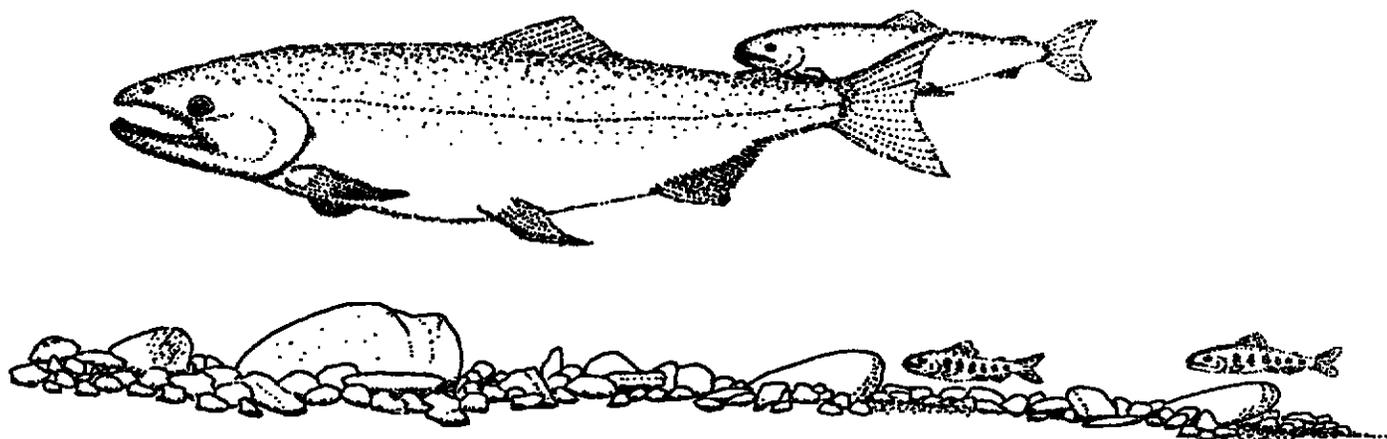


U.S. DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE



MACROHABITAT SELECTION BY JUVENILE COHO
SALMON IN THE MAINSTEM CLEARWATER
RIVER, WASHINGTON



WESTERN WASHINGTON FISHERY RESOURCE OFFICE

OLYMPIA, WASHINGTON

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**Macrohabitat Selection by Juvenile Coho Salmon in
the Mainstem Clearwater River, Washington**

by

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ABSTRACT

The strong relationship between woody debris and juvenile coho salmon has been well established for small streams. However, no one has yet to investigate the relationship in larger streams. This paper describes summer habitat selection by juvenile coho salmon (*Oncorhynchus kisutch*) in the mainstem Clearwater River (mean discharge = 39 m³/s). The effect of woody debris was assessed by estimating coho salmon abundance in areas with and without woody debris. The effect of physical habitat variables on coho salmon abundance near woody debris, such as woody debris size and density, riverine habitat, substrate, water depth, and current velocity was evaluated using either a one- or two-way analysis of variance, analysis of covariance, or linear regression. General linear modelling procedures were used to determine which variables together explained the greatest amount of variability in estimated coho salmon abundance at the stations sampled.

Of the variables measure, the presence of woody debris was the most important variable influencing summer rearing distribution of juvenile coho salmon in the Clearwater River. Similar numbers of juvenile coho salmon were observed at introduced and natural woody debris accumulations, while significantly fewer (zero in most cases) were observed in areas lacking woody debris. Juvenile coho salmon preferred large, dense structures in pool habitats to a greater degree than small, sparse structures. Woody debris structures in glide habitats also were frequently used by large numbers of juvenile coho salmon. Debris surface area and density were the most common variables included in general linear models and explained a majority of the variability in coho salmon summer rearing distribution. Riverine habitat (pool, glide, riffle) and an interaction term between debris surface area and riverine habitat were also common variables included in general linear models. The positive influence of debris surface area on coho salmon abundance was generally greater in pools than in glides and riffles. Coho salmon abundance was generally positively influenced by increasing water depth, however, the influence was only occasionally statistically significant. In contrast to findings from small streams, coho salmon abundance was not significantly influenced by current velocity. However, large variability in estimated coho salmon abundance and the influence of other variables (i.e., debris density and surface area) may have overshadowed the significance of current velocity. These results suggest that further habitat enhancement in the mainstem Clearwater River should focus on the placement of large, dense woody debris accumulation in pools.

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INTRODUCTION

Restoration of salmonid habitat has received much attention in the past decade (Reeves et al. 1991). Sedell and Luchessa (1982) state that emphasis should be placed on restoring habitat complexity to mainstem channels of 4th- to 7th-order streams. These areas provide over 70 percent of productive stream length available to migrating fish and have, based on historical records, been significantly altered from their pristine state through removal of woody debris resulting in reduced habitat complexity. However, there are presently two factors limiting habitat restoration in large rivers. The first is the limited ability to introduce stable structures which can withstand the high flows within these channels (Frissel and Nawa 1992). The second is the limited knowledge of habitat use by salmonids in these large rivers. Prior to completing habitat enhancement for a particular fish, one must understand the habitat requirements of all its life stages (Moore and Gregory 1988; Nickelson et al. 1992b) and determine which life stages are limited by habitat availability (Nickelson et al. 1992b). Information regarding the summer habitat preferences of many salmonids, including juvenile coho salmon (*Oncorhynchus kisutch*), comes predominantly from experiences in small streams (e.g., Bisson et al. 1982, 1988; Bugert et al. 1991). In contrast, habitat preferences of summer rearing coho salmon in large rivers is represented by a single study (Lister and Genoe 1970).

Preferred habitats of juvenile coho salmon could differ between large and small streams. Microhabitat selection by rainbow trout (*O. mykiss*) has been related to channel size (Baltz and Moyle 1984). Changes in fish communities are often associated with varying stream size (Beecher et al. 1988) which may result in the presence of new, or the loss of old predators and competitors. Changes in fish communities can influence salmonid habitat use (Fausch and White 1981; Baltz et al. 1982; Schlosser 1987; Bugert and Bjornn 1991). Temperature differences associated with large streams may alter habitat use, either by changing preferred habitats (Baltz et al. 1987) or by altering the outcomes of competitive interactions (Baltz et al. 1982; Reeves et al. 1987). Thus, coho salmon in large river channels may select different habitats than those reported in the literature for small streams.

Woody debris is an important component of juvenile salmonid habitat in lotic systems (Bisson et al. 1987), providing protection from extreme current velocities (McMahon and Hartman 1989; Shirvell 1990; Fausch 1993) and predators (Everest and Chapman 1972; Grant and Noakes 1987). Coho salmon densities have been reduced following removal of woody debris (Bryant 1982; Dolloff 1982; Elliot 1986). However, coho salmon distribution and survival in a semi-artificial rearing channel was not consistently related to woody debris cover (Quinn et al. 1994; Spalding et al. 1995). This suggests that pools formed by woody debris may actually be more important than the cover provided by woody debris for summer rearing juvenile coho salmon. The combination of woody debris and deep pools may be ideal, as Lonzarich and Quinn (1995) observed greater coho salmon densities in pools with woody debris than in pools of equal depth lacking woody debris. Coho salmon densities were

greatest in the deepest pools containing woody debris (Lonzarich and Quinn 1995).

Large mainstem rivers such as the Clearwater generally possess pools much deeper than those commonly found in smaller streams. It is unclear if the presence of woody debris in these large pools will influence the abundance of coho salmon or distribution within these large pools. The greater abundance and diversity of the predator community likely to be observed in these larger rivers could increase the importance of woody debris cover compared to small streams. This is supported by the observation that juvenile coho salmon are less willing than other Pacific salmon to take risks during feeding (Abrahams and Healey 1993), which results in reduced attack distance to food following the presentation of model predators (Dill and Fraser 1984). The objectives of this study were to determine whether woody debris influences the distribution and abundance of coho salmon in the Clearwater River and the relative importance of other habitat variables singly and in combination in influencing habitat use by summer rearing juvenile coho salmon in this relatively large stream channel.

Study Area

The present study was completed in the mainstem Clearwater River located on the north coast of Washington State (Figure 1). The Clearwater River originates from the west slope of the Olympic Mountains, flows west to southwest for 58 km to its confluence with the Queets River (Winter 1992). The river's drainage area of approximately 350 km² (Cederholm and Scarlett 1982) receives over 350 cm of rain annually (Cederholm and Scarlett 1991). The river is fed primarily by surface runoff and ground water (Winter 1992). Median discharge near the town of Clearwater for the years 1932 and 1938-1949 ranged from about 3.7 m³/s to 9.3 m³/s from June to September; a peak flood of 1,059 m³/s was recorded 3 November 1955 (Amerman and Orsborn 1987). The river gradient is low to moderate and river habitat is composed primarily of pools and glides with relatively short riffle sections. A majority of the coho production occurs in tributary streams, with the mainstem serving as juvenile summer rearing habitat (Phinney and Bucknell 1975). The study reach extended from Bull Creek (Rkm 30) to a creek described as 0031 Creek (Rkm 10) and was divided into seven sub reaches including: Bull Creek to Deception Creek, Deception Creek to Peterson Creek, Peterson Creek to Gross Bridge, Gross Bridge to Shale Creek, Shale Creek to Elkhorn Creek, and Elkhorn Creek to Hunt Creek (Figure 1).

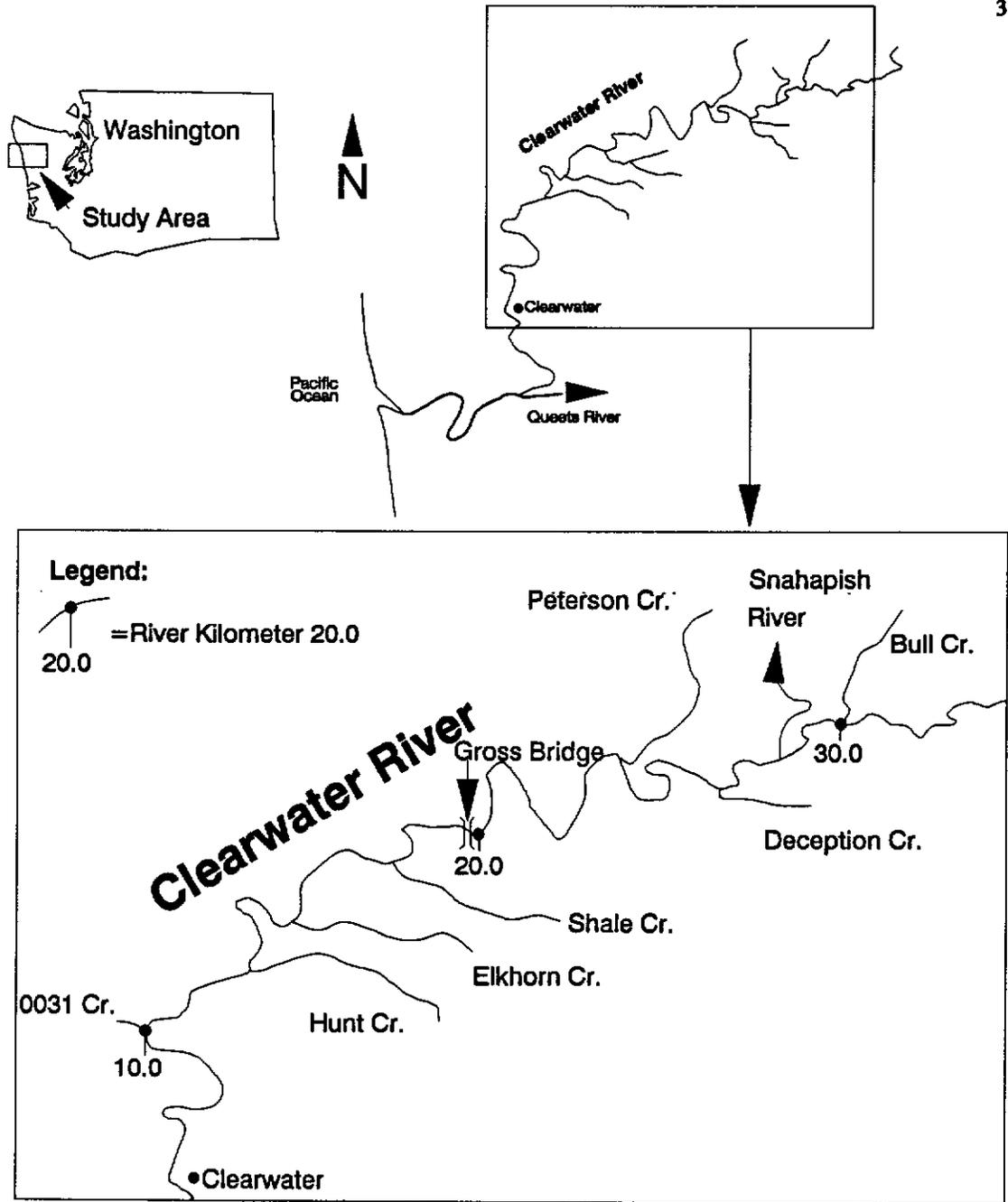


Figure 1. Study area of the mainstem Clearwater River.

MATERIALS AND METHODS

Habitat use by juvenile coho salmon was assessed by examining abundance at three types of woody debris sampling stations within the mainstem. The three debris types (stations) were areas with naturally occurring woody debris, areas containing introduced woody debris, and areas lacking woody debris (controls). Introduced woody debris bundles were installed by a 10-person crew during early May at predetermined stations within each reach. Two or three sitka spruce (*Picea sitchensis*) or western hemlock (*Tsuga heterophylla*) trees, averaging 10-20 cm diameter at the base, were removed from the adjacent riparian zone and carried to the river's edge, where they were laid parallel and joined at their butt ends with rope or a large metal spike. The bundle of trees was then rolled into the river and then floated to the desired position, where it was lashed in a submerged position to an existing tree or rock.

Juvenile coho salmon abundances were estimated at several ($n=4$ to 100) of these three debris station types in early summer (June/July) and late summer (August/September). Two snorkelers entered the river upstream of the station to be surveyed and proceeded downstream, counting juvenile coho salmon as they moved past the station. Once well downstream of the station, the snorkelers moved upstream past the station again to make a second estimate. The snorkelers then discussed their individual estimates and came to a consensus, which became the estimate of coho salmon abundance at that station.

Juvenile coho salmon density (fish/m² debris surface area) and abundance at the three debris types (natural, introduced, control) were compared using a Kruskal-Wallis test and Dunn's multiple comparisons test (Zar 1984). The surface area of the debris stations was measured during late summer surveys in 1990 and 1992, and for both the early and late summer surveys in 1993 to compensate for differing surface areas of introduced and natural woody debris stations. The surface area of control stations was measured as the entire area snorkeled because no woody debris was present at these stations. Debris surface areas were not measured during early summer surveys of 1990 and 1992, which prevented the calculation of coho salmon densities during these surveys. Therefore, coho salmon abundance estimates rather than density were used for these comparisons. The distribution of coho salmon abundance estimates from early summer 1990 and 1992 was skewed towards samples with few fish (0-50) (skewed left) and thus was transformed using the square root transformation ($X' = (X + 0.5)^{1/2}$) prior to statistical analysis.

The effects of several physical habitat variables on coho salmon abundance were evaluated at stations with woody debris (natural or introduced). Physical habitat variables (water depth, velocity, riverine habitat type, woody debris surface area, debris species, woody debris density, and substrate) were measured after the area had been snorkeled to estimate abundance. Water depth was measured to

the nearest 3 cm at two locations, on the outer edge of the debris station and half-way from the outer edge of the station to the shore (Figure 2). Current velocity was measured to the nearest 3 cm/s with a Swoffer model 2100 current meter. Current velocities were measured at the two locations where water depth was measured and also just upstream and downstream of each debris station (Figure 2). All velocities were measured at approximately 60% of total depth. Woody debris length was measured on an axis from the upstream edge to the downstream edge of the woody debris accumulation. Woody debris width was calculated as the average distance the debris extended from the near-shore edge to the mid-stream edge of the debris accumulation. Woody debris length and width were used to calculate woody debris surface area. Riverine habitat was designated as pool, riffle, or glide, as defined by Bisson et al. (1982). Debris density was visually classified as dense, medium, or sparse and reflected the complexity of cover produced by the debris. Predominant debris plant species and underlying substrate were classified as described in Tables 1 and 2. Physical habitat variables were measured only after the late summer surveys during 1990 and 1992 and following both the early and late summer surveys in 1993.

The effects of the individual habitat variables and debris station type on estimated coho salmon abundance (transformed) were evaluated using two-way analysis of variance (ANOVA) or analysis of covariance (ANCOVA). The interaction between station type and the individual habitat variables also was examined. The effect of the environmental variable on coho salmon abundance was tested individually for each debris station type if a significant interaction existed. These individual tests were completed using a one-way ANOVA and Tukey multiple comparisons (categorical variables-habitat, density, etc.) or linear regression (continuous variables-depth, current velocity, etc.). General linear modelling was used to identify those variables which, in combination, were important in explaining variation in abundance estimates of juvenile coho salmon at introduced and natural debris stations. "Best" models were developed by beginning with the most significant single variable (based on individual variable analysis) and adding the next significant variable and the interaction between the two. Variables were kept in the model if they were significant at the 0.1 alpha level in the General Linear Model. Remaining variables were included in the model in the order of their probability of significance based on single variable analyses. Effects of habitat variables were evaluated for introduced and natural woody debris both individually and in combination.

Table 1. Classifications of debris species in accumulations used by coho salmon.

Species	Description
Alder	Debris accumulation composed of single or multiple alder trees, which had branches attached.
SWD	An accumulation of several small (< 10 cm diameter) logs and branches regardless of species.
LWD	An accumulation of several large logs (> 10 cm diameter and 2 m in length) regardless of species.
Rootwad	The rootwad of a tree which was for the most part intact and which made up a majority of the cover.
Spruce	One or more spruce trees.
Hemlock	One or more hemlock trees.
Spruce/Hemlock	Debris accumulation composed of both spruce and hemlock trees.

Table 2. Classification system used to designate the substrate below woody debris stations (Adapted and modified from Cummins 1962)

Substrate	Description/Particle Size Range (mm)
Silt	0.0039-0.0625
Sand	0.0625-2
Gravel	2-64
Cobble	64-256
Boulder	> 256
Bedrock	Exposed underlying rock not distinguishable as a boulder
Debris	Bottom covered with terrestrial debris such as leaf litter and/or small woody debris

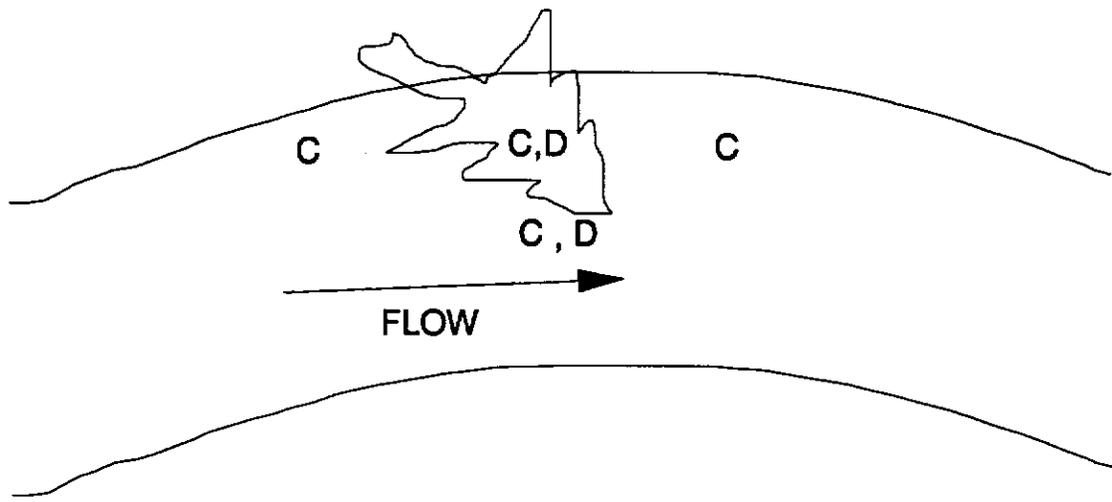


Figure 2. Locations where water depth (D) and current velocity (C) were measured.

RESULTS

Relative Abundance by Debris Type

Coho salmon occupied areas with woody debris more often than areas lacking woody debris (Table 3 and 4). When the data were analyzed using estimated coho salmon abundance (transformed), more coho salmon were observed at stations with natural or introduced woody debris than control stations (Table 3). Coho salmon abundance also was greater at introduced than natural debris stations during August 1991, June 1993, and August 1993. No difference in coho salmon abundance existed between introduced and natural debris stations during August and September 1990 or June 1991 and 1992.

Table 3. Mean coho salmon abundance estimates and Kruskal-Wallis and Dunn test results comparing estimated coho salmon abundance at introduced and natural debris and control stations during early and late summer 1990-1993.

Year		Station Type			Kruskal -Wallis	Dunn	
		Introduced	Natural	Control	<i>P</i>	Result	<i>P</i>
August 1990	Mean	43.65	45.79	0	0.0018	I=N	>0.5000
	SD	52.87	51.46	0		I>C	<0.0001
	n	48	38	4		N>C	<0.0001
Sept. 1990	Mean	35.33	36.47	0	0.0016	I=N	>0.5000
	SD	36.35	44.78	0		I>C	<0.0010
	n	46	34	4		N>C	<0.0010
June 1991	Mean	66.16	49.95	—	0.0224*	I>N	0.0224
	SD	65.66	69.63	—			
	n	38	127	0			
June 1992	Mean	33.0	34.80	0.59	0.0001	I=N	0.1085
	SD	51.49	67.68	2.06		I>C	<0.0001
	n	32	100	22		N>C	<0.0001
August 1992	Mean	19.47	18.81	0	0.0001	I>N	<0.0001
	SD	25.79	58.13	0		I>C	<0.0001
	n	32	100	19		N>C	<0.0001
July 1993	Mean	55.14	36.67	1.53	0.0001	I>N	0.0083
	SD	39.62	57.74	4.70		I>C	<0.0001
	n	29	99	19		N>C	<0.0001
August 1993	Mean	59.10	28.61	0	0.0001	I>N	<0.0001
	SD	49.62	64.86	0		I>C	<0.0001
	n	30	95	19		N>C	<0.0001

*Wilcoxon Sign Rank Test

The above analysis does not account for differences in the size of the debris accumulation. Debris surface area was measured during September 1990, August 1992, and June and August 1993, allowing the comparison of coho salmon densities (coho salmon/m² debris) at the three station types. Coho salmon densities at control stations were calculated using the surface area of the entire area snorkeled (areas were similar in size to introduced and natural debris stations). Coho salmon densities were greater at introduced and natural woody debris accumulations than at control areas during all years (Table 4). They were also greater at introduced than natural debris accumulations in all years except September 1990 (Table 4).

Table 4. Mean coho salmon densities (coho/m² debris) and Kruskal-Wallis and Dunn test results comparing mean densities at introduced and natural debris and control stations lacking woody debris during late summer 1990, 1992, and early and late summer 1993.

Year		Station Type			Kruskal-Wallis	Dunn	
		Introduced	Natural	Control	<i>P</i>	Result	<i>P</i>
Sept. 1990	Mean	1.996	2.694	0	0.0033	I=N	>0.5000
	SD	2.331	3.769	0		I>C	0.0018
	n	46	34	4		N>C	<0.0001
August 1992	Mean	0.691	0.314	0	0.0001	I>N	<0.0001
	SD	0.774	0.794	0		I>C	<0.0001
	n	32	100	20		N>C	<0.0001
July 1993	Mean	3.521	1.706	0.085	0.0001	I>N	<0.0001
	SD	3.116	3.319	0.225		I>C	<0.0001
	n	29	99	19		N>C	<0.0001
August 1993	Mean	4.092	0.728	0	0.0001	I>N	<0.0001
	SD	4.285	1.271	0		I>C	<0.0001
	n	30	95	19		N>C	<0.0001

Influence of Habitat Variables on Abundance

Coho salmon occupied the densest woody debris accumulations (Figure 3). More coho salmon were observed in dense than either medium or sparse debris accumulations during all years (Figure 3). More coho salmon were observed at medium debris than sparse debris accumulations during July and August 1993, but not during 1990 and 1992. A significant interaction (two-way ANOVA: $P=0.0167$) existed between debris density and station type during 1992, requiring the analysis of the effects of debris density on coho salmon abundance be completed separately for introduced and natural debris stations. More coho salmon were observed in dense natural debris accumulations than either medium or sparse during 1992. No difference in coho salmon abundance was observed between medium and sparse natural debris stations. No introduced stations were classified as sparse during 1992.

The riverine habitat (pool, glide, riffle) in which the woody debris was located influenced coho salmon abundance (Figure 4). More coho salmon were observed at introduced and natural debris accumulations located in pools than at glides or riffles in four of six comparisons. These differences were significant for introduced and natural debris accumulations during 1992 and natural debris accumulations during July and August 1993. In contrast, coho salmon abundance was greater at introduced debris accumulations located in glides than pools during July and August 1993, but was significant only during July 1993 (Figure 4). More coho salmon generally occupied debris accumulations located in glides than riffles; however, differences were statistically significant only during 1992 and August 1993 (natural debris accumulations). A significant interaction existed between station and habitat type during July (two-way ANOVA: $P=0.0010$) and August 1993 (two-way ANOVA: $P=0.0209$). Therefore, statistical testing for the effect of riverine habitat on coho salmon abundance was completed separately for each station type for data collected during July and August 1993.

The tree species which constituted a majority of the natural and introduced debris accumulations did not significantly influence coho salmon abundance (Figure 5). Station type did not significantly influence the analysis for the effect of tree species on coho salmon abundance (number of coho/debris accumulation) during any year (two-way ANOVA: $P=0.2283-0.0.6578$). No differences in coho salmon abundance were observed at introduced and natural debris accumulations composed of different tree/vegetation species during any year (two-way ANOVA: $P=0.0578-0.6952$).

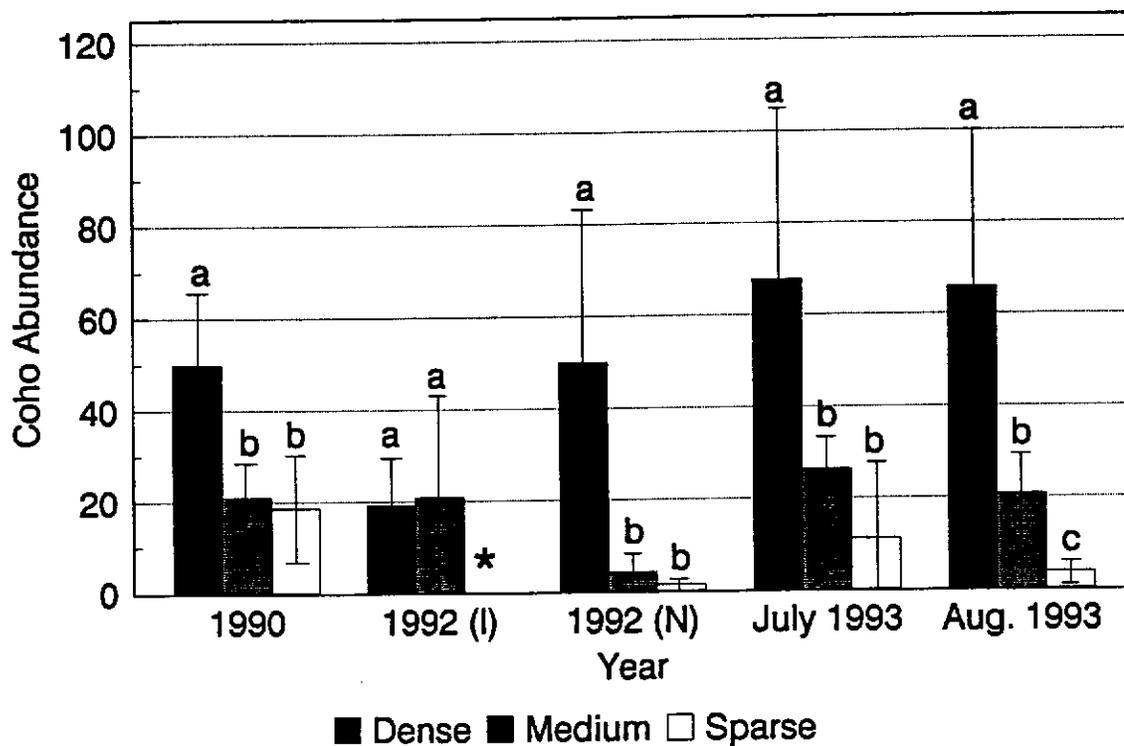


Figure 3.

Mean (\pm 2 SE) coho salmon abundance (#/debris accumulation) at natural and introduced debris (combined) accumulations of different density during 1990, 1992, and August 1993 and natural (N) and introduced (I) (separate) debris accumulations during 1992. Data for 1992 were analyzed separately for debris of different densities because a significant interaction existed between the factors station type and density. For debris accumulations of different density, bars with different letters are significantly different (two-way ANOVA and Tukey test: $P < 0.05$). (* = no stations classified as sparse).

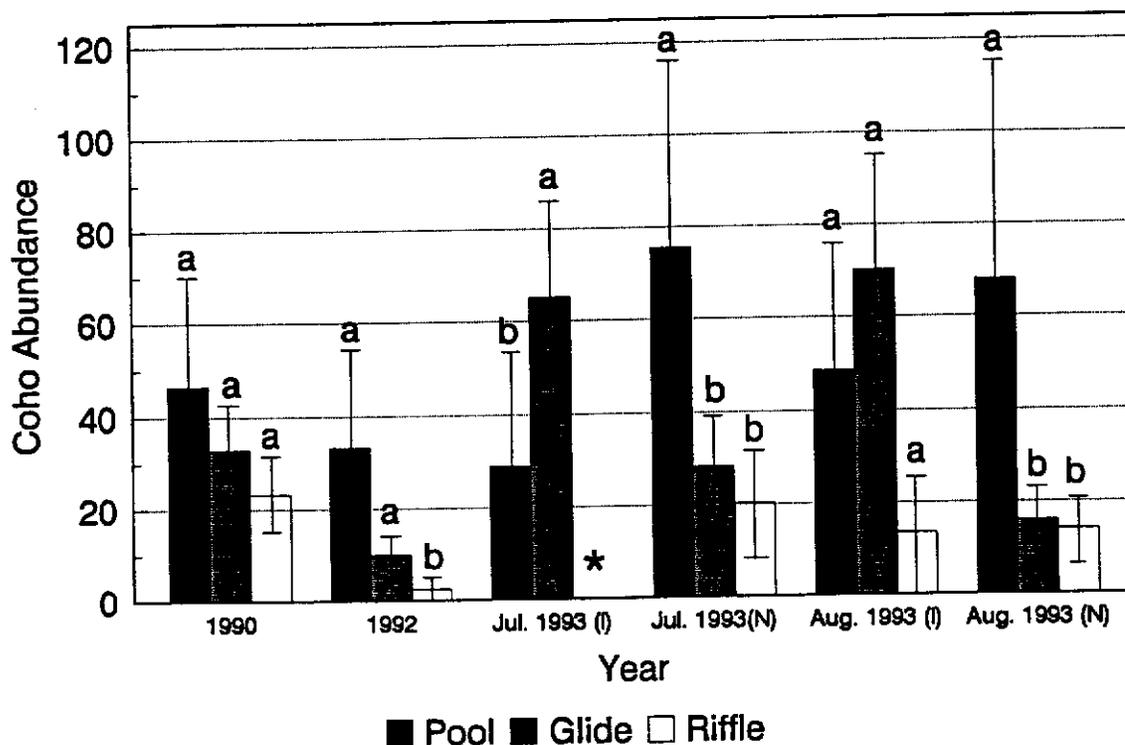


Figure 4.

Mean (± 2 SE) coho salmon abundance (# coho/debris accumulation) at natural and introduced debris accumulations located in different riverine habitat, 1990, 1992-1993. Coho salmon abundance at debris accumulations located in different habitats were analyzed separately for introduced (I) and natural (N) debris accumulations during July and August 1993 because a significant interaction existed between the factors station type (I or N) and habitat. For debris accumulations in different habitats, bars with different letters are significantly different (two-way ANOVA and Tukey tests: $P < 0.05$). (* = no stations located in riffles).

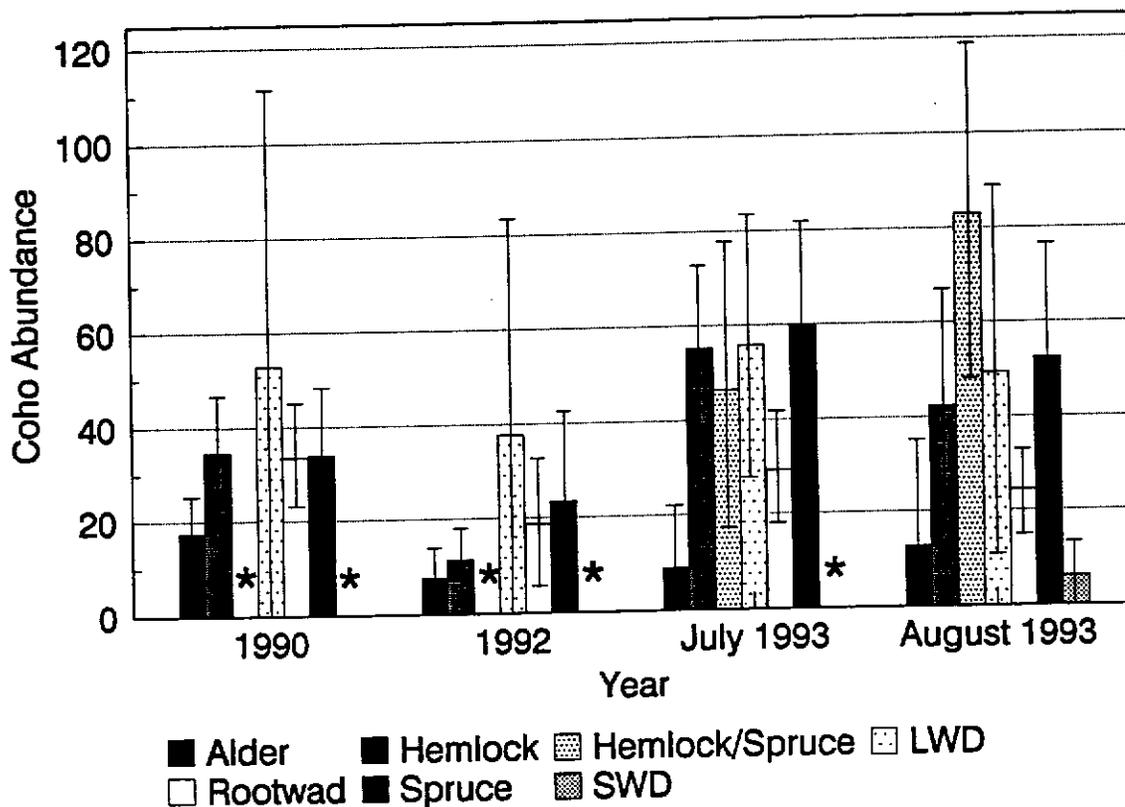


Figure 5. Mean (\pm 2 SE) coho salmon abundance (# coho/debris accumulation) at natural and introduced debris accumulations composed of different species of wood. (* = no debris stations classified as SWD or hemlock/spruce) (SWD = small woody debris; LWD = large woody debris).

The predominant substrate under the debris accumulation did not correlate with coho salmon abundance (Figure 6). Station type had a significant effect on the analysis for the effects of substrate on coho salmon abundance during July and August 1993 (two-way ANOVA: July 1993: $P=0.0152$; August 1993: $P=0.0001$) but not during 1990 or 1992 (two-way ANOVA: 1990: $P=0.8398$; 1992: $P=0.1159$). Thus, the analysis for the July and August 1993 data sets was completed separately for introduced and natural debris stations. Coho salmon abundance (number of coho/debris accumulation) was not influenced by the substrate under introduced and natural debris stations during 1990 and 1992 (two-way ANOVA: $P=0.1159-0.5443$). Substrate under introduced and natural debris stations also did not influence coho salmon abundance during July and August 1993 (ANOVA: Introduced: $P=0.5-0.9470$; Natural: $P=0.0833-0.4799$).

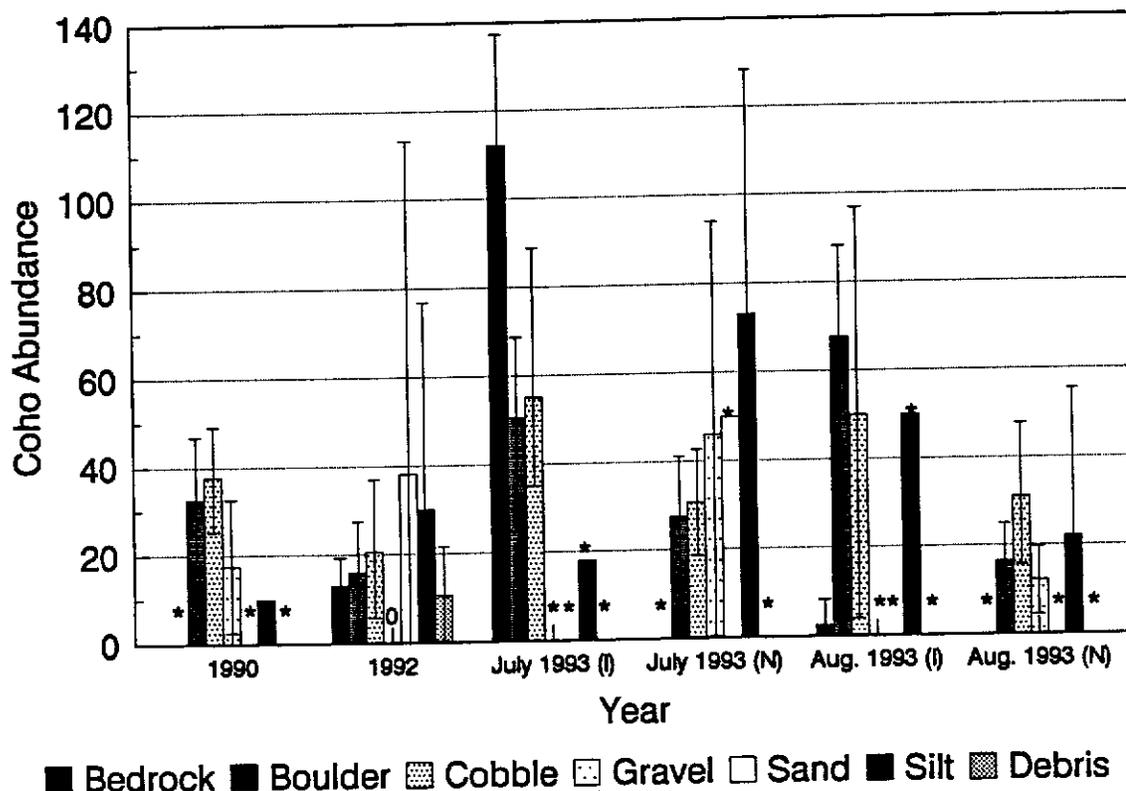


Figure 6. Mean (\pm 2 SE) coho salmon abundance (# coho/debris accumulation) in relation to the substrate below natural and introduced debris accumulations. (I)=introduced debris station, (N)=Natural debris station (* = $n=0$ or $n=1$, not included in statistical analysis).

The influence of the location of the debris station (i.e., whether or not it was located in a back eddy) was examined during 1993. Coho salmon abundances were not statistically greater (Sign Rank Test: July 1993: $P=0.8008$; August 1993: $P=0.4335$) greater at debris accumulations located in back eddies (July 1993: Mean=81.7, SD=142.3, $n=7$; August 1993: Mean=75.1, SD=160.2, $n=9$) then at those located elsewhere (July 1993: Mean=33.3, SD=45.7, $n=92$; August 1993: Mean=32.9, SD=45.3, $n=116$).

Coho salmon abundance was generally positively influenced by the size of woody debris accumulations (Figure 7). The effect of debris surface area on coho salmon abundance was different for introduced and natural debris accumulations for all surveys (ANCOVA: 1992: $P=0.0036$; July 1993 $P=0.0001$; August 1993: $P=0.0001$), except 1990 (ANCOVA: $P=0.9594$). These significant

interactions require the analysis for the effect of debris surface areas on coho salmon abundance be completed separately for each station type. Coho salmon abundance increased significantly with increases in debris surface area in every case, except at introduced debris stations during July and August 1993 (Figure 7).

Depth on the outer edge of debris did not consistently influence coho salmon abundance (number of coho/debris accumulation) (Figure 8). Significant interactions between station types during July (ANCOVA: $P=0.0170$) and August 1993 (ANCOVA: $P=0.0025$) required that the analysis for the effects of depth on coho salmon abundance be completed separately for introduced and natural debris stations during these two surveys. Coho salmon abundance was positively influenced by increasing water depth at introduced and natural debris stations during 1992 and natural debris stations during July and August 1993. Although, coho salmon abundance was positively influenced by water depth on the outer edge of natural and introduced debris stations during 1990, the effect was not statistically significant (Figure 8). Coho salmon abundance was not significantly influenced by water depth on the outer edge of introduced debris accumulations during July and August 1993. Very little of the variability in coho salmon abundance was explained by depth on the outer edge of debris accumulations alone (Figure 8).

The depth halfway from shore to the outer edge of the debris station generally did not influence coho salmon abundance (number of coho/debris accumulation) (Figure 9). Station type significantly influenced the results of the analysis during July (ANCOVA: $P=0.0127$) and August 1993 (ANCOVA: $P=0.0003$), requiring the influence of depth halfway from shore to the outer edge of the debris on coho salmon abundance be analyzed separately for introduced and natural debris stations. Depth halfway from shore to the outer edge of the debris station did not influence coho salmon abundance (number coho/debris accumulation) at introduced and natural debris stations during 1990 or at natural or introduced debris stations tested independently during July and August 1993. However, coho salmon abundance was positively related to depth half way from shore to the outer edge of the debris station during 1992 (Figure 9).

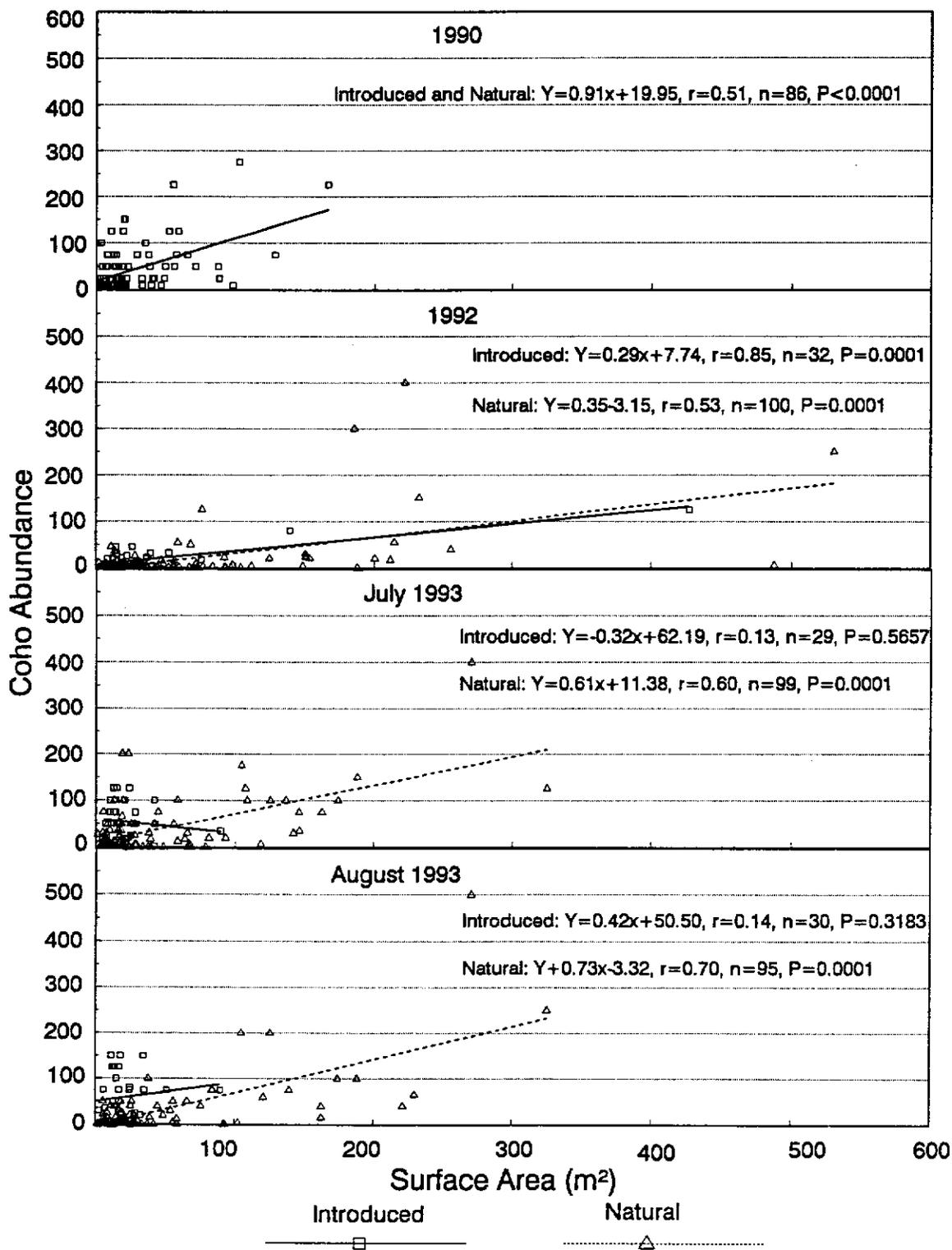


Figure 7.

Relationship between coho salmon abundance (# coho/debris accumulation) and debris surface area of natural and introduced debris stations, 1990, 1992-1993.

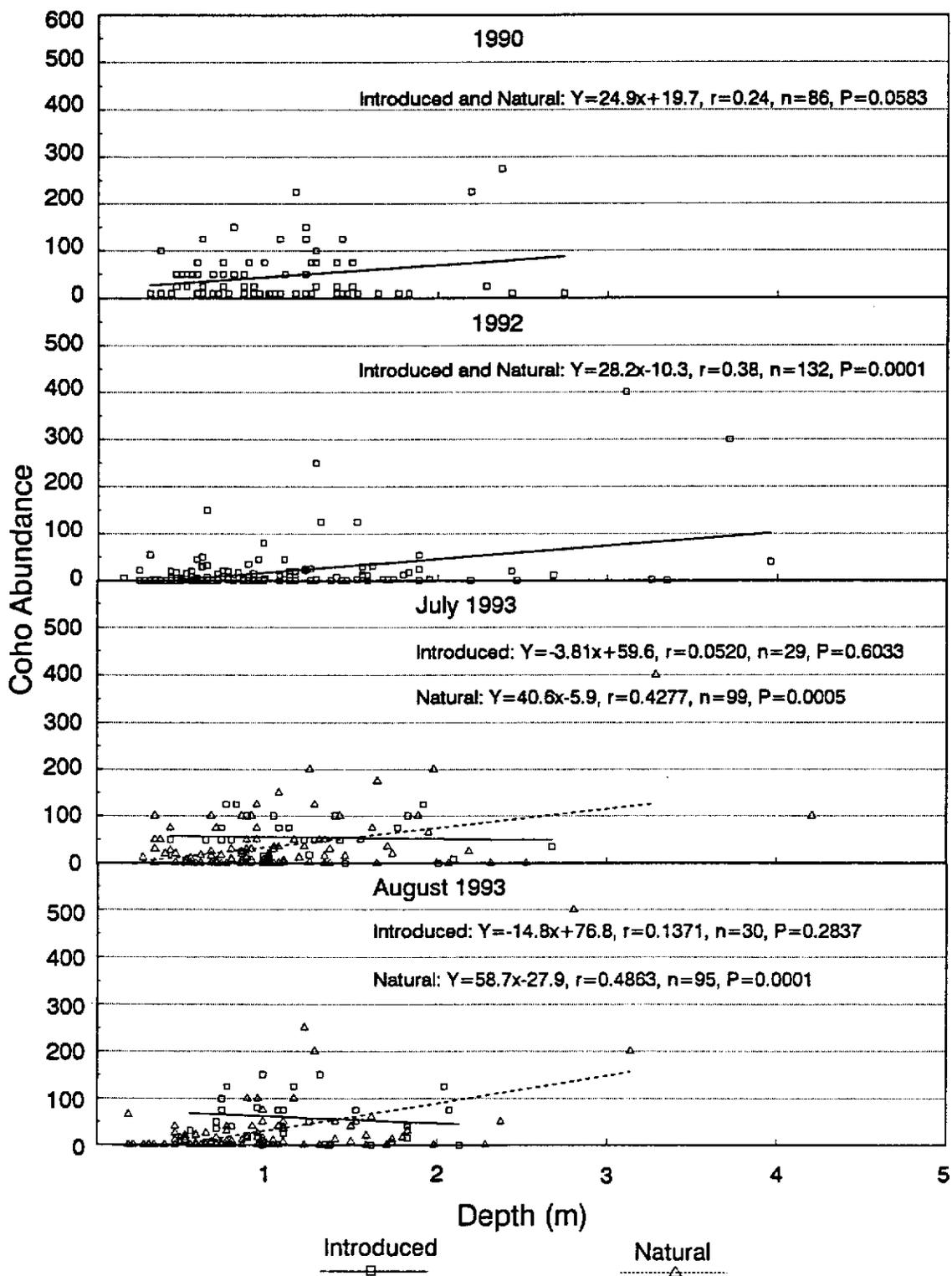


Figure 8. The relationship between coho salmon abundance (# coho/debris accumulation) and the depth on the outer edge of natural and introduced debris accumulations, 1990, 1992-1993.

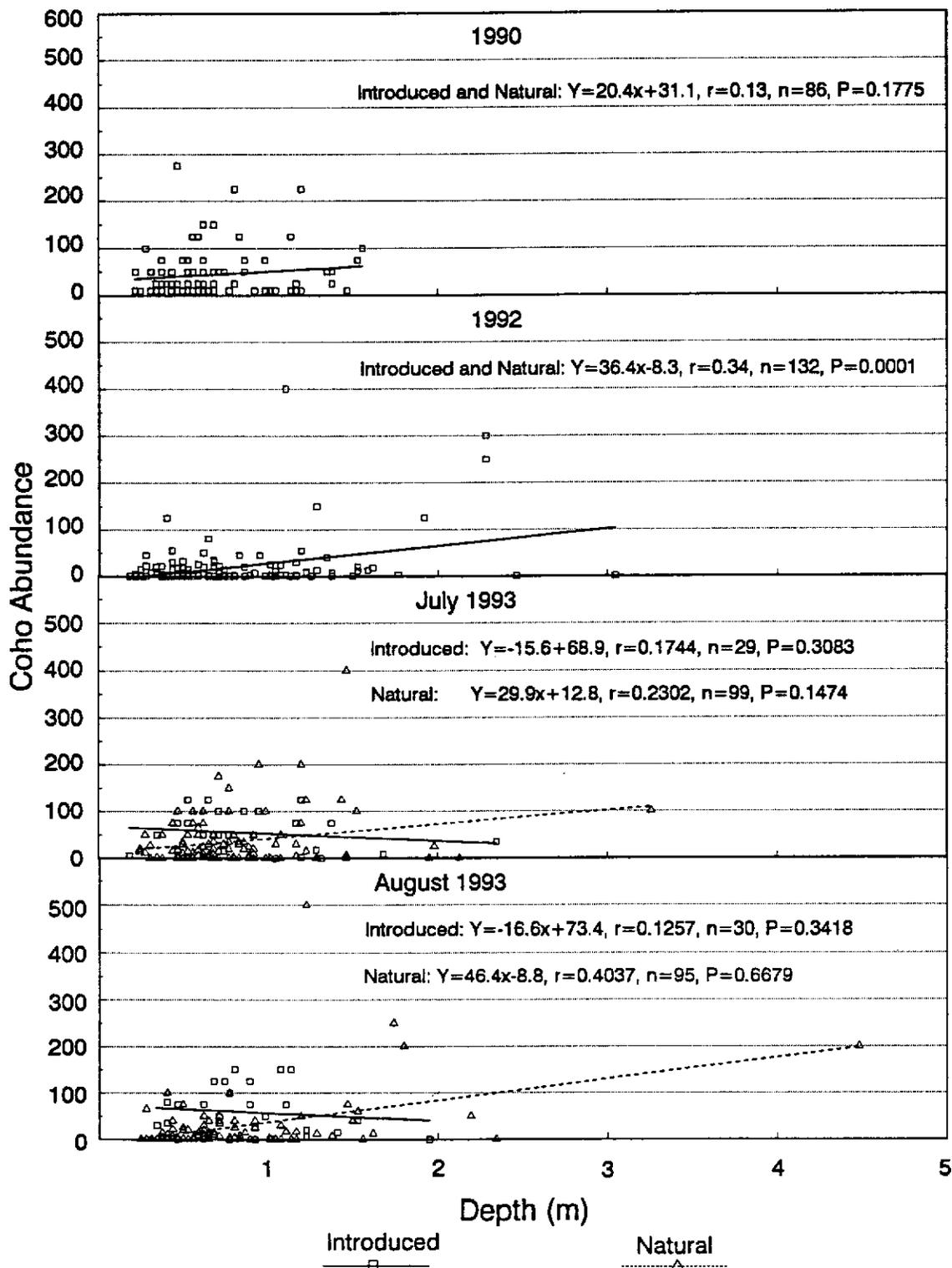


Figure 9.

The relationship between coho salmon abundance (# coho/debris accumulation) and the depth half way from shore of natural and introduced debris accumulations, 1990, 1992-1993.

Current velocities measured upstream, downstream, on the outer edge, and in the center of debris stations were not correlated with coho salmon abundance (Table 5). Station type significantly (ANCOVA: $P=0.0004-0.0383$) influenced the analysis for the July and August 1993 data sets for all four locations where current velocities were measured. The influence of current velocities at all four locations on coho salmon abundance for these two data sets was analyzed separately for introduced and natural debris stations. Although the relationship was not significant, coho salmon abundance was generally negatively related to increasing current velocities, except at introduced debris accumulations during July 1993, when coho salmon abundance was positively related to current velocities upstream and downstream of the debris station (Table 5).

General Linear Models

Introduced and Natural Debris Combined

Coho salmon at introduced and natural debris accumulations were influenced most by the combination of debris surface area, debris density, and riverine habitat (Table 6). Debris surface area and debris density were significant variables in all general linear models for each survey. These two variables alone contributed to a majority of the variability explained by the strongest overall model (1990, 79%; 1992, 77%; July 1993, 91%; August 1993, 91%). An interactive term in which debris surface area was significantly related to riverine habitat type was also a significant variable in the strongest models in 1990, 1992 and August 1993. Increasing debris surface area in pools had a greater effect on coho salmon abundance (number of coho/debris accumulation) than increasing debris surface area in glides or riffles (Figure 10); however, this effect was significant only in 1992 (ANCOVA: 1990: $P=0.2281$; August 1993: $P=0.0691$; 1992: $P=0.0095$; Tukey: Pool > Glide: $P=0.0464$; Pool > Riffle: $P=0.0098$). Riverine habitat itself was not a significant term in these models but was included because the debris surface area-riverine habitat interactive term was statistically significant. During July 1993, either riverine habitat or current velocity on the outer edge of the debris accumulations could be combined with debris surface area and debris density to yield the strongest model (Table 6). During this survey, coho abundance was affected nearly equally in pool and glide habitat, with the fewest fish residing in debris accumulations located in riffles (Table 6). Increasing numbers of coho salmon were associated with decreasing current velocities on the outer edge of the debris accumulation (Table 6).

Table 5. Results of ANCOVA (combined) and linear regression (introduced and natural) analysis of the effects of current velocities on coho salmon abundance at introduced and natural debris accumulations during 1990, 1992, July 1993, and August 1993. Linear regression was used to analyze data for introduced and natural debris accumulations separately when station type significantly influenced the results. The analysis of introduced and natural debris was completed with combined (combined) data if no significant difference was observed between the two station types.

Date	Debris type	Regression equation	n	r	P
Current Velocity on the Outer Edge					
1990	Combined	$Y = -31.6x + 51.6$	78	0.10	0.5602
1992	Combined	$Y = -13.1x + 20.5$	132	0.05	0.7959
July 1993	Introduced	$Y = -52.6x + 61.8$	29	0.14	0.7724
July 1993	Natural	$Y = -37.9x + 46.0$	99	0.20	0.0642
August 1993	Introduced	$Y = -47.8x + 63.2$	30	0.08	0.8129
August 1993	Natural	$Y = -26.3x + 34.3$	95	0.11	0.5890
Current Velocity in the Center					
1990	Combined	$Y = 30.4x + 44.1$	80	0.07	0.8969
1992	Combined	$Y = -149.3x + 21.5$	132	0.11	0.0974
July 1993	Introduced	$Y = 639.2x + 59.2$	29	0.24	0.3646
July 1993	Natural	$Y = 105.5x + 42.3$	99	0.16	0.0653
August 1993	Introduced	$Y = -630.3x + 61.6$	30	0.17	0.6043
August 1993	Natural	$Y = -28.5x + 30.7$	95	0.07	0.4314
Current Velocity Upstream					
1990	Combined	$Y = -3.1x + 46.9$	79	0.01	0.7842
1992	Combined	$Y = -28.3x + 21.1$	132	0.08	0.3561
July 1993	Introduced	$Y = 11.8x + 54.4$	29	0.02	0.0711
July 1993	Natural	$Y = -8.1x + 36.2$	98	0.10	0.6640
August 1993	Introduced	$Y = -9.7x + 59.6$	30	0.02	0.6983
August 1993	Natural	$Y = -6.0x + 29.3$	94	0.02	0.9791
Current Velocity Downstream					
1990	Combined	$Y = -10.8x + 46.8$	80	0.06	0.9446
1992	Combined	$Y = -12.7x + 20.1$	132	0.04	0.6759
July 1993	Introduced	$Y = 281.3x + 50.3$	29	0.36	0.0905
July 1993	Natural	$Y = -49.4x + 41.6$	99	0.14	0.1473
August 1993	Introduced	$Y = -5.8x + 59.8$	29	0.004	0.9647
August 1993	Natural	$Y = -27.9x + 131.8$	95	0.08	0.6679

Table 6. "Best" general linear models of coho salmon abundance (# coho/debris accumulation, transformed) with physical variables of natural and introduced debris accumulations combined. Sums of Squares (SS), significance level, correlation coefficients, and fitted models for different class variables are also listed.

Date	Type III SS	Significance	Density	Habitat	Area*Habitat	P	R
1990	Area	0.0012	0.0200	0.4237	Area*Habitat 0.0436	0.0001	0.4300
Trans =	3.98	+ 0.003 Area	+ 1.05 Dense - 0.44 Medium - 0.62 Sparse	+ 0.69 Glide - 0.17 Pool - 0.52 Riffle	- 0.0020 Area*Glide + 0.0026 Area*Pool - 0.0007 Area*Riffle		
1992	Area	0.0021	Density 0.0001	Habitat 0.4566	Area*Habitat 0.0001	0.0001	0.7625
Trans =	1.71	+ 0.012 Area	+ 1.51 Dense - 0.48 Medium - 1.02 Sparse	+ 0.38 Glide - 0.21 Pool - 0.16 Riffle	- 0.009 Area*Glide + 0.017 Area*Pool - 0.009 Area*Riffle		
July 1993	Area	0.0001	Density 0.0001	Habitat 0.0140		0.0001	0.6786
Trans =	3.36	+ 0.028 Area	+ 2.26 Dense + 0.09 Medium - 2.36 Sparse	+ 0.70 Glide + 0.53 Pool - 1.22 Riffle			
Trans =	4.24	+ 0.029 Area	Density 0.0001	Outer Current 0.0019		0.0001	0.6753
August 1993	Area	0.0001	+ 2.23 Dense + 0.15 Medium - 2.38 Sparse	- 3.02 Outer Current			
Trans =	2.78	+ 0.029 Area	Density 0.0001	Habitat 0.3280	Area*Habitat 0.0196	0.0001	0.7682
Trans =	2.78	+ 0.029 Area	+ 2.48 Dense - 0.48 Medium - 2.01 Sparse	+ 0.53 Glide + 0.11 Pool - 0.64 Riffle	- 0.0091 Area*Glide + 0.016 Area*Pool - 0.007 Area*Riffle		

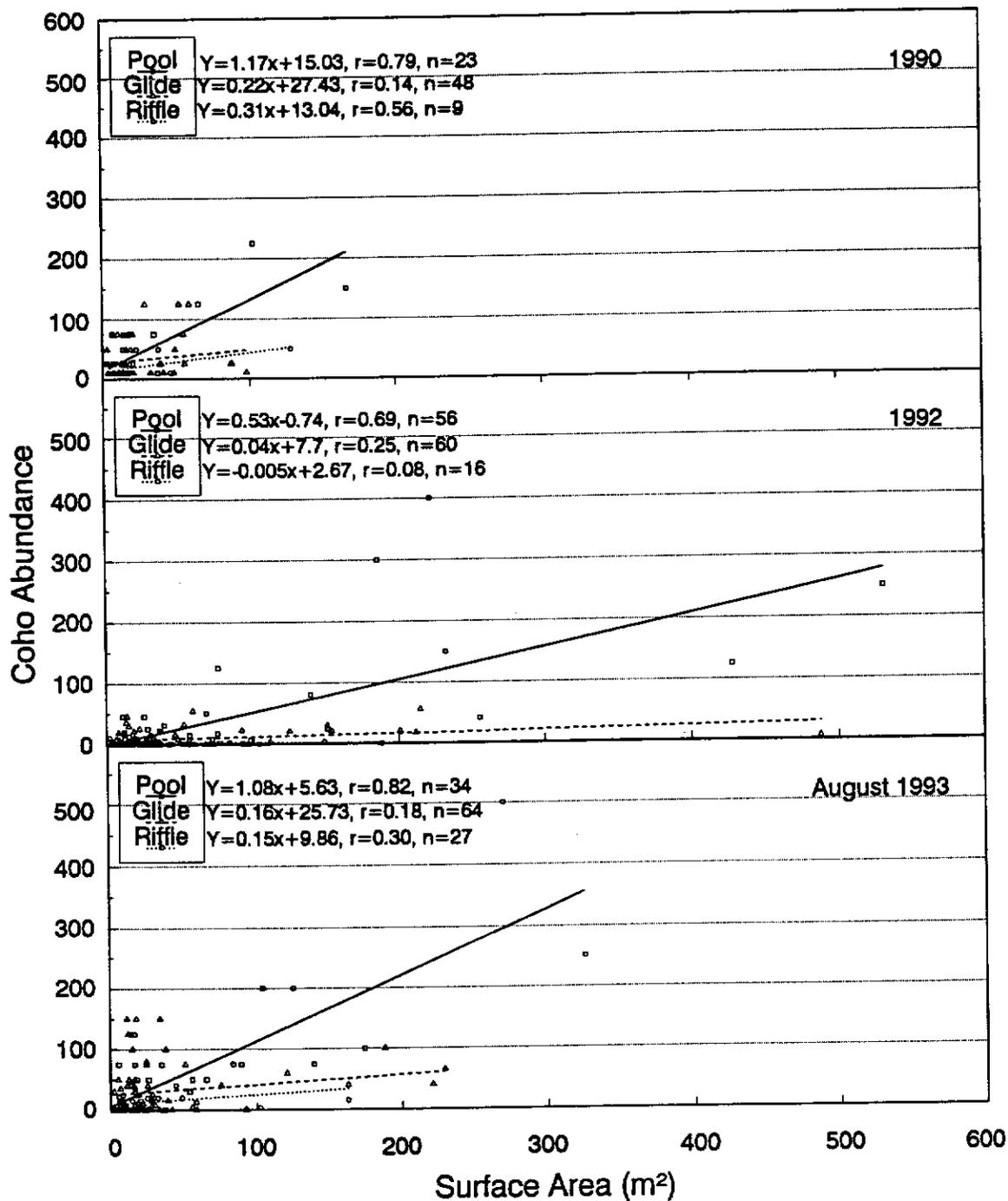


Figure 10. Relation between debris surface area, riverine habitat and coho salmon abundance (# coho/debris accumulation) for the combined introduced and natural debris analysis 1990, 1992-1993.

Natural Debris

The strongest models developed for natural debris accumulations contained the same variables as those for natural and introduced debris accumulations combined except for August 1993 (Table 7). Again, debris surface area and debris density were significant variables in all models and explained much of the overall variability explained by the strongest full model (1990: 49%; 1992: 86%; July 1993: 89%; August 1993: 84%). In contrast to the combined introduced and natural debris analysis, riverine habitat was a significant variable for the natural debris only analysis for 1990. As with the combined debris analysis, debris surface area was significantly related to riverine habitat type for 1990, 1992, and August 1993 (not in the best model for August 1993). In partial contrast to the combined debris analysis of 1990, increasing debris surface area had a positive effect on coho salmon abundance in pools and riffles for the natural debris analysis, but increasing debris surface area in glides did not affect coho salmon abundance (Figure 11). The effect of increasing debris surface on coho salmon abundance was significantly greater in pools than in glides and riffles during 1992 (ANCOVA: $P=0.0079$; Tukey: Pool > Glide: $P=0.0137$; Pool > Riffle: $P=0.0095$) and August 1993 (ANCOVA: $P=0.0086$; Tukey: Pool > Glide and Riffle: $P<0.0001$), but not in 1990 (ANCOVA: $P=0.5254$).

Two models, which explained nearly the same amount of variability in coho salmon abundance were developed for natural debris stations using August 1993 data (Table 7). These models differed from the strongest model for introduced and natural debris combined (Table 6). The model explaining the most variability in coho salmon abundance at natural debris accumulations during August 1993 contained the variables debris surface area, debris density, outer depth, and an interaction term between outer depth and debris surface area. Coho salmon abundance increased with increasing debris surface area and outer depth (Figure 12). Outer depth was not itself significant in this model but was included because the interactive term was significant. The second model developed for natural debris accumulations during August 1993 included the variables debris surface area, debris density, outer depth, and an interactive term between debris surface area and debris density. This model explained nearly as much variability as the first; however, all the terms in the second model were significant (Table 7). Increasing the surface area of dense debris accumulations had a significantly (ANCOVA: $P=0.0001$; Tukey Dense > Medium and Sparse: $P<0.0001$; Medium > Sparse: $P=0.0039$) greater impact on coho salmon abundance than increasing the debris surface area of medium or sparsely dense accumulations (Figure 13). More variation was explained by the natural debris model containing surface area, density, habitat and the interaction term between habitat and surface area for August 1993 (Table 7) than was explained by the same model in the combined analysis (Table 6).

Table 7. "Best" general linear models of coho salmon abundance (transformed) with physical variables of natural debris accumulations. Sums of Squares (SS), significance level, correlation coefficients, and fitted models for different class variable are also listed.

Date	Type III SS	Significance			P	R
1990	Trans = 1.61	Area	Density	Habitat	Area*Habitat	0.7808
		0.0201	0.0470	0.0023	0.0009	
		+ 0.014 Area	+ 1.05 Dense + 0.79 Medium - 1.85 Sparse	+ 3.43 Glide - 0.78 Pool - 2.64 Riffle	- 0.013 Area*Glide - 0.003 Area*Pool + 0.016 Area*Riffle	
1992	Trans = 1.70	Area	Density	Habitat	Area*Habitat	0.7874
		0.0018	0.0001	0.7380	0.0001	
		+ 0.013 Area	+ 1.73 Dense - 0.73 Medium - 0.99 Sparse	+ 0.26 Glide - 0.21 Pool - 0.06 Riffle	- 0.010 Area*Glide + 0.018 Area*Pool - 0.009 Area*Riffle	
July 1993	Trans = 3.37	Area	Density	Habitat		0.7201
		0.0001	0.0001	0.0083		
		+ 0.029 Area	+ 1.84 Dense + 0.33 Medium - 2.17 Sparse	+ 1.22 Pool + 0.09 Glide - 1.32 Riffle		
Trans = 3.95		Area	Density	Outer Current		0.7194
		0.0001	0.0001	0.0022		
		+ 0.032 Area	+ 1.85 Dense + 0.33 Medium + 2.18 Sparse	- 2.98 Outer Current		

Table 7. cont.

Date	Type III SS Significance	P	R
August 1993	Area 0.0161	0.0001	0.8638
Trans = 1.64	+ 0.015 Area Density 0.0001 + 1.45 Dense - 1.42 Medium - 0.23 Sparse	Area*Outer Depth 0.0003 + 0.017 Area*Outer Depth	
Trans = 0.68	Area 0.001 + 0.024 Area Density 0.0117 + 1.15 Dense - 0.44 Medium - 0.72 Sparse	Outer Depth 0.0001 + 1.92 Outer Depth Area*Density 0.0082 + 0.018 Area*Dense + 0.006 Area*Medium - 0.024 Area*Sparse	0.0001 0.8585
Trans = 2.41	Area 0.0001 + 0.031 Area Density 0.0001 + 1.45 Dense + 0.05 Medium - 1.50 Sparse	Habitat 0.7677 - 0.25 Glide + 0.24 Pool + 0.02 Riffle	0.0001 0.8398

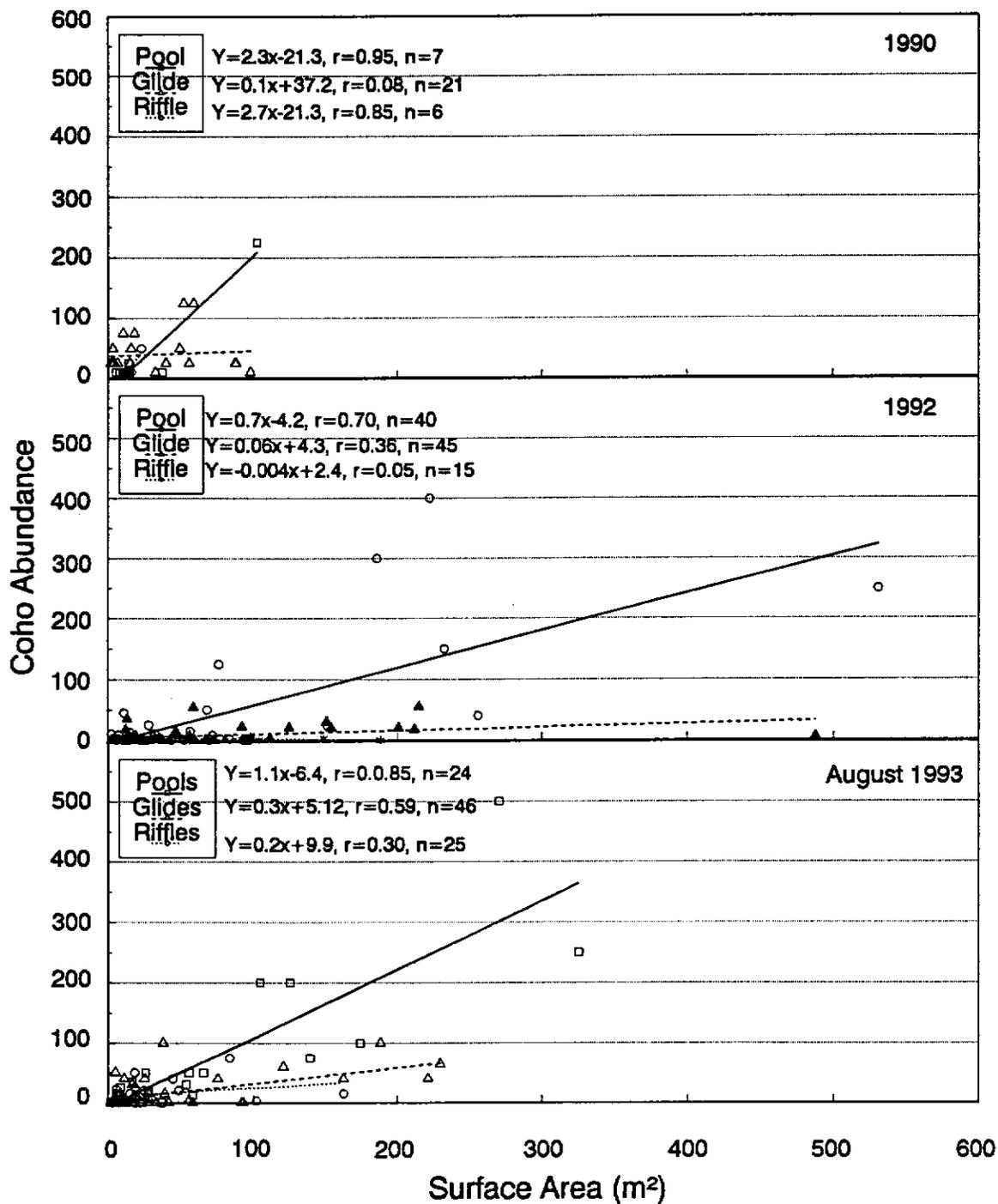


Figure 11. Relationship between debris surface area, riverine habitat and coho salmon abundance (# coho/debris accumulation) for natural debris accumulations 1990, 1992, and August 1993.

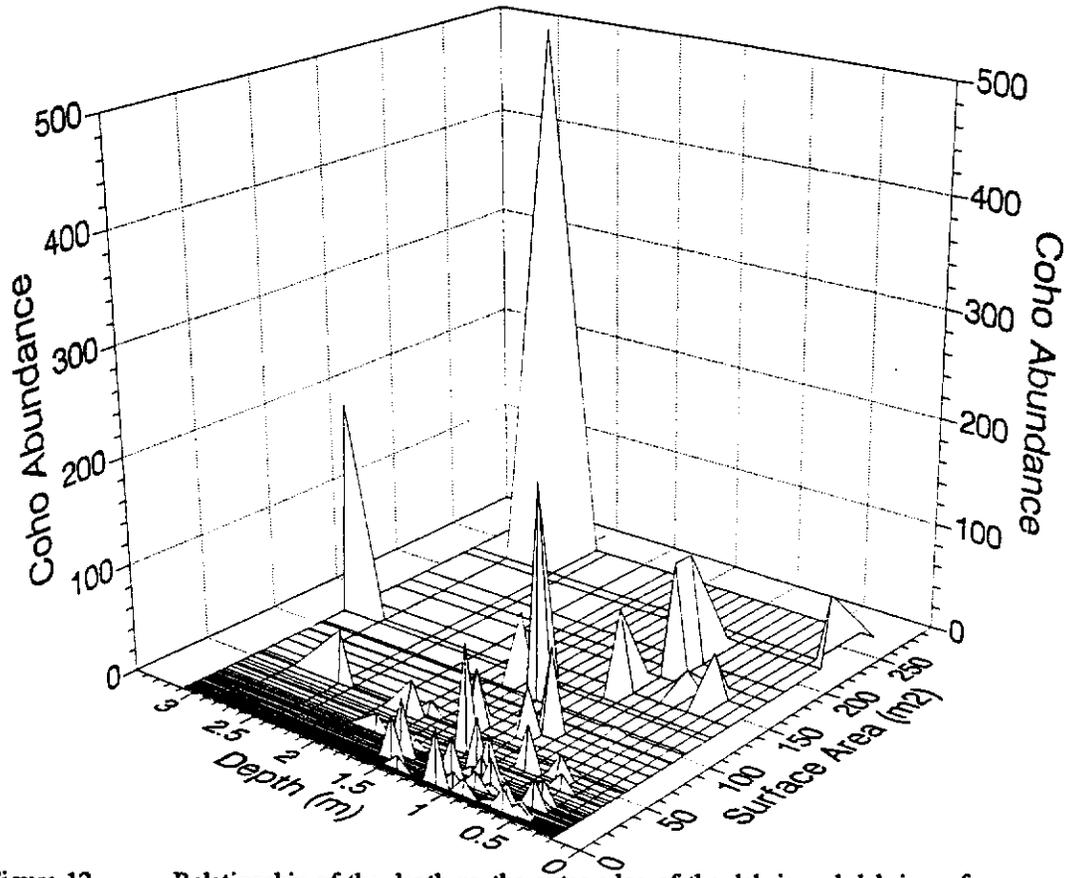


Figure 12. Relationship of the depth on the outer edge of the debris and debris surface area on coho salmon abundance (# coho/debris accumulation), August 1993.

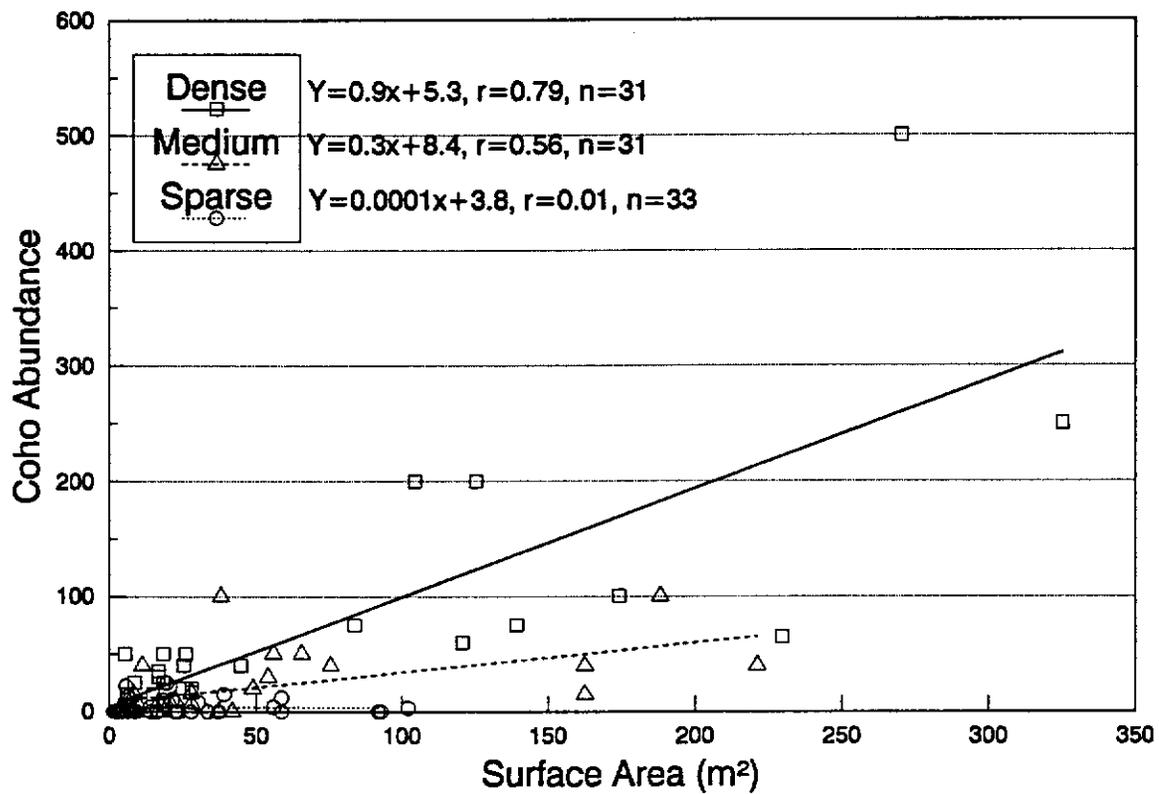


Figure 13. Relationship between coho salmon abundance (# coho/debris accumulation) and debris surface area at natural debris accumulations of different density, August 1993.

Introduced Debris

The strongest models developed for coho salmon abundance at introduced debris accumulations were somewhat different than those developed for natural debris accumulations (Table 8). Debris surface area and debris density were included in all models; however, debris density was not a significant variable in the model developed using the 1992 data. It was included in the model because of the significant interaction between debris surface area and debris density. Again, these two variables contributed to a majority of the variability explained by the strongest full model (1990--100%, 1992 area only 55%, and August 1993--52%). During 1990, debris density and debris surface area explained 36% of the variability in coho abundance (number coho/debris accumulation). Estimates from the equation show that dense accumulations attracted more coho salmon than either medium or sparse accumulations. Debris density and debris surface area were the only variables present in the strongest model. For 1992, debris density, although not significant, was included because of the significant interactive term between debris surface area and debris density. Increasing debris surface area may have had a greater effect on coho salmon abundance at debris accumulations of medium density than those with dense classifications (Figure 14), although, this difference was not statistically significant (ANCOVA: $P=0.9555$). No significant model could be developed for July 1993.

The strongest model for introduced debris developed using the August 1993 data included debris surface area, debris density, tree species, depth in the center of the debris, and the current velocity downstream of the debris (Table 8). Debris surface area and the current velocity downstream of the debris positively influenced coho abundance (number of coho/debris accumulation). Dense and sparse debris had a positive effect on coho salmon abundance, while medium accumulations had a negative effect. More coho salmon were associated with debris accumulations composed of a combination of hemlock and spruce trees, followed by those composed only of spruce and finally hemlock. Coho abundance was inversely associated with the depth in the center of the debris accumulation.

Table 8. "Best" general linear models of coho salmon abundance (transformed) with physical variables of introduced debris accumulations. Sums of Squares (SS), significance level, correlation coefficients, and fitted models for the different class variables are also listed.

Date	Type III SS	Significance	P	R
1990		Area 0.0046	0.0001	0.6013
Trans =	4.34	+ 0.003 Area Density + 1.24 Dense - 0.96 Medium - 0.28 Sparse		
1992		Area 0.0001	0.0001	0.7355
Trans =	2.24	+ 0.038 Area Density + 1.56 Dense - 1.56 Medium		
July 1993			No Significant Models	
August 1993	Area 0.0161	Density 0.0002	0.0011	0.8044
Trans =	5.11 + 0.091 Area	+ 3.99 Dense - 4.11 medium + 0.13 Sparse	Back Current 0.0170 + 46.98 Back Current	
		Species 0.0050	Mid Depth 0.0231	
		+ 2.67 Hemlock/Spruce - 0.52 Spruce - 2.14 Hemlock	- 3.42 Mid Depth	
Trans =	5.46 + 0.104 Area	Density 0.0004	Outer Depth 0.0572	0.0001
		+ 3.49 Dense - 4.56 Medium + 1.07 Sparse	- 2.55 Outer Depth	0.7871
		Species 0.0127	Back Current 0.0404	
		+ 2.45 Hemlock/Spruce - 0.51 Spruce - 1.93 Hemlock	+ 40.4 Back Current	

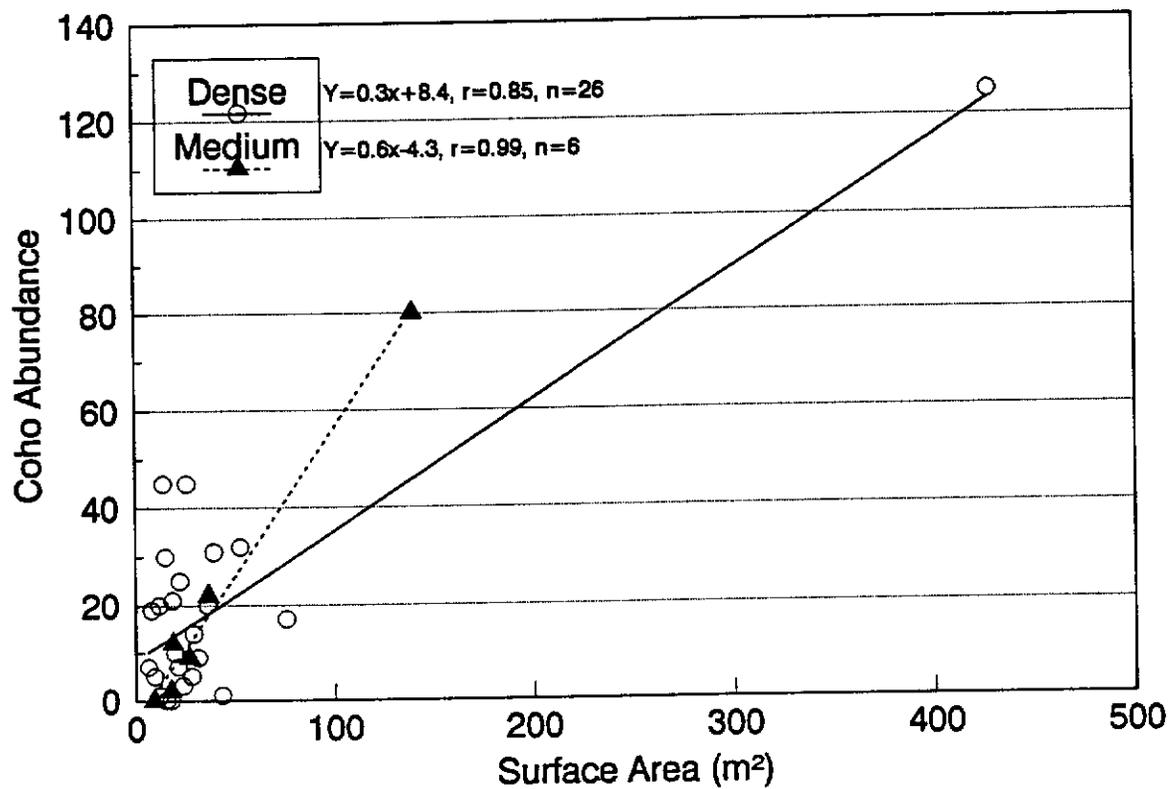


Figure 14. Relationship of coho salmon abundance (# coho/debris accumulation) with debris surface area at introduced debris accumulations of different density, 1992.

DISCUSSION

The presence of woody debris was the most important factor influencing the distribution of summer rearing juvenile coho salmon in the mainstem Clearwater River. More juvenile coho salmon were present at the largest, most dense debris accumulations. Increasing debris surface area in pools generally had a greater positive impact on coho salmon abundance than increasing debris surface area in glides and riffles.

Juvenile coho salmon in the mainstem Clearwater River were more abundant in areas containing woody debris. Woody debris is an important salmonid habitat component of streams, responsible for functions such as pool formation (Bisson et al. 1987), provision of cover from predators (Everest and Chapman 1972; Bisson et al. 1987; Grant and Noakes 1987), and protection from extreme current velocities (McMahon and Hartman 1989; Shirvell 1990; Fausch 1993). We hypothesize that woody debris in the mainstem Clearwater River primarily provides cover from predators, although, cover from high current velocities may be important during fall migration to wall-base channels. Coho salmon generally selected focal positions upstream of woody debris cover and were observed fleeing from otters (*Lutra canadensis*), cutthroat trout (*O. clarki clarki*), and common mergansers (*Mergus merganser*) during microhabitat observations (Peters 1996). Many debris accumulations were located in areas with current velocities well below those favored by coho salmon (10 cm/s: Murphy et al. 1989; 20 cm/s: Dolloff and Reeves 1990) and no relationship between coho salmon abundance and velocity was observed. Nevertheless, other studies have shown that protection from current velocities appears to be an important function of woody debris in riffles (Peters 1996). Although woody debris results in the formation of some pools in the mainstem Clearwater River, bedrock outcroppings and large boulders are the primary pool forming structures of this system. When present, woody debris is generally a secondary feature of these pools, having been deposited in slack water areas where it serves as cover habitat for juvenile coho salmon.

The mainstem Clearwater River has many potential predators of juvenile coho salmon, including the common merganser, great blue heron (*Ardea herodias*), belted kingfisher (*Ceryle alcyon*), river otter, and cutthroat trout. Wood (1987) showed that broods of common mergansers may consume large numbers of coho salmon fry during the summer. Merganser broods were seen along the study reach during most surveys. River otters also may consume large numbers of juvenile coho salmon (Dolloff 1993) and were observed in the study area. Dense cover associated with woody debris could prevent these predators from observing, pursuing, and capturing juvenile coho salmon, which might explain the greater abundance of coho salmon near dense debris accumulations. The distance at which young-of-the-year brook trout react to (flee from) an approaching predator is shorter in areas of high cover than low cover, which may increase foraging opportunities in these areas (Grant and Noakes

1987). Tabor and Wurtsbaugh (1991) showed that juvenile rainbow trout in reservoirs apparently selected inshore cover from predators even though more abundant food resources were located offshore. Juvenile coho salmon are relatively unwilling to expose themselves to predators when compared to other Pacific salmon (Abrahams and Healey 1993). The distance at which coho salmon will move to obtain food items is reduced in the presence of predators (Dill and Fraser 1984). Thus, the use of areas containing woody debris by juvenile coho salmon in the mainstem Clearwater River may be a result of balancing foraging opportunities while reducing risk of predation mortality.

The influence of woody debris on coho salmon distribution has received much attention recently and contradictory results have been presented. The distribution and density of coho salmon in a semi-natural stream channel were not directly associated with woody debris cover during summer months (Quinn et al. 1994; Spalding et al. 1995). However, coho salmon abundance was related to woody debris cover in another study completed in the same semi-natural stream channel, although water depth was an equally important factor influencing distribution (Lonzarich and Quinn 1995). The fewest coho salmon were observed in shallow areas lacking woody debris (Lonzarich and Quinn 1995). Experimental trials completed by Quinn et al. (1994) and Spalding et al. (1995) lacked aquatic predators which may influence salmonid distribution (e.g., Schlosser 1987; Bugert and Bjornn 1991). In contrast, potential predatory fish were included in the study completed by Lonzarich and Quinn (1995), which may have resulted in the observed differences in woody debris use by juvenile coho salmon in these experiments.

Juvenile coho salmon in the Big Qualicum River, Vancouver Island, B.C., were associated with bank cover early in the summer but shifted to midstream locations as they grew (Lister and Genoe 1970). In contrast, distance to cover decreased as coho salmon size increased in small streams of Prince of Wales Island, Alaska (Dolloff and Reeves 1990). In the present study, woody debris also appeared to be more important later in the summer when the fish were larger. Fausch (1993) determined that coho salmon rarely used artificial cover (plexiglass structures) in the Salmon River, B.C, and then only as refuge from current velocities rather than for overhead cover. However, the experimental units were located in runs with mean depths of 28-49 cm and the overhead cover was located only 10 cm above the substrate. This may have been too close to the substrate for coho salmon since they prefer mid-water focal positions (Dolloff and Reeves 1990, Bugert and Bjornn 1991, Bugert et al. 1991), which would have been approximately 14-24 cm above the bottom. A more likely cause of the discrepancy between Fausch (1993) and the present study is the scale at which habitat use was examined. Fausch (1993) discusses microhabitat selection while we measured macrohabitat use. Microhabitat refers to habitat variables measured at the focal position of individual fish, whereas macrohabitat describes larger scale distributions of fish (i.e., abundance in pool, riffle, glide). Focal positions (microhabitat use) of coho salmon in the mainstem Clearwater River were generally not

directly associated with woody debris cover and were up to 10 m from woody debris cover (Peters 1996). However, coho salmon often fled to woody debris cover when threatened by predators (Peters 1996). It is possible that, when threatened, coho salmon in Fausch's (1993) experiment would have sought the cover provided. This point shows the importance of comparing habitat selection information using similar index scales as well as the benefits to be gained by using both micro and macro scales in habitat selection studies (Bozek and Rahel 1991).

Coho salmon abundance in small streams is highest in pools (Hartman 1965; Bisson et al. 1982, 1988; Nickelson et al. 1992a). Coho salmon abundance in the mainstem Clearwater River also was greatest at woody debris accumulations located in pools and was generally positively related to depth on the outer edge of the debris. Although pools were the preferred habitat, glides were often used by large numbers of juvenile coho salmon. Juvenile coho salmon prefer areas with slow current velocities in small streams (Bustard and Narver 1975; Murphy et al. 1989). Murphy et al. (1989) (<10 cm/s) and Dolloff and Reeves (1990) (<20 cm/s) observed the highest densities of coho salmon in still or slow water. Bustard and Narver (1975) found that coho salmon preferred areas with current velocities below 15 cm/s during the winter. Coho salmon in the mainstem Clearwater River selected focal positions with current velocities less than 10 cm/s (Peters 1996). Although the relationship was not significant, coho salmon abundance was generally inversely related to increasing current velocities ranging from 0-116 cm/s at all locations where flow was measured in the present study. The lack of a significant relationship between current velocities and coho salmon abundance in the present study was likely caused by the large variability of coho salmon abundance estimates and the significance of other environmental variables (i.e. debris density and surface area). Based on this information, current velocities may not be an important variable to measure when determining macrohabitat use of salmonids. In contrast, this appears to be an important variable to measure when determining microhabitat use.

The species of woody debris affected coho salmon abundance during the final year of the study. This was likely due to the inherent differences in density of different types of debris. Debris accumulations composed of LWD, or introduced spruce or hemlock trees, were often denser than alder trees and SWD. No debris accumulations composed of SWD were classified as dense and the ratio of the three density classifications differed from an expected ratio (1/3:1/3:1/3) of dense:medium:sparse debris classifications (χ^2 : $P=0.0144$). Debris accumulations composed of spruce, hemlock and spruce/hemlock combinations did not conform to the expected ratio (χ^2 spruce: $P=0.0318$; hemlock: $P<0.0001$; hemlock/spruce: $P=0.0498$), but these species had more dense accumulations than expected. Debris accumulations composed of LWD, rootwads, and alder did not differ from the expected ratios.

Results from this study suggest that further enhancement in the mainstem Clearwater River

should focus on placement of large, dense woody debris bundles in pools. Structures placed in pools also will have a greater probability of surviving high winter flows, a potential problem for enhancing the Clearwater River with woody debris structures. However, several large natural debris accumulations were present in pools during the entire study period, indicating that stable woody debris could be introduced into pools.

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