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Evaluation of Juvenile Brown Trout and Steelhead Competition in the Great Lakes Tributaries

John F. Kocik

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John F. Kocik

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EVALUATION OF JUVENILE BROWN TROUT AND STEELHEAD
COMPETITION IN GREAT LAKES TRIBUTARIES

by

John Francis Kocik

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

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Department of Fisheries and Wildlife

1992

ABSTRACT

EVALUATION OF JUVENILE BROWN TROUT AND STEELHEAD COMPETITION IN GREAT LAKES TRIBUTARIES

by

John Francis Kocik

The importance of competition between steelhead (Oncorhynchus mykiss) and brown trout (Salmo trutta) was determined in a three part project. Field and laboratory experiments assessed the effects of introducing steelhead fry on brown trout growth, survival, and habitat use. I examined brown trout abundance, survival, size, growth, and condition in allopatry and in sympatry with steelhead in Gilchrist Creek, Michigan and in an artificial stream. In the field, I established a test and control section on the stream. I measured the abundance and vital statistics of salmonines at these stations during 1989. In 1990 and 1991, steelhead fry were scatter-stocked in the test section. From 1990 to 1992, I continued population assessments. Laboratory trials assessed the impact of age-0 steelhead upon age-0 brown trout in a completely randomized design. Four replicate cells contained 14 allopatric brown trout and 4 cells contained 7 sympatric brown trout with 7 steelhead. In field and laboratory studies, the impact of steelhead was negligible. Steelhead had no impact on brown trout abundance or survival. Steelhead had a minor impact on brown trout growth in Gilchrist Creek. However, the impact had little effect on brown trout size, relative to

intraspecific and abiotic factors. In the artificial stream, I observed no impact on growth. The earlier emergence times of brown trout gives them a size advantage over steelhead. This size advantage decreases over time since steelhead grow faster. At the post-emergence stage, these species appear to interact to the detriment of steelhead. However, if emergence times become closer, the advantage of brown trout over steelhead may be lost. These studies indicated that steelhead superimposition of brown trout redds and factors narrowing the emergence gap between these species may adversely impact brown trout. Habitat use of these species was similar. Water depth, cover, and substrate used during the age-0 growing season was not significantly different. Steelhead did use slower mean column velocities. Steelhead were suspended in the water column whereas brown trout were benthic. Despite overlap in habitat use, no difference in brown trout habitat occurred between sympatry or allopatry. Vertical stratification of these species may reduce interactions during the age-0 growth period.

To Linda

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CHAPTER 1

COMPETITION BETWEEN BROWN TROUT AND STEELHEAD IN A GREAT LAKES TRIBUTARY

ABSTRACT

I examined competitive interactions between juvenile (age-0 and age-1) steelhead (Oncorhynchus mykiss) and brown trout (Salmo trutta) in Gilchrist Creek, Michigan. I assessed the abundance and vital statistics of allopatric juvenile brown trout in two stream sections (test and control) in 1989. In 1990 and 1991, steelhead fry were scatter stocked in the downstream test section. After these introductions, I continued population assessments in both sections. Steelhead populations established were generally low but within the range found in the region. There was no measurable impact of steelhead on juvenile brown trout abundance, survival, or size. There was an effect of steelhead on age-0 brown trout growth, but it was insufficient to counter year-to-year size variations. Brown trout were larger at emergence, which was probably a major factor in their successful interactions with juvenile steelhead. However, higher steelhead growth rates diminished this difference over the first growing season. If factors such as spawner-alevin interactions, differing emergence times, and climactic variability alter the initial size advantage of brown trout, the result of juvenile competition may be altered. Future research should be focused on quantification of these other parameters.

INTRODUCTION

The indigenous salmonid fauna of Michigan rivers consisted of grayling (Thymallius tricolor) and brook trout (Salvelinus fontinalis). Habitat destruction, overfishing, and the introduction of exotic species led to the extinction of Michigan grayling and decimation of brook trout stocks (Kruger 1985; Kruger et al. 1985). In response to the decline of these fish, fishery biologists have introduced numerous salmonines to Michigan streams since the late 1800's (Parsons 1973). Currently, a multispecies salmonine complex exists in Michigan tributaries of the Great Lakes and the region as a whole, consisting of the brook trout and six exotic species (Table 1). Thus, the result of stocking, colonization, and range expansion has been that most streams contain exotic species or reestablished stocks of native species (Parsons 1973; Kruger et al. 1985).

The introductions have resulted in salmonine species combinations unique to the Great Lakes region since several species do not co-occur in their native distributions. These species have similar ecological requirements that could potentially foster interspecific competition (Jones 1991). Hearn (1987) and Fausch (1988) both conducted

Table 1. Salmonines that use riverine environments and their predominant life-history patterns in the Great Lakes Region. Riverine fish complete their life-cycle in river systems. Migratory fish exhibit predictable movement from riverine to Great Lakes' lacustrine ecosystems. References cited in table: a)MacCrimmon and Marshall 1968; b)Biette et al. 1981; c)Kruger et al. 1985; d)Kocik and Taylor 1987; e)Jones 1991.

Common Name	Scientific Name	Life History
pink salmon	<u>Oncorhynchus gorbuscha</u>	migratory ^d
coho salmon	<u>Oncorhynchus kisutch</u>	migratory ^d
steelhead	<u>Oncorhynchus mykiss</u>	migratory ^b
Chinook salmon	<u>Oncorhynchus tshawytscha</u>	migratory ^d
brook trout	<u>Salvelinus fontinalis</u>	riverine ^{a,c}
Atlantic salmon	<u>Salmo salar</u>	migratory ^e
brown trout	<u>Salmo trutta</u>	riverine ^{a,c}

extensive reviews of competition between stream salmonines. Both authors stress the importance of coevolution in the successful resource partitioning of sympatric salmonine populations. Given these facts, tributaries with salmonine species from different geographic origins are prime candidates for competitive interactions that may be detrimental to the success of one or both species.

The effects of salmonine competition in Great Lakes tributaries has received limited attention. Carl (1983) examined relative abundance of chinook salmon, coho salmon, and steelhead. He found no evidence of negative interactions between these species. He attributed limited

competition to spatial and temporal segregation. Fausch (1984) and Fausch and White (1986) examined competition between brook trout, brown trout, and coho salmon. Both studies reported that coho salmon exhibited competitive superiority for food and space over brook trout and brown trout. Competition between brown trout and brook trout was dependent upon age, size, and temperature (Fausch and White 1986). However, brown trout were typically dominant over brook trout (Fausch and White 1981).

Knowledge of competition between brown trout and steelhead would enhance our understanding of stream salmonines in Great Lakes tributaries. These salmonines have been established in the Great Lakes region the longest (over 100 years), and many populations are naturally reproducing (MacCrimmon and Marshall 1968; Biette et al. 1981; Seelbach 1987). Successful colonization has resulted in both species becoming well distributed throughout the Great Lakes region (MacCrimmon and Marshall 1968; Seelbach 1987). Life-history differences make knowledge of their interrelationships important since each species represents distinctive ecological and fishery resources.

Brown trout in the Great Lakes typically utilize streams for their entire life-history (MacCrimmon and Marshall 1968). A few migratory populations exist, but these are rare in Great Lakes populations (Scholl et al. 1984). Brown trout provide a unique resource, spending

their entire life in the riverine environment. With the demise of indigenous salmonines, brown trout represent the only riverine-resident salmonine in many systems (MacCrimmon and Marshall 1968). As the largest fish in many of these coldwater systems, they may influence ecosystem structure and function (Alexander 1979). Brown trout also sustain year-round fisheries in many Great Lakes tributaries (Kruger et al. 1985).

Steelhead in the Great Lakes are migratory; they use the riverine environment for spawning and juvenile nursery areas until age-2 (Biette et al. 1981; Seelbach 1987). Their distribution overlaps with brown trout in streams that flow unobstructed into the Great Lakes. Steelhead also provide an important and distinct fishery resource (Kruger et al. 1985). A factor contributing to their importance as a fishery resource is their extended adult residence in stream environments prior to spawning (Biette et al. 1981). As such, the loss of either of these species would represent a change in the structure of these ecosystems and their fishery resources from past decades.

In the early 1980's, anglers indicated that they felt there had been a decline in the quality of the Pere Marquette River brown trout fishery (Kruger et al. 1985). Kruger (1985) observed an inverse relationship between brown trout and steelhead abundance in the Pere Marquette River from 1970-1983. In addition, brown trout growth in size

classes equivalent to steelhead parr (< 200 mm) was below the state average. However, once brown trout exceed the size at which steelhead outmigrate, their growth rates were above the state average. Kruger (1985) suggested that competition between these species might be occurring at the juvenile stage.

Ziegler (1988) examined age-0 brown trout and steelhead food habits and habitat use in one sympatric and two allopatric populations. She concluded that the species used similar habitats and food but found no differences in either parameter in sympatry or allopatry. She also noted no difference in relative abundance of age-0 fish in allopatry or sympatry (Ziegler 1988). However, age-1 brown trout were more abundant in allopatric than sympatric populations. She suggested that competition between these fish might occur during their first winter to the detriment of brown trout growth and survival.

Understanding the potential interactions between steelhead and brown trout is important. Both species have many naturally reproducing populations that provide distinct and highly valuable sport fisheries (Kruger 1985). To manage streams for optimal populations of salmonines, biologists need to know if competitive interactions occur. In addition, ascertaining the life-history stage and mode of competition will contribute to a clearer understanding of sympatric salmonine ecology.

The goal of this research is to determine the extent and mode of competition between juvenile (age-0 and age-1) steelhead and brown trout. I define competition as the negative impact of the presence of one species on the population dynamics of another species. I hypothesize that juvenile steelhead compete for resources with brown trout to the detriment of juvenile brown trout. Analyses of the brown trout population parameters of density, survival, growth, and condition should provide evidence of the impact of juvenile steelhead.

I measured brown trout population parameters in Gilchrist Creek in the northern lower peninsula of Michigan for three years. In the first year of the study (1989), I examined the stream in its current state: exclusively brown trout. In the second and third years of the study, I introduced steelhead to the downstream section of Gilchrist Creek. In this chapter, I describe the results of this introduction.

METHODS

Study Site

Gilchrist Creek is a second order coldwater stream located in Montmorency County, Michigan (Figure 1). The creek flows northeast through forested land into the Thunder Bay River and Lake Huron. The soils in this region are primarily glacial sands, and infiltration into deep aquifers maintains highly stable flow regimes (P. Seelbach, MDNR pers. comm.). Primary substrates are sand with long expanses of gravel. This stream type is typical of many Michigan Great Lakes tributaries harboring brown trout and steelhead.

I selected the stream based upon its high brown trout abundance and isolation from migratory Great Lakes salmonines due to downstream dams on the river system. Brown trout have been the predominant salmonine species in the stream since at least the 1960's (Gowing, MDNR, Unpublished data). Within Gilchrist Creek, I established two study sections. Section 1 was the upstream control section; section 2 was the downstream test section (Figure 1). The two study sections were 2 km apart. Within each study section, I established three 100 m study reaches separated by 25 m buffer zones.

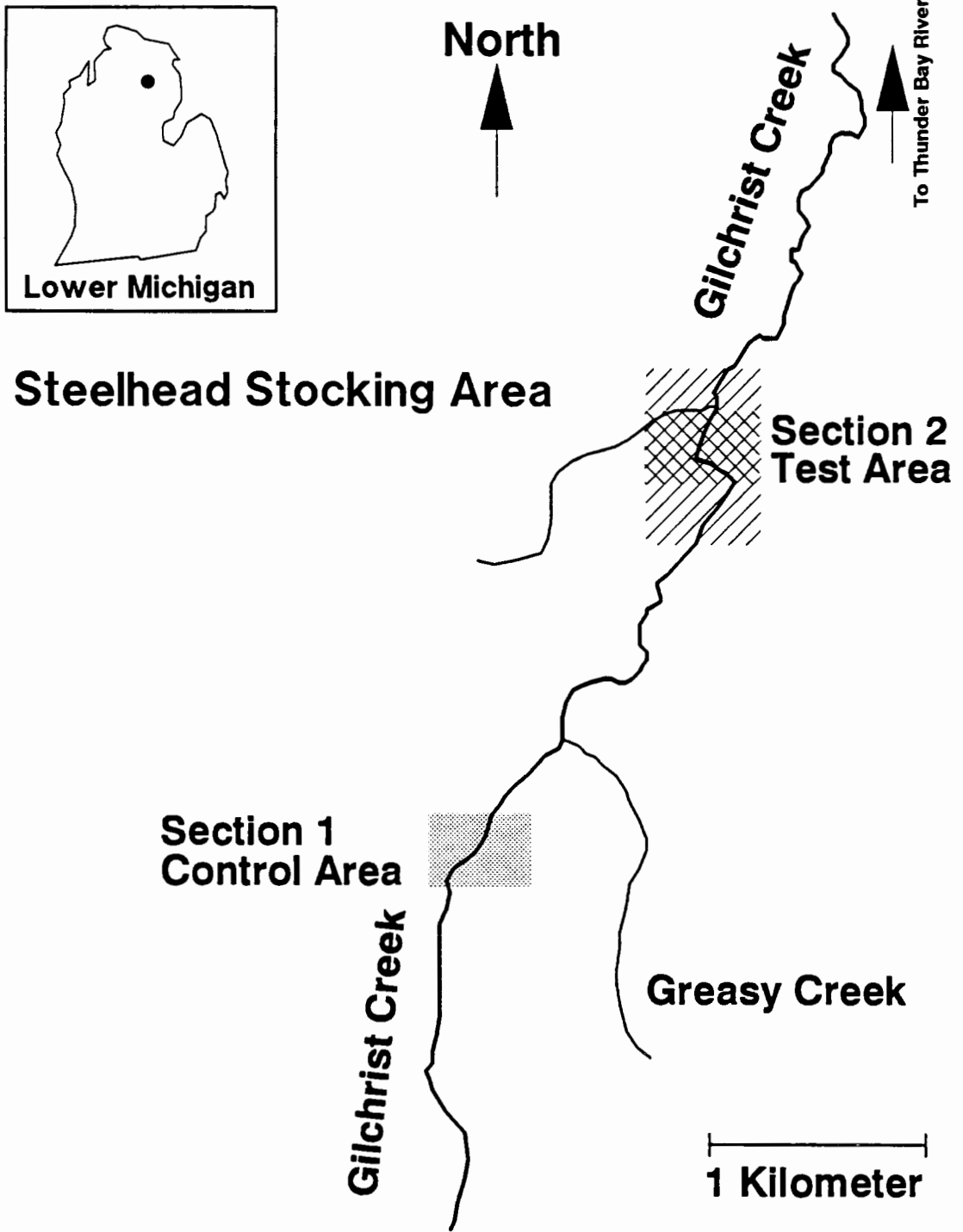


Figure 1. Location of Gilchrist Creek and test and control areas.

Study Design:

The structure of this experiment quantifies competitive impacts of steelhead upon brown trout population dynamics. This was accomplished by comparing juvenile brown trout (below age-2) abundance, survival, growth, and condition in allopatry and in sympatry with introduced steelhead. I collected baseline population data from sections 1 and 2 starting in June 1989. At this point, both sections contained allopatric brown trout populations (pre-treatment). In the spring of 1990, I introduced steelhead fry into section 2 of Gilchrist Creek, making it a sympatric (test) treatment. Section 1 remained an allopatric (control) brown trout population. I continued post-treatment population assessments through June 1992 to measure steelhead impacts upon brown trout. I tested the impact of steelhead upon brown trout using pre- versus post-treatment comparisons within sections and between-section comparisons (test versus control) within years.

Steelhead Introduction:

To simulate natural steelhead colonization, I stocked steelhead swim-up fry in 1990 and 1991. Since it was impractical and undesirable to impede within-stream fish movements, I used knowledge of steelhead behavior to isolate them in only one of the two study sections. Steelhead fry dispersion is reported to be minimal and predominantly

downstream (Hume and Parkinson 1987, 1988). By stocking steelhead only in the downstream area surrounding section 2 (test area), I successfully isolated allopatric and sympatric populations. We stocked a total of 700 m of stream length inclusive of section 2 (Figure 1).

I could not locate any post-emergence population estimates of steelhead fry for Great Lakes tributaries. Therefore, I used fall population densities to calculate stocking rates. The fall densities of age-0 fry in the Great Lakes region range from 681 fish/ha to 43,771 fish/ha (Seelbach 1986). Reviewing these data, I determined that a fall density of 3,500 steelhead/ha to be a realistic target for Gilchrist Creek. I based this value on steelhead densities in nearby streams with similar habitat availability and stream productivity (P. Seelbach, MDNR pers. comm.).

With the fall target density established, I examined reports of fry stocking survival. Hume and Parkinson (1987) summarized data from fry stocking for steelhead, Atlantic salmon, and brown trout from 10 studies. Using these data, I predicted steelhead survival from stocking to fall would be about 10%. I then used this survival rate to calculate spring stocking rates. Actual 1990 stocking densities were 35,534 fry / ha. In 1991, I used survival data from 1990 (minimum 2.5 %) to calculate stocking densities. In 1991, I stocked 242,415 fry /ha.

I obtained steelhead fry from the Michigan Department of Natural Resources (MDNR) Wolf Lake Hatchery. These fry were progeny of wild steelhead collected at the Little Manistee River. We transported fish to Gilchrist Creek and released them in stream margins in the center of each 100 m² surface area (unit) of stream within the stocking section (Wentworth and La Bar 1984). On 30 May 1990, steelhead fry averaging 25.5 mm (\pm 0.199 S.E.) and 0.122 g (\pm 0.003 S.E.) were stocked at a rate of 355 fry per unit. In 1991, average fry size was 27.1 mm (\pm 0.212 S.E.) and 0.143 g (\pm 0.004 S.E.). Fry were stocked at a rate of 2424 fry/unit on 23 May.

Salmonine Population Assessments

I collected population data from June 1989 to 1992. Procedures were the same before and after steelhead introduction. Assessments were made three times a year: post salmonine emergence (June), post growing season (October), and late winter (February). I conducted assessments within each 100 m study reach.

Abundance estimates were made using the Petersen mark-recapture method with a 250 volt D.C. electrofishing unit (Ricker 1975; Peterson and Cederholm 1984). A 24-hour redistribution period separated the marking and recapture runs. I marked all salmonines using a site-specific partial fin clip. Salmonines collected on the marking run were

measured for total length (mm) and weight (g). On the recapture run, all fish were measured for total length and only unmarked fish were weighed. Using this protocol, I could calculate cohort population estimates, and sample sizes for vital statistics were maximized. I collected scales from all fish during the October collection and from all fish over 150 mm during other collections. Fish were aged using length-frequency analysis and scale reading (MacDonald 1987). This procedure allowed separation of fish into age groups.

I calculated salmonine abundance by age class for each species in each study reach using Chapman's adjusted Petersen estimate (Ricker 1975). Using these data, the instantaneous mortality rate (Z) was calculated for each age class and study reach. The following equation was used (Ricker 1975):

$$Z = -(\log_e N_{t+1} - \log_e N_t)$$

Where:

Z = instantaneous mortality rate
 N_{t+1} = population estimate of study reach at time $t+1$
 N_t = population estimate of study reach at time t

Z was calculated for age-0 and age-1 fish on a seasonal basis. Growing season mortality was estimated using June and October abundance. Winter mortality reflected losses from October to the following February. Spring mortality quantified losses from February to June. Since the number

of steelhead stocked was also known, I calculated their stocking mortality from initial stocking to June sampling.

Mean lengths were used to calculate instantaneous daily growth rate (μ) for each stream reach. These estimates were also conducted on a seasonal basis. I calculated μ using the following equation (Ricker 1975):

$$\mu = (\log_e TL_t - \log_e TL_{t-1}) / T$$

Where:

μ = instantaneous daily growth rate
 TL = mean total length (mm)
 t = time at the end of growth period
 t-1 = time at beginning of growth period
 T = time interval in days

To assess differences in the condition of salmonines between treatments, ordinary least squares regression of the weight (W) on total length (TL) was used ($\log_e W = \log_e a + b \log_e TL$) as recommended by Cone (1989). This method is unbiased since the slope of an ordinary least squares regression can be used as the condition index (Cone 1989). Condition indices were calculated for each study reach by age classes.

Statistical Assessment Methods

The design of this experiment allowed comparisons of juvenile brown trout abundance, survival, growth, and

condition to assess the impact of steelhead. Analyses of these parameters was conducted by cohort. To clarify cohorts and relate changes to life-history periods (ie. post-emergence, post-growing season, and late winter), I assigned the birth date of these fish to be April 15. This date closely corresponds to brown trout emergence from redds. Using this method, age-0 fish were sampled in June, October, and February of their first year of life. By sampling in their second June they would be considered age-1. Using this aging scheme, I conducted analyses separately for age-0 and age-1 cohorts.

I partitioned statistical analysis by month for point estimates (density and size) and by season for rate variables (Z and μ). However, Z and μ are ratio data that are not typically normally distributed. To account for non-normality, I transformed these data using the RT-1 procedure (Conover and Iman 1981). To examine the differences in brown trout between test and control sections in Gilchrist Creek, I used analysis of variance (ANOVA) and selected sets of single degree-of-freedom contrasts (Steel and Torrie 1980). I designed contrasts to test biologically meaningful hypotheses (Table 2). Three comparisons examined differences between sites within years (test versus control). The final two compared pre- versus post-treatment effects within a section. I set the significance levels for ANOVA's at $\alpha = 0.05$ and used the Bonferroni routine to

adjust for non-orthogonal contrasts (Ott 1988). Using this routine, an error rate of $\alpha = 0.01$ was used for these contrasts.

I tested for differences in condition between test and control sections within sampling periods using analysis of covariance (ANCOVA). Using this design, ANCOVA compared slopes (condition index) for significant ($\alpha = 0.05$) differences (Snedecor and Cochran 1982). This test allowed effective comparisons of fish condition between reaches and sections. To determine which reaches were significantly different, I used a Tukey-Kramer multiple comparison test (Miller 1986).

Effects of Salmonine Density on Brown Trout Size

To further discern differences between the impact of steelhead on brown trout, I constructed a multiple regression model. This model examined the relationship between brown trout total length (Y) and brown trout density (X1) and steelhead density (X2). I constructed separate models for age-0 and age-1 brown trout and steelhead from site 2.

Table 2. Selected sets of single degree-of-freedom linear contrasts used to test for the effect of steelhead upon juvenile brown trout population parameters. The numbers correspond to data comparisons made. Across rows sum equals 0. Data values with different signs are the comparisons being made.

Comparison	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Age-0	1989 Cohort		1990 Cohort		1991 Cohort	
<u>Between Sites by Year</u>						
1989	-1	1	0	0	0	0
1990	0	0	-1	1	0	0
1991	0	0	0	0	-1	1
<u>Pre- vs Post-Treatment</u>						
Site 1	2	0	-1	0	-1	0
Site 2	0	2	0	-1	0	-1
Age-1	1988 Cohort		1989 Cohort		1990 Cohort	
<u>Between Sites by Year</u>						
1989	-1	1	0	0	0	0
1990	0	0	-1	1	0	0
1991	0	0	0	0	-1	1
<u>Pre- vs Post-Treatment</u>						
Site 1	-1	0	-1	0	2	0
Site 2	0	-1	0	-1	0	2

RESULTS

Steelhead Introduction and Population Assessment:

Steelhead stocking proceeded well in both years. Transport mortality was low ($< 0.03\%$). Temperature conditions were excellent with the average stream temperature and average bag temperature varying by no more than 0.3°C . Fry showed no stress and swam immediately to cover upon release. Stocking of steelhead swim-up fry established steelhead cohorts in the test section of Gilchrist Creek in both years. Steelhead were not found in the control section.

The population densities and mortality patterns of age-0 steelhead were similar between 1990 and 1991 (Table 3). Analysis of steelhead density using ANOVA found no significant differences in population density ($P > 0.05$) in June, October, or February samples between years. Age-0 steelhead density averaged 4620 fish in June, 1781 fish/ha in October and 368 fish/ha in February. No significant differences were noted in summer or winter instantaneous mortality rates between the two years ($P > 0.05$). Instantaneous mortality in the growing season averaged 1.06 while in the winter it averaged 1.57. However, stocking to June mortality was significantly higher in 1991 (4.31) than

Table 3. Steelhead abundance (S.E.- standard error) and corresponding instantaneous mortality rates (Z) for 1990 and 1991 cohorts in the test section of Gilchrist Creek. P represents the significance level of ANOVA comparisons of cohort Z values.

Sampling Period	1990 Cohort			1991 Cohort			P
	Abundance		Z	Abundance		Z	
	#/ha	(S.E.)		#/ha	(S.E.)		
Stocking	35534			242415			
June	4982	(1288)	2.03	4259	(1656)	4.31	0.03
October	2366	(1564)	1.11	1196	(171)	1.01	0.94
February	250	(157)	2.24	486	(79)	0.90	0.35
June	260	(66)	-0.42				
October	197	(26)	0.26				
February	92	(26)	0.78				

it was in 1990 (2.03) ($P < 0.05$).

Steelhead fry size and instantaneous growth rates were similar between 1990 and 1991 cohorts (Table 4). Fry were stocked at a significantly larger size in 1991 (27.1 mm) than in 1990 (25.5 mm). This initial size difference ($P < 0.05$) was maintained in June where age-0 steelhead averaged 37.8 mm in 1990 and 41.9 mm in 1991. However, by October and February, age-0 steelhead were not significantly different between years as summer growth rates were significantly ($P < 0.05$) higher in 1990 (0.0070) than in 1991 (0.0055). This growth difference was apparent only in summer growth. No significant differences in growth occurred during the winter period ($P > 0.05$).

Table 4. Steelhead total length (TL) and weight (WT) and corresponding instantaneous growth rates for 1990 and 1991 cohorts in test section of Gilchrist Creek.

Sampling Period	1990 Cohort			1991 Cohort		
	TL mm S.E.	WT g S.E.	Inst. Growth	TL mm S.E.	WT g S.E.	Inst. Growth
Stocking	25.5 0.20	0.12 0.003		27.1 0.21	0.14 0.004	
June	37.6 0.32	0.46 0.025	0.0158	41.1 0.50	0.67 0.029	0.0135
October	77.7 0.84	4.53 0.150	0.0070	80.4 1.20	4.98 0.268	0.0055
February	83.6 2.08	5.16 0.415	0.0008	84.8 1.45	5.35 0.291	0.0005
June	138.3 2.07	25.04 1.254	0.0034			
October	164.3 3.56	38.17 2.805	0.0015			
February	168.3 5.36	41.43 4.073	0.0001			

Brown Trout Abundance and Mortality

Age-0 brown trout abundance was not significantly different ($P > 0.05$) in June or October samples for any contrast (Table 5; Appendix 1). Differences did exist in February samples. Abundance of the 1989 cohort was higher in site 2 than in site 1 ($P < 0.005$). Brown trout density in site 1 averaged 1,656/ha, while site 2 densities averaged 2,892/ha. The high abundance in site 2 also contributed to a significant difference in pre-treatment versus post-

Table 5. Average abundance of age-0 brown trout per hectare and standard error (S.E.) in control (site 1) and test (site 2) sections of Gilchrist Creek for 1989-1991 cohorts. The * denotes presence of same age steelhead cohort.

Sampling Period	1989 Cohort		1990 Cohort		1991 Cohort	
	Site 1	Site 2	Site 1	Site 2*	Site 1	Site 2*
	#/ha S.E.	#/ha S.E.	#/ha S.E.	#/ha S.E.	#/ha S.E.	#/ha S.E.
June	23110	118710	4115	5627	6481	4825
	14014	104183	1196	1039	1223	1867
October	5627	1998	1919	3116	2472	1814
	3326	329	263	657	500	421
February	1656	2892	1196	1643	1670	1117
	224	316	237	329	263	79

treatment contrasts ($P < 0.001$). These post-treatment densities averaged 1,643/ha and 1,117/ha for 1990 and 1991 cohorts.

Analysis of instantaneous mortality rates supported observations of density analysis. Summer mortality was not significantly different ($P > 0.05$) for any contrasts (Table 6; Appendix 1). Age-0 winter mortality was significantly different ($P = 0.002$) in the between-site comparison for 1989. In February 1989, instantaneous mortality rates were 0.38 in section 2 as compared to 0.90 in section 1. Pre-versus post-treatment comparisons for section 2 were also significant ($P = 0.002$). These differences were caused by high brown trout abundance in the test section during February 1990. Two of the three reaches in site 2 exhibited this trend.

Table 6. Instantaneous mortality (Z) rates for age-0 brown trout cohorts 1989-1991 in control (site 1) and test (site 2) sections of Gilchrist Creek. Summer represents June-October. Winter represents October-February. Spring represents February-June. The * denotes presence of same age steelhead cohort.

Season	1989 Cohort		1990 Cohort		1991 Cohort	
	Site 1	Site 2	Site 1	Site 2*	Site 1	Site 2*
Summer	1.33	2.93	0.69	0.60	0.97	0.88
Winter	0.90	0.38	0.48	0.63	0.38	0.44
Spring	0.11	0.83	0.16	0.92		

Spring mortality was significantly ($P < 0.001$) higher in the test section than in the control section for both 1989 and 1990 cohorts. However, I found no significant differences in comparisons between pre- and post-treatment periods for the section 1 ($P = 0.738$) or section 2 ($P = 0.443$).

For age-1 brown trout, densities were not significantly different ($P > 0.05$) for any between site comparisons within years (Table 7; Appendix 1). However, pre- and post-treatment comparisons of cohorts for section 1 were significant. The 1988 and 1989 age-1 brown trout cohorts were more abundant in June, October, and February samples than was the 1990 cohort ($P < 0.010$). Since these differences occurred in the control section, factors other than steelhead were responsible for the change in overall age-1 abundance.

Table 7. Average abundance of age-1 brown trout per hectare and standard error (S.E.) in control (site 1) and test (site 2) sections of Gilchrist Creek for 1988-1990 cohorts. The * denotes presence of same age steelhead cohort.

Sampling Period	1988 Cohort		1989 Cohort		1990 Cohort	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2*
	#/ha S.E.	#/ha S.E.	#/ha S.E.	#/ha S.E.	#/ha S.E.	#/ha S.E.
June	3563	841	1499	1302	999	1643
	1328	234	250	276	105	329
October	1209	592	999	776	933	670
	158	53	39	105	184	157
February	868	171	762	460	868	644
	184	53	158	53	105	184

Analysis of instantaneous mortality rates yielded somewhat different results (Table 8; Appendix 1). Summer and spring mortality rates were not significantly different ($P > 0.01$) for any contrast. The only instantaneous mortality rate that was significant was the section 2 comparison pre- versus post-treatment ($P = 0.005$). This difference was driven by the extremely low instantaneous mortality rate of the 1990 cohort in the winter of 1991-1992 (0.045). As a result, survival was higher in sympatry with age-0 steelhead in section 2. The effect of steelhead on age-1 abundance appears to be insignificant.

Table 8. Instantaneous mortality (Z) rates for age-1 brown trout cohorts 1988-1990 in control (site 1) and test (site 2) sections of Gilchrist Creek. Summer represents June-October. Winter represents October-February. Spring represents February to June of the next year. The * denotes presence of same age steelhead cohort.

Season	1988 Cohort		1989 Cohort		1990 Cohort	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2*
Summer	0.960	0.303	0.379	0.487	0.108	0.146
Winter	0.373	1.359	0.304	0.511	0.387	0.045
Spring	0.849	0.202	0.347	0.577		

Brown Trout Size and Growth

The size and growth of age-0 brown trout was variable throughout the course of the study (Table 9 and Table 10). Since total length and weight were highly correlated ($r^2 = 0.97$), statistical comparisons of size yielded comparable results using either variable. As such, only length data are presented.

In June, between-site comparisons within years found no significant difference ($P > 0.05$) in size of age-0 brown trout (Table 9; Appendix 2). However, significant size differences existed in February (1990, 1991) and October (1990). In all three cases, age-0 brown trout were larger in the control section than the test section ($P < 0.002$). Only the February 1990 data were from a pre-treatment sample.

Pre- versus post-treatment comparisons of total length were also complex (Table 9). Results were significant

Table 9. Average total length (TL) and weight (WT) of age-0 brown trout and standard errors (S.E.) for these measurements. Separate data are given for the control (site 1) and test (site 2) sections of Gilchrist Creek for 1989-1991 cohorts. The * denotes presence of same age steelhead cohort.

Date	1989 Cohort		1990 Cohort		1991 Cohort	
	Site 1	Site 2	Site 1	Site 2*	Site 1	Site 2*
TL (mm) S.E.						
June	47.2 0.31	45.1 0.26	54.5 0.42	52.5 0.39	58.4 0.67	58.6 0.56
October	86.9 0.62	82.8 0.65	95.6 0.72	82.4 0.61	91.1 0.86	89.0 1.09
February	94.9 1.04	84.8 0.87	99.2 0.82	89.9 0.78	97.6 0.82	93.1 1.01
WT (g) S.E.						
June	1.11 0.036	1.10 0.032	1.97 0.201	1.51 0.055	2.15 0.073	2.02 0.059
October	7.26 0.282	6.88 0.297	8.32 0.225	5.49 0.137	8.37 0.288	7.34 0.327
February	7.89 0.256	5.83 0.191	9.06 0.234	6.79 0.202	8.12 0.207	7.19 0.227

Table 10. Seasonal instantaneous growth rates for age-0 brown trout cohorts 1989-1991 in control (site 1) and test (site 2) sections of Gilchrist Creek. Summer represents June-October. Winter represents October-February. Spring represents February to June of the next year. The * denotes presence of same age steelhead cohort.

Season	1989 Cohort		1990 Cohort		1991 Cohort	
	Site 1	Site 2	Site 1	Site 2*	Site 1	Site 2*
Summer	0.0049	0.0048	0.0054	0.0043	0.0038	0.0036
Winter	0.0006	0.0002	0.0003	0.0007	0.0006	0.0004
Spring	0.0033	0.0037	0.0028	0.0035		

in 4 out of 6 contrasts. June comparisons found the 1989 cohort to be significantly smaller than the 1990 or 1991 cohorts in both test and control sites ($P = 0.001$). The treatment effects were also significant in section 1 in October ($P = 0.006$) and in section 2 in February ($P = 0.005$). However, in both these cases, brown trout were larger post-treatment than pre-treatment. As such, size differences between years were of greater magnitude.

Growth rate comparisons provide a clearer examination of size data since the confounding effect of initial sizes is downplayed (Table 10). Only one significant between site comparison was found (Appendix 2). Age-0 summer growth rates were significantly higher ($p = 0.001$) in section 1 than in section 2 for the 1990 cohort. A single significant within-site comparison was also found. The summer growth of age-0 brown trout was significantly ($P = 0.001$) slower post-treatment than pre-treatment in section 2. The same comparison in the control section revealed no such effect ($P = 0.183$).

Age-1 brown trout size and growth followed a similar pattern to age-0 fish (Table 11 and Table 12). Two significant differences were found in between-site comparisons (Appendix 2). In October 1989, age-1 fish were significantly larger ($P = 0.007$) in section 2. In June 1990, age-1 fish were again larger in section 2. All other between-site comparisons were nonsignificant. Pre-treatment

Table 11. Average total length (TL) and weight (WT) of age-1 brown trout and standard errors (S.E.) for these measurements. Separate data are given for the control (site 1) and test (site 2) sections of Gilchrist Creek for 1988-1990 cohorts. The * denotes presence of same age steelhead cohort.

Date	1988 Cohort		1989 Cohort		1990 Cohort	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2*
<u>TL (mm) S.E.</u>						
June	124.9 1.01	132.3 1.20	141.4 1.32	132.2 1.61	145.4 1.41	143.3 1.42
October	154.5 1.29	165.8 1.64	161.7 1.41	156.9 1.69	171.8 1.80	167.0 2.15
February	163.4 1.97	167.3 4.02	170.8 1.81	163.9 2.60	180.9 4.53	180.7 3.13
<u>WT (g) S.E.</u>						
June	20.51 0.514	24.68 0.678	32.51 0.928	26.13 0.993	31.85 0.906	28.9 0.832
October	34.17 0.873	41.84 1.348	39.32 1.034	36.40 1.170	47.84 1.551	42.35 1.695
February	39.86 1.522	41.73 3.093	47.70 1.549	40.42 1.937	54.32 4.019	53.97 2.869

Table 12. Seasonal instantaneous growth rates for age-1 brown trout cohorts 1988-1990 in control (site 1) and test (site 2) sections of Gilchrist Creek. Summer represents June-October. Winter represents October-February. Spring represents February to June of the next year. The * denotes presence of same age steelhead cohort.

Season	1988 Cohort		1989 Cohort		1990 Cohort	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2*
Summer	0.0017	0.0018	0.0012	0.0016	0.0014	0.0013
Winter	0.0004	0.0004	0.0005	0.0004	0.0005	0.0003
Spring	0.0027	0.0021	0.0020	0.0027		

versus post-treatment differences were significant in section 1 in June and October and in section 2 in June samples. In all three cases, age-1 brown trout were larger post-treatment than pre-treatment. These data seem to indicate no negative effect of steelhead on age-1 size. Analysis of instantaneous growth rates supports size data (Table 12; Appendix 2). No significant differences in growth rates were found in between-site or within-site comparisons.

Brown Trout Condition

Analysis of length-weight regressions yielded excellent models for age-0 and age-1 brown trout. All slopes were significant ($P < 0.01$) and the mean coefficient of variations were 0.91 and 0.96 for age-0 and age-1 brown trout. The mean slope was 2.93 for age-0 brown trout and 2.51 for age-1 fish. Comparisons of differences between stream reaches during each sampling period (blocked by month and year) were performed by ANCOVA. All ANCOVA were significant ($P < 0.05$). Tukey-Kramer multiple comparison tests were used to determine which stream reaches were significantly different. No specific pattern of fish condition comparisons between reaches in section 1 and section 2 was found. Reaches that had the greatest condition factor at one time period had the lowest in the next. As such, this analysis indicated that condition was

independent of the presence of steelhead.

Multiple Regression Models

To discern the role of interspecific competition and intraspecific competition, multiple regression models were constructed for age-0 and age-1 brown trout. These models used brown trout length as the dependent variable and brown trout and steelhead abundance as the independent variables. Each model contained only data from fish of the same age group. The model for age-0 brown trout was significant ($P < 0.01$) and the r^2 for the model was 0.38. The number of steelhead and the number of brown trout were both inversely related to age-0 size ($P < 0.01$). Parameter estimates were -0.002 for brown trout abundance and -0.049 for steelhead abundance. As such, density effects of both species are inversely related to brown trout size and account for 38% of the observed size variation.

The model for age-1 brown trout was significant ($P < 0.01$) and the r^2 was 0.46. An inverse relationship between density and size was apparent but only the estimate for brown trout abundance was significant ($P < 0.01$). The parameter estimate for this variable was -0.41, indicating that at age-1, intraspecific competition was more important than was interspecific competition. It is important to remember that steelhead abundance was low by age-1 and that this could affect the outcome of interactions.

DISCUSSION

Competition Theory and Interpretation of Results

The outcome of interactions between two species of fish is a complex process involving habitat segregation (innate temporal or spatial differences), interactive segregation (competition related behavioral interactions), and the varying effects of abiotic factors (Hearn 1987). The importance of each of these factors in the outcome of competition depends on the species involved. One central theme of salmonine competition studies has been the importance of size (Chapman 1966; Fausch and White 1986; Hearn 1987). Larger fish tend to dominate in intraspecific and interspecific conflicts. In addition to size, the comparative abundance of the two species can have an impact on the outcome of competition. It is the relationship of size to competition and the effects of competition upon abundance that work in concert to form a relationship between the population dynamics of two species.

In interpreting the results of this experiment, I assessed the impact of steelhead upon brown trout population dynamics. In addition, understanding the relative success of steelhead stocking and their survival can provide insights into interactions between these species. As such,

I will examine the abundance and size relationships of both species to gain a better understanding of the mechanisms that may regulate their populations.

Steelhead and Brown Trout Abundance

Steelhead introductions established average fall densities of 1791 age-0 and 197 age-1 steelhead/ha. Comparable densities were achieved in both years despite a 7-fold increase in stocking in 1991. Densities of age-0 steelhead were within the range (1,000-23,000/ha) reported in the Great Lakes region while age-1 densities were below (210-3700/ha) reported values (Seelbach 1986). Overall, densities obtained were low compared to other Great Lakes populations. Populations were also low compared to those obtained by a fry stocking project in Lake Superior tributaries (Close and Anderson 1992); they achieved late summer densities averaging 19,250 fish/ha. A major difference between the two introductions was that the Lake Superior streams contained few resident salmonines (Close and Anderson 1992).

During the course of this study, brown trout densities remained high. The average autumn density of brown trout was 3389 age-0 and 863 age-1 fish/ha. The only significant population level response noted was the decrease in winter abundance of brown trout in section 2 of Gilchrist Creek. This section contained the highest winter density of age-0

brown trout in the 1989-1990 winter when brown trout were in allopatry. Brown trout form over-winter aggregations as colder temperatures trigger reductions in territorial behavior and dominance hierarchies (Bachman 1984; Cunjak and Power 1986). It is possible that this section contained favorable age-0 wintering habitat, which concentrated brown trout from nearby stream sections. Since no immigration was apparent after steelhead introduction, this could be interpreted as evidence of competition for wintering habitat. However, combined brown trout and steelhead abundance in this section was lower in 1991 and 1992 winters than brown trout abundance in 1990. Given the lower overall salmonine abundance, I feel that the presence of steelhead was not a deterrent to any potential age-0 brown trout immigration.

Any impact of age-1 steelhead on age-1 brown trout abundance was not apparent during the course of this study. Although differences in abundance occurred in both sites, none could be ascribed to the presence of steelhead. This was not surprising given the low numbers of steelhead present by age-1.

Data indicated no impact of steelhead upon brown trout abundance. This could be a result of the low numbers of steelhead resulting from stocking. Given high salmonine productivity in this system, I anticipated the establishment of a larger steelhead population. Instantaneous mortality

rates for steelhead were highest between stocking and June assessments. High initial mortality was also observed in other steelhead fry stocking experiments (Wentworth and LaBar 1984; Hume and Parkinson 1987; Close and Anderson 1992). They implicated competition and spring flooding as probable causes of mortality. Gilchrist Creek was highly stable in discharge and no major flooding was seen in the spring of 1990 or 1991. This would diminish the mortality due to floods. I suspect that interactions with juvenile brown trout (competition) and larger brown trout (predation) were major causes of steelhead mortality in this study (Alexander 1977).

Steelhead and Brown Trout Size and Growth

Average size of steelhead fry compared favorably with other studies in the Great Lakes. In this study, age-0 fry averaged 79 mm and age-1 fish averaged 164 mm in autumn. Seelbach (MDNR, pers. comm.) reported autumn size ranges of 50-80 mm and 112-196 mm for age-0 and age-1 steelhead in the Great Lakes region. As such, steelhead were large relative to other Great Lakes populations.

Brown trout were also large compared to populations found elsewhere in Michigan (Merna et al. 1981; Alexander 1985). Age-0 brown trout averaged 89 mm and age-1 averaged 163 mm. Size of brown trout varied between years. None of these differences was attributable to steelhead and occurred

in both sites. In between-site comparisons, size was not different in June. Differences did occur in some autumn and winter samples. These results show that steelhead played a minor role in the size obtained by brown trout. Data from laboratory studies reinforces this observation (Chapter 2). Other factors influencing brown trout size and abundance were probably more important. Year-to-year and between-site differences indicate that factors such as intraspecific population dynamics or abiotic factors played an important role (Elliot 1984a, 1984b; Newman and Waters 1989). I feel these factors were the major ones causing observed size differences.

Despite the lack of impact of steelhead on the overall size of brown trout, an impact on growth rate was indicated. Tests of treatment effects on summer growth were highly significant in the test section and not in the control section. The slower growth of brown trout in sympatry with steelhead indicates that steelhead interaction may inhibit brown trout growth. Rose (1986) found that steelhead in a Lake Superior tributary inhibited brook trout growth. This is similar to the results of my experiment since brook trout also emerge earlier than steelhead and were at a size advantage. However, Rose (1986) concluded that steelhead adversely impacted brook trout growth to the extent that their wintering mortality was increased. The large response of brook trout may be due to inherent differences between

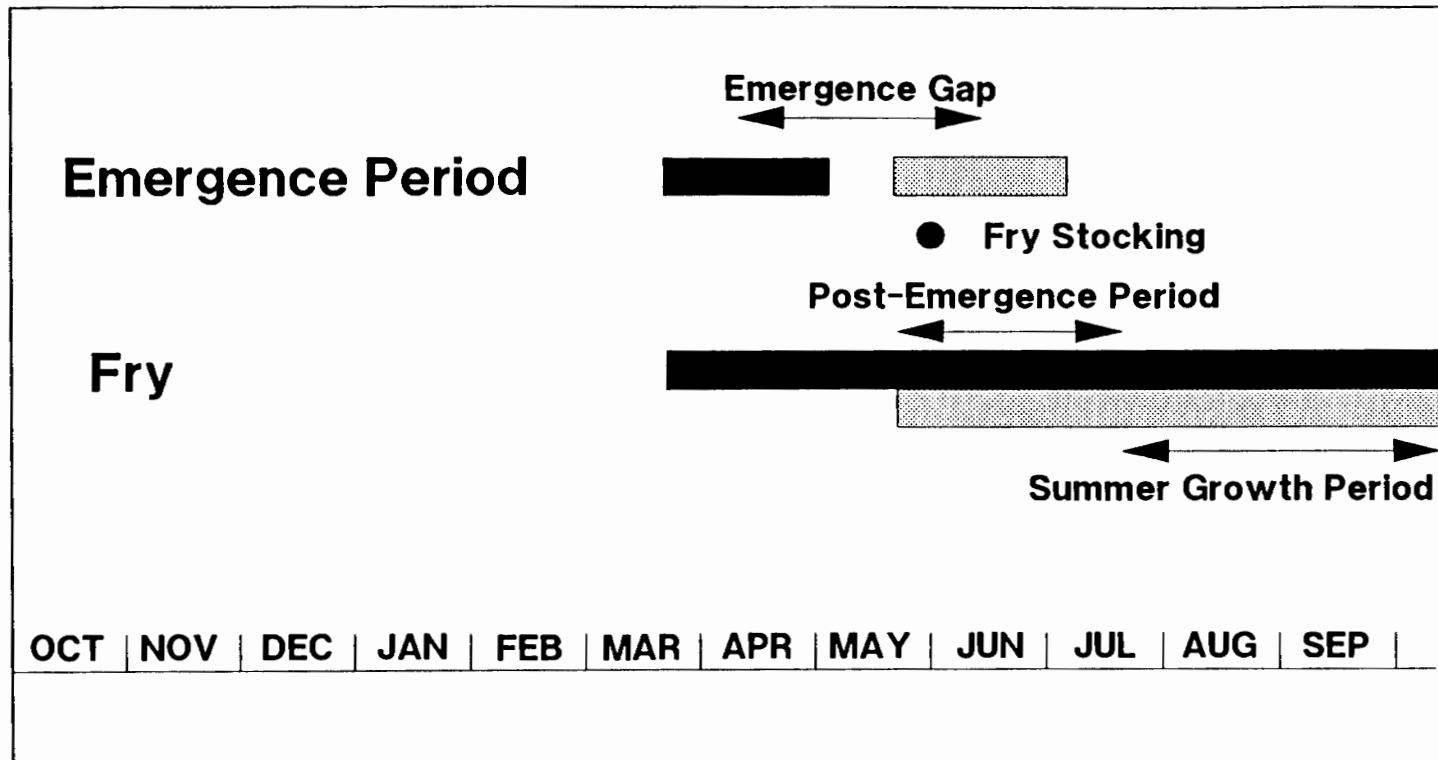
brook trout and brown trout. However, the brook trout also did not have as great a size advantage as the brown trout in this study. The results of both studies indicate that despite a size disadvantage, steelhead may be able to impact the growth of larger salmonine species of the same cohort. This could be important since climactic factors could change the relative size structures of the two species and, hence, the outcome of interspecific interactions.

Combined Effects of Size and Abundance

The impact of juvenile steelhead on juvenile brown trout population dynamics in this study was insignificant. Analysis of these results in the context of present knowledge of salmonine competition ecology, variations in life-history, and climactic conditions allows a better understanding of interactions between these species. I present a conceptual model of these species juvenile interactions (Figure 2). This model allows interpretation of the results of this experiment as well as emphasizing other areas of competition and future research needs.

Emergence Gap

The difference in emergence times leads to a difference in size of juvenile salmonines. At hatch and emergence, steelhead and brown trout are roughly the same size (Auer 1982). However, different spawning and incubation times



Key: **Brown Trout** **Steelhead**

Figure 2. Conceptual model of interactions between juvenile brown trout and steelhead in riverine environments illustrating areas of spatial and temporal overlap.

create a temporally regulated size difference. The earlier spawning and emergence of brown trout gives them a distinct size advantage. In Gilchrist Creek, emergence is usually complete by the end of April (Chapter 3). Reported emergence dates for some Lake Michigan tributaries are as late as mid-May (Fausch and White 1986). Steelhead stocking did not occur until late May, corresponding to peak natural emergence (Seelbach 1986). The length of the emergence gap gave brown trout at least a 30 day head start in exogenous growth (Figure 2).

Post-Emergent Stage

The effect of the emergence gap was manifested during the post-emergence stage (Figure 2). In Gilchrist Creek, age-0 brown trout were 30% larger than steelhead in June. This size advantage is important in competitive interactions between riverine salmonines (Fausch and White 1986; Hearn 1987). Direct competition is highly probable since both species heavily utilize stream margins until mid-summer (Sheppard and Johnson 1985; Chapter 3). Agonistic behavior between salmonines starts at both an intraspecific and interspecific level shortly after emergence. Salmonines exhibit confrontational behavior, and dominance hierarchies or territories are formed (Jenkins 1969; Fausch and White 1986; Hearn 1987). Fish gaining the most profitable positions are most likely to dominate (Fausch 1984).

Since diet, feeding strategy, and habitat use of these species overlaps substantially, interactions between the species are likely (Elliot 1973; Cada et al. 1987; Ziegler 1988; Chapter 3). Vertical segregation of fry has been proposed as an isolating mechanism between these species (Chapter 3). However, the shallow nature of marginal habitats might negate this isolation mechanism. Thus, direct interactions between emergent steelhead and established brown trout probably occurred. Given the results of this experiment and the relative size of these species, brown trout should dominate at this post-emergence stage. Subordinate fish typically exhibit lower growth, higher mortality, and many emigrate from the area (Chapman 1962; Hearn 1987). In my study, these factors gave brown trout juveniles a numerical advantage over steelhead that they maintained.

Summer Growth Stage

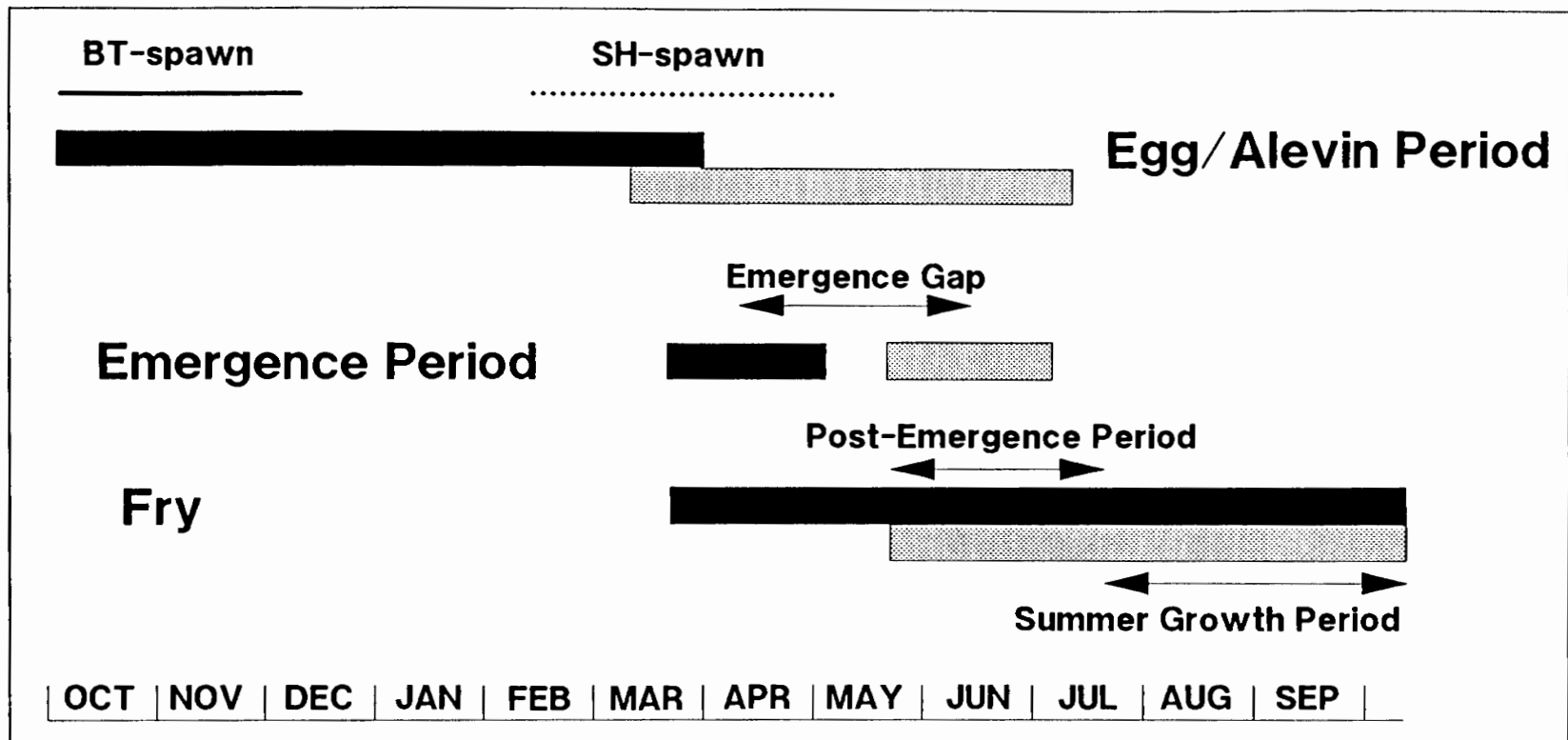
The summer growth stage is characterized by the habitat shift of age-0 fish to slightly deeper and faster water (Sheppard and Johnson 1985; Chapter 3) (Figure 3). From this point onward, habitat use by the two cohorts will be very similar until steelhead outmigration (Chapter 1; Raleigh et al. 1984, 1986; Ziegler 1988). Another important element, the faster growth rate of steelhead, allows them to reduce size difference with brown trout. This higher growth rate

for steelhead has also been seen in other Great Lakes studies (Kruger 1985; Ziegler 1988). As such, the size difference between species becomes neutralized as a factor in competitive interactions. However, with the shift to somewhat deeper water, vertical stratification could act as a habitat segregation mechanism (Chapter 3). The influence of segregation might be to reduce or eliminate potential competition (Allee 1982; Hearn 1987).

In my study, no impact of steelhead on brown trout abundance or growth was seen during summer growth periods or thereafter. This may have been the result of low steelhead abundance and/or habitat segregation. Had the gap in emergence not given brown trout the initial competitive advantage at the post-emergence period, the impact of steelhead might increase at this time.

Other Life-History Stages

Due to differing life-histories, interactions between these two species in riverine environments are limited to only parts of each species' life history (Figure 2 and Figure 3). This study only examined the relationship between juvenile brown trout and steelhead. This is the longest period of interaction, and previous research indicated that competition might be occurring here (Kruger 1985; Ziegler 1988). However, it is not the only time period where these fish interact.



Key:

Brown Trout



Steelhead



Figure 3. Conceptual model of interactions between brown trout and steelhead in riverine environments at all life history stages.

Interactions at the spawning and egg-alevin stage may also be important (Figure 3). In the Great Lakes region, brown trout typically spawn from October to November, and emergence from redds occurs from March to May (Elliot 1984b; Chapter 3). Steelhead spawning occurs from December to June (Seelbach 1986). Given the overlap in dates, steelhead redd superimposition could physically damage or dislodge brown trout prematurely from redds (Figure 3). During this overlap in gravel use, steelhead could potentially diminish the abundance of a brown trout cohort. The temporal relationship between steelhead spawning and brown trout emergence would determine the extent and impact of these interactions. It has been suggested that available gravel spawning areas are limited in Great Lakes streams, leading to superimposition and egg overseeding (Seelbach 1986; Kocik and Taylor 1987, 1991). If spawning steelhead were overabundant, all spawning gravel in a stream reach might be excavated during redd construction. If this were the case, the impact of temporal overlap between these life-history stages could be substantial. The relationship between these species at these life-history stages warrants a thorough investigation and should be a direction for future research.

Impacts of Differing Climate

Under environmental conditions observed in this experiment, juvenile brown trout were not adversely impacted

by steelhead. However, annual variations in climate create an opportunity for differing outcomes of brown trout-steelhead interactions. Two stages of interactions could be influenced: the steelhead superimposition period and the emergence gap (Figure 3). Since brown trout are autumn spawners and steelhead are spring spawners, atypical or changing conditions during these period could affect interactions between these species. For example, a cold winter followed by a warm spring could cause a greater overlap in steelhead superimposition of brown trout redds due to delayed brown trout alevin development. This would decrease brown trout abundance. In addition, the emergence gap could be shortened. Elliot (1984a) noted up to a 50 day difference in brown trout emergence times with temperature being the predominant factor in these differences. The impact of a shift of this magnitude would be the reduction or loss of the brown trout size advantage at the post-emergence stage. In concert, the result could be a stronger steelhead year class at the expense of brown trout.

This can be illustrated in comparisons of brown trout size in June between years. In June of 1990 and 1991, brown trout were 30% larger than steelhead. However, if steelhead were introduced in 1989 they would have been only 13% smaller. This could be enough to make a significant difference in the outcome of competition. This seems especially important given the results of studies of brook

trout and steelhead interactions (Rose 1986). Thus, results of this study should be used with care in regions with different or more variable winter and spring climates.

Implications

In this study, interactions between juvenile brown trout and steelhead appear to favor brown trout. The major arena of competition of juveniles appears to be the post-emergent stage. This stage is critical in determining future juvenile abundance. After this stage, the juveniles appear to be compatible (Chapter 2; Chapter 3). As such, this study provides new directions for assessment of competition between these species: spawner-alevin interactions and climatic influences. Culmination of these studies will complete the assessment of life-history stage interactions between these species.

Given the results of juvenile competition experiments, it appears that with adequate temporal segregation, the two species can coexist. It should be noted that steelhead are very similar in stream ecology to Atlantic salmon, which coexist with brown trout in many systems (Gibson and Cunjak 1986; Seelbach 1987; Hearn 1987). This evidence suggests that coexistence of these species is possible. However, the effects of human perturbations on Atlantic salmon-brown trout systems (Hearn 1987) has caused a loss of balance in some populations to the detriment of one of the species.

The long history of natural reproduction of brown trout and steelhead in the Great Lakes indicates their success in these systems. It is possible that continued changes in the Great Lakes lacustrine ecosystems and climate changes are responsible for changes in the balance between brown trout and steelhead (Scavia 1991).

CHAPTER 2

IMPACT OF AGE-0 STEELHEAD UPON AGE-0 BROWN TROUT IN AN ARTIFICIAL STREAM EXPERIMENT DURING THE FIRST SUMMER

ABSTRACT

I examined the impact of age-0 steelhead (Oncorhynchus mykiss) on age-0 brown trout (Salmo trutta) during their first summer in an artificial stream experiment. I ran a completely randomized design experiment with 4 replicates and two treatments. The control treatment was allopatric brown trout, and the test treatment was sympatric brown trout with steelhead. A total of 14 fish were placed in each experimental cell with control cells containing 14 brown trout and test cells containing 7 brown trout and 7 steelhead. The experiment ran for 99 days. Water temperatures and habitat types were similar to those encountered by wild trout. Fish were fed invertebrates twice daily during the experiment. No effect of steelhead on brown trout survival or growth was detected. Density-dependent interactions appeared to impact both survival and growth of brown trout. However, intraspecific interactions within brown trout populations were more important than interspecific interactions with steelhead. The results of this experiment indicate that steelhead have a minimal impact on brown trout and the species can coexist during their first summer of life.

INTRODUCTION

Interspecific competition between stream dwelling salmonines has been implicated as an important factor in their population dynamics (Hearn 1987; Fausch 1988). Concern over competition in riverine salmonines in the Great Lakes region is high since many of the species are exotics, habitat use is similar, and most species combinations have not coevolved (Carl 1983; Fausch 1984; Fausch and White 1986). Of particular interest has been competition between brown trout and steelhead (Kruger et al. 1985; Kruger 1985; Ziegler 1988; Chapter 1).

Michigan anglers, concerned over the apparent decline of resident brown trout populations, felt that oncorhynchids were adversely affecting the brown trout fishery. Kruger (1985) concluded that brown trout abundance had declined and that juvenile growth was relatively slow in the Pere Marquette River. He also observed an inverse relationship between brown trout abundance and steelhead abundance. These results suggested that steelhead may interact detrimentally with juvenile brown trout. In a study of 3 Michigan rivers, Ziegler (1988) found that age-0 fish of both species use similar habitat and food. Given the results of Kruger (1986) and Ziegler (1988), the need for a

clearer understanding of competition between these salmonines became apparent.

I assessed brown trout population dynamics and habitat use in a brown trout stream in northern Michigan (Chapter 1; Chapter 3). In these investigations, I found the effects of steelhead juveniles on brown trout to be minimal. To further assess the potential for brown trout-steelhead juvenile competition, an artificial stream experiment was conducted. Artificial stream experiments provide valuable supplements to field studies since abiotic variability can be minimized (Kalleberg 1958; Li and Brocksen 1977). In natural ecosystems, food and space can limit the abundance and growth of stream salmonines (Chapman 1966; Fausch and White 1986; Cada et al. 1987). These parameters can also vary between systems and within longitudinal sections of the a stream (Elliot 1984a; Cada et al. 1987). Artificial stream experiments allow measured and replicated food availability, habitat volume, and fish density. As such, artificial stream experiments allow for true replication for statistical analysis.

Artificial stream experiments have been successfully used to analyze competition in stream dwelling salmonines (Kalleberg 1958; Li and Brocksen 1977; Fausch 1984; Fausch and White 1986). Previous artificial stream experiments have illustrated that salmonines form dominance hierarchies in artificial streams (Li and Brocksen 1977; Fausch and

White 1986). These hierarchies allow dominant fish to use the most energetically profitable stream positions. As a result, the dominant fish species grew better and exhibited higher survival (Kalleberg 1958; Li and Brocksen 1977; Fausch 1984; Fausch and White 1986). Thus, the results of behavioral interactions and the formation of dominance hierarchies can be measured by assessing growth and mortality rates.

The goal of this research was to assess the impact of age-0 steelhead upon age-0 brown trout survival and growth in an artificial stream. Competition was assessed through comparisons of brown trout in allopatry and in sympatry with steelhead. The experimental design removed abiotic and biotic variability found in natural systems. By regulating densities, diet quantity and quality, and habitat, the effects of steelhead competition upon juvenile brown trout population dynamics were evaluated.

METHODS

Stream Design and Macrohabitat

I conducted the competition experiment in a recirculating artificial stream channel with the inside dimensions of 60 cm x 60 cm. The channel was partitioned into 8 experimental cells (Figure 4). Experimental cells were 1 m in length. Cells were divided by 5 mm mesh nylon screens held in place by plexiglass frames with edges made fish-proof using nylon tubing. The screens had a negligible affect on overall velocity while preventing fish passage between cells.

Flow was maintained through using of two 1 hp water pumps adapted to generate 4 jets of water. The filtration system pump supplemented the main pumps while running an above ground pool filter. I placed sand, filter floss, and charcoal into the pool filter to create a biofilter. The entire volume of water was filtered two times an hour.

Mercury-vapor and fluorescent lights were used to light the stream. The mercury vapor lights took approximately 30 minutes to reach full intensity. As such, sunrise and sunset effects were created by these lights. Light cycles followed ambient norms and were controlled by an electronic timer. Analysis of variance was used to compare differences

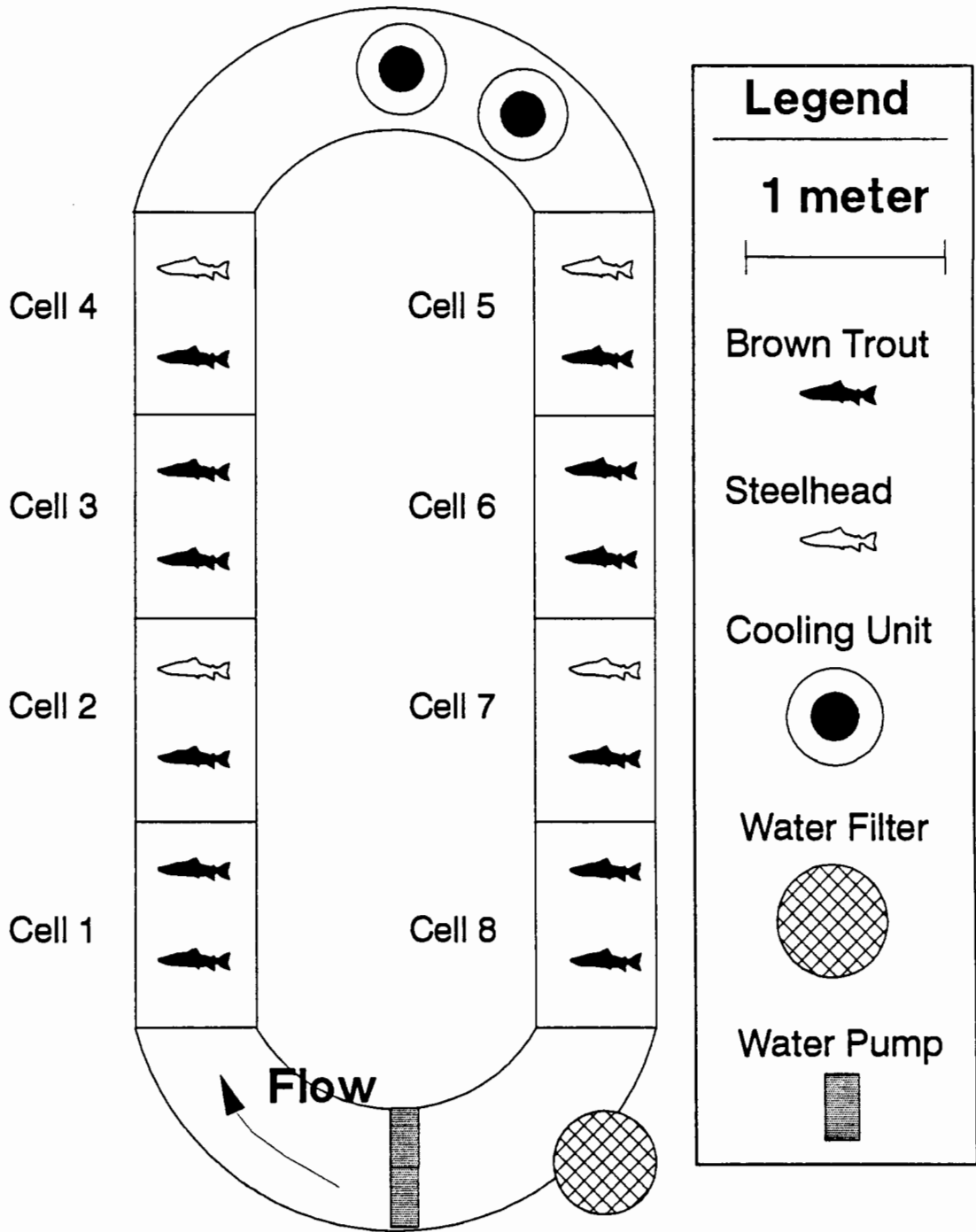


Figure 4. Artificial stream design and experimental structure.

in maximum light intensity between cells. No significant differences were found ($P > 0.05$), and the mean light intensity at the water surface was 950 lux.

Two 1 hp chiller units were used to maintain stream temperatures. I used temperature data from my previous field studies in Gilchrist Creek as a guide to regulate temperature in the artificial stream (Kocik 1990, unpublished data). The mean monthly artificial stream temperatures were 15.7°C , 16.6°C , 13.2°C , and 12.9°C for June, July, August, and September. Daily temperature fluctuations as high as 1.5°C were observed, due to increased heating by lights and changes in building airflow. These fluctuations were similar to natural fluctuations with the highest temperatures in the middle of the day. The velocity profile of the stream kept the water mixed and at a uniform temperature at all stream cell locations.

Stream Cells and Microhabitat

Each cell was a replicate in regards to microhabitat variables of depth, velocity, substrate, and cover. The water depth in all cells was maintained at 30.5 cm for the duration of the experiment. Water added at feeding countered evaporation and excess would drain off through a standpipe.

Mean column velocity was measured at 20 replicate locations in each cell. Eight of these represented

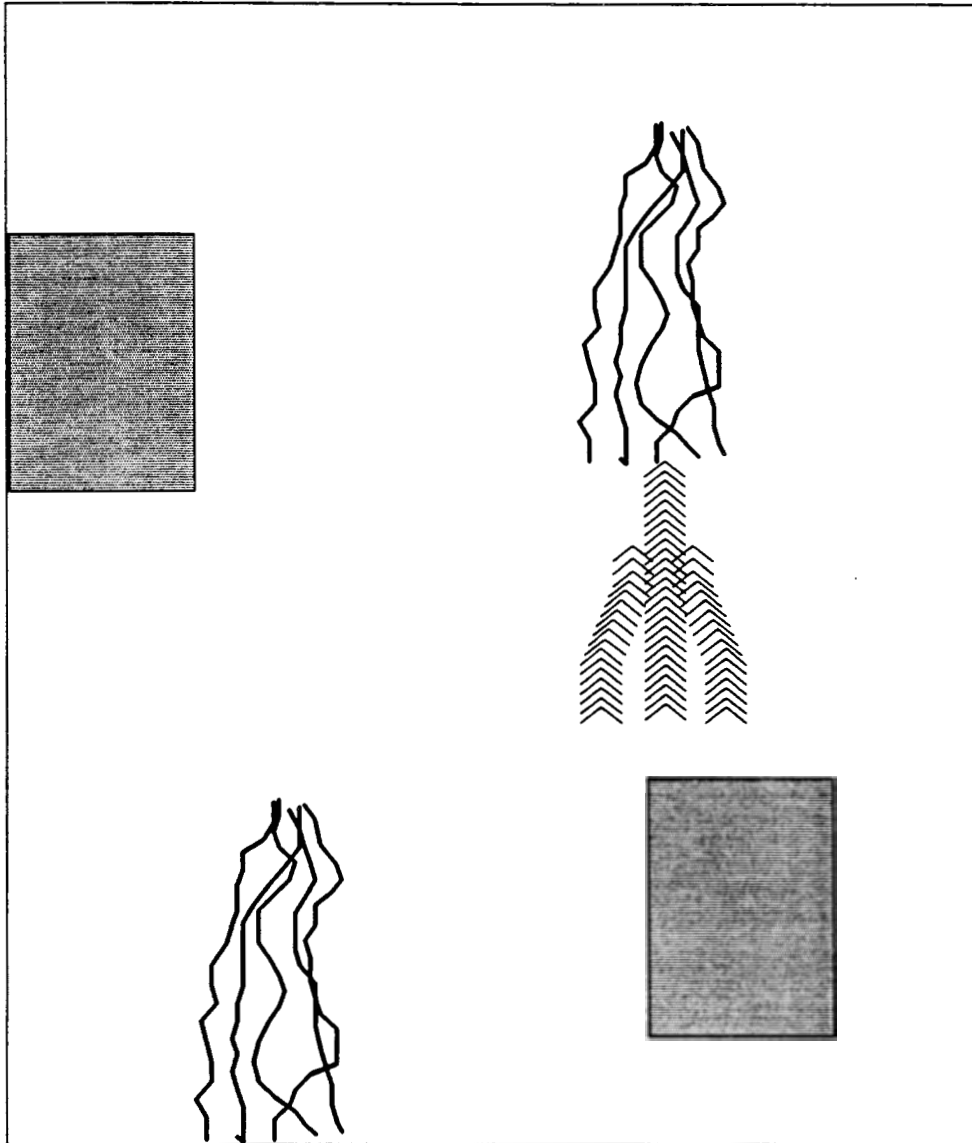
positions in stream cover and 12 were in open water. There was no significant difference in water velocity at either location set between cells (ANOVA, $P > 0.05$). Average open water velocities were 13 cm/s. In cover locations the mean was 11.4 cm/s. The overall average was 12.4 cm/s. Water depth and water velocities were low but within ranges utilized by both species in field experiments (Chapter 3).

The substrate was identical in all cells; clean gravel ranging in size from 4 to 8 mm comprised the substrate. All cover types were artificial to ensure uniformity for replication. Each cell had 5 individual cover structures placed in identical locations in relationship to the cell ends and sides (Figure 5). Three artificial plants were placed in each cell: two corkscrew vallisneria (Vallisneria spiralis) and one ambulia (Limnophila heterophyllia). The vallisneria were 30 cm in length and the ambulia were 25 cm long. These species were chosen due to their similar appearance and size to aquatic plants utilized by these fish in field studies (Chapter 3). Artificial logs were made from gray 15 cm pvc pipe cut in half laterally and cut into 21 cm lengths. These logs were then placed in the gravel with two thirds of the pipe exposed.

Fish Procurement and Holding

Wild brown trout and hatchery incubated progeny of wild steelhead were used in this experiment. Brown trout were

UPSTREAM



DOWNSTREAM

Corkscrew Vallisneria (*Vallisneria spiralis*)

Ambulia (*Limnophila heterophyllia*)

Artificial Log 

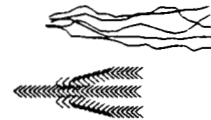


Figure 5. Artificial stream cell illustrating habitat size and placement.

collected by D.C. electrofishing from Gilchrist Creek, Montmorency County Michigan. They were transported back to the laboratory in a 190 l cooler with aeration units and ice. A total of 130 brown trout were available at the start of the experiment. I received 200 steelhead swim-up fry from the Michigan Department of Natural Resources Wolf Lake Hatchery. The progenitors of these fish were wild steelhead collected at the Little Manistee River Weir and Egg Collection Station.

Until introduced into the experimental stream, brown trout and steelhead were kept isolated in a separate living stream unit. Fish were fed live and frozen brine shrimp (Artemia sp.) twice daily while in the holding tank. Brown trout were kept in the holding tank for 15 days prior to introduction into the artificial stream. Steelhead were kept in the holding tank 32 days. The longer holding period allowed steelhead to reach a size where they would not go through the cell partitions (30 mm). In addition, brown trout were able to establish a hierarchy in the artificial stream prior to steelhead introduction.

Experimental Design

To test the impact of steelhead on brown trout survival and growth, I used a completely randomized design with two treatments. Control cells would have initial populations of 14 brown trout. Test cells initially contained 7 brown

trout. After the 17 day acclimation period for the brown trout, 7 steelhead were introduced to test cells.

Initial brown trout introductions were made on 21 June 1991. I randomly selected brown trout from the holding tank using a 15 x 20 cm hand net. To facilitate handling and minimize stress, fish were anesthetized using tricaine methanesulfonate at a concentration of 50 mg/l. I measured all brown trout for total length (nearest mm) and weight (nearest 0.001 g). I then placed fish in separate recovery/holding buckets that represented a test or control cell. Placement of fish in test or control cells was alternated to minimize any selective effect of the netting. Fish ranged in length from 48 to 74 mm. I compared fish total length and weights using an ANOVA and LSD comparison to check for differences between holding buckets. No significant differences were detected ($P > 0.05$). Test and control buckets were randomly assigned to test and control cells in the stream and fish were released. This yielded an experimental design with 14 brown trout in control cells 1, 3, 7, and 9 (allopatric) and 7 brown trout in test cells 2, 4, 6, and 8 (sympatric). During the first week of the brown trout acclimation period, any brown trout that died were replaced with brown trout of similar (within 4 mm) size from the holding tank. The replacement was conducted to minimize the effects of transfer mortality from the holding tank to the artificial stream.

On 8 July 1991, I placed 7 steelhead in cells 2, 4, 6, and 8. Steelhead were randomly selected in the same manner as brown trout. Their sizes ranged from 35 to 42 mm. I compared steelhead total lengths and weights using an ANOVA and LSD comparison to check for differences between cells. No significant difference between cells was detected ($P > 0.05$). Steelhead mortalities were replaced with identical sized fish for one week following introduction. Brown trout were not replaced at this point. After the 7 day steelhead introduction period, no mortalities were replaced.

After initial introductions and subsequent replacements, fish were removed for two periodic vital statistic assessments (15 August and 4 September 1991) and at the end of the experiment (27 September 1991). The collection and measurement protocol was the same for all three collections. During these checks, I collected all fish in a cell using a 10 x 15 cm hand net. Fish were anesthetized using tricaine methanesulfonate at a concentration of 50 mg/l. Fish were identified to species and measured for total length and weight. They were then allowed to recover from anesthesia in an oxygenated recovery bucket. Once all fish had regained their equilibrium, they were returned to the stream cell. Fish not accounted for at this point were considered mortalities. Carcasses were usually located during fish removal from a cell. All carcasses were accounted for at culmination of the

experiment. All cells were handled individually.

Feeding and Maintenance Regimes

I fed fish twice daily in experimental cells using live, frozen, or freeze-dried invertebrates. Diet was varied throughout the experiment but was always identical for all cells. Using the temperature specific relationship between maximum food ration eaten per day and fish weight (Elliot 1975), I calculated feeding biomass. A total of 10% of fish body weight per day provided ample food. I recalculated food amounts every time fish were removed for measurement. Fish were fed at approximately 07:00 and at 16:00 each day. Foods were introduced through a funnel and tube that released food at the gravel level in the center of each cell at the upstream cell divider.

A mixture of food types was used to ensure that nutrient requirements of the fish were met (Elliot 1975). Predominant food types were frozen brine shrimp, frozen bloodworms, and frozen and freeze-dried krill. Amounts of each food were alternated each feeding period between frozen foods, with one food making up 2/3rd of the frozen ration and a second 1/3rd of the frozen ration. Frozen foods comprised 92 % of the biomass of the daily diet. Freeze-dried krill or live foods were used to supplement the diet. Freeze-dried krill was fed about every third feeding period. I also maintained live cultures of mosquitos, brine shrimp,

and Chironomus riparius. These foods were introduced as they became abundant enough to use as food.

Stream cells were vacuumed with the filtration system intake hose each time fish were removed from the cells. This helped remove excrements and food wastes. The filter was back flushed as needed (when filter back-pressure doubled), approximately every two weeks. Water removed from the tank during back-flushing was replaced with clean water from a water storage tank that was cooled to the same temperature as the artificial stream.

Rate Calculations and Statistical Analysis

To identify critical time periods, I calculated mortality and growth rates over specific time periods. The pre-steelhead period ranged from initial brown trout introduction to steelhead introduction (Table 13). After steelhead introduction, the experiment was divided into three phases. The early phase ran from steelhead introduction until experiment check 1 (37 days). The middle phase ran from experimental check 1 until experimental check 2 (20 days). The late phase ran from experimental check 2 until the end of the experiment (23 days). This periodic analysis of the post-steelhead introduction phases was designed to find differences as the size ratio of steelhead to brown trout changed (ie. do steelhead have a greater effect as they approach the size of brown trout).

Table 13. The timing of fish introductions, collections, and subsequent time period references.

Date (Julian)	Experimental Operation	Time Period Reference
21 Jun (172)	Brown Trout Introduction	
8 Jul (189)	Brown Trout Measurements	Pre-Steelhead
9 Jul (190)	Steelhead Introduction	
15 Aug (227)	Experimental Check 1	Early Phase
4 Sep (247)	Experimental Check 2	Middle Phase
27 Sep (270)	Experiment End	Late Phase

At each time period, the number of each species and total salmonine density in each cell was known. Given this abundance data, I calculated the instantaneous mortality rate (Z) for each cell and species for each period and for the duration of the experiment. I also calculated the overall survival rate (S) of each species in each cell. The following equations were used (Ricker 1975):

$$Z = - (\log_e N_{t+1} - \log_e N_t) \text{ and } S = (N_{t+1} / N_t) * 100$$

Where:

- Z = instantaneous mortality rate
- S = overall survival rate
- N_{t+1} = population of cell at time $t+1$
- N_t = population estimate of cell at time t

In order to assess the impact of changing salmonine densities in cells as differential survival changed abundance, I analyzed the size of brown trout at each collection compared to overall salmonine, brown trout, and

steelhead abundances. These models were least squares regressions of fish length to each abundance. If models were significant, the slopes of the models were compared using analysis of covariance (ANCOVA). Using this design, ANCOVA compared slopes for significant ($\alpha = 0.05$) differences (Snedecor and Cochran 1982). By assessing the effects of fish density on fish size, any confounding effect on fish growth could be explained.

Mean lengths were used to calculate instantaneous daily growth (μ) for each cell using the following equation (Ricker 1975):

$$u = (\log_e TL_t - \log_e TL_{t-1}) / T$$

Where:

u = instantaneous daily growth rate
 TL_t = mean total length (mm) at start of growth period
 TL_{t-1} = mean total length (mm) at end of growth period
 T = time interval in days

Instantaneous growth rates were calculated for each time period and for the overall experiment. Total length and weight data were averaged for each cell to allow direct comparisons of fish size at specific points in time.

To assess differences in the condition of salmonines between treatments, ordinary least squares regression of the weight W on total length TL was used ($\log_e W = \log_e a + b \log_e TL$) as recommended by Cone (1989). Using this method, the calculation of condition is unbiased since the slope of an ordinary least squares regression can be used as the

condition index (Cone 1989). This model was used to calculate this index for brown trout prior to steelhead introduction and for both species at the end of the experiment.

The structure of this experiment was designed to test the impact of YOY steelhead upon YOY brown trout abundance, survival, growth, and condition under replicate experimental conditions. Statistical analysis was partitioned by sampling date for point estimates and by periods for rate variables. To examine the differences in brown trout between test and control sections, I used analysis of variance (ANOVA) ($\alpha = 0.05$) (Steel and Torrie 1980). This method was used to compare abundance, survival, and growth. Analysis of instantaneous growth and mortality rates and overall survival can be confounded, since ratio data are usually not normally distributed (Steel and Torrie 1980). Since small sample sizes precluded effective tests of normality, I transformed the data using the RT-1 transformation (Conover and Iman 1981). Individual observations were ranked according to their relative value, and statistical tests were performed on the ranked data. This transformation provides a more rigorous substitute to the non-parametric Kruskal-Wallis test through a standard ANOVA (Conover and Iman 1981).

RESULTS

Brown Trout Mortality

The number of brown trout in all cells decreased over time (Figure 6). In control cells, brown trout density at the conclusion of the experiment fell to a low of 6 in cell 1 and a high of 9 in cells 8 and 3. In the test cells, abundance fell to a low of 4 in cell 2 and a high of 5 in cell 4. These data yielded an average instantaneous mortality rate of 0.6516 in the control sections and 0.3467 in the test sections for the duration of the experiment. This difference was non-significant ($P > 0.05$). Comparisons of instantaneous mortality rates during specific time periods were only significant during the early phase of the experimental period. During this time, instantaneous mortality was higher in the control section (0.4186) than in the test section (0.1613).

Comparisons of overall survival rates (S) also showed this trend. Overall survival was higher in test sections (71.3%) than in control sections (53.5%) ($P < 0.10$). The early phase of the experimental period was different with survival averaging 85.8% in the test sections and 65.8 % in the control sections ($P < 0.05$).

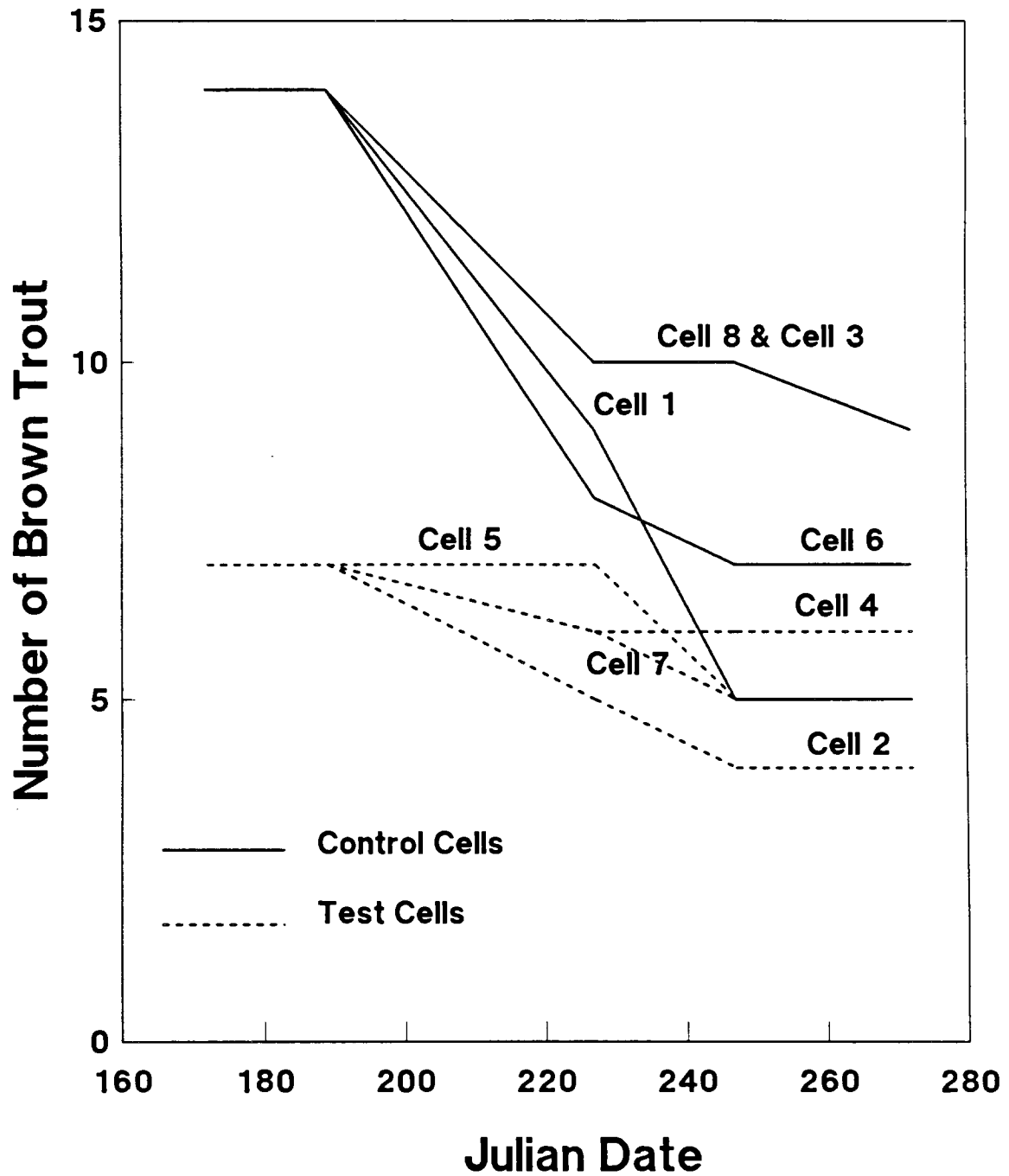


Figure 6. Number of brown trout in allopatry and sympatry surviving in individual artificial stream cells.

Brown Trout Size and Growth

The total length of brown trout did not significantly differ between test and control cells at the onset of the experiment ($P = 0.18$) (Figure 7). Fish in the control cells averaged 60.0 mm and 2.16 g. In the test section, brown trout averaged 57.6 mm and 1.91 g. By 15 August, fish in the test cells (72.3 mm, 3.84 g) were slightly larger than fish in control cells (74.5 mm, 4.18 g) but differences were not significant ($P = 0.39$). Brown trout in the test sections continued to widen the gap with their counterparts in the control sections. However, the difference was still nonsignificant at the end of the experiment ($P = 0.15$).

Analysis of growth rates supports the observations of the analysis of fish length and weight differences. Instantaneous growth rates from the start of the experiment to the end show that brown trout in the test section grew faster than those in the control section ($P < 0.05$). The mean instantaneous growth rate in the control section was 0.0039; in the test section it averaged 0.0050. Comparisons during different time periods were only significant during the early phase of the experimental period. During this time period, the mean instantaneous growth rate in the control section was 0.0009, while in the test section it averaged 0.0013.

Fish condition in cells was measured using the slope of the $\log_e W - \log_e TL$ least squares regression. At the

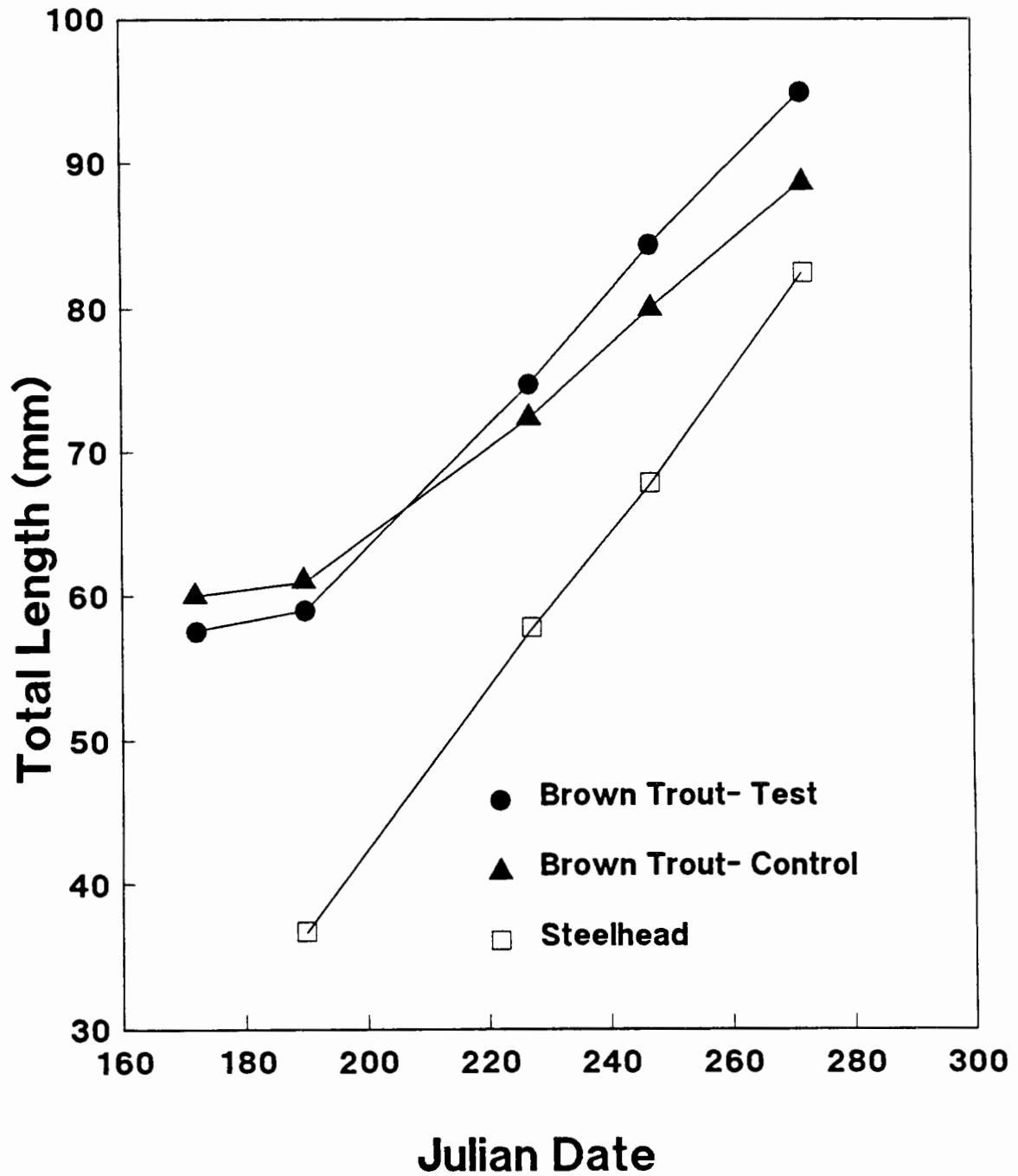


Figure 7. Mean total length (mm) over experimental time for brown trout in allopatry and sympatry and for steelhead in sympatry.

point of steelhead introduction into the stream, no significant differences in the condition of the fish existed (ANCOVA, $P > 0.05$). At this point, the average condition (slope) was 2.94. At the end of the experiment, the condition of fish had improved to an average of 3.04, and the difference between test and control sections was still nonsignificant ($P > 0.05$).

Steelhead Population Parameters

Steelhead mortality was generally low. For all cells containing steelhead, the mean instantaneous mortality rate over the duration of the experiment was 0.1501 ± 0.0526 S.E. This translates to an overall average survival of 71.5 %.

Growth of steelhead was quite rapid (Figure 7). At the start of the experiment, steelhead averaged 38.7 mm and 0.45 g. By the end of the trials they grew to an average of 82.5 mm and 6.14 g. The instantaneous growth rates of steelhead over the course of the experiment averaged 0.0093 ± 0.0001 . This growth rate was significantly higher than brown trout growth rates ($P < 0.05$). This is illustrated in an examination of the ratio of mean steelhead total length to mean brown trout total length. At the start of the experiment, steelhead were 0.6575 times smaller than brown trout. By the end of the experiment, this ratio increased to 0.8979 the size of brown trout. Steelhead growth was good in all cells, and ANOVA comparisons of the mean total

length or weight of steelhead between cells were nonsignificant at all time periods ($P > 0.05$).

The condition factor of steelhead averaged 3.39 at their introduction to the artificial stream. No significant differences in condition were noted in between-cell comparisons (ANCOVA; $P > 0.05$). By the end of the experiment, average condition had decreased to 2.87. However, there was no significant difference between the test cells ($P > 0.05$).

Density Effects on Brown Trout

To test for effects of overall salmonine, brown trout, and steelhead densities on size, I modeled the relationship of brown trout mean total length to abundance. Overall salmonine abundance (total number of brown trout and steelhead in a cell) was inversely related to brown trout size for control sections ($P < 0.01$). In test sections, it had no effect on brown trout size ($P = 0.73$). Brown trout abundance was inversely related to brown trout size in both test and control sections ($P < 0.01$). ANCOVA of the slope of these two models was not significant ($P > 0.05$). Steelhead density had no effect upon brown trout size ($P = 0.22$).

DISCUSSION

Steelhead Effects on Brown Trout Survival

Age-0 steelhead had no apparent effect upon age-0 brown trout survival in artificial stream experiments. In fact, survival rates of brown trout in sympatry with steelhead were greater than those of allopatric brown trout. These results support field studies that indicate no effect of age-0 steelhead upon age-0 brown trout (Chapter 1). Higher mortality in allopatric cells indicates that intraspecific competition may be a more important factor in regulating brown trout abundance in this experiment. Intraspecific competition of brown trout has been noted in other artificial stream studies (Hartman 1963; Fausch and White 1986) and in natural systems (Elliot 1984a).

Steelhead Effects on Brown Trout Growth

Brown trout growth rates during the course of this experiment were comparable to those observed in wild fish (Chapter 1). Steelhead growth rates were somewhat higher than those in the companion field study (Chapter 1). However, they were comparable to fry stocked in a British Columbia stream (Hume and Parkinson 1988).

No effect of steelhead on brown trout growth was

observed. In fact, brown trout growth rates were higher in sympatry. Analysis of total length illustrated this point and indicated that in a longer experimental period, test section brown trout may have grown significantly larger. This potential "positive effect" of steelhead was probably a result of the effects of salmonine density on growth.

Analysis of models of brown trout size to overall salmonine, brown trout, and steelhead abundances clearly showed the relationship of density to growth. Since fish in all cells were not significantly different at the beginning of the experiment, size was an unbiased measure of growth. The total number of salmonines or steelhead in test cells had an insignificant effect on brown trout size. However, the number of brown trout had a negative impact on brown trout size in both test and control treatments. Thus, at this life history stage and size distribution, intraspecific competition between brown trout (density dependence) has a greater effect than interspecific competition with steelhead.

I feel that mortality was higher in the control cells since brown trout carrying capacity was much lower than initial populations. In test cells, the lower initial densities resulted in a lower brown trout mortality to reach carrying capacity. Initial fish densities in this experiment were also similar to those in comparable artificial stream experiments (Fausch 1984; Fausch and White

1986). However, since my studies were run much longer, the carrying capacity of the cells decreased as territory size increased (Chapman 1962; Hearn 1987).

All mortality was assumed to be due to behavioral interactions since no signs of diseases were observed. The level of aggressiveness of brown trout can be severe enough to cause mortality due to physical damage (Kalleberg 1958). I observed agonistic behavior between and within species in all cells, although no quantitative assessment was conducted. Frequently, dominant fish would chase subordinates to the point where they would jump out of the stream (This accounted for 60% of total mortality). Although an artificial response, this could be considered comparable to emigration from a stream reach in a natural system. In natural systems, the result of emigration from inferiority in the dominance hierarchy is typically downstream displacement and subsequently death (Chapman 1962).

Implications for Natural Systems

The results of this study illustrate that, in their first growing season, steelhead are likely to have little or no impact on survival or growth of age-0 brown trout. Previous research had indicated that the age-0 or age-1 stages were likely arenas of competition (Kruger et al. 1985; Ziegler 1988). The results of this study reject the

hypothesis that the age-0 summer growth period is a critical one for interaction between these two species. These conclusions have been supported by my research in a natural stream system (Chapter 1). In that study, I found that the presence of steelhead had negligible effects on brown trout size and no effects on abundance. For both size and abundance, factors related to year-to-year differences in abiotic conditions and/or intraspecies factors had a more important effect on brown trout population dynamics. In this artificial stream study with environmental variables controlled and equal size fish at the start of the experiment, results were similar. I conclude that interactions between these fish are minimal during the summer growth period.

I feel that one of the factors that allows coexistence is vertical stratification between the species (Ziegler 1988; Chapter 3). Vertical stratification was consistently observed in artificial stream experiments. Steelhead were suspended in the water column and brown trout were closely associated with the bottom. This may be the mechanism that allows coexistence between these species. However, prior to movement to summer habitats, both species utilize shallower margin habitat (Sheppard and Johnson 1985; Raleigh et al. 1984, 1986; Chapter 3). In these shallow habitats, vertical stratification could break down and competition could occur. I feel that this happened in my field studies and that the

larger size of brown trout at this time allowed for a competitive advantage (Fausch and White 1986; Ziegler 1988; Chapter 1). Field research also showed that the impact of steelhead in the first winter and yearling period were minimal under low steelhead densities.

The results of this study indicate that during the age-0 summer growth period, brown trout and steelhead can coexist in a riverine environment. While evidence for interspecies compatibility is substantial at this life-history stage, other life-history stages must be taken into account. Of particular interest is the period shortly after steelhead emergence when both species utilize stream margins. Assessment of competition at this stage would give further insights into juvenile competition. Also of interest is the steelhead spawning stage where interactions with brown trout alevins may occur (Chapter 1). The effect of climate variations on the temporal segregation (or lack of segregation) of alevin and post-emergent stages is also important. The extent of overlap in spawning as well as the size and time of each species' emergence would influence the outcome of these experiments (Fausch and White 1986; Chapter 1; Chapter 3).

Managers should observe caution in creating sympatric populations of these two species where a healthy, naturally reproducing allopatric population of one of these species exists. The effect of such an introduction on the

established population would be uncertain. My results only assessed the impact of steelhead on brown trout at the summer growth stage. Interactions to the detriment of brown trout were minimal, but the impact upon steelhead was not examined. In addition, until further information is available on other overlapping life-history stages (ie. spawner-alevin interactions and climatic effects on temporal segregation) of these species, the full impact will not be known. Until this information is quantified, I urge managers to consider the potential impact these species may have on each other at all life-history stages before combining these species in a riverine environment.

CHAPTER 3

HABITAT USE OF JUVENILE BROWN TROUT IN A GREAT LAKES TRIBUTARY AND THE IMPACT OF JUVENILE STEELHEAD

ABSTRACT

Habitat utilization is described for juvenile brown trout (Salmo trutta) in allopatry and in sympatry with steelhead (Oncorhynchus mykiss). I conducted this study in Gilchrist Creek, where I had introduced steelhead fry to a portion of the river. Underwater habitat use observations were made seasonally from 1989 to 1992. Few winter observations were made as both species occupied complex timber and could not be readily observed. In spring, age-0 brown trout occupied margins soon after emergence. By July they had moved into deeper water. Age-0 brown trout cover was predominately aquatic vegetation associated with fine sediments. No seasonal shift was noted in age-1 brown trout. Compared to age-0 brown trout, they occupied positions in deeper, faster water and used downed timber and gravel more frequently. Comparison of age-0 brown trout and steelhead showed that they use similar water depths, substrates, and cover during summer and autumn. Steelhead used slower velocities. Comparisons of age-0 brown trout habitat use in sympatry and allopatry found no measurable habitat shift of brown trout. Vertical stratification appeared to be an effective isolation mechanism between these species during the majority of the growing season.

INTRODUCTION

Research concerning competition between riverine salmonines has been conducted for over 40 years (Hearn 1987). Currently, this topic has seen renewed interest due to extensive reviews by Hearn (1987) and Fausch (1988). In addition, concern over biodiversity has kindled new interest in the impacts of exotic species on indigenous species and established fauna (Rinne and Minckley 1985; Ross 1991).

Investigations of competition have often focused on measuring niche shifts or changes in population dynamics of one species in the presence (or absence) of another species (Fausch 1986). Habitat use and segregation have been used to define niches and the role of competition in niche development and maintenance. As such, this research direction has frequently focused on the differing habitat use of a species when it co-occurs with a potential competitor (Chapman 1966; Cunjak and Power 1986; Baltz and Moyle 1984; Gibson and Cunjak 1986; Rose 1986). A trend seen in many of these studies is that coevolved species have less overlap in habitat use and are segregated temporally as well as spatially (Allee 1982; Cunjak and Green 1983; Gibson and Cunjak 1986; Hearn 1987). In interactions between exotic and indigenous species, coevolved adaptations do not

always act to segregate species in their use of habitat. This frequently results in the decline in abundance of one of the competing species. The outcome of competition between exotic and indigenous forms seems dependent upon the number and types of species involved and the quality of stream habitat (compared to historic ecosystems). Ross (1991) found that exotics were typically more successful in regions with low numbers of native species and/or degraded habitats. Given pristine conditions and multiple indigenous fauna, native species were more likely to flourish.

The scenario described by Ross (1991) appears realistic for Great Lakes tributaries in the northern portion of Michigan's lower peninsula. The alteration of stream habitat and the introduction of exotic species has dramatically changed the salmonine fauna in these river systems over the past century. The current state of most Great Lakes tributaries are salmonine populations dominated by exotic fish in altered watersheds (Kruger 1985). This creates a rather unique situation, since the riverine salmonine fauna is comprised of predominately introduced species (Carl 1983; Fausch 1984; Fausch and White 1986). Hence, these streams contain exotics in species combinations that have not coevolved.

Brown trout and steelhead are two of these species. These two species have both been very successful in colonizing Great Lakes ecosystems and many rivers harbor

wild, self-sustaining populations (MacCrimmon and Marshall 1968; Biette et al. 1981) Recent changes in brown trout growth and abundance have led to concern about negative impacts of steelhead juveniles upon juvenile brown trout (Kruger 1985; Kruger et al. 1985; Ziegler 1988; Chapter 1). Given the past success of natural reproduction of both species and current concern over adverse impacts of steelhead upon brown trout, knowledge of the habitat use of these species is critical to understanding interactions between these species.

This study was undertaken as part of a project to determine the effects of steelhead upon brown trout (Chapter 1). A stream containing an allopatric brown trout population was stocked with steelhead fry to assess shifts in juvenile brown trout population parameters and habitat use. This chapter describes my assessment of the introduction of steelhead upon brown trout habitat use. The purpose of the investigation was to determine if steelhead caused any shifts in juvenile (less than age-2) brown trout habitat use.

METHODS

Study Site and Design

Gilchrist Creek is a second order stream located in Montmorency County, Michigan (Figure 8). It flows northeast through forested land into the Thunder Bay River and ultimately Lake Huron. The stream is typical of this region of Michigan being coldwater and characterized by highly stable flow regimes (P. Seelbach, MDNR pers. comm.). The salmonine fauna of this stream was exclusively wild brown trout (Chapter 1).

Investigation of steelhead impact on brown trout habitat use was conducted in conjunction with assessment of their impact on brown trout population dynamics (Chapter 1). The study introduced steelhead to a downstream section of Gilchrist Creek in late May 1990 and 1991. Populations of steelhead were moderate (autumn densities averaged 1781/ha) in density compared to other Great Lakes tributaries (Chapter 1). Study sections were established representing a test (downstream) and control (upstream) section separated by 2 km (Figure 8). These study sections measured 350 meters in length and averaged 7.5 m in width.

Habitat use of brown trout and steelhead was assessed by observing fish while diving the entire length of the

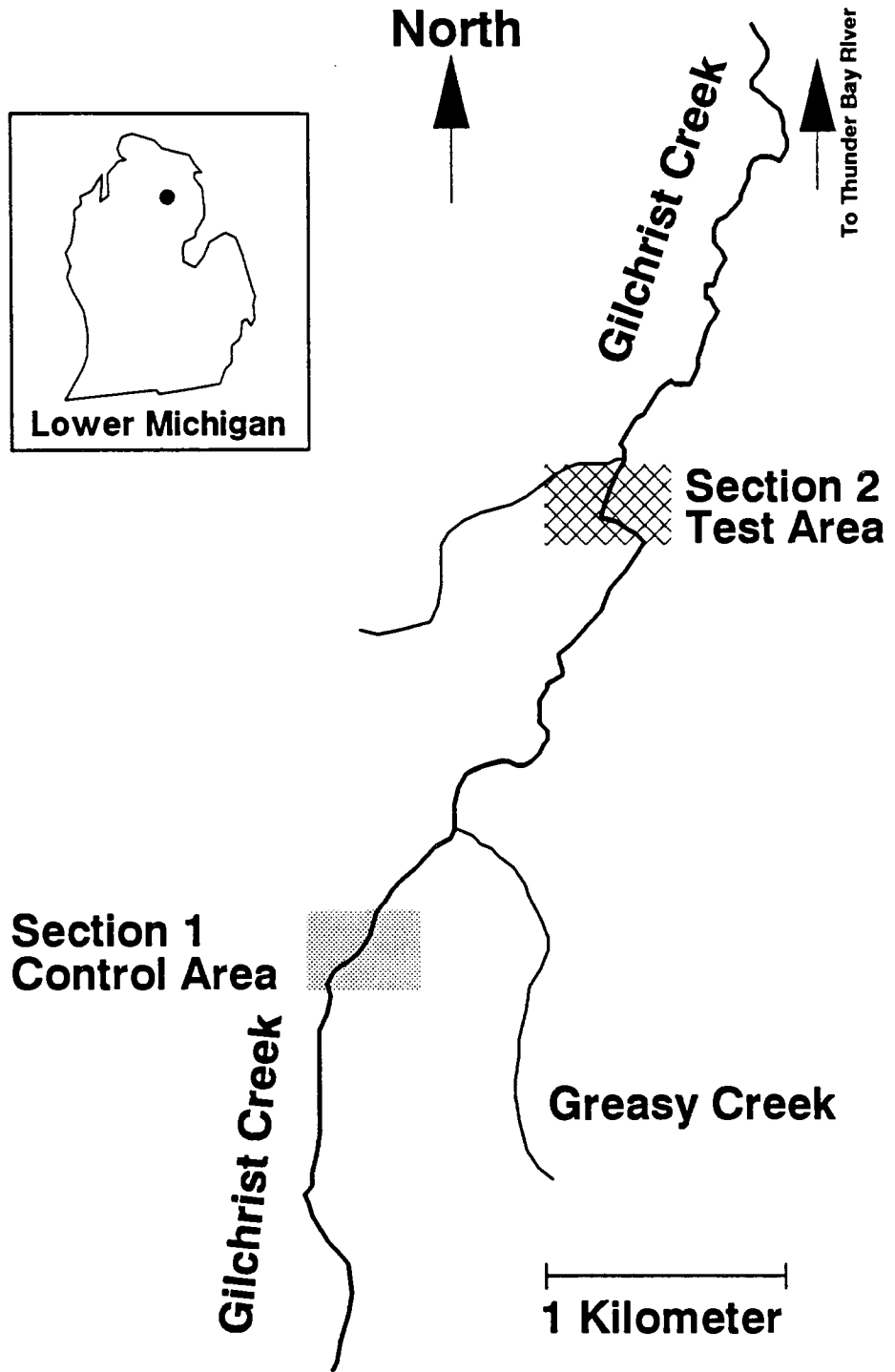


Figure 8. Map of Gilchrist Creek and study sections where dives were conducted.

study section four times a year. Assessments started in May 1989 and ended in April 1992. The design of the study allowed one year's worth of observations for brown trout in allopatry and two years with one allopatric section and one sympatric section.

Salmonine Habitat Use Observations

A single diver made underwater observations of salmonine habitat use seasonally. Observations were conducted in spring, summer, autumn, and winter each year (Table 14). I made measurements under similar discharge conditions and only under conditions of high water clarity. Differences in sampling dates within seasons were the result of unseasonably high and/or discolored flows or logistical difficulties. During dives, discharges ranged from 0.85 to 1.28 m³/sec and averaged 1.09 m³/sec.

Table 14. Diving dates for habitat use surveys.

Season	1989-90	1990-91	1991-92
Spring	05-06 May	27-28 April	18-19 May
Summer	07-08 August	10-11 July	24-25 August
Autumn	03-04 October	09-10 September	-----
Winter	-----	19-20 January	02-03 February

Dives started no earlier than 09:00 and ended no later than 15:00. This was done to ensure maximum light penetration to increase visibility. The time required to

dive an entire 350 m study site varied with fish abundance and water clarity, ranging from 2.0 hours to 3.5 hours.

The diver would start at the downstream section of a study reach and slowly crawl and swim across and upstream in a zigzag pattern (Cunjak and Power 1986; Moore and Gregory 1988). When a fish was sighted, the diver would identify the fish to species and use underwater landmarks to mark the fishes position and estimate fish length (Cunjak and Power 1986; Ziegler 1988). For data to be recorded, the fish must have been in an undisturbed state when first sighted. The diver would then move into the area where the fish was located and place a lead weight with a numbered fluorescent flag at the focal position of the fish (Fausch and White 1981). The diver would then relay information to an assistant located approximately 10 m behind the diver. Information reported by the diver was the weight number, species, fish length (nearest cm), the substrate the fish was over, the cover the fish was relating to, the position relative to cover, and the position in the water column. Substrate and cover categories are those of Bovee (1986) (Appendix 3 and Appendix 4). The proximity of fish to cover was recorded as greater than 0.5 m and less than 1 m from, less than 0.5 m from, or in cover. Proximity to cover was related by collapsing the vertical dimension (ie. a fish could be "in" overhead cover). The location in the water column was recorded as benthic or suspended.

The diver's assistant would pick up the flagged weight, placing the base of a top-set wading rod in this position. The person would then measure the habitat variables of water depth and mean column velocity. These were measured using the top-set wading rod and a portable electromagnetic flow meter. This type of meter allowed for accurate measurements of velocity even in the midst of heavy vegetative cover. These data were then added to data recorded by the diver to complete a data set for an individual fish.

Comparisons of Habitat Use

Since two habitat variables were quantitative measures and two were categorical, different statistical methods were needed to make comparisons between seasons, age groups, and species. Depth and velocity measurements represented the only quantitative habitat variables. Preliminary analysis of these variables data indicated most data were not normally distributed (Shapiro-Wilk Test, $P > 0.05$). As such, I used a nonparametric comparison, the Kruskal-Wallis (K-W) test, for comparisons of multiple groups of observations (significant at $\alpha < 0.05$). Substrate and cover data are qualitative variables and as such were not suited to this analysis. To test for differences in the distribution of fish between these habitat variables, the Kolmogorov-Smirnov (K-S) two-sample test was used.

RESULTS

Brown Trout Habitat Use

A total of 477 age-0 and 145 age-1 brown trout were observed. Differences in sample size occurred between seasons. Only 6% of the observations of age-0 brown trout and 13% of age-1 samples came from winter samples. These winter samples were omitted from statistical analysis due to the low number of observations. However, the observations during this period were useful in providing insights into assessment methods for future studies of overwinter habitat use.

For the remaining seasons, I compared habitat use within age groups using the K-W test for depth and velocity data. Since no multiple comparison statistic is suitable for qualitative data (substrate and cover), I visually examined their frequency distributions. No significant differences were noted for age-1 brown trout ($P > 0.05$). As such, age-1 habitat use was similar spring through autumn, and these data were pooled. Differences were significant for age-0 brown trout. Statistical and graphical analysis indicated that the spring sample was likely the outlier. I reanalyzed the summer and fall data with spring removed. Tests were nonsignificant ($P > 0.10$) for all four habitat

variables, so data were pooled for summer-autumn.

Comparisons of age-0 brown trout habitat use between spring and summer-autumn were significant for three of four variables. In the spring, age-0 brown trout were located in water averaging 34 cm in depth with a mean column velocity of 22 cm/sec. In the summer, they shifted to deeper (44 cm) and faster (33 cm/sec) water ($P < 0.01$; Figure 9 and Figure 10). In the spring, age-0 brown trout were found over predominately silt and sand substrates (Figure 11). These two substrates comprised 86% of spring observations. In the summer-autumn period, habitat use significantly ($P < 0.05$) shifted to a greater variety of substrates. During this period, use of sand and silt declined to 65% and, more use was made of gravel substrates. Utilization of cover did not vary significantly ($P > 0.10$) between spring and summer-autumn (Figure 12). During both periods, aquatic vegetation was the most commonly utilized cover. However, as the season progressed, fish use of downed timber and overhanging vegetation increased slightly.

Comparison of summer-autumn habitat use of age-0 brown trout was also significantly different from age-1 brown trout. These comparisons were significant for all four habitat variables. Age-0 fish used water averaging 44 cm in depth and 33 cm/sec velocity. The age-1 brown trout utilized significantly ($P < 0.01$) deeper and faster waters (Figure 13 and Figure 14). The mean depth used by age-1

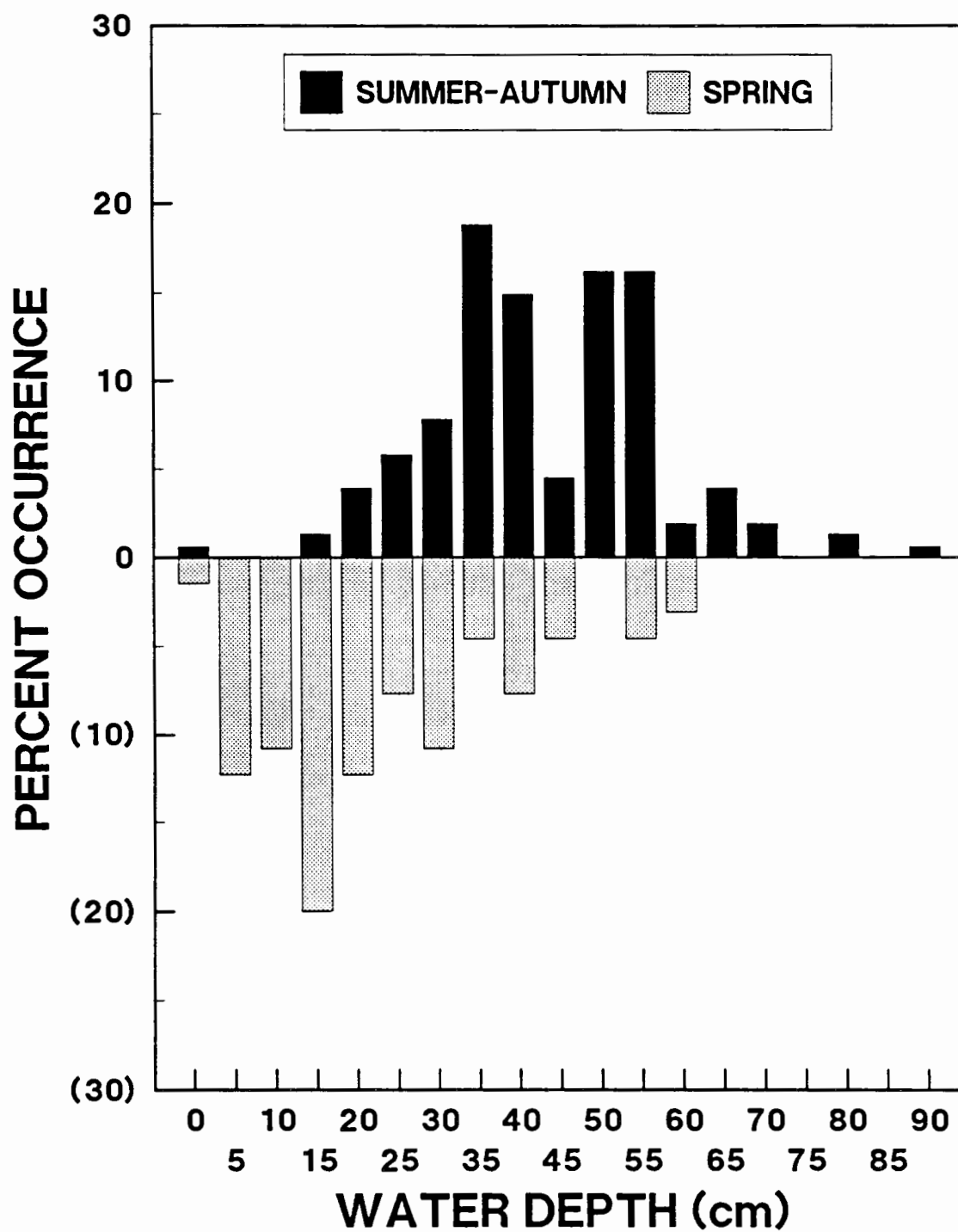


Figure 9. Comparison of water depths utilized by age-0 brown trout between spring and the summer-autumn time periods.

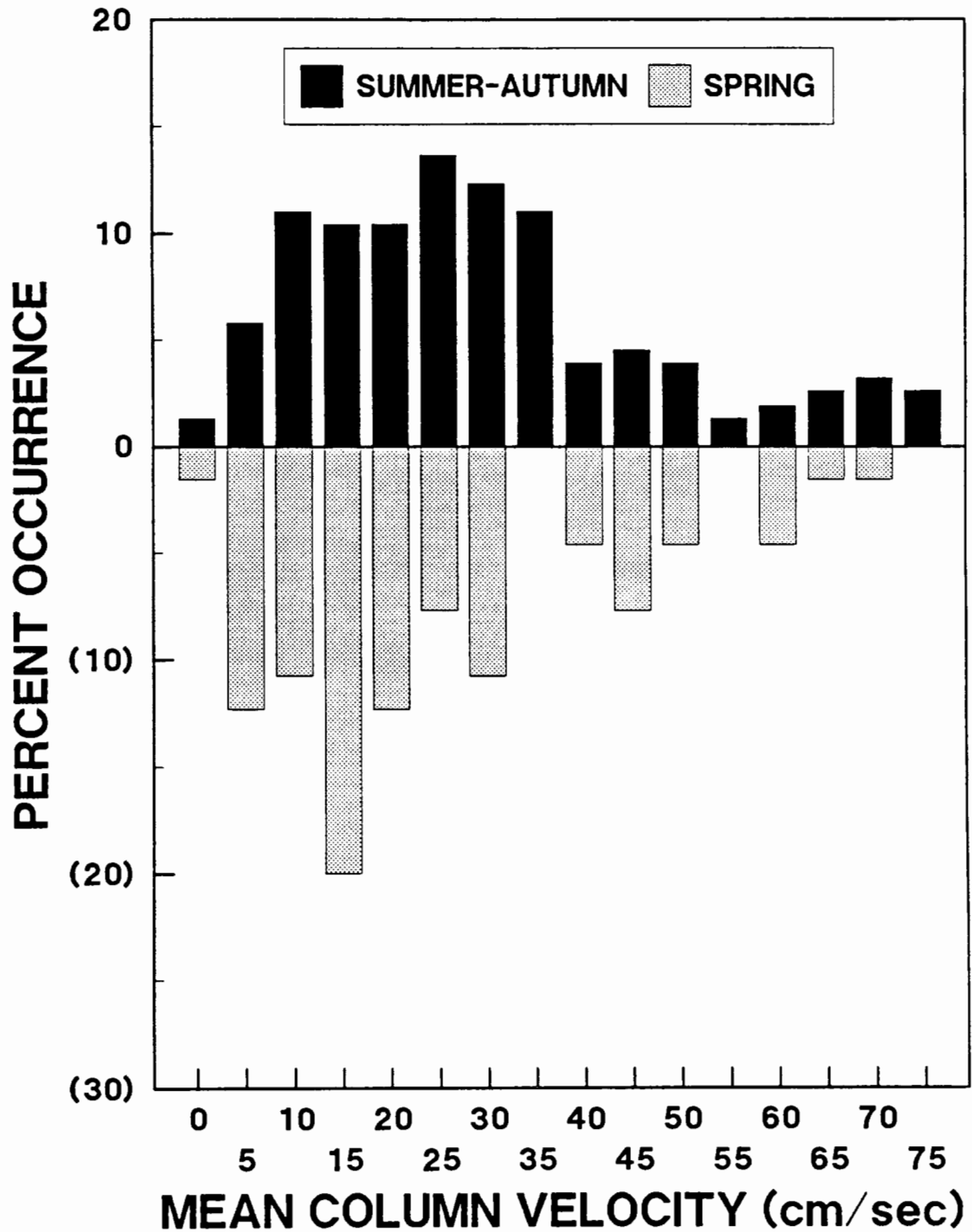


Figure 10.

Comparison of mean column velocities utilized by age-0 brown trout between spring and the summer-autumn time periods.

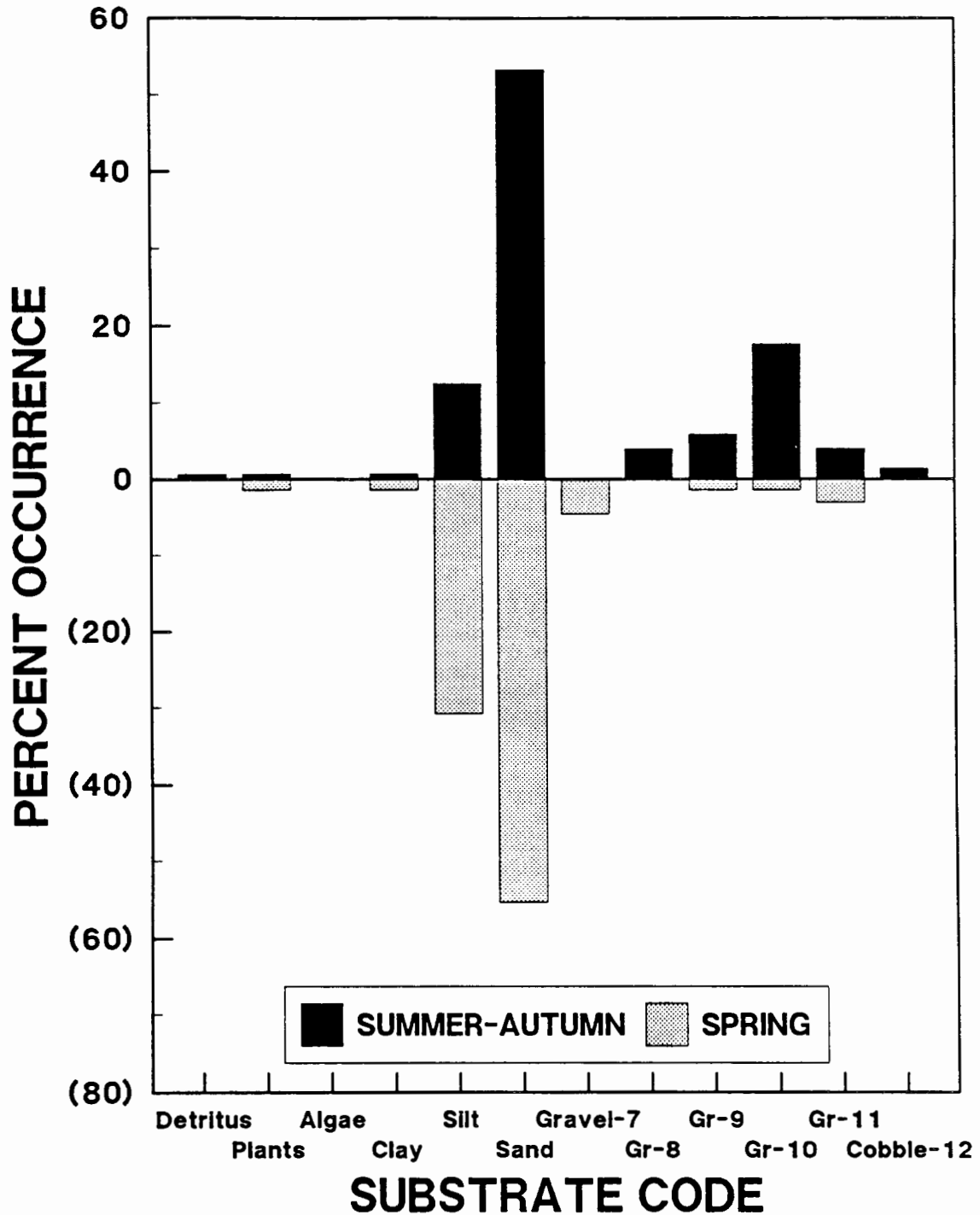


Figure 11.

Comparison of substrate types utilized by age-0 brown trout between spring and the summer-autumn time periods. Detailed descriptions of substrates are in Appendix 3.

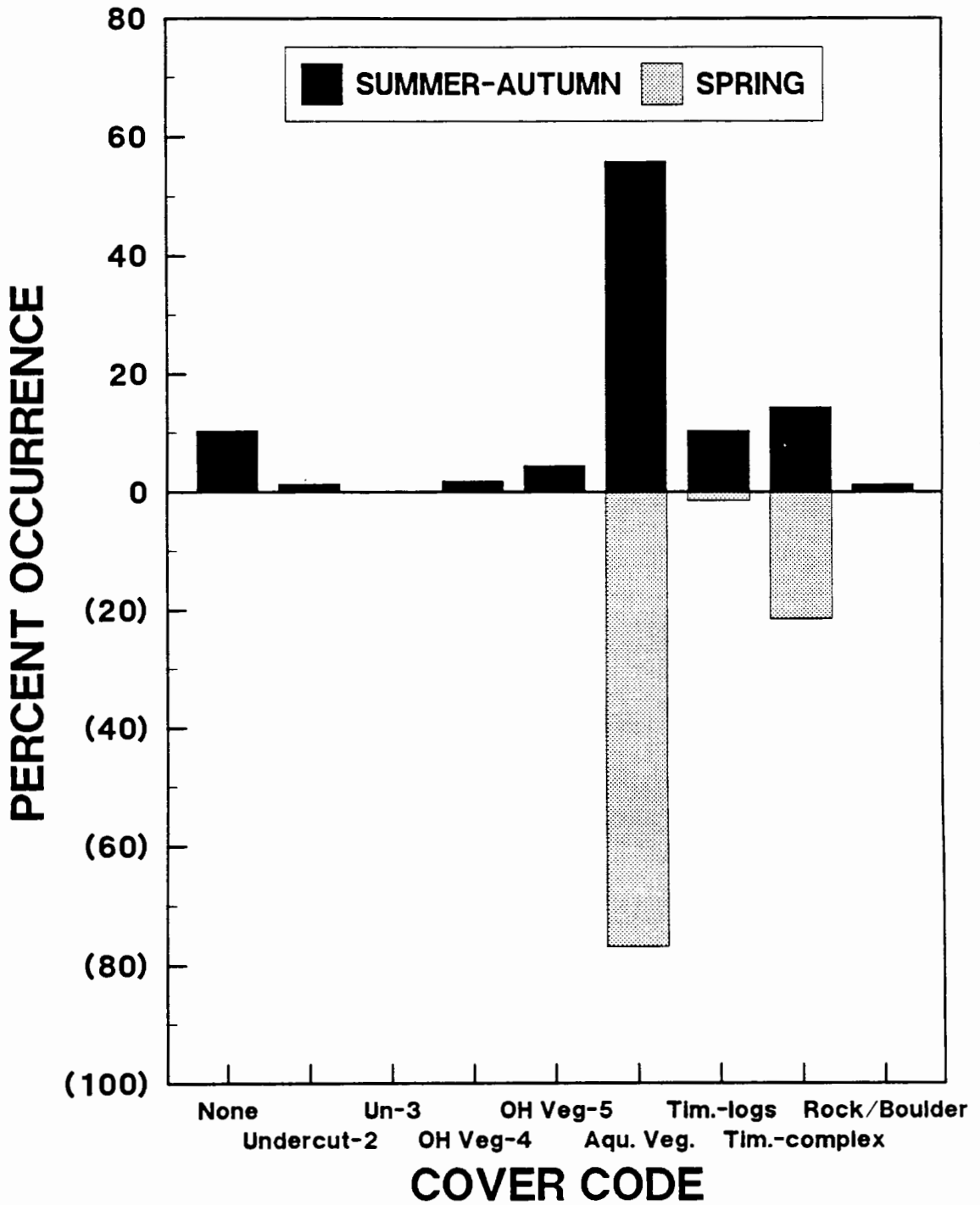


Figure 12.

Comparison of cover types utilized by age-0 brown trout between spring and the summer-autumn time periods. Detailed descriptions of substrates are in Appendix 4.

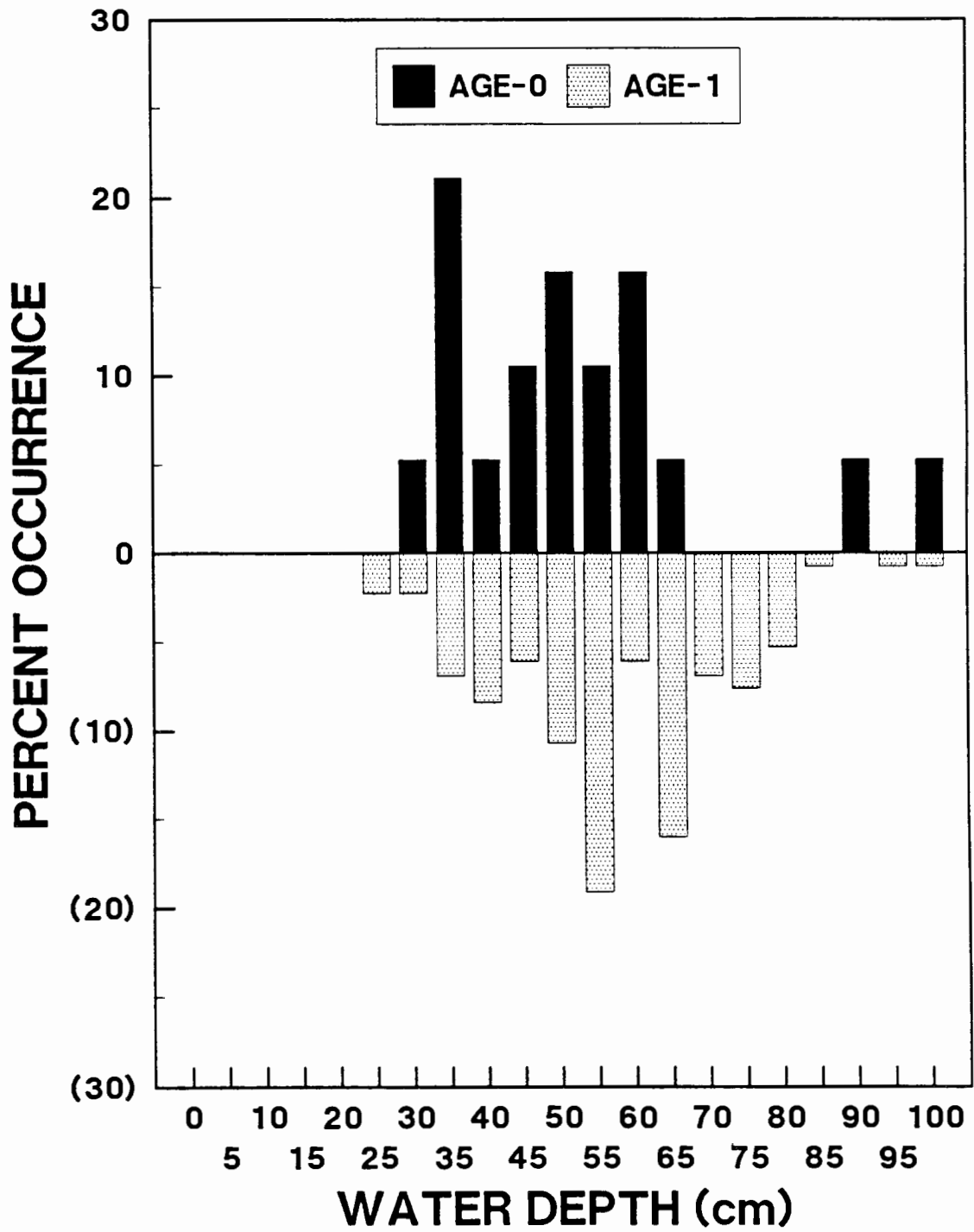


Figure 13. Comparison of water depths utilized by age-0 and age-1 brown trout.

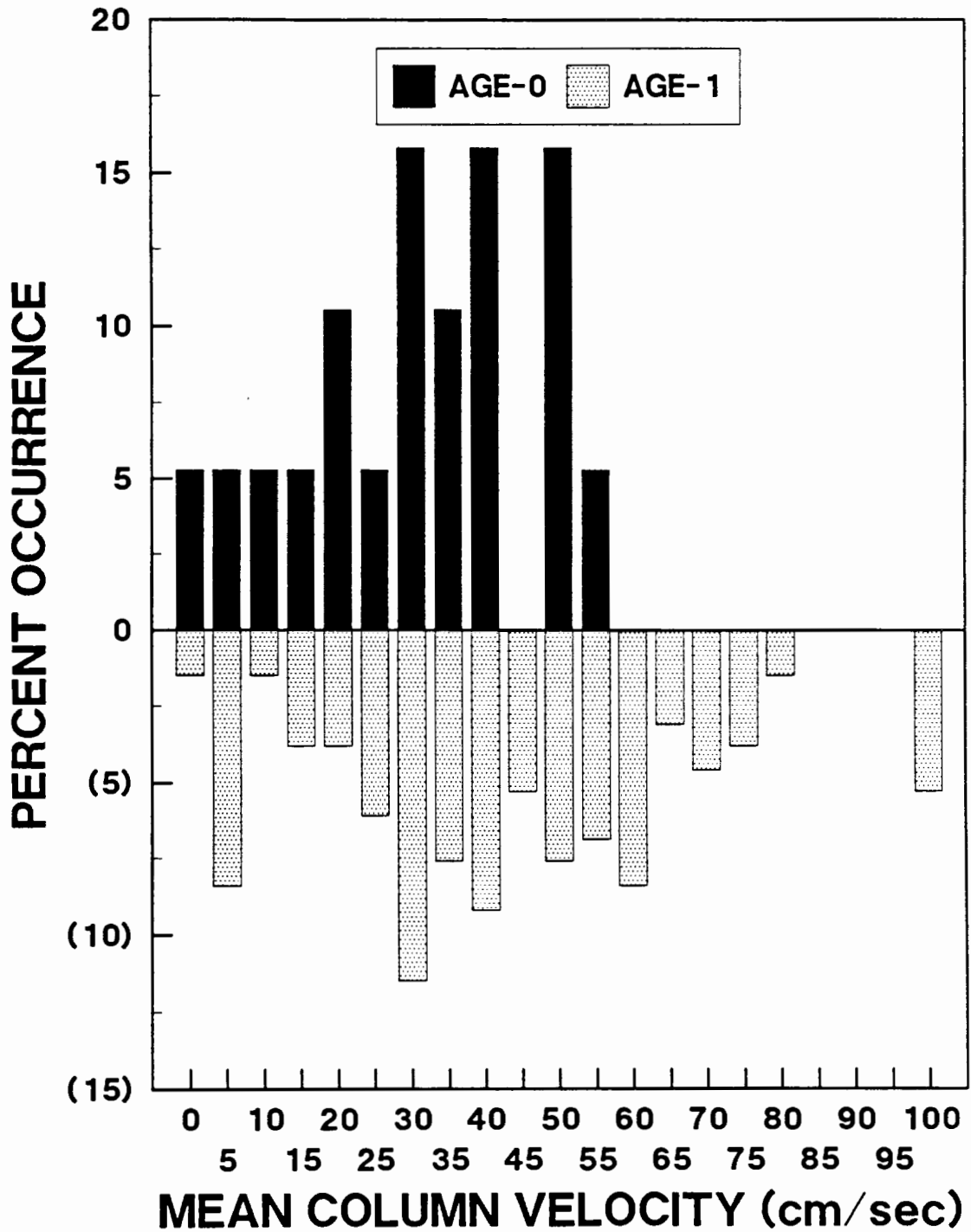


Figure 14. Comparison of mean column velocities utilized by age-0 and age-1 brown trout.

brown trout was 54 cm and mean velocity was 41 cm/sec. Use of substrate and cover also shifted significantly ($P < 0.01$) (Figure 15 and Figure 16). Age-0 brown trout utilized predominately silt and sand (65%). The use of these fine materials declined to only 36% of age-1 observations. The older brown trout switched to using gravel more frequently, 60% of observations as compared to 31% for age-0 fish. Use of cover went through a similar shift (Figure 16). Age-0 brown trout were found predominantly in aquatic vegetation (56%). As the fish entered their second growing season, use of downed timber became more important. Age-1 brown trout were found in logs for 20% of observations and in submerged branches or roots for 25%. Use of both cover types by age-0 fish was only 25%. An increase in the use of overhead cover from 6% at age-0 to 13% at age-1 also occurred.

The horizontal and vertical relationship of brown trout to cover and substrate was consistent in all observations. Brown trout showed a very tight relationship to cover. For age-0 brown trout, 85% of observations were made directly in the cover. Another 12% were within 50 cm of cover when sighted. The remainder of fish (3%) were greater than 50 cm but less than 1 m from cover. Age-1 brown trout showed a slightly different relationship to cover. While they were also most often found in cover (84%), the second most common location was greater than 50 cm but less than 1 m from

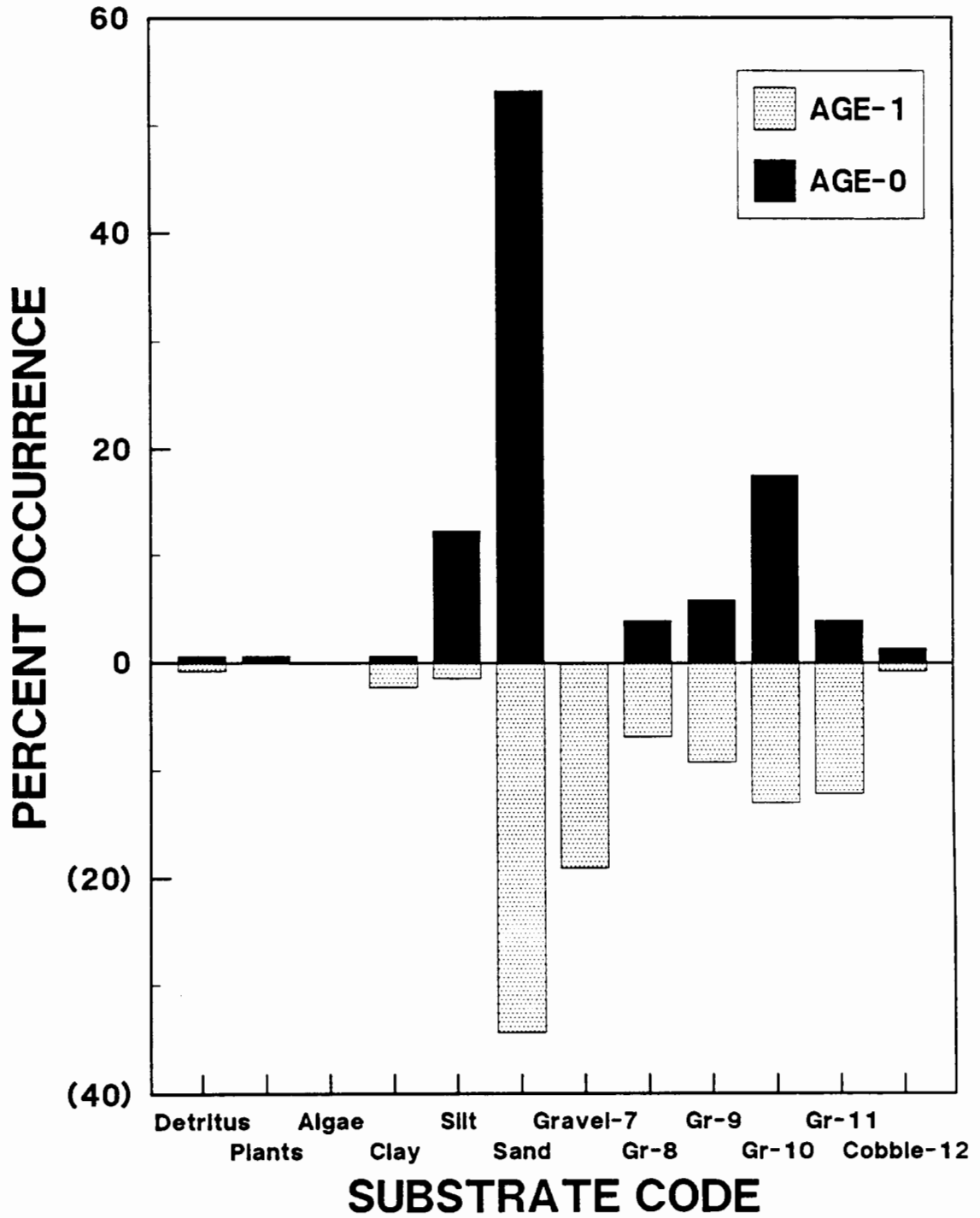


Figure 15.

Comparison of substrate types utilized by age-0 and age-1 brown trout. Detailed descriptions of substrates are in Appendix 3.

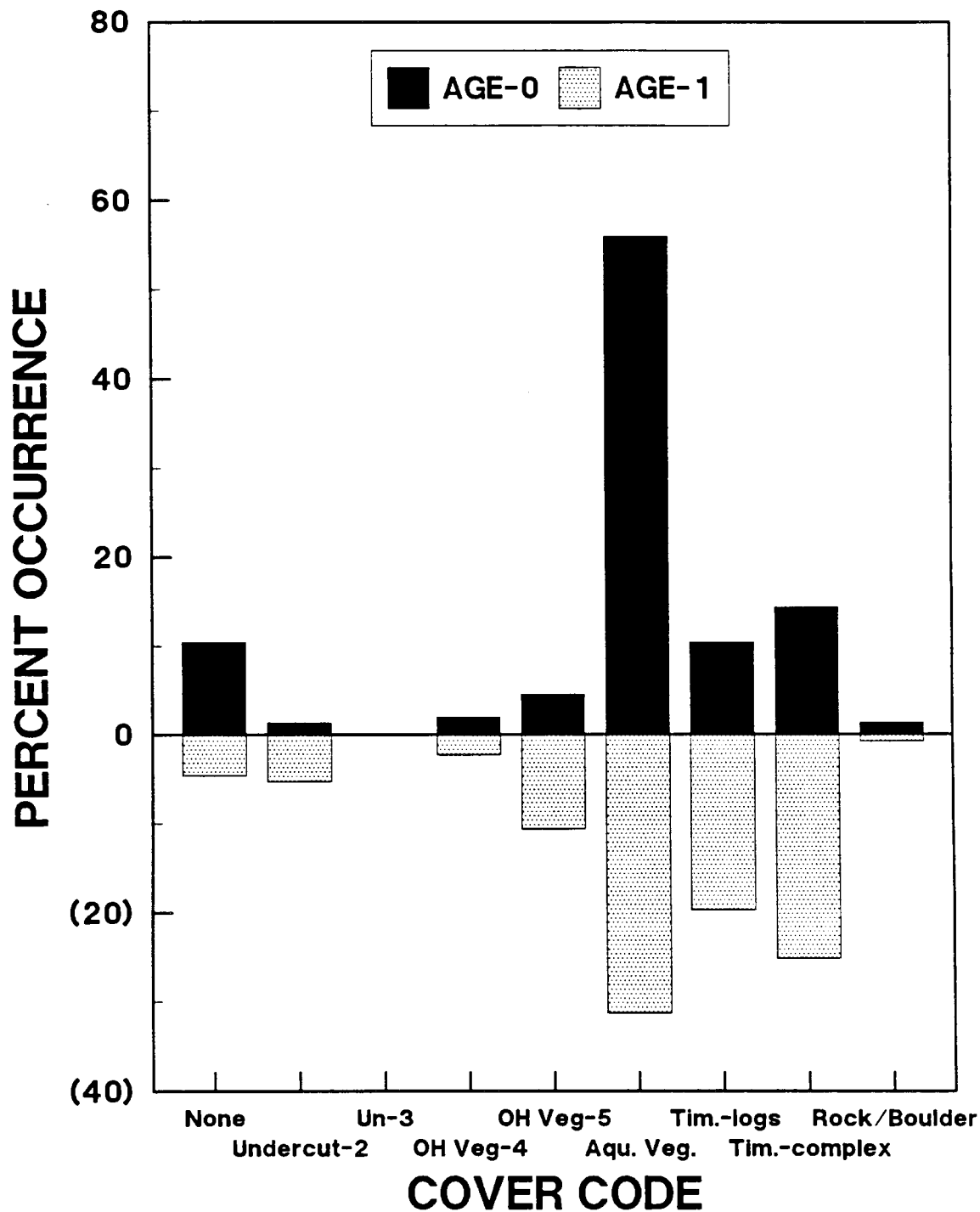


Figure 16.

Comparison of cover types utilized by age-0 and age-1 brown trout. Detailed descriptions of cover types are in Appendix 4.

cover (13%). The remaining 3% were found in the middle of these two positions. Brown trout of age-0 and age-1 were also most frequently (> 90%) sighted in very close proximity to the bottom. Divers noted that it was quite common for the anal, pelvic, and pectoral fins to be in direct contact with the substrate.

Steelhead Habitat Use and Impact on Brown Trout

Age-0 steelhead comprised 57 observations and age-1 steelhead only four observations. Given the low number of observations for age-1 steelhead, only anecdotal conclusions can be made regarding competition at this age. However, evaluations of habitat use similarities and differences between age-0 brown trout and steelhead were possible. Comparisons were made between summer-autumn habitat use of brown trout and observations for the same period for steelhead. Again, winter observations of steelhead were too low to statistically assess. Spring observations of steelhead were not made since steelhead were not stocked until late May (Note: wild steelhead would emerge at approximately the same time).

Comparisons of habitat use of steelhead and brown trout showed significant differences in only one of the 4 habitat variables ($P > 0.05$). Age-0 steelhead utilized water averaging 45 cm deep with a mean column velocity of 23 cm/sec. The difference in water depth was not significantly

($P > 0.10$) different from that utilized by brown trout (Figure 17). Water speed was significantly ($P < 0.01$) slower than that utilized by brown trout (Figure 18). No significant ($P > 0.10$) difference in use of cover or substrate occurred (Figure 19 and Figure 20). Steelhead used predominately sand and silt (81%) substrates like their brown trout cohorts. The predominant cover type for both species was aquatic vegetation, with steelhead found in this cover in 65% of observations. Use of other cover types was in approximately the same proportions.

The horizontal and vertical juxtaposition to cover and substrate varied somewhat from that of brown trout. Steelhead were closely related to cover, but not to the same extent as were brown trout. Of all steelhead observed, 74% were in cover and 22% were within 50 cm of cover. The remaining 4% were greater than 50 cm but less than 1 m from cover. Their vertical relationship to cover was very different. Over 90% of all steelhead observed were suspended in the water column. Contact of fins with the bottom was very rare for steelhead observed in this study.

The great amount of overlap in habitat use between these species implies the potential for competition and associated shifts in habitat use. To examine any changes, I compared habitat use of allopatric brown trout to that of brown trout in sympatry with steelhead. I found no significant difference in brown trout habitat use between

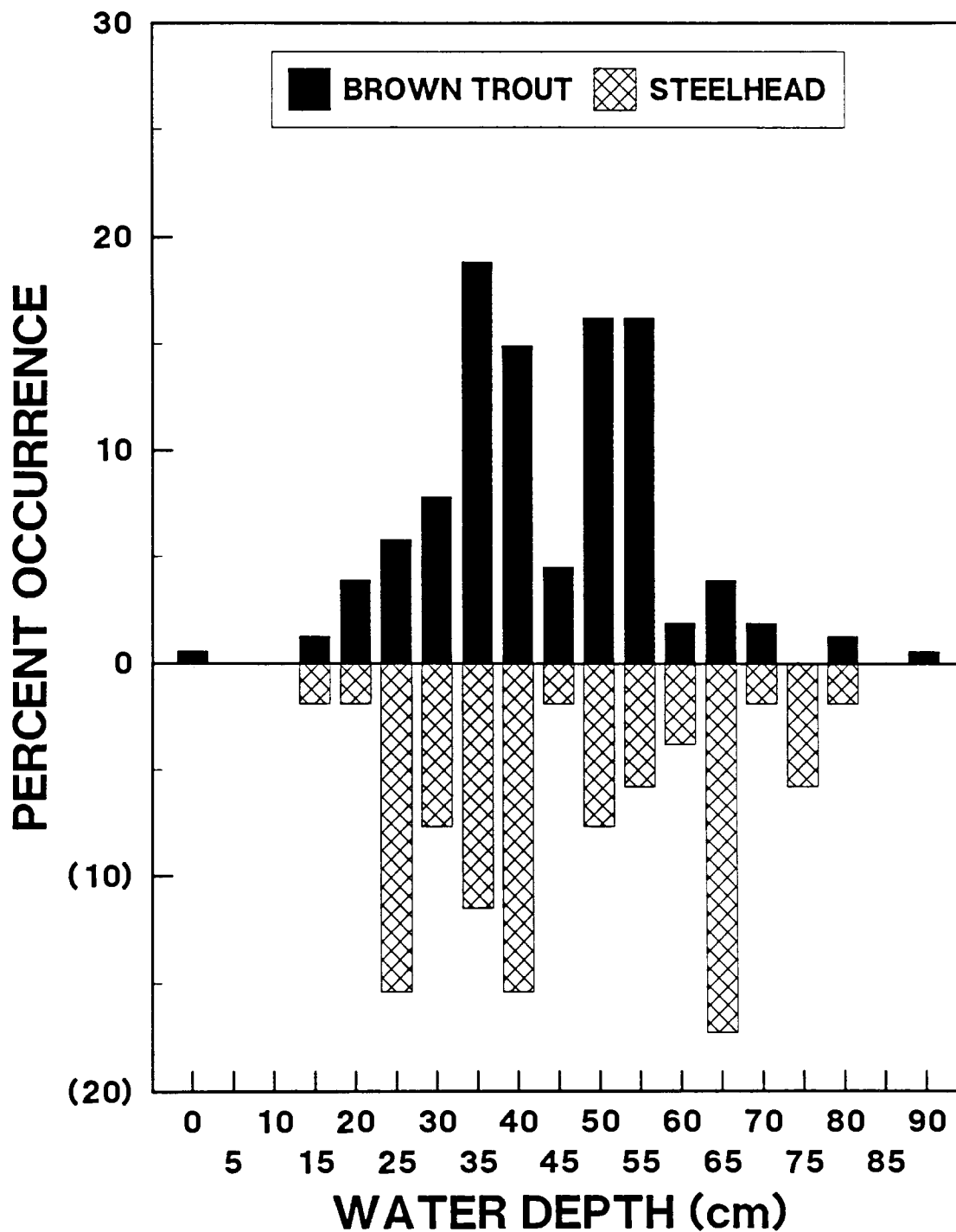


Figure 17. Comparison of water depth utilized by age-0 brown trout and steelhead.

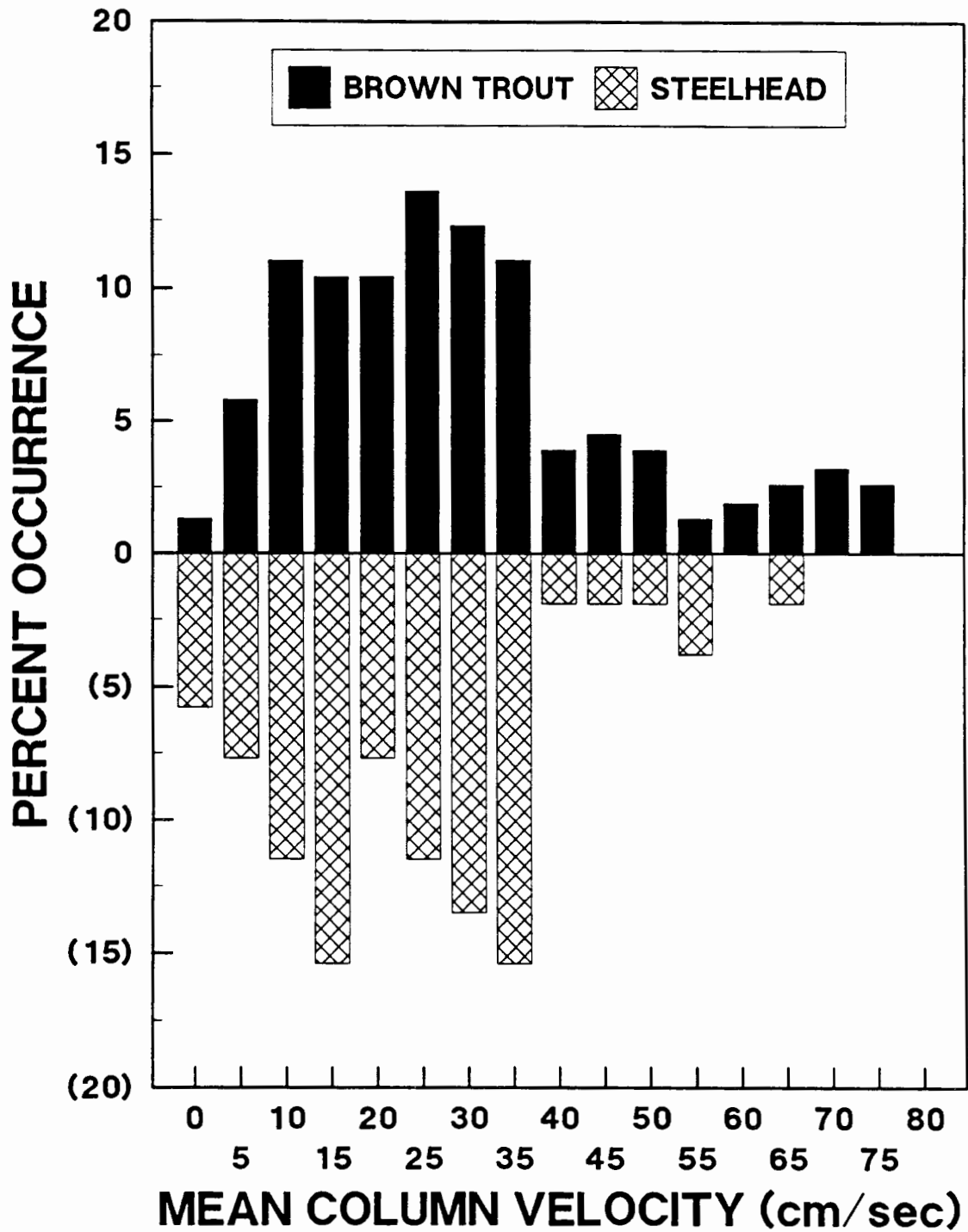


Figure 18. Comparison of mean column velocities utilized by age-0 brown trout and steelhead.

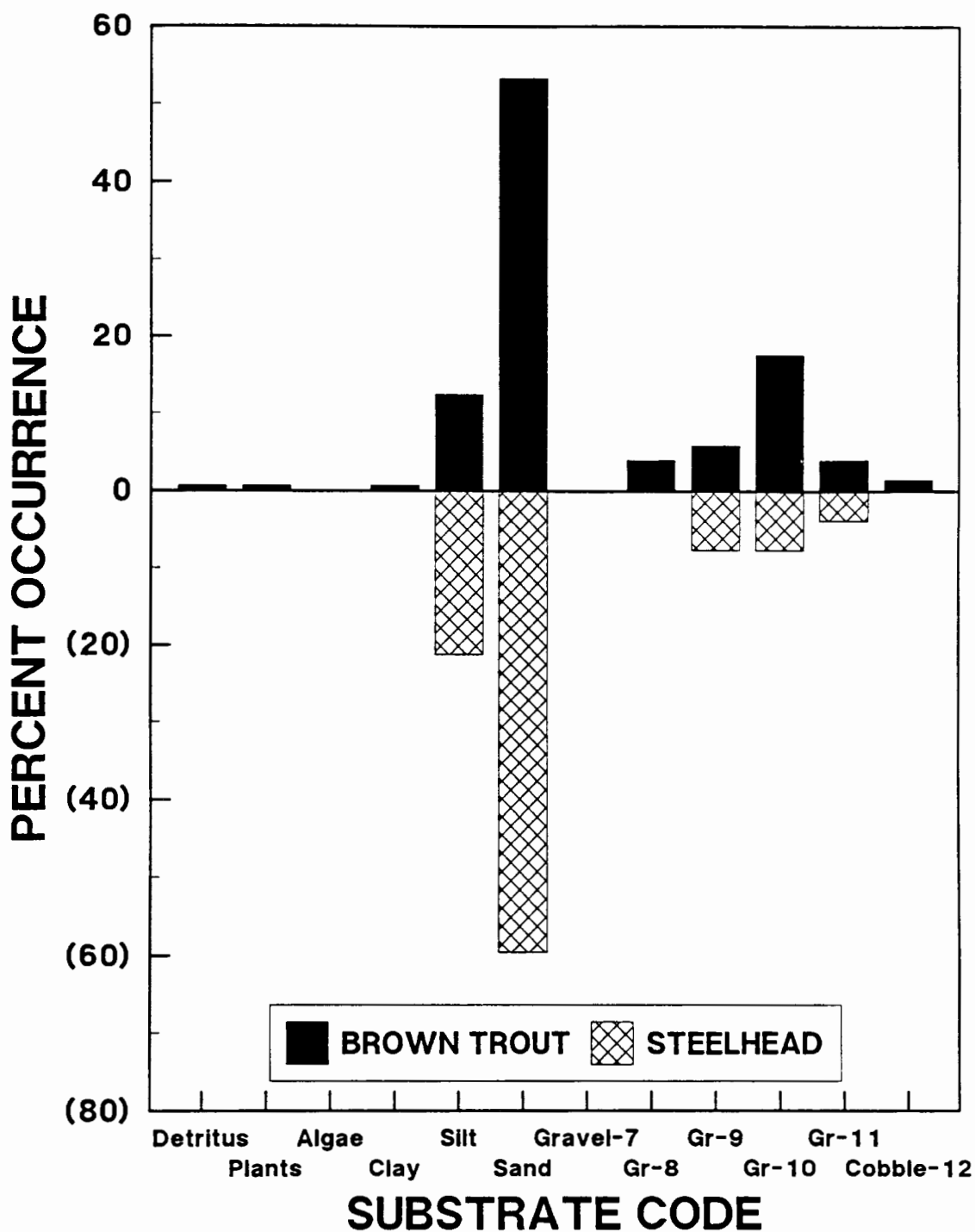


Figure 19. Comparison of substrates utilized by age-0 brown trout and steelhead. Complete descriptions of substrates are given in Appendix 3.

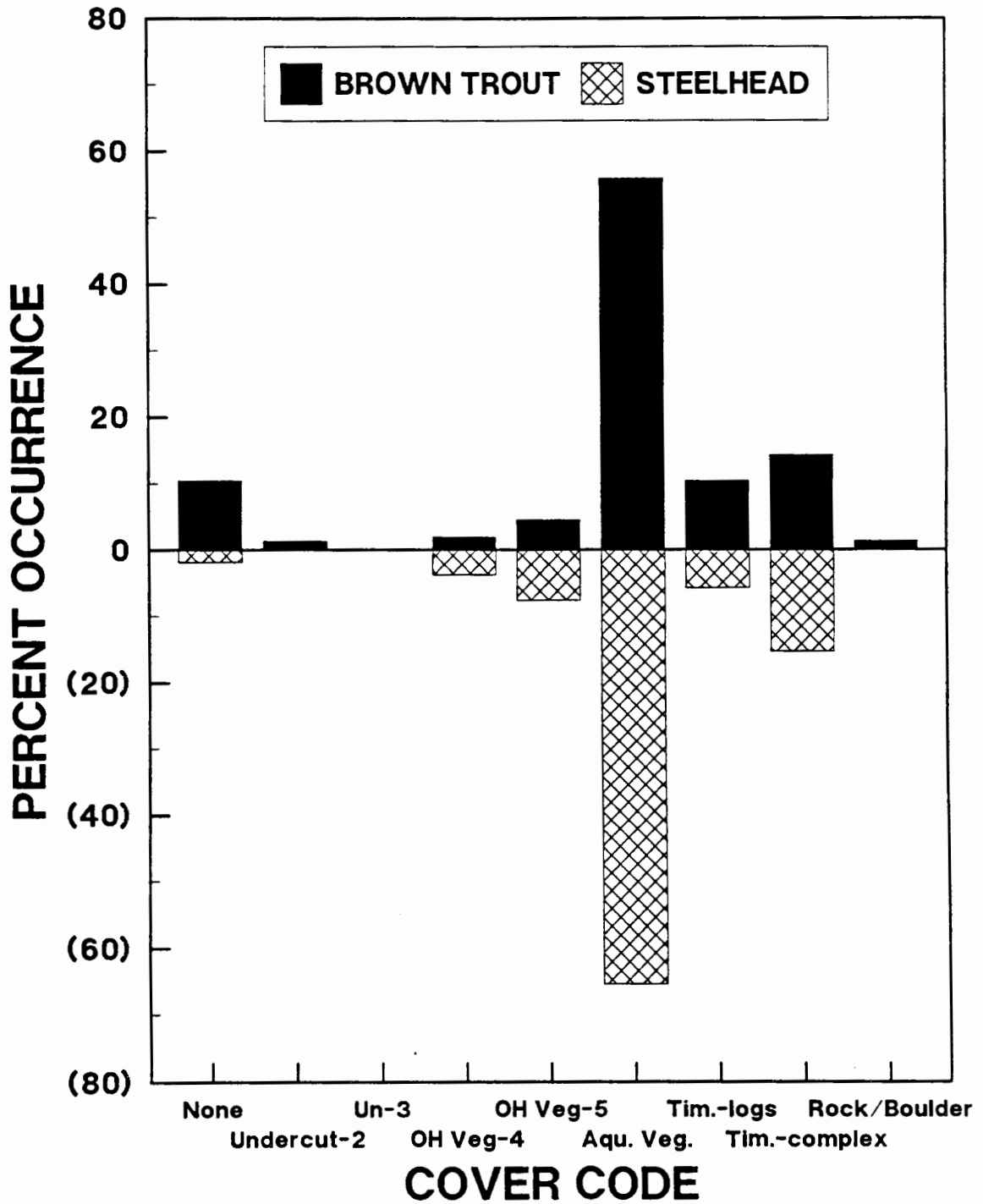


Figure 20.

Comparison of cover utilized by age-0 brown trout and steelhead. Complete descriptions of cover types are given in Appendix 4.

sympatry and allopatry for depth or cover variables ($P > 0.10$). However, significant differences were observed in mean column velocity and substrate. In sympatry, brown trout were found in slower water and utilized gravel to a greater extent. However, the magnitude of both of these shifts was in the opposite direction of the variables most frequently used by steelhead. Given the opposite direction of habitat shifts (ie. to habitats utilized by steelhead), I suspect that differences were driven by competition between brown trout cohorts or some other factor.

DISCUSSION

Brown Trout Habitat Use

Habitat use of age-0 and age-1 brown trout generally follow the habitat use patterns of brown trout populations in other regions (Cunjak and Power 1986; Raleigh et al. 1986; Ziegler 1988; Chaverocche and Sabaton 1989). Limited habitat use data are available for brown trout in the Great Lakes region (Gowan 1984; Ziegler 1988). Habitat utilization assessed in this study compares favorably to their results. My examination of habitat use on a seasonal basis provides some additional insights. Little is known of the habitat use of brown trout soon after emergence, ie. fish less than 50 mm (Raleigh et al. 1986). My spring assessments provided information on the habitat use of these newly emerged fish. These fish typically stayed in the stream margins in slow, shallow water. Aquatic vegetation was heavily used as cover and, as such, substrates were typically fines. Age-0 brown trout used aquatic vegetation quite frequently when it was available (Mortensen 1977a, 1977b; Mann et al. 1989). As the season progressed through summer and autumn, these age-0 fish moved to deeper faster water and utilized downed timber cover and gravel substrate more frequently. While not well documented for brown trout,

this habitat shift has been observed in other salmonine species (Chapman and Bjornn 1969; Symons and Heland 1978; Moore and Gregory 1988; Dauble et al. 1989).

Habitat use of age-1 brown trout did not vary between spring and fall. Habitat use of this age group was again similar to that reported by other authors (Gowan 1984; Raleigh et al. 1986; Hanson et al. 1987). These fish used deeper and faster water than age-0 fish. It is thought that the presence of these older fish may limit the use of deeper water by age-0 brown trout (Kennedy and Strange 1986). While my study has no direct evidence of this intraspecific competition between age groups, habitat use was partitioned by age groups.

Wintering habitat of brown trout was not effectively assessed through diving in this study; observations of both age-0 and age-1 brown trout were low. This is in contrast to the number of fish residing in the stream sections as indicated by winter electrofishing (Chapter 1). In the winter, salmonines are often found buried in substrates or associated with heavy cover (Rimmer et al. 1983; Cunjak and Power 1986; Cunjak 1988; Heggenes and Saltveit 1990). Both large substrates and heavy cover were searched in the manner described by these authors without success. I suspect that the observational differences were due to habitat availability and complexity. I feel that fish in this study were associated with complex timber and hidden in crevices.

Therefore, they were not visible to divers without frightening the fish. It was fairly common for divers to scare multiple fish from complex cover without making an adequate observation. This hypothesis is supported by observations during electrofishing. As such, I feel that fish were hidden in this cover in aggregates and that winter habitat use is similar to that noted by Cunjak and Power (1986).

Steelhead Habitat Use and Impact on Brown Trout

Steelhead habitat use was assessed only for age-0 steelhead due to low numbers of age-1 observations. They were first observed in summer since they were not present during spring dives. Habitat use by age-0 steelhead during the growing season is similar to that noted by other authors (Baltz and Moyle 1981; Raleigh et al. 1984; Sheppard and Johnson 1985; Ziegler 1988). Steelhead exhibited no significant shift in habitat use between summer and fall samples. By the time that fish were sampled in July and August, it is likely that they had already shifted habitats from stream margins to deeper waters. Another study in the Great Lakes observed steelhead fry to be using margin habitat as late as June (Sheppard and Johnson 1985). Since this transition is dependent upon size, and fish in Gilchrist Creek were large, the speculation of a habitat shift is probably safe. Steelhead habitat shifts during

their first growing season are well documented (Raleigh et al. 1984; Sheppard and Johnson 1985). Since behavior of age-0 fish is similar to reported values, their habitat at age-1 is also likely to be similar.

Comparisons of the summer and fall habitat use of steelhead and brown trout showed that each species used the same range of habitat variables. Only water velocity was significantly different, with steelhead utilizing slower waters. This difference corresponds to published habitat suitability curves for juveniles of both species (Raleigh et al. 1984; 1986). Ziegler (1988) found similar habitat use patterns in her examination of allopatric and sympatric populations of both species in three rivers. Similarities in habitat use between these two species has also been noted in other regions (Jenkins 1969; Raleigh et al. 1984, 1986; Cada et al. 1987).

Despite the large overlap in habitat use in all four variables, no shifts in brown trout habitat use could be attributed to steelhead presence. There are three probable explanations: 1) brown trout typically predominate in competition, 2) competition between the two species is negated by vertical stratification, or 3) the abundance of steelhead was not large enough to impact brown trout. Since brown trout maintain a size advantage through age-2 (Chapter 1), it is possible that they have an advantage in habitat use. Trout dominance hierarchies and use of preferred

feeding stations (optimal habitat) typically go to larger fish (Chapman 1966; Fausch 1984; Fausch and White 1986). This scenario seems likely given the larger size of brown trout juveniles. If this is true, then interspecific competition between the two species would favor brown trout at the juvenile life stage.

Vertical stratification in the water column could play a major role in coexistence of brown trout and steelhead in similar habitats. I observed steelhead to be suspended in the water column almost exclusively while brown trout remained close to the bottom. Ziegler (1988) also noted this vertical stratification. This type of stratification has been implicated as a segregation mechanism allowing the coexistence of salmonines (Allee 1982; Cunjak and Green 1983). This segregation has been termed habitat segregation (Hearn 1987). In habitat segregation, two species have innate differences in habitat use regardless of the other species' presence. This is supported by the fact that Ziegler (1988) observed differences in height in the water column in allopatric populations of both species as well as in sympatry. This segregation could be a major isolating factor between these species, allowing coexistence of these salmonines at the juvenile stage.

The abundance of steelhead in this study was relatively low by Great Lakes standards (Chapter 1). The ratio of steelhead to brown trout averaged 0.7:1 in June and 0.4:1 by

October. Since steelhead frequently outnumber brown trout in Great Lakes tributaries (Ziegler 1987), the low ratio of steelhead to brown trout may have affected the outcome of habitat use. The higher the ratio of steelhead, the more probable that individual steelhead will be larger than individual brown trout. Given higher steelhead densities, the steelhead may have been able to impact brown trout habitat use.

This study has shown that steelhead under relatively low densities have no impact on juvenile brown trout habitat use. Analysis of three plausible explanations for the lack of steelhead impact helps explain the interactions between these species. Given the results of this study, I feel that brown trout and steelhead have innate habitat isolation (vertical stratification) that contributes to their utilization of similar habitats. In addition, the size advantage and numerical advantage that brown trout have would benefit them in any interactive competition that could occur. A shift in species abundance or relative size at emergence could alter this relationship. This shift could be caused by differences in spawner abundance and/or the time of peak spawning (Chapter 1). Under such conditions, the balance might be tipped toward greater steelhead success to the detriment of brown trout.

APPENDICES

Appendix 1. P values for ANOVA models and linear contrasts for population estimates and instantaneous mortality rates for juvenile brown trout. Models significant at $P < 0.05$ and contrasts significant at $P < 0.01$. The * denotes comparisons of allopatric brown trout and brown trout in sympatry with steelhead.

Age-0		Between Sites			Pre vs Post	
Sampling Period	Model	1989	1990*	1991*	Site 1	Site 2*
<u>Population Estimates</u>						
June	0.401	0.141	0.981	0.979	0.741	0.052
October	0.434	0.096	0.563	0.750	0.072	0.795
Feb.	0.005	0.005	0.239	0.152	0.496	0.001
<u>Instantaneous Mortality</u>						
Summer	0.644	0.227	0.768	0.797	0.684	0.193
Winter	0.019	0.002	0.394	0.709	0.166	0.002
Spring	0.001	0.001	0.001		0.738	0.443
Age-1		Between Sites			Pre vs Post	
Sampling Period	Model	1988	1989	1990*	Site 1	Site 2*
<u>Population Estimates</u>						
June	0.037	0.685	0.051	0.575	0.006	0.804
October	0.015	0.053	0.244	0.455	0.003	0.206
February	0.021	0.243	0.734	0.074	0.003	0.136
<u>Instantaneous Mortality</u>						
Summer	0.276	0.150	0.693	0.939	0.084	0.277
Winter	0.021	0.027	0.441	0.812	0.220	0.005
Spring	0.475	0.152	0.653		0.283	0.395

Appendix 2. P values for ANOVA models and linear contrasts for total length and instantaneous growth rates of age-0 and age-1 brown trout. Models significant at $P < 0.05$ and contrasts significant at $P < 0.01$. The * denotes comparisons of allopatric brown trout and brown trout in sympatry with steelhead.

TOTAL LENGTH COMPARISONS

Age Class	Model	Between Sites			Pre vs Post	
		1989	1990*	1991*	Site 1	Site 2*
<u>Age-0</u>						
June	0.001	0.103	0.136	0.750	0.001	0.001
October	0.001	0.087	0.001	0.507	0.006	0.144
February	0.001	0.001	0.002	0.110	0.092	0.005
<u>Age-1</u>						
		1988	1989	1990*	Site 1	Site 2*
June	0.001	0.030	0.001	0.475	0.001	0.002
October	0.001	0.007	0.117	0.201	0.001	0.496
February	0.164	0.145	0.383	0.324	0.042	0.536

INSTANTANEOUS GROWTH RATE COMPARISONS

Sampling Period	Model	Site 1 vs. Site 2			Pre vs Post	
		1989	1990*	1991*	Site 1	Site 2*
<u>Age-0</u>						
Summer	0.001	0.888	0.001	0.220	0.183	0.001
Winter	0.096	0.070	0.033	0.294	0.466	0.400
Spring	0.090	0.457	0.027		0.114	0.027
<u>Age-1</u>						
		1988	1989	1990*	Site 1	Site 2*
Summer	0.034	0.340	0.081	0.816	0.533	0.027
Winter	0.929	0.956	0.978	0.398	0.750	0.496
Spring	0.682	0.319	0.593		0.582	0.326

Appendix 3. Generalized substrate classes (From Bovee 1986).

#	Class Name	Size Range (mm)
01	Organic Detritus	
02	Vascular Plants	
03	Attached Algae	
04	Clay	0.00024 - 0.004
05	Silt	0.004 - 0.062
06	Sand	0.062 - 2.0
07	Very Fine Gravel	2 - 4
08	Fine Gravel	4 - 8
09	Medium Gravel	8 - 16
10	Coarse Gravel	16 - 32
11	Very Coarse Gravel	32 - 64
12	Small Cobbles	64 - 128
13	Large Cobbles	128 - 256
14	Small Boulders	256 - 512
15	Medium Boulders	512 - 1024
16	Large Boulders	1024 - 2048
17	Very Large Boulders	> 2048
18	Bedrock Plain, unfractured	
19	Bedrock Plain, jointed	
20	Bedrock Tilted, perpendicular	
21	Bedrock Tilted, parallel	

Appendix 4. Descriptions of cover types. Adapted from
Bovee (1986).

#	Cover Code Class Name
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- logs
8	down timber- branches or roots
9	rock/ boulder
a/b	to combine 2 habitat codes

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