. However, interaction between brown and steelhead trout may affect over-winter survival or have more pronounced affects on these species at later points in their life history. Future research should be designed to investigate population controlling mechanisms of brown and steelhead trout and to determine the results of interaction between these ecologically similar species throughout their life history.

Summary

Juvenile brown and steelhead trout in the Little Manistee, Pere Marquette, and Boardman Rivers were found to utilize the same food and space resources. Both species ate primarily chironomid and simulid larvae which were approximately the same size. Steelhead trout in the Pere Marquette River did ingest smaller prey compared to the other trout populations. However, these data were based on a limited sample size.

Analysis of habitat utilization indicated that both brown and steelhead trout are commonly associated with cover, particularly down timber. No major differences in utilization were observed for sympatric versus allopatric populations of these trout. However, differences in physical parameters such as depth and velocity did allow distinction to be made between trout populations from different rivers. Sympatric brown and steelhead trout were difficult to classify into species categories through the measurement of physical and biological variables as there was little difference in the values of these variables between species.

In general, sympatric populations of brown and steelhead trout did not appear to exhibit niche shifts from those observed for allopatric populations. Growth of both species was the same regardless of their distribution (allopatric or sympatric). The only indication that interaction between these species may have a negative effect is in relative abundance. The abundance of sympatric brown trout diminished across the season and was on the average lower than that of the allopatric population. This observation may be the result of inherent variability in between river comparisons but interaction with steelhead trout may also play a role in the regulation of brown trout populations. In order to evaluate this possibility, it is necessary to manipulate the density of steelhead trout and observe the responses of the sympatric brown trout population.

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