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THE ROLE OF LOW FLOW HABITAT AND INTERSPECIFIC COMPETITION
IN LIMITING ANADROMOUS PARR ABUNDANCE IN NORTH SHORE STREAMS

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Donald E. Woods, Fisheries Research Manager

THE ROLE OF LOW FLOW HABITAT AND INTERSPECIFIC COMPETITION

IN LIMITING ANADROMOUS PARR ABUNDANCE IN NORTH SHORE STREAMS[1]

by

Tracy L. Close
Fisheries Biologist

and
David A. Belford
Fisheries Biologist

and
Steven E. Colvin
Fisheries Biologist

and
Charles S. Anderson
Coldwater Fisheries Research Supervisor

Minnesota Department of Natural Resources
Section of Fisheries

ABSTRACT

We investigated the roles of summer low flow habitat and
interspecies competition as limiting factors of chinook salmon
(Oncorhynchus tshawytscha), Atlantic salmon (Salmo salar), and
steelhead (O. mykiss, formerly Salmo gairdneri) parr in North Shore
streams. Macro-and micro-habitat availability and use by allopatric
and sympatric populations were analyzed by analysis of variance
(ANOVA) and multiple regression. Summer densities of age 0 and
age 1 or older (1+) age classes were highly variable and were
independent of measured low flow habitat variables and the densities
of potentially competing species. Steelhead and Atlantic salmon parr
preferred fast-water habitats and avoided pools. Chinook salmon parr
were found in deeper water than steelhead parr and Atlantic salmon
parr, but snout velocities were similar. Overhead cover was a
significant component of habitat use models for all ages of steelhead
and Atlantic salmon, but overhead cover did not limit abundance. We
concluded that low flow habitat is not a major limiting factor, and
we found no evidence of interspecific competition in sympatry. The
year-to-year and stream-to-stream variations in fish density suggest
that other environmental factors normally limit salmonid abundance to
less than the low flow carrying capacity.

INTRODUCTION

Understanding the dynamics and behavior of steelhead
Oncorhynchus mykiss (formerly Salmo gairdneri), Atlantic salmon
S. salar, and chinook salmon O. tshawytscha parr is the key to
intensively managing the Lake Superior anadromous fish stocks
intensively. Steelhead residing 2-3 years in streams contribute 88%
to the returning adult stocks (Hassinger et al. 1974). Hassinger
(1981) and Close et al. (1984) suggest adult returns are primarily a
function of the number and fitness of smolts. To increase the
fitness and production of anadromous smolts, the factors affecting
growth and survival of parr must be determined.

Smolt production could be influenced by the amount of suitable
summer rearing habitat. Binns and Eisermann (1979) found that trout
abundance was limited primarily by the amount of summer habitat and
flow stability, and they developed a model that precisely predicted
fish density from habitat characteristics. Summer habitat in North
Shore streams may have a similar impact on juvenile salmonid
densities because there is little groundwater input for summer base
flow. We investigated the relationship between low flow macrohabitat
variables and juvenile salmonid densities to determine the limiting
factors in North Shore streams.

Interspecific competition for space can also influence species
distribution and abundance (Fausch and White 1981; Whitworth and
Strange 1983; Larson and Moore 1985). Competition for rearing space
between chinook salmon, Atlantic salmon, and steelhead could limit
parr abundances in North Shore streams, so the importance of
competition for space must be determined to guide multispecies

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management. We measured microhabitat availability and use by each species in allopatric and sympatric populations. An overlap in microhabitat use by allopatric species indicated there was a potential for competition while a change in microhabitat use by sympatric species was assumed to indicate the occurrence of competition (Fausch and White 1981).

This study examined the role of summer habitat and interspecific competition as factors limiting abundance of anadromous salmonid parr. Our goal was to apply our findings by developing recommendations for stocking, for multi-species management, and for habitat improvement to maximize smolt output of North Shore streams.

STUDY AREAS

This study included 12 study sectors in five streams on the North Shore of Lake Superior (Table 1). North Shore streams are characterized by small watersheds and little groundwater input. Headwater reaches are inhabited by brook trout <u>Salvelinus</u> <u>fontinalis</u>, and natural reproduction of anadromous salmonids is limited by water falls and cascades to 156 km in 58 streams (Hassinger et al. 1974). Stocking of salmonid fry above the barriers and barrier modification (step pockets) are current management practices to increase smolt output.

METHODS

Stocking and Fish Density

Chinook salmon, Atlantic salmon, and steelhead swim-up fry were stocked in 1984-1986 in 300 m study sectors at a total density of 5 salmonid fry/m^2 (wetted surface area) in allopatric and sympatric combinations (Table 1). The 300 m study sectors were subdivided into

Table 1. Stocking quotas (swim-up fry) for study sectors.

Study stream	Sector[a]	Steelhead	Atlantic salmon	Chinook salmon
Lester River	1	5,000	5,000	5,000
Lester River	2	5,000	5,000	--
Lester River	3	5,500	5,500	--
Gooseberry River	1	5,000	5,000	5,000
Gooseberry River	2	8,500	--	8,500
Gooseberry River	3	13,500	--	--
Two Island River	1	--	3,500	3,500
Two Island River	2	--	--	7,500
Two Island River	3	--	--	9,000
W. Br. Split Rock	1	9,000	--	--
E. Br. Split Rock	1	--	9,000	--

[a] Sector number increased upstream.

25 m sections. Eggs were incubated at stream temperatures so that fry swim-up coincided with naturally hatched fish. Chinook salmon and Atlantic salmon were stocked in May and steelhead were stocked in June.

Salmonid densities in each 25 m section were estimated once each year from June to October in 1984-1986 by electrofishing using the removal method of Carle and Strub (1978). Captured fish were given a caudal fin clip and released back to the area where they were captured. We alternated upper, lower, and both lobe fin clips to validate our assumption that movement of fish between sections was minimal. We assumed that migration into and out of the 300 m sectors was minimal during the sampling interval. Typically, two electrofishing passes spaced 24 h apart were used to estimate the population size. Average densities (unweighted) for each 300 m sector are reported here, but the 25 m section densities were used in

regression analyses.   Electrofishing was performed using a Smith-Root Type 11 backpack unit.

Macrohabitat Use

Water velocity-depth categories and overhead cover types (Table 2) were diagrammatically mapped using the method of Oswood and Barber (1982). Oswood and Barber suggested two depth categories, shallow (<0.5 m) and deep ($\geq$0.5 m). North Shore streams have large areas of shallow water so we added a very shallow fast category that included depths <0.15 m. The percent area of each substrate type was estimated in each 25 m study section and the length of the thalweg was measured.

The relationship of macrohabitat variables to juvenile densities was determined by step-wise multiple regression analysis (Draper and Smith 1981). For regression Model 1, dependent variables were section densities of similar aged salmonid cohorts and independent variables were percent of total section area of each macrohabitat category and thalweg length. Only significant variables (P <0.05) were included in the final model. Transformations of the dependent and independent variables were investigated with the methods suggested by Weisberg (1985), but the models could not be improved significantly (P >0.05). We assessed multicolinearity in the independent variables by noting coefficient stability during stepwise regression and concluded multicolinearity was not excessive.

Regression Model 2 included year and stream indicator variables (Neter et al. 1985) to determine the possible effects of unmeasured year-to-year and stream-to-stream variations. We compared the coefficients of determination (R^2) of the two models with the same

Table 2. Water velocity-depth, overhead cover, and substrate
         categories used in diagrammatic mapping.

Category (code)	Description
Very shallow slow (VSS)	Area of water <0.15 m deep and water velocity <0.3 m/s.
Very shallow fast (VSF)	Area of water <0.15 m deep and water velocity >0.3 m/s.
Shallow slow (SS)	Area of water >0.15 m and <0.5 m deep and water velocity <0.3 m/s.
Shallow fast (SF)	Area of water >0.15 m and <0.5 m deep and water velocity >0.3 m/s.
Deep slow (DS)	Area of water >0.5 m deep and water velocity <0.3 m/s.
Deep fast (DF)	Area of water >0.5 m deep and water velocity >0.3 m/s.
Forest debris (FD)	Area of fallen trees and branches in the sampling station (fish cover).
Undercut banks (UB)	Area of eroded stream banks which offer overhead cover for fish.
Riparian vegetation (RV)	Area of overhanging vegetation along stream banks.
Boulder (1)	Rock particles >250 mm diameter.
Rubble (2)	Rock particles .250 mm and >75 mm diameter.
Gravel (3)	Rock particles .75 mm and >3 mm diameter.
Sand (4)	Rock particles .3 mm diameter.
Silt (5)	Fine material with little grittiness.
Clay (6)	Compact, sticky material.
Muck (7)	Decomposed organic matter, usually black.
Detritus (8)	Organic material composed of sticks, leaves, decaying plants, etc.

dependent variable to determine the relative importance of unmeasured variables.

Microhabitat Use

Microhabitat available to parr was determined in 1987 by making measurements at 1 m intervals along transects (perpendicular to the center line) spaced 25 m apart. Our goal was to sample 100 locations in each 300 m study sector. If the number of measurement points in a sector totaled less than 70, the number was increased by spacing transects 12.5 m apart. Mean water column velocity (at 0.6 the water depth from the surface), bottom water velocity (at 3.0 cm above the stream bottom), water depth, and dominant substrate within a diameter of 1 m were recorded at each point. All water velocities were measured with a pygmy Price-type velocity meter.

Microhabitat use by parr was also determined in 1987 by direct underwater observations by skin divers in six study sectors (Table 3). Snout velocities (focal point velocity) of undisturbed fish were measured with a midget Bentzel flow-speed tube (Everest 1967). Divers also measured water depth and distance of the fish above the substrate. A person following the divers measured mean water column velocity, and recorded the dominant substrate category within a 1 m diameter circle. Two or three 25 m sections were electrofished in 1987 in each sector where microhabitat data were collected. Densities were estimated and compared to averages for those sections in previous years to be sure that conclusions about species interactions were not the result of "unusual" densities.

A series of analysis of variance tests (ANOVA) was used to determine if significant differences in the microhabitats used by

Table 3. Stream sectors sampled for microhabitat use by fish. Species
codes are RBT-steelhead, ATS-Atlantic salmon, and CHS-chinook
salmon.

Stream	Sector	Sampling period	Species	Mean total-length (SD)
W. Branch Split Rock	1	July 1-6	RBT	42.4 (6.4)
E. Branch Split Rock	1	July 7-8	ATS	55.9 (6.1)
Two Island	2	June 10-19	CHS	54.9 (6.4)
Lester	1	June 22-26	RBT	37.9 (6.5)
			ATS	59.2 (8.5)
Lester	2	August 10-21	RBT	54.3 (7.5)
			ATS	72.7 (5.6)
Lester	3	July 15-August 7	RBT	52.3 (6.1)
			ATS	70.1 (5.6)

allopatric populations of Atlantic salmon, steelhead, and chinook
salmon existed. We assumed that there was correlation between the
variables, but even after logorithmic transformation, unequal
variance-covariance matrices prevented the use of multivariate
analysis of variance (MANOVA). Thus, an ANOVA test was performed for
each of the five variables measured at $P = 0.01$ level (0.05 divided
by 5) to control the overall Type I error at $P = 0.05$ (Harris 1975).
If log transformation failed to equalize variances, a Kruskal-Wallis
(nonparametric) test was performed to determine equality of
distributions (Neter et al. 1985). Pairwise multiple comparisons
(Tukey's technique for ANOVA's and Bonferroni's technique for
Kruskal-Wallis') were made if the test rejected the null hypothesis
(Neter et al. 1985). A similar analysis was performed on the
available habitat in the study sectors to aid in determining if
available habitat influenced the habitat use of the salmonids.

Lester River sectors 2 and 3, which had similar sympatric community structures, were sampled to determine if habitat availability influenced microhabitat use by steelhead and Atlantic salmon. Analysis of the available microhabitat, however, indicated that the sectors did not differ significantly in habitat availability (ANOVA, $P > 0.05$).

Habitat preference (except substrate) was evaluated by a Mann-Whitney test of the equality of the distributions of used and available habitat. Preference for dominant substrate was evaluated with a Kolmogorov-Smirnov test (Snedecor and Cochran 1967). Fish snout velocities were compared with available "bottom" velocities since most fish were within 5 cm of the stream bottom. If the null hypothesis of random selection was rejected, we inspected the histograms of used and available habitat to determine what habitat was preferred.

Species Interaction

Species interactions at the macrohabitat level were analyzed using multiple regression analysis. Section densities of other potentially competing fish species (excluding the cohort modeled) were added as independent variables to each Regression Model 2, thus controlling significant macrohabitat, year-to-year, and stream-to-stream variables. Competition with other fish species was indicated when a fish species contributed significantly ($P < 0.05$) to the model and yielded a negative coefficient.

A series of ANOVA's similar to those described above was carried out to determine if species interactions influenced microhabitat selection. These ANOVA's compared the difference between the mean use

of a habitat variable by the allopatric populations of steelhead and
Atlantic salmon with the difference of mean use by the sympatric
populations of the two species. We assumed that an increase in the
difference of mean habitat use of a variable indicated that a niche
change had occurred.

<div align="center">RESULTS</div>

Fish Densities

Densities of young-of-the-year (Y-O-Y) steelhead (Table 4)
and Atlantic salmon (Table 5) varied between 1.1-22.7 and 0.1-85.2
fish/100 m^2, respectively. Chinook salmon densities (<0.1-0.9
Y-O-Y fish/100 m^2) were consistently low, probably due to early
smoltification. The greatest densities of Y-O-Y steelhead and
Atlantic salmon occurred in allopatric populations. In the
Gooseberry River sector 3, however, allopatric Y-O-Y steelhead
densities were similar to sympatric populations indicating that
stream variation may have been responsible for the greater allopatric
densities. Densities of Y-O-Y varied by year, but no consistent
pattern was apparent.

Densities of steelhead and Atlantic salmon older than age 1 (1+)
were 0-14.5 and 0-2.6 fish/100 m^2, respectively (Tables 4 and 5).
Variations in fish density did not appear to be related to the
presence of potentially competing species. Densities of age 1+
steelhead were highest in 1984 and densities of both species were
lowest in the Gooseberry River.

Macrohabitat Use

Macrohabitat use by steelhead and Atlantic salmon were modeled,
but that of chinook salmon was not as they were smolting during

Table 4. Average (unweighted) densities (no./100 m^2) of steelhead (RBT) parr in 300 m study sectors. The sector number follows the river name. ATS and CHS indicate that Atlantic salmon and chinook salmon, respectively, were in sympatry.

	RBT		RBT-ATS		RBT-CHS	RBT-ATS-CHS	
		West Branch					
Year	Gooseberry 3	Split Rock River	Lester 2	Lester 3	Gooseberry 2	Lester 1	Gooseberry 1
			YOY RBT				
1984	[a]	12.9	4.5	1.5	3.3	4.4	1.6
1985	2.7	14.9	3.1	2.8	3.0	8.7	1.1
1986	3.6	22.7	1.8	1.9	6.3	1.7	2.4
			1+ RBT				
1984	[a]	14.5	13.0	1.6	0.8	2.2	0.2
1985	<0.1	3.7	1.2	0.3	<0.1	0.9	<0.1
1986	0.1	1.5	2.5	0.	0.1	1.1	<0.1

[a] Not sampled.

Table 5. Average (unweighted) densities (no./100 m^2) of Atlantic salmon (ATS) parr in 300 m study sectors. The sector number follows the river name. RBT and CHS indicate that steelhead and chinook salmon were present in sympatry.

| | ATS | ATS–RBT | | ATS–CHS | ATS–RBT–CHS | |
| | East Branch | | | | | |
Year	Split Rock River	Lester 2	Lester 3	Two Island 1	Lester 1	Gooseberry 1
				YOY ATS		
1984	85.2	12.4	2.1	0.6	11.8	5.0
1985	3.8	0.1	0.4	[a]	2.8	0.8
1986	59.0	1.0	1.2	2.0	1.0	1.6
				1+ ATS		
1985	0.4	1.0	0.6	[a]	2.6	0.1
1986	1.2	0.2	0.1	0.7	0.1	<0.1

[a] Not sampled.

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our sampling period. Macrohabitat variables (Model 1) explained 40% and 23% of the variation in Y-O-Y steelhead and Atlantic salmon densities, respectively (Table 6). Shallow water (SF, VSF, and SS categories) and cover (RV and FD categories) were important in explaining Y-O-Y steelhead densities. Although the coefficient of determination was lower for Y-O-Y Atlantic salmon, only the amount of SF and boulder habitat accounted for the explained variation.

The greatest increase in R^2 resulting from the addition of indicators was in the Y-O-Y Atlantic salmon model. Addition of year and stream indicators increased the R^2 value of the Y-O-Y Atlantic salmon model by 0.31. Addition of the stream indicator variable to the Y-O-Y steelhead model raised the R^2 by only 0.18.

Macrohabitat variables (Model 1) explained only 20% and 5% of the variation in densities of 1+ steelhead and Atlantic salmon, respectively. Cover (FD, Boulder, and RV categories) had the greatest positive relationship to 1+ steelhead densities. Only the percent of SF habitat had a significant relationship to densities of 1+ Atlantic salmon.

With the addition of the indicator variables in the analysis (Model 2), the explanation of 1+ steelhead and Atlantic salmon densities increased 19% and 9%, respectively. Year variation helped explain the variation of densities of both species, while stream variation was also significant in the 1+ steelhead model.

Microhabitat Use

Steelhead, chinook salmon, and Atlantic salmon in allopatric communities differed significantly (P <0.05) in microhabitat use (Fig. 1). Significant differences were found in water depth, distance

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Table 6. Significant (P <0.05) variables with their coefficients and p-values (P) for regression Model 1 (habitat variables only) and Model 2 (habitat and year and stream indicator variables).

Species	Age	Model 1				Model 2			
		Variable[a]	Coefficient	P	R^2	Variable[a]	Coefficient	P	R^2
Steelhead	0+	Y-intercept	-0.038	0.002	0.40	Y-intercept	0.015	0.006	0.58
		SF	0.149	<0.001		Stream[b]		<0.001	
		RV	0.595	<0.001		SF	0.064	<0.001	
		VSF	0.088	<0.001		VSF	0.034	0.029	
		FD	0.440	<0.001					
		SS	0.045	0.007					
	1+[d]	Y-intercept	-0.012	0.084	0.20	Y-intercept	0.078	0.072	0.39
		FD	0.634	<0.001		Year		<0.001	
		Boulder	0.114	<0.001		Stream[c]		<0.001	
		RV	0.313	0.003		DS	0.054	<0.001	
		DF	-0.149	0.019		Boulder	0.088	<0.001	
		Sand	0.053	0.045		FD	0.347	0.002	
						Thalweg	-0.003	0.037	
Atlantic salmon	0+	Y-intercept	0.053	0.062	0.23	Y-intercept	0.018	0.550	0.54
		Boulder	0.626	<0.001		Stream		<0.001	
		SF	0.154	0.014		Year		<0.001	
						SF	0.105	0.026	
	1+[d]	Y-intercept	0.002	0.408	0.05	Y-intercept	0.000	0.822	0.14
		SF	0.009	0.002		Year		<0.001	
						SF	0.009	0.001	

[a] Habitat variable abbreviations are given in Tables 2 and 3.
[b] Stream-to-stream variation indicator variables. A single coefficient cannot be calculated.
[c] Year-to-year variation indicator variables. A single coefficient cannot be calculated.
[d] This group includes all fish of that species equal to or greater than age 1+.

above the substrate, and dominant substrate, but not in mean or snout water velocities (Table 7). The average Atlantic salmon located itself about 1.4 cm above the substrate in boulder/rubble substrate and was significantly (P <0.01) closer to the bottom than steelhead or chinook salmon. Atlantic salmon also selected coarser substrates than steelhead or chinook salmon, but coarser substrates were more available to the Atlantic salmon. Chinook salmon occupied water 28.0 cm deep on the average which was significantly (P <0.01) deeper than Atlantic salmon or steelhead. Average mean water column velocities (14.1-15.1 cm/s) and snout velocities (11.2-12.7 cm/s) were not significantly (P >0.01) different.

All three species generally selected a preferred habitat for all variables except dominant substrate under both allopatric and sympatric conditions (Figs. 1-4). Steelhead, Atlantic salmon, and chinook salmon selected for significantly (P <0.05) faster and deeper water than generally available. In the Lester River sector 1, however, steelhead (mean total length of 37.9 mm) chose the abundant 0-10 cm/s mean and snout water velocities in proportion to availability (Fig. 2). Atlantic salmon in Lester River sector 1 selected significantly (P <0.05) larger substrates than generally available, but in all other cases, fish selected substrate in proportion to availability.

Species Interactions

Macrohabitat--A negative relationship existed between 1+ steelhead and chinook salmon (P = 0.015) in our regression model, but this relationship was probably a statistical aberation since chinook

Table 7. Comparison of microhabitat used by allopatric steelhead, Atlantic salmon and chinook salmon (ANOVA, P=0.01). Species with different letters in a group differed significantly for that variable (Tukey's pairwise comparisons).

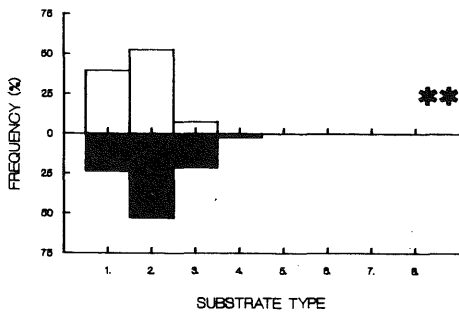| Species	N	River	Sector	Water depth (cm) Mean(SD)	Group	Distance above bottom (cm) Mean(SD)	Group	Mean velocity (cm/s) Mean(SD)	Group	Snout velocity (cm/s) Mean(SD)	Group	Dominant substrate rating[a] Mean(SD)	Group
RBT	95	W. Br. Split Rock	1	20.9(7.8)	A	4.8(4.5)	B	14.2(11.1)	A	12.7(7.2)	A	2.4(0.8)	B
ATS	53	E. Br. Split Rock	1	21.1(6.9)	A	1.4(1.6)	A	14.1(10.2)	A	12.5(9.4)	A	1.7(0.6)	A
CHS	28	Two Island	2	28.0(9.5)	B	3.2(1.7)	B	15.1(9.0)	A	11.2(4.0)	A	2.8(0.7)	B

[a] Dominant substrate ratings are given in Table 4.

salmon densities were so low. A positive relationship existed between Y-O-Y steelhead and 1+ Atlantic salmon (P <0.001).

Microhabitat--Microhabitat use by steelhead and Atlantic salmon differed more in sympatry than allopatry in only the Lester River sector 1; in the other two sectors, habitat use converged. In the Lester River sector 1, the difference between the mean use of water depth, water column velocity, and snout velocity by steelhead and Atlantic salmon increased significantly (P <0.01; Table 8) over allopatry, while the availabilities of these microhabitat variables were similar (P <0.013). This difference was attributed to the steelhead using slower, shallower water in the Lester River sector 1 than in allopatry, while Atlantic salmon habitat use was similar to that in allopatry. Habitat use by sympatric steelhead and Atlantic salmon in the Lester River sectors 2 and 3 was significantly more similar than in allopatry (P <0.05), since these species used significantly more similar substrate in sympatry than in allopatry (P <0.01). No change was found in the distance above the substrate in sympatry versus allopatry.

Table 8. Comparison of the differences between micro-habitat use of allopatric steelhead (W. Branch Split Rock River) and Atlantic salmon (E. Branch Split Rock River) with sympatric populations in the Lester River (ANOVA, P=0.01). Differences in mean habitat use with different letters in a group were significantly different for that variable (Tukey's pairwise comparisons).

Species	N	River	Sector	Water depth (cm) Mean (SD)	Difference between means	Group	Distance above substrate (cm)[a] Mean (SD)	Difference between means	Group	Mean velocity (cm/s) Mean (SD)	Difference between means	Group	Snout velocity (cm/s) Mean (SD)	Difference between means	Group	Dominant substrate rating[b] Mean (SD)	Difference between means	Group
RBT	95	W. Br. Split Rock	1	20.9(7.8)		A	4.8(4.5)		A	14.2(11.1)		A	12.7(7.2)		A	2.4(0.8)		A
					−0.2			3.4			0.1			0.2			0.7	
ATS	53	E. Br. Split Rock	1	21.1(6.9)			1.4(4.5)			14.1(10.2)			12.5(9.4)			1.7(0.6)		
RBT	63	Lester	1	15.7(5.9)		B	3.7(2.5)		A	9.2(8.8)		B	8.9(5.8)		B	2.5(0.7)		AB
					−6.2			2.3			−11.2			−5.4			0.3	
ATS	40	Lester		21.9(6.5)			1.4(1.5)			20.4(13.1)			14.3(8.7)			2.2(0.7)		
RBT	49	Lester	2	24.7(8.3)		AB	5.2(5.4)		A	19.3(13.1)		A	13.0(8.2)		AB	2.3(0.9)		B
					−3.7			3.1			0			−1.3			0	
ATS	34	Lester		28.4(11.6)			2.1(2.6)			19.3(15.4)			14.3(9.5)			2.3(1.1)		
RBT	44	Lester	3	26.6(7.5)		A	4.0(2.9)		A	15.3(9.8)		AB	11.6(7.0)		AB	2.1(0.9)		B
					0.7			1.6			−5.8			−2.3			−0.2	
ATS	40	Lester		25.9(9.0)			2.4(2.0)			21.1(15.1)			13.9(8.2)			2.3(0.7)		

[a] Kruskal-Wallis test with Bonferroni pairwise multiple comparisons.
[b] Dominant substrate ratings are given in Table 4.

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DISCUSSION

Neither summer (low flow) habitat nor interspecific competition were consistent limiting factors during this study. Summer flows, and thus available habitat, were similar each year and sympatric stocking rates were identical each year, but fall densities were extremely variable. Binns and Eiserman (1979) were able to predict fish densities reliably with a model using one-time ratings of low flow habitat quality and flow stability as independent variables, indicating that summer habitat was a very important limiting factor. Our findings, however, suggest that a model similar to the Binns and Eiserman model would not reliably predict salmonid parr densities on the North Shore.

We hypothesize that three climatic factors act as limiting factors for age 0 parr. North Shore streams are characterized by high discharges resulting from spring rains, and we suspect that spate flows frequently limit age 0 abundance. Work by several authors indicates that spate flows limit stream fish populations (Anderson and Nehring 1985, House and Boehne 1986, Hume and Parkinson 1987). Our study supports this because Y-O-Y Atlantic salmon, which were stocked earlier in the spring than steelhead and were thus more exposed to spring spates, exhibited more year-to-year variation in density. The occurrence of low summer flows and low groundwater input suggests that stream temperature may become high enough to cause mortality. Acid rain may also be a source of mortality (Lacroix and Townsend 1986), however work by Waters (1986) suggests that acid rain has not had a measurable affect on invertebrates which act as a biological indicator of acid rain damage in North Shore streams.

Figure 1.   (On the following two pages)
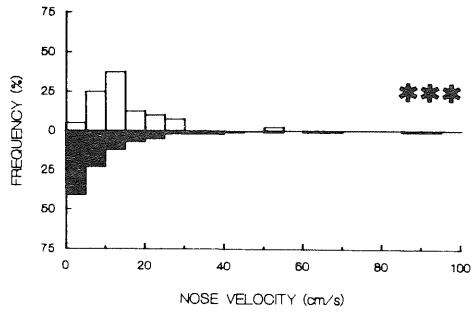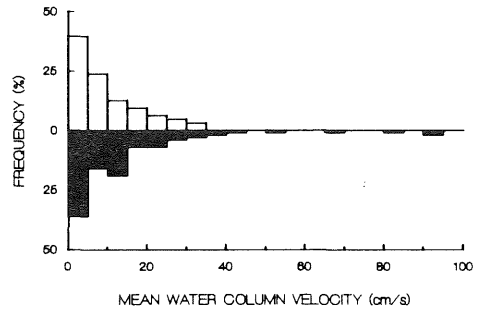Microhabitat use and availability for allopatric Atlantic
salmon (use N = 53, availability N = 89), chinook salmon
(use N = 28, avail. N = 101), and steelhead (use N = 95,
avail. N = 114). Asterisks denote significant differences
between use and availability distributions at the
following probability ranges: * = $0.05 \geq P > 0.01$,
** = $0.01 \geq P > 0.001$, *** = $P \geq 0.001$.

EAST BRANCH SPLIT ROCK RIVER
ATLANTIC SALMON

□ USE
■ AVAILABILITY

***

WATER DEPTH (cm)

SUBSTRATE TYPE

**

MEAN WATER COLUMN VELOCITY (cm/s)

*

NOSE VELOCITY (cm/s)

*

DISTANCE ABOVE SUBSTRATE (cm)
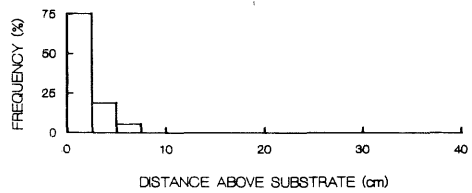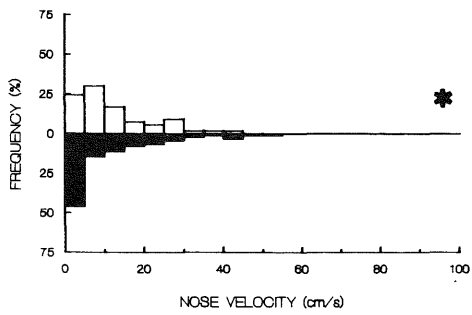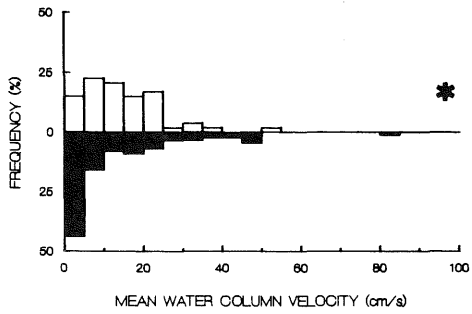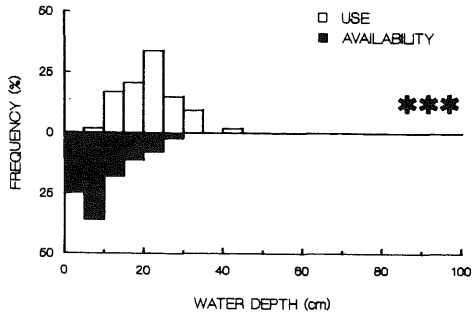
TWO ISLAND RIVER
CHINOOK SALMON

□ USE
■ AVAILABILITY

*

WATER DEPTH (cm)

SUBSTRATE TYPE

MEAN WATER COLUMN VELOCITY (cm/s)

***

NOSE VELOCITY (cm/s)

***

DISTANCE ABOVE SUBSTRATE (cm)
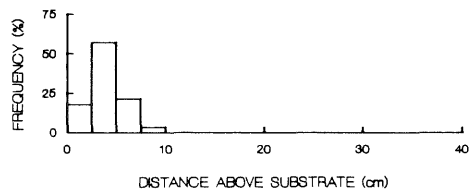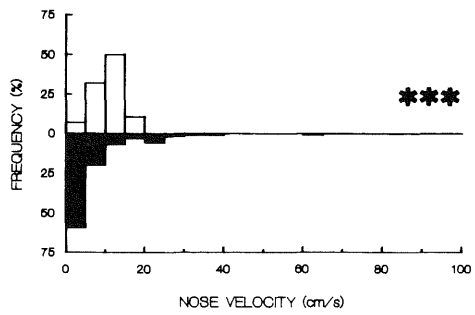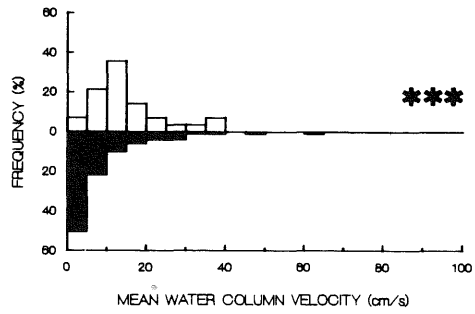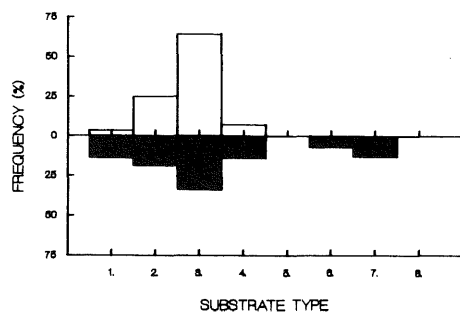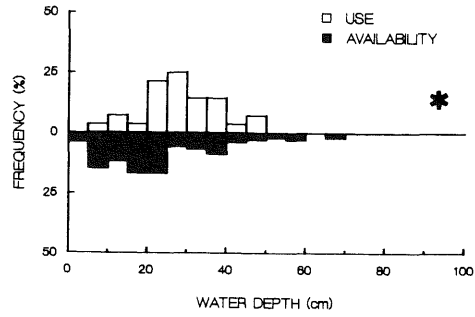
WEST BRANCH SPLIT ROCK RIVER
RAINBOW TROUT

□ USE
■ AVAILABILITY

***

FREQUENCY (%)

WATER DEPTH (cm)

SUBSTRATE TYPE

MEAN WATER COLUMN VELOCITY (cm/s)

NOSE VELOCITY (cm/s)

DISTANCE ABOVE SUBSTRATE (cm)

21
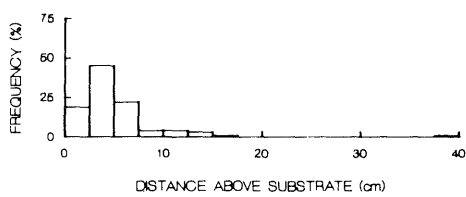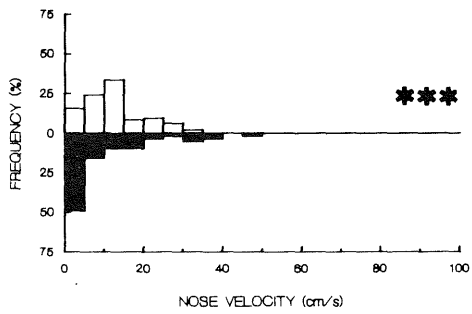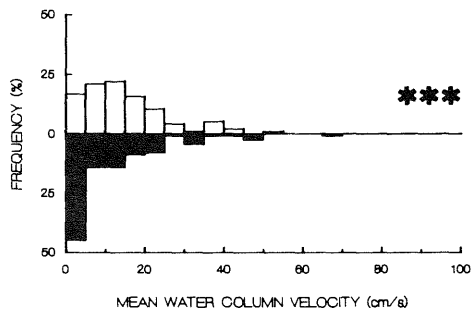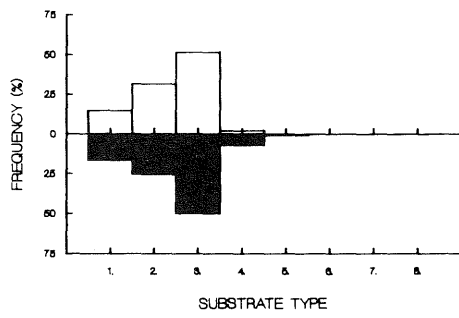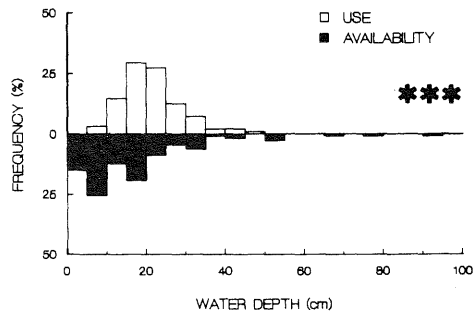
Figure 2. Microhabitat use and availability for sympatric Atlantic
          salmon (use N = 40, avail. N = 100) and steelhead
          (use N = 63) at Lester River site 1.

LESTER RIVER SITE 1
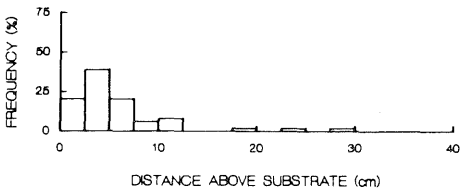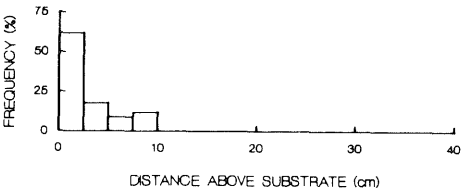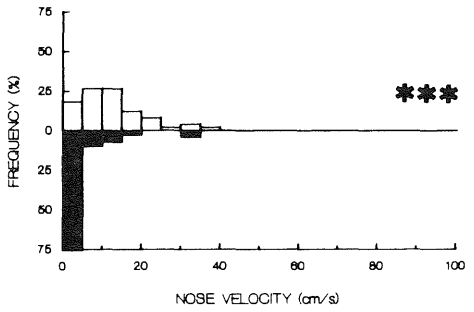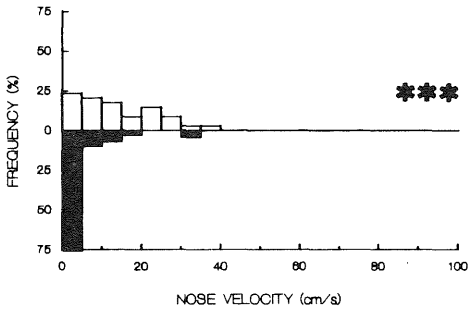ATLANTIC SALMON
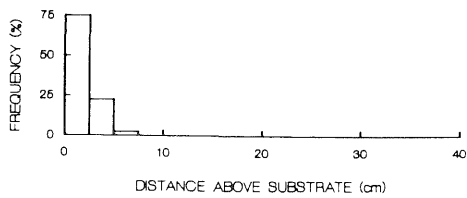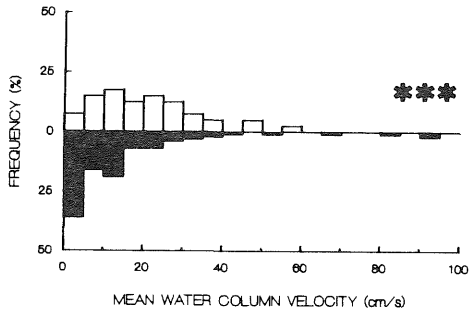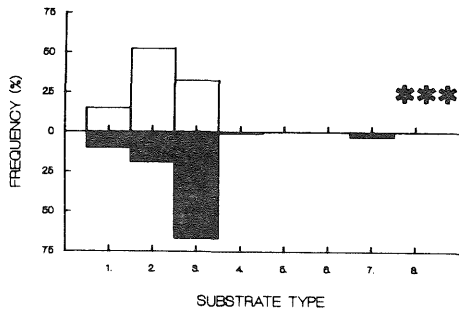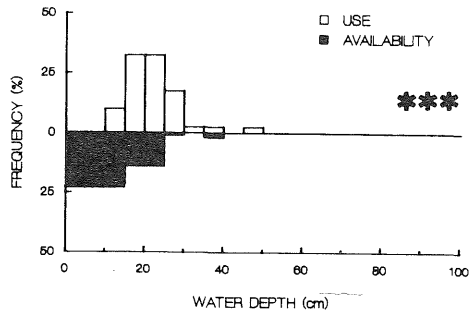
LESTER RIVER SITE 1
RAINBOW TROUT
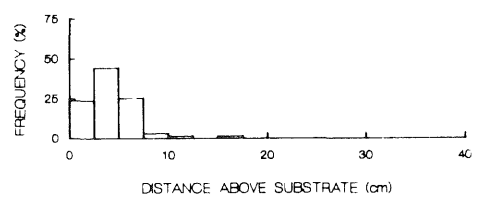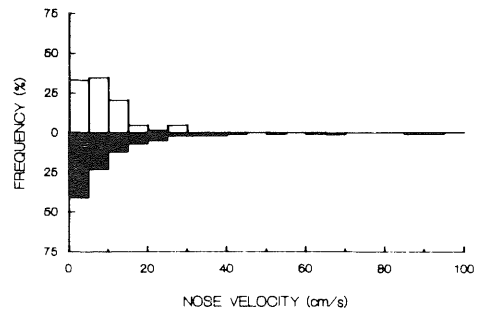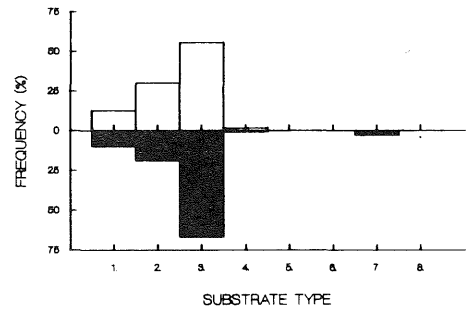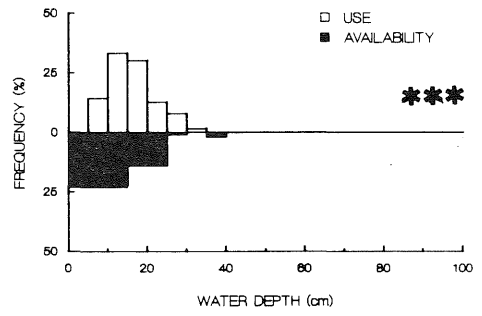
Figure 3. Microhabitat use and availability for sympatric Atlantic
           salmon (use N = 34, avail. N = 70) and steelhead
           (use N = 49) at Lester River site 2.

LESTER RIVER SITE 2
ATLANTIC SALMON
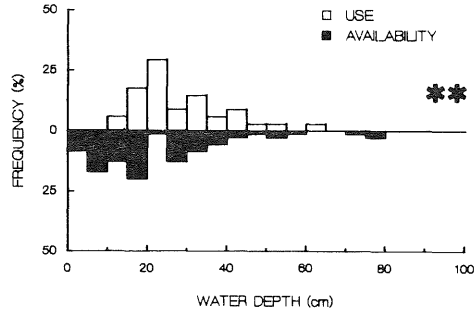
LESTER RIVER SITE 2
RAINBOW TROUT

25
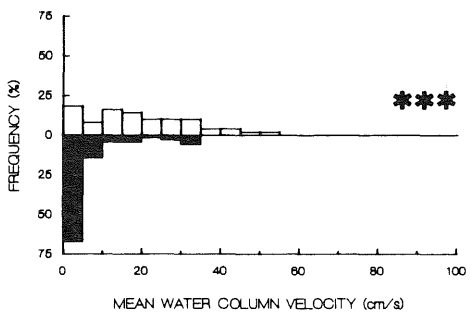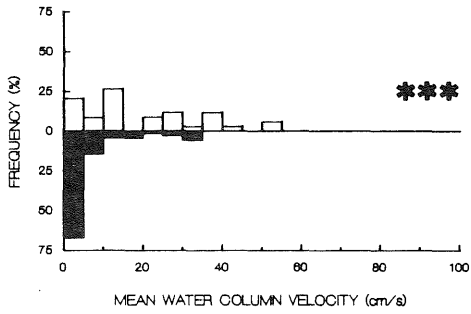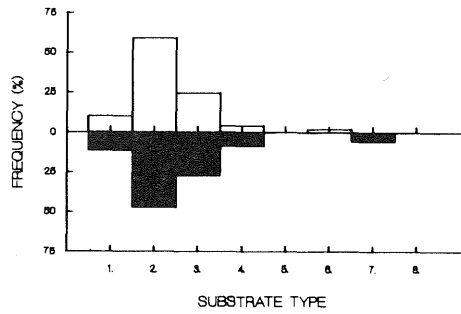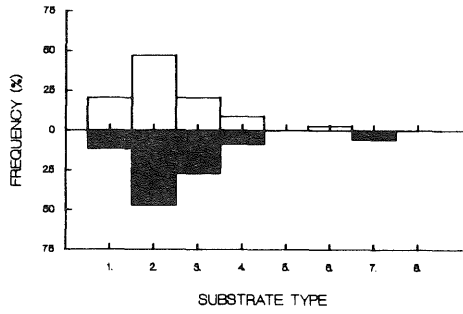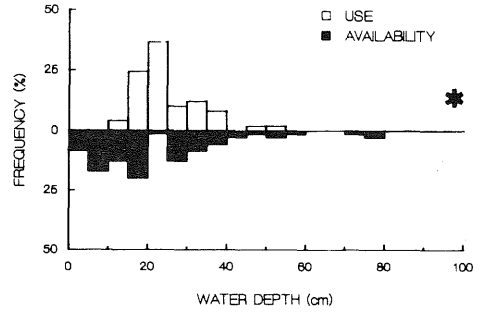
Figure 4. Microhabitat use and availability for sympatric Atlantic
           salmon (use N = 40, avail. N = 88) and steelhead
           (use N = 44) at Lester River site 3.

LESTER RIVER SITE 3
ATLANTIC SALMON

☐ USE
■ AVAILABILITY

✳✳✳

FREQUENCY (%)

WATER DEPTH (cm)

FREQUENCY (%)

SUBSTRATE TYPE

FREQUENCY (%)

✳✳✳

MEAN WATER COLUMN VELOCITY (cm/s)

FREQUENCY (%)

✳✳✳

NOSE VELOCITY (cm/s)

FREQUENCY (%)

DISTANCE ABOVE SUBSTRATE (cm)
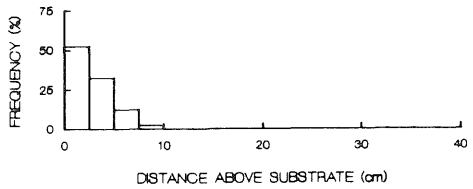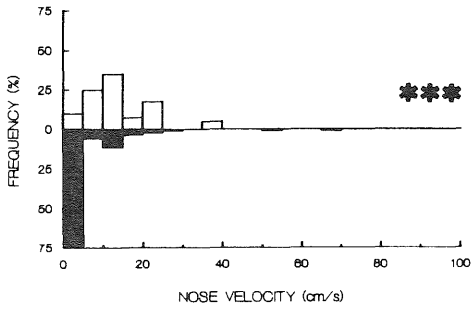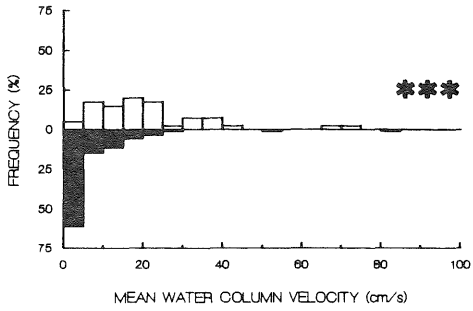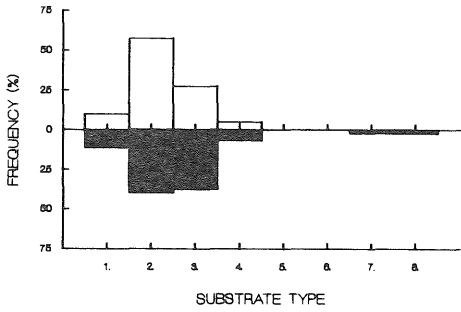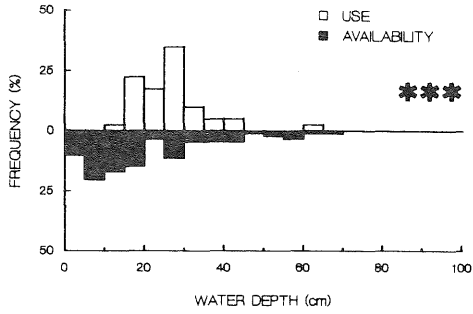
LESTER RIVER SITE 3
RAINBOW TROUT

☐ USE
■ AVAILABILITY

✳✳✳

FREQUENCY (%)

WATER DEPTH (cm)

FREQUENCY (%)

✳

SUBSTRATE TYPE

FREQUENCY (%)

✳✳✳

MEAN WATER COLUMN VELOCITY (cm/s)

FREQUENCY (%)

✳✳✳

NOSE VELOCITY (cm/s)

FREQUENCY (%)

DISTANCE ABOVE SUBSTRATE (cm)

27
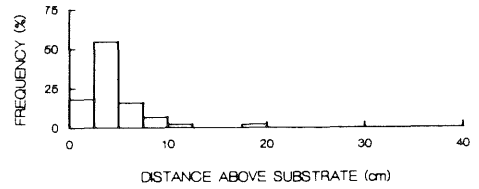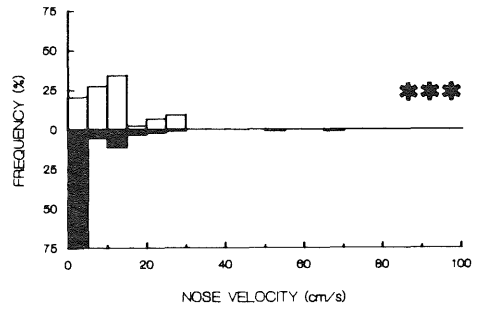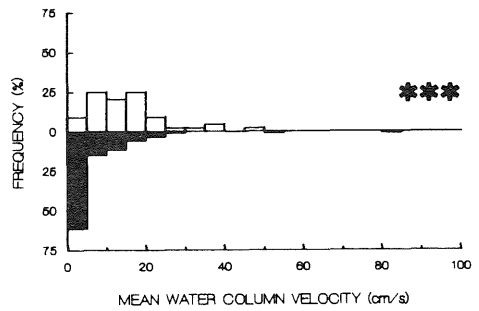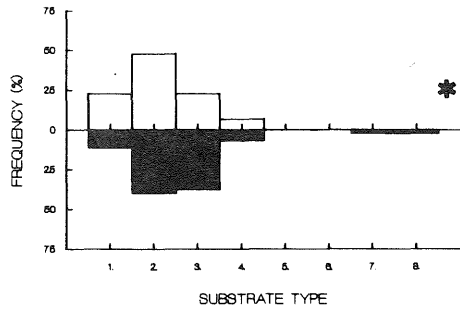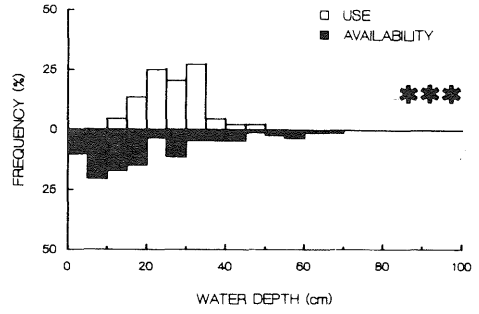
We hypothesize that density reductions occurring between age 0 and age 1 are caused primarily by winter mortality. We could not find a strong correlation between age 1 density and any of our habitat variables and we concluded that densities were too low for summer habitat to limit age 1+ abundance. Work by Bjornn (1971) and Wentworth and LaBar (1984) found that winter mortality was an important limiting factor for stream fish populations.

Chinook salmon fry are unlikely to compete with steelhead fry, but may compete with Atlantic salmon fry. Chinook salmon smolted as early as the middle of June, limiting the time period that competition with steelhead and Atlantic salmon could occur. Cohabitating steelhead fry, which emerge in June, would be smaller and in shallower and slower water than chinook salmon, reducing the potential for competition (Everest and Chapman 1972). Chinook salmon fry and Atlantic salmon fry, however, emerge at about the same time, so interspecies competition is possible. We observed that chinook salmon grew faster than Atlantic salmon, so any competition may decrease as chinook salmon parr move into deeper, swifter microhabitats than those used by Atlantic salmon (Chapman and Bjornn 1969, Lister and Genoe 1970).

Our macrohabitat data suggest that steelhead and Atlantic salmon parr are potential competitors for space. The significant variables in Model 1 indicate that shallow depths and fast water are important to age 0 steelhead and all ages of Atlantic salmon. Macrohabitat use by steelhead was similar to that found by Chapman and Bjornn (1969), and Everest and Chapman (1972). Atlantic salmon have been found to occupy wide ranges of depths and water velocities, and even use pools

(Saunders and Gee 1964, Elson 1967, de Graaf and Bain 1986). Pool
use by Atlantic salmon was found to increase with increasing age
(de Graaf and Bain 1986), but we found virtually all age 1 Atlantic
salmon in fast water, and we did not observe any Atlantic salmon older
than age 1. Pools were abundant in all sectors stocked with Atlantic
salmon, but they were rarely used, suggesting that the strain of
Atlantic salmon stocked in Minnesota prefers faster water if it is
available.

Our microhabitat data also indicated the potential for
competition between steelhead and Atlantic salmon parr, but suggests
that chinook salmon parr do not compete with either steelhead or
Atlantic salmon parr. Microhabitats of allopatric steelhead and
Atlantic salmon were similar except for distance off the bottom and
dominant substrate. The observed difference in average distance off
bottom of 3.4 cm would not prevent competition, however, because we
observed chasing behavior from interspecific encounters at greater
distances. Similarly, the dominant substrate variables were
significantly different for Atlantic salmon and steelhead, but use
appeared to be strongly correlated with availability (Figs. 1-4)
indicating the difference was not controlled by competition. Our
observations of microhabitat use by chinook salmon parr indicated that
water depths were significantly greater than for steelhead or Atlantic
salmon, suggesting that chinook salmon may prefer pools. Everest and
Chapman (1972) also observed that chinook salmon preferred greater
depths than steelhead.

Although we suspect that interspecific competition between
steelhead and Atlantic salmon has the potential to occur under the

right circumstances, we don't think it occurred in our study sectors. We base this conclusion on two results. First, fish densities were not related to the densities or the presence of potentially competing species. Secondly, the only biologically and statistically significant change in habitat use between allopatric and sympatric populations can be attributed to differences in fish size when the various streams were sampled. Microhabitat measurements in Lester River, Sector 1, were done early in the season when the fish were relatively small (Table 5), and use of shallower, slower water was expected. We hypothesize that late summer and fall densities of salmonids are usually below low flow carrying capacity in North Shore streams. When densities are below carrying capacity, competition is precluded because resource demand does not exceed supply (Jaeger 1974).

MANAGEMENT IMPLICATIONS

In North Shore streams where fish densities vary considerably, short-term evaluations of management activities may lead to incorrect conclusions. We suggest that a reliable predictive model for anadromous parr is needed before natural variation can be adequately removed as a confounding variable in evaluations. In lieu of a model, we suggest that evaluations of management activities be based on long-term assessments with three or more years of data both before and after treatment.

Habitat improvements for anadromous parr should be done only on an experimental basis until the hierarchy of limiting factors can be determined. Our findings suggest that anadromous parr are not normally limited by cover, but rather are limited by the harsh North

Shore environment. Habitat improvements to reduce mortality caused by flooding and winter stream conditions may be successful and should be evaluated. In streams where winter survival is exceptional, age 1+ populations may be cover limited and experimental addition of cover is warranted. Cover structures should be placed immediately adjacent to fast water.

The probability that juvenile chinook salmon impact other species is very low. The short stream rearing and rapid growth by chinook salmon that we observed suggest that if impacts occur, it will be chinook salmon that are impacted by older and larger individuals of other species. These conclusions are valid only as long as the existing Lake Superior strain of chinook salmon is stocked.

In streams where age 0 densities are usually low, stocking more that one species may result in more efficient use of the streams. If floods do indeed limit parr populations, parr may only be vulnerable to displacement for a limited time, and stocking fry on more than one occasion may avoid some floods. We suspect that the carrying capacity for Y-0-Y salmonids in North Shore streams is 50 to 85 parr/100m^2 (observed in East Branch Split Rock, 1984) during summer low flow. Streams at or near carrying capacity are where demand for microhabitats can exceed supply and potential competitors such as steelhead and Atlantic salmon should not be stocked together.

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