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PHYSICAL FACTORS INFLUENCING FISH POPULATIONS
IN POOLS OF A TROUT STREAM

by

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VITA

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ABSTRACT

The relationship between physical parameters and fish populations of 19 pools of Little Prickly Pear Creek, Montana, was studied during the summers of 1965 and 1966. The pools were mapped and their fish populations sampled. Differences in surface area, volume, average depth, average current velocity, total cover and percent cover accounted for 75, 77 and 70 percent of the variation in numbers of total trout, brown trout and rainbow trout respectively. Current velocity and total cover were the most important factors, and together they accounted for most of the explained variation. Each of these two factors contributed significantly to total trout numbers. Cover was the most important factor for brown trout, and current velocity was most important for rainbow trout. The number of trout per unit of cover (cover quality) and the number per unit of pool surface area (pool quality) increased significantly as current velocity became greater. Deep-slow pools with a large amount of cover had the most stable populations with brown trout being more stable than rainbow trout. Suckers were most common in large, deep-slow pools with extensive cover. The importance of cover to trout is discussed in terms of security and photonegative response, and current velocity in terms of space-food relationships.

INTRODUCTION

An important environmental requirement of trout in streams is shelter, generally associated with pools. Several workers have shown the value of overall habitat quality in relation to trout population levels in sections of streams. The stream improvement work of Tarzwell (1937, 1938); Shetter, Clark and Hazzard (1946); and Saunders and Smith (1962) showed that population levels respond to an increase in shelter and food. Gunderson (1966) found that an ungrazed stream section with higher percentages of deep water types and more cover had a population of brown trout (over 6 inches long) that was 27 and 44 percent greater by number and weight respectively than a grazed section of the same stream with shallower water and less cover. Boussu (1954) showed that removal of undercut banks and brush in a section of stream caused a decrease in numbers and weight of trout, with decreases being greatest for larger fish. Shuck (1945) reported that volume and depth of water were significant factors in determining the population density of larger brown trout in a section of stream.

The social behavior of fish in relation to habitat conditions is an important consideration. The investigations of Kalleberg (1958) and Newman (1956) showed that salmonids are territorial and establish a social hierarchy within the overall population. Thus there is competition for the limited number of favorable positions within a stream. This indicates population levels may be self-limiting based on the quality of the habitat.

I evaluated the physical aspects of habitat quality of pools on Little Prickly Pear Creek, Montana, from July, 1965, to September, 1966. The objectives were to determine: (1) which physical factors were most important in determining standing crops of fish and (2) population stability.

DESCRIPTION OF THE STUDY AREA

Little Prickly Pear Creek is a small trout stream located 30 miles northwest of Helena, Montana. This stream arises on the east slope of the continental divide approximately 4,600 feet above sea level and flows northeasterly for about 35 miles. It enters the Missouri River 3 miles downstream from Wolf Creek, Montana, at an elevation of 3,300 feet. The drainage basin encompasses an area of 394 square miles consisting primarily of grassland slopes with open stands of conifers. Analyses done by the Soil Conservation Service show that the soils of the drainage basin are weakly calcareous, being derived mainly from weathered argillite rock with smaller contributions from weathered quartzite and igneous rocks.

The study area included 16 pools and a 940 foot section of stream referred to as the stability area. The latter contained three pools and the interconnected riffles above each pool. All pools were within a 6.2 mile length of stream from 0.7 mile above the mouth of Trinity Creek to 0.2 mile below the mouth of Big Sheep Creek (Figure 1).

Little Prickly Pear Creek is a mountain stream with high flows during the spring runoff and low flows during the summer, fall and winter. Flow data from the Sieben Gage Station indicate the peak of the spring runoff generally occurs in May with mean monthly discharge ranging from 70.2 to 354.0 cfs. Low summer flows occur in August with the mean monthly discharge varying from 11.5 to 51.7 cfs. Water conditions during the study period varied from high water in 1965 to more normal flows in 1966. The mean monthly discharges at the Sieben Gage Station for July, August and

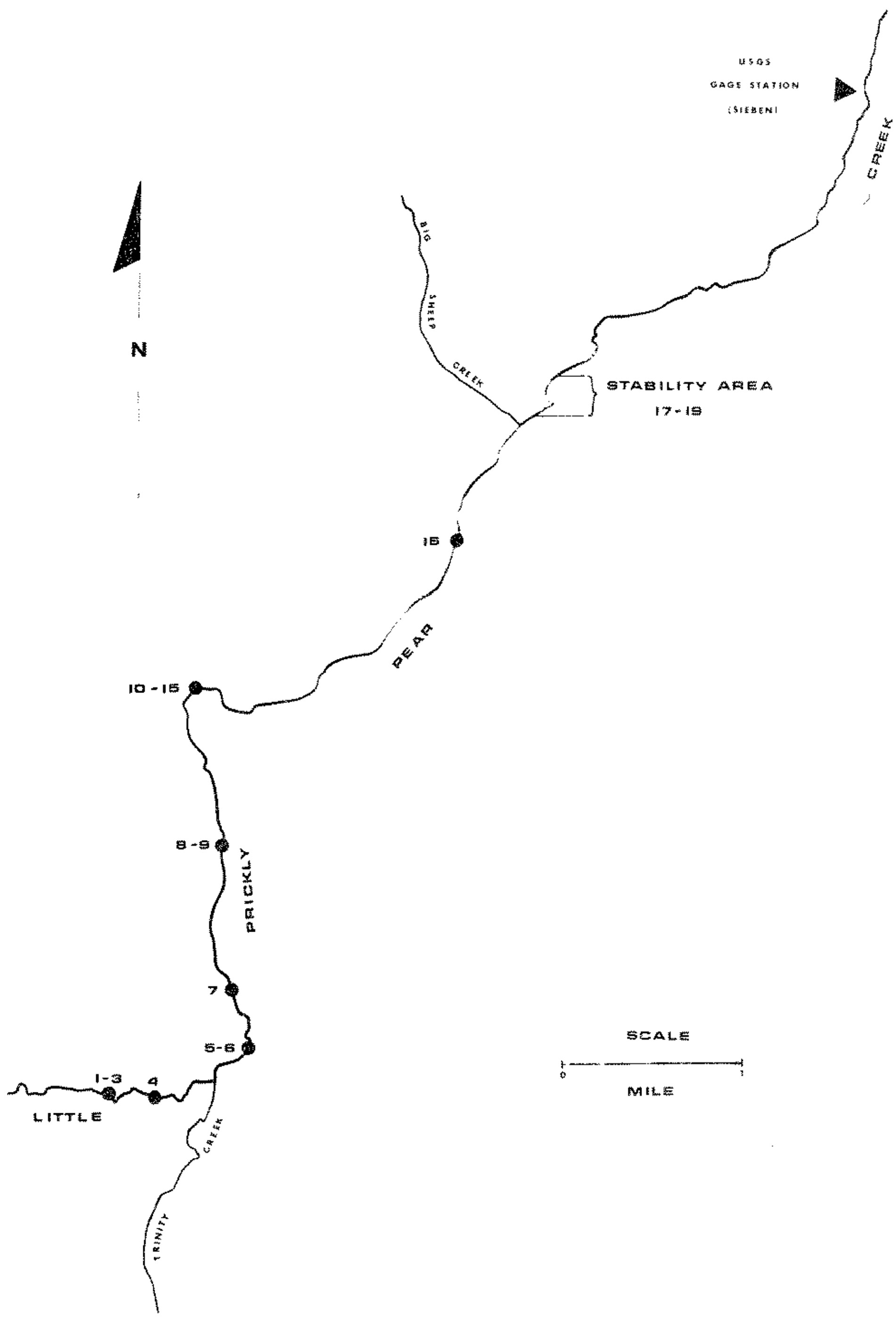

Figure 1. Study area of Little Prickly Pear Creek showing the approximate location of pools and the stability area.

September, 1965, were 92.2, 51.7 and 85.5 cfs respectively; and for 1966, 33.4, 14.1 and 20.4 cfs respectively. During periods of low flow, stream widths averaged from 20 to 30 feet with depths in most pools not exceeding 5 feet. Discharge and stream size increased progressively downstream.

Chemical analyses were made during the summers of 1965 and 1966 in the section of stream from the mouth of Canyon Creek to the Sieben Gage Station. Alkalinity ranged from 3.9 to 4.9 milliequivalents per liter, pH from 7.6 to 8.7, conductivity (K_{25}) from 350 to 445 micromhos, and total hardness from 210 to 235 ppm. Mean monthly temperatures for July, August and September, 1962-65, at the Sieben Gage Station ranged from 41.0 to 64.7 F (Swedberg, 1965).

The species of fish taken in the study area in order of decreasing abundance were: brown trout (*Salmo trutta*), longnose sucker (*Catostomus catostomus*), rainbow trout (*Salmo gairdneri*), mountain whitefish (*Prosopium* williamsoni), brook trout (*Salvelinus fontinalis*) and white sucker (*Catostomus commersoni*). Mottled sculpin (*Cottus bairdi*), although numerous, were not considered in this study. There has been no stocking of fish in the stream since 1954.

METHODS

For purposes of this study a pool was defined as any relatively large stream area capable of providing shelter for larger fish. The pools ranged from deep-slow portions of the stream to areas of shallow-fast water associated with cover. Physical characteristics used to select pools were size (surface area), depth, current velocity and cover. Pools selected were distinct units, limited above and below by the presence of shallow water types without cover. This minimized the error of overlapping home territories of fish from adjacent pools.

All pools were mapped between August 9 and September 12, 1966, at a low stabilized flow of 16 to 32 cfs. Transects were established at 10-foot intervals and depths were taken every foot along each transect. Current velocities were measured with a Gurley current meter at 0.4 of the observed depth every 2 feet along each transect. The water comprising a pool was classified into types based on depth and current velocity (Table 1). Cover was mapped and this included brush, overhanging vegetation, undercut banks and miscellaneous types. The term brush was used to describe dead submerged woody portions of bank vegetation occasionally

Table 1. Criteria of water-type classification

Water type	Depth (feet)	Current velocity (feet per second)
Slow-Shallow (SS)	0.1-1.5	-1.00
Deep-Slow (DS)	+1.5	-1.00
Shallow-Fast (SF)	0.1-1.5	+1.00
Deep-Fast (DF)	+1.5	+1.00

strengthened by live growth. Overhanging vegetation was live growth that provided an overhead canopy less than one foot above the water's surface. Miscellaneous cover included underwater shelves provided by clay and rock, tree roots and debris. Pool boundaries were delineated by depth and cover. The surface area included within the pool was deeper than 1.4 feet and areas with cover regardless of depth. Surface area, water-type composition and extent of cover were determined with a planimeter from the maps. Average depth, average current velocity and pool volume were calculated for each pool. Figure 2 is a representative pool map showing water types, cover and the pool boundary.

The fish populations of all areas were sampled between August 3 and September 1, 1965, and between July 11 and July 27, 1966. Discharges at the time of fish sampling in 1965 ranged from 37 to 73 cfs compared with 28 to 43 cfs in 1966. The stability area was also sampled December 20, 1965, and April 1, 1966. Sampling was done by electrofishing using a 300 volt, 850 watt direct current unit. Individual pools were isolated with blocking nets and at least three passes were made through each area. Captured fish were anesthetized with MS-222 (Tricaine Methanesulfonate), measured to the nearest 0.1 inch total length and weighed to the nearest 0.01 pound. Trout from 7.0 to 8.0 inches long or longer were tagged with plastic band jaw tags. Whitefish were tagged with metal opercle tags and suckers with plastic dart tags inserted at the base of the dorsal fin. Trout smaller than 4.0 inches and whitefish and suckers smaller than 7.0 inches were not included in this study since they were seldom present in the pools sampled.

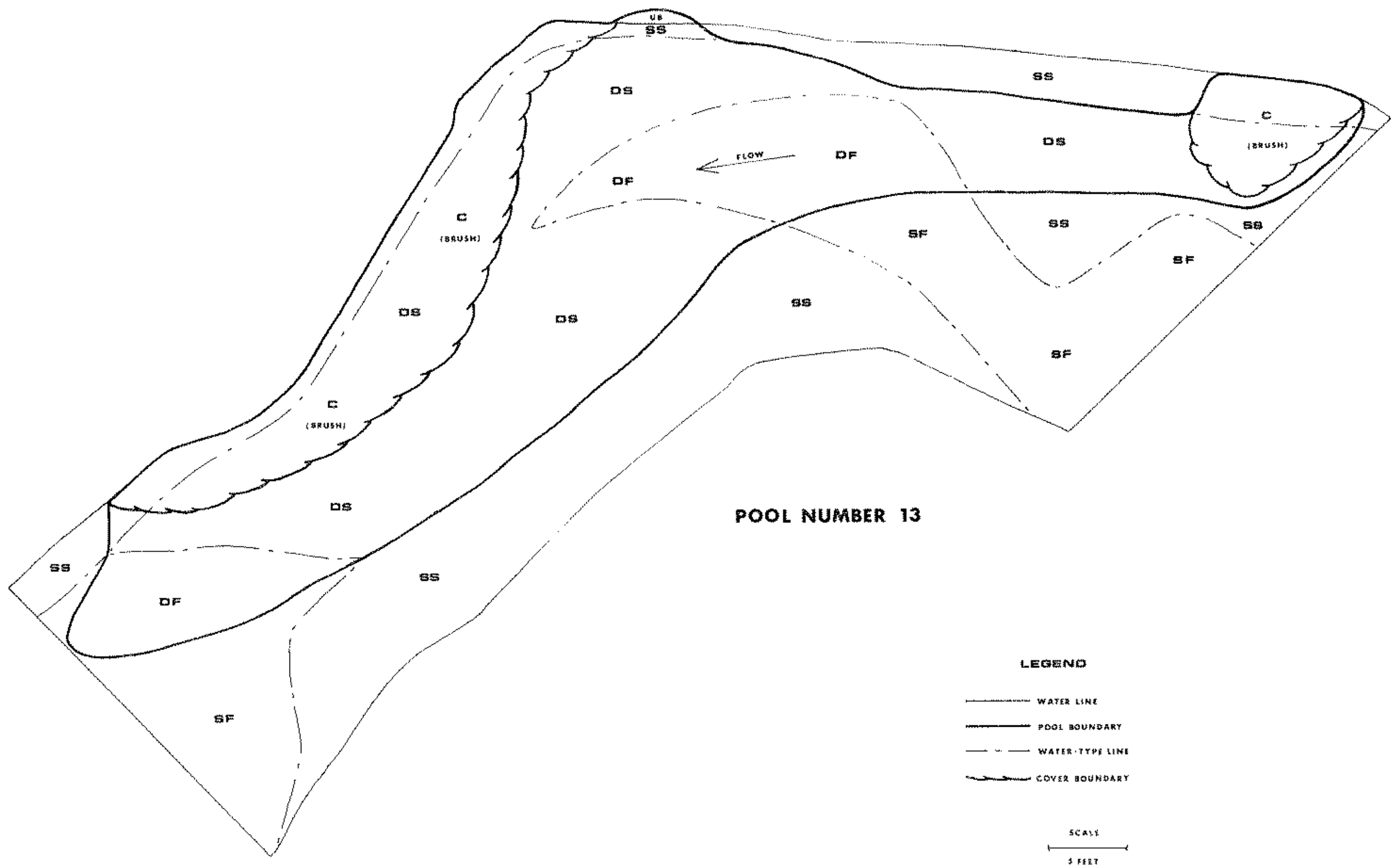

Figure 2. Representative pool map showing water types, cover and pool boundary.

The efficiency of fish sampling (ratio of marked to unmarked in a second sample) was determined in the stability area and a large pool. Trout 4.0 to 6.9 inches had a range of 72 to 78 percent while those 7.0 inches and over had a range of 84 to 100 percent. Sampling efficiency for suckers was 56 percent. There were too few whitefish present for efficiency determination. Elser (1967) with more extensive sampling in the same general stream section had similar efficiencies.

The data were analyzed in a multiple linear regression and analysis of variance according to Bailey (1959) and Snedecor (1956) to determine the relationships between physical parameters and fish populations of pools.

RESULTS

Physical Parameters of Pools

Physical data for pools are presented in Table 2. Pools ranged in surface area from 273.9 to 1,849.3 square feet with volumes from 593.4 to 4,068.5 cubic feet. Average depths varied from 1.3 to 2.5 feet and average current velocities from 0.30 to 1.67 f.p.s. (feet per second). The predominant water type was deep-slow in 14 pools, deep-fast in 4 pools and slow-shallow in 1 pool. The slow-shallow pool also had a high percentage of fast water types. Slow-water pools were generally deep, and/or large, and often located on sharp bends of the stream (Figures 3 and 4). Fast-water pools were smaller, shallower and associated with straight stream channels (Figures 5 and 6).

Cover ranged as high as 496.8 square feet and made up as much as 51.7 percent of the pool surface area. Larger pools generally contained more cover than smaller pools. Brush made up 77.0 percent, undercut banks 10.6 percent, overhanging vegetation 7.3 percent and miscellaneous types 5.1 percent of all pool cover. The important plant species constituting cover were willow (*Salix* sp.) and dogwood (*Cornus* sp.).

Fish Populations of Pools

Trout 4.0 to 6.9 inches were primarily yearling fish (Bishop, 1955; Elser, 1967). These comprised 27 percent of the trout sampled in 1965 and 39 percent in 1966 but less than 7 percent of the weight in either year. Since the pools selected were not considered the primary habitat of small trout and since their abundance did not correlate with pool

Table 2. Physical parameters of pools at low flow (16-32 cfs) in the summer of 1966

Pool no.	Pool size: Surface area ft^2	Pool size: Vol ft^3	Avg depth (ft)	Avg current vel (f.p.s.)	Predominant water types [1/]	Total cover (ft^2) [1/]
1	585.4	1,053.7	1.8	0.78	DS (52.3%) DF (29.0%)	253.8 (43.4%)
2	1,453.7	2,471.3	1.7	0.30	DS (75.5%) SS (24.5%)	294.3 (20.2%)
3	496.6	1,092.5	2.2	0.32	DS (81.3%) DF (9.4%)	46.2 (9.3%)
4	838.2	1,676.4	2.0	0.42	DS (96.2%) SS (3.8%)	46.7 (5.6%)
5	888.6	1,866.1	2.1	0.48	DS (77.7%) DF (15.5%)	54.9 (6.2%)
6	1,612.6	3,386.5	2.1	0.63	DS (82.6%) DF (11.7%)	496.8 (30.8%)
7	487.2	730.8	1.5	1.67	DF (51.4%) SF (29.2%)	144.5 (29.7%)
8	367.3	808.1	2.2	0.89	DS (68.0%) DF (25.4%)	79.4 (21.6%)
9	576.6	1,153.2	2.0	0.81	DS (54.2%) DF 35.6%)	158.6 (27.5%)

Table 2. Continued

Pool no.	Pool size: Surface area ft^2	Vol ft^3	Avg depth (ft)	Avg current vel (f.p.s.)	Predominant water types [1]	Total cover (ft^2) [1]
10	562.6	1,068.9	1.9	0.77	DS (65.6%) DF (27.9%)	30.4 (5.4%)
11	1,849.3	4,068.5	2.2	0.52	DS (82.0%) SS (8.4%)	200.6 (10.9%)
12	1,629.7	3,748.3	2.3	0.67	DS (78.0%) DF (16.8%)	158.8 (9.7%)
13	1,069.9	2,674.8	2.5	0.69	DS (69.5%) DF (21.2%)	289.6 (27.1%)
14	667.1	1,200.8	1.8	1.00	DF (45.3%) DS (33.5%)	186.4 (27.9%)
15	655.3	1,441.7	2.2	0.94	DS (50.9%) DF (41.7%)	65.8 (10.0%)
16	700.0	1,330.0	1.9	1.02	DF (54.7%) DS (31.4%)	134.5 (19.2%)
17	456.5	593.4	1.3	1.22	SS (41.7%) DF (28.6%)	236.0 (51.7%)
18	433.1	693.0	1.6	1.32	DF (68.1%) SS (20.6%)	79.0 (18.2%)
19	273.9	684.8	2.5	0.85	DS (65.6%) DF (34.4%)	00.0 (0.0%)

1/ Percentage figures in parentheses represent percent of surface area.

Figure 3. Deep-slow pool with little cover.

Figure 4. Deep-slow pool with extensive brush cover.

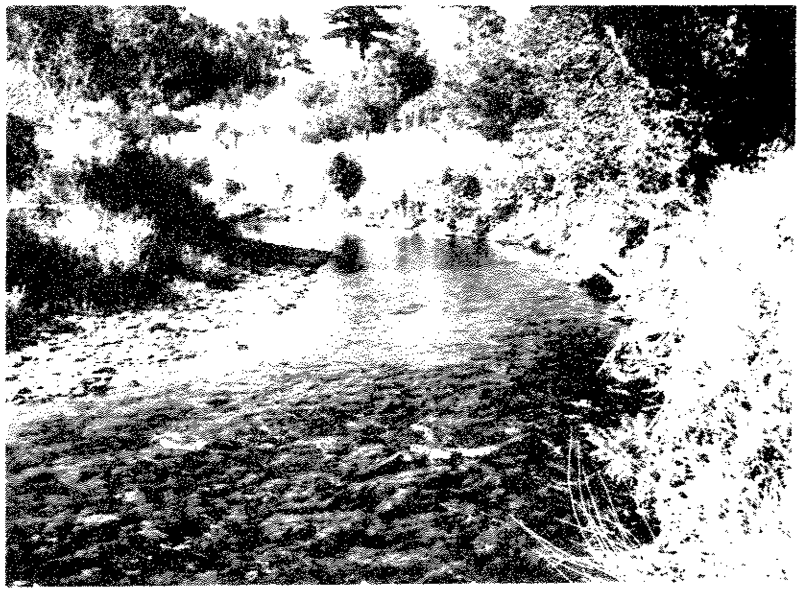

Figure 5. Deep-fast pool with limited cover provided by undercut bank.

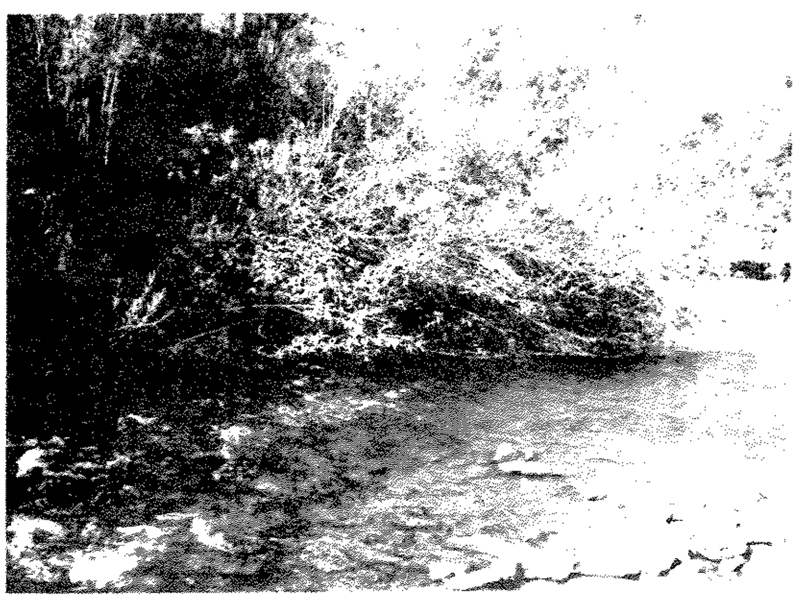

Figure 6. Deep-fast pool showing swift current associated with dense brush cover.

physical parameters, this group was excluded from the statistical analyses. Any actual preference of the yearling trout for specific pool conditions may have been obscured by the dominance of larger fish (Newman, 1956).

Standing crops of larger fish (over 6.9 inches) found in the study pools are presented in Table 3. In 1965, trout comprised 53 percent, suckers 35 percent and whitefish 12 percent of the 461 fish collected in all pools. In 1966, trout made up 63 percent, suckers 31 percent and whitefish 6 percent of 393 fish. Brown trout constituted about 60 percent of the trout for both years. The number of trout collected in 1965 and 1966 was the same, but numbers varied between years in five pools. Numbers increased in three pools and declined in two pools from 1965 to 1966. Whitefish and sucker populations varied greatly in individual pools and in total numbers between years.

In 1966, populations of larger trout in the 19 individual pools ranged from 2 to 34 fish with 6 pools having less than 6 trout. Brown trout were the numerically predominant trout in 11 pools and comprised from 60 to 80 percent of the trout in 9 pools. Rainbow trout were predominant in 2 pools and made up from 40 to 50 percent of the trout in 8 pools. Eleven brook trout were present in 8 pools, but no more than 3 were found in any one pool. The average length of brown trout in various pools ranged from 10.3 to 12.8 inches compared with 10.1 to 11.4 for rainbow.

In 1965, whitefish were found in 13 pools with from 1 to 6 fish per pool, while in 1966 they occurred in only 9 pools with 1 to 13 fish. In

Table 3. Fish populations of pools studied in the summers of 1965 and 1966

Pool no.	Year	Total trout No.	Total trout Wt.	Brown trout No.	Brown trout Wt.	Rainbow trout No.	Rainbow trout Wt.	Whitefish No.	Whitefish Wt.	Suckers No.	Suckers Wt.
		Standing crops of fish over 6.9 inches									
1	1965	13	8.91	7	7.20	6	1.71	6	9.48	1	1.14
	1966	14	7.19	6	3.68	8	3.51	13	17.96	0	0.00
2	1965	15	6.34	8	3.95	5	1.88	1	1.62	7	10.42
	1966	17	6.24	12	5.07	2	0.53	0	0.00	10	12.88
3	1965	5	1.30	1	0.39	4	0.91	4	5.80	0	0.00
	1966	2	1.17	1	0.38	1	0.79	0	0.00	2	2.91
4	1965	2	1.22	1	0.36	0	0.00	2	2.62	13	18.72
	1966	4	1.59	3	1.42	0	0.00	0	0.00	1	1.04
5	1965	6	1.70	1	0.33	5	1.37	2	1.22	0	0.00
	1966	2	1.03	0	0.00	1	0.80	1	0.29	0	0.00
6	1965	24	11.57	14	8.55	9	2.84	2	2.65	12	13.95
	1966	31	17.36	24	14.19	6	2.92	2	2.29	20	30.32
7	1965	32	19.51	22	15.18	10	4.33	8	7.60	3	5.22
	1966	34	24.76	19	15.26	14	8.93	1	0.48	0	0.00
8	1965	14	6.12	4	2.53	10	3.59	0	0.00	0	0.00
	1966	16	7.29	7	3.26	7	3.64	0	0.00	1	1.43
9	1965	6	2.18	4	1.65	2	0.53	6	11.57	0	0.00
	1966	20	16.07	13	11.04	7	5.03	0	0.00	3	4.94
10	1965	11	5.82	3	2.03	8	3.79	0	0.00	13	20.84
	1966	4	2.16	2	0.97	2	1.19	0	0.00	0	0.00
11	1965	16	8.78	11	7.24	5	1.54	7	12.20	32	52.90
	1966	15	6.91	10	4.50	5	2.41	1	1.10	20	30.12

Table 3. Continued.

Pool no.	Year	Standing crops of fish over 6.9 inches									
		Total trout		Brown trout		Rainbow trout		Whitefish		Suckers	
		No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
12	1965	12	9.88	9	7.99	3	1.89	6	4.68	4	5.30
	1966	7	6.86	5	6.07	2	0.79	2	1.08	4	6.38
13	1965	6	2.38	6	2.38	0	0.00	4	5.65	32	45.53
	1966	5	3.05	4	2.44	1	0.61	0	0.00	10	10.77
14	1965	21	11.86	16	10.64	5	1.22	2	2.29	14	20.54
	1966	11	7.47	7	5.84	4	1.63	3	4.95	11	16.67
15	1965	11	5.44	5	3.45	6	1.99	4	7.13	1	1.75
	1966	7	2.35	3	0.76	3	1.46	1	0.47	0	0.00
16	1965	9	5.11	4	2.94	5	2.17	0	0.00	5	8.86
	1966	21	11.56	11	7.30	10	4.26	1	0.13	15	23.01
17	1965	25	14.25	14	8.63	11	5.62	0	0.00	19	30.35
	1966	19	8.70	9	4.94	9	3.60	0	0.00	22	31.25
18	1965	15	6.55	12	5.94	2	0.48	0	0.00	1	1.50
	1966	13	8.25	10	6.63	3	1.62	0	0.00	0	0.00
19	1965	4	2.03	2	1.46	2	0.57	0	0.00	3	4.94
	1966	5	2.45	1	1.02	4	1.43	0	0.00	2	4.38
Totals	1965	247	130.95	144	92.84	98	36.43	54	74.51	160	241.96
	1966	247	142.46	147	94.77	89	45.15	25	28.75	121	176.10

1965, suckers ranged from 1 to 32 per pool in 15 pools; and, in 1966, they ranged from 1 to 22 per pool in 13 pools. In many of the pools suckers were predominant by number and/or weight. Fluctuations in the numbers of whitefish and suckers between years did not appear to have any effect on trout populations.

Relationship of Pool Physical Parameters to Trout Populations

A multiple linear regression was set up with pool surface area, volume, average depth, average current velocity, percent cover and total cover as the independent variables and number of trout per pool as the dependent variable. Following the initial regression analysis the independent variables that added little to the overall relationship were removed and the regression recalculated to find the factors that significantly influenced trout numbers. Weights were not used since they paralleled numbers. Regression lines were computed for all trout, rainbow trout and brown trout. Only the trout populations for 1966 were used in the statistical analyses since pool physical parameters were measured in that year only and the low water levels of 1966 increased sampling efficiency (Elser, 1967).

The six physical parameters accounted for 75, 77 and 70 percent of the variation in the numbers of total trout, brown trout and rainbow trout respectively. The multiple regressions involving all physical factors were significant at the 0.05 level, and the multiple correlation coefficients ranged from 0.84 to 0.88. Pool area, volume and depth accounted for very little of the variation in numbers. Percent cover added little to the relationship since it was closely correlated with total cover and its effect had already been accounted for by the latter. Current velocity and total cover were the most important factors. Together they accounted for 66, 66 and 59 percent of the variation in numbers of total trout, brown trout and rainbow trout respectively. The regressions with these variables were highly significant (0.01 level), and the multiple correlation coefficients ranged from 0.77 to 0.81 (Table 4).

There were differences in the relative importance of current velocity and cover to the three groups of trout as shown by the partial regression coefficients and the significance of their corresponding T values (Table 4). Each of these two factors contributed significantly to total trout numbers and were of nearly equal importance. Cover was the most important factor for brown trout indicating that they utilized cover even at the slower current velocities measured. However, faster current velocities contributed to an increase in brown trout numbers above that expected on the basis of cover alone. Current velocity was the only significant factor for rainbow trout and in analysis 4 (Table 4) accounted for 51 percent of the variance in rainbow trout numbers. However, the fast-water pools utilized by rainbow trout also had a relatively large amount of cover.

The number of trout per unit area of cover (cover quality) and the number per unit of pool surface area (pool quality) increased significantly as current velocity became greater. This is shown by the regression analyses with number of trout per 50 square feet of cover and per 50

Table 4. Results of multiple regression analyses with current velocity and total cover as the independent variables

Analysis	Trout group	Independent variables	Partial regr coef	T 1/	F 2/	Multiple R 3/	R^2 4/
1	Total trout	Current vel (f.p.s.)	+15.1191	3.85**	15.25**	0.81	0.66
		Total cover (ft^2)	+ 0.0481	4.28**			
2	Brown trout	Current vel (f.p.s.)	+ 7.5957	2.85*	15.26**	0.81	0.66
		Total cover (ft^2)	+ 0.0378	4.96**			
3	Rainbow trout	Current vel (f.p.s.)	+ 7.8560	4.59**	11.60**	0.77	0.59
		Total cover (ft^2)	+ 0.0090	1.83			
4	Rainbow trout	Current vel (f.p.s.)	+ 7.5739	4.16**	17.38**	0.71	0.51

1/ T refers to student-type test to determine if the partial regression coefficient is significantly greater than zero.
2/ F tests significance of overall regression.
3/ Multiple correlation coefficient.
4/ R^2 is amount of variance explained by the independent variables.
** Significant at 0.01 level.
* Significant at 0.05 level.

square feet of pool surface area against current velocity (Figures 7 and 8). These regressions were significant at the 0.01 level. Current velocity accounted for 42 percent of the variation in number of trout per unit area of cover and for 66 percent of that in number per unit of pool surface area.

Relationship of Pool Physical Parameters to Other Fish Species

Suckers were excluded from the statistical analyses because of poor sampling efficiency (56 percent) and because a large number of those sampled may not have been resident in the pools due to spawning movement. Although little emphasis could be placed on habitat preference by suckers, they were most common in large pools with a predominance of deep-slow water and extensive cover. The small number of whitefish collected precluded any attempt to determine the habitat preference of this species.

Population Stability

Another measure of pool quality is population stability. Annual population stability was determined for all pools from August, 1965, to July, 1966, on the basis of tag returns. The number of tagged fish (231) was adjusted for those known to have been caught by anglers (20). Of 211 available tagged trout, 47 or 22 percent were found in the home pools one year later. Brown trout populations were most stable with 30 percent recovered in home pools compared with 13 percent for rainbow trout. Deep-slow pools with a large amount of cover had the most stable populations. Fast-water pools and those with little cover had the greatest population

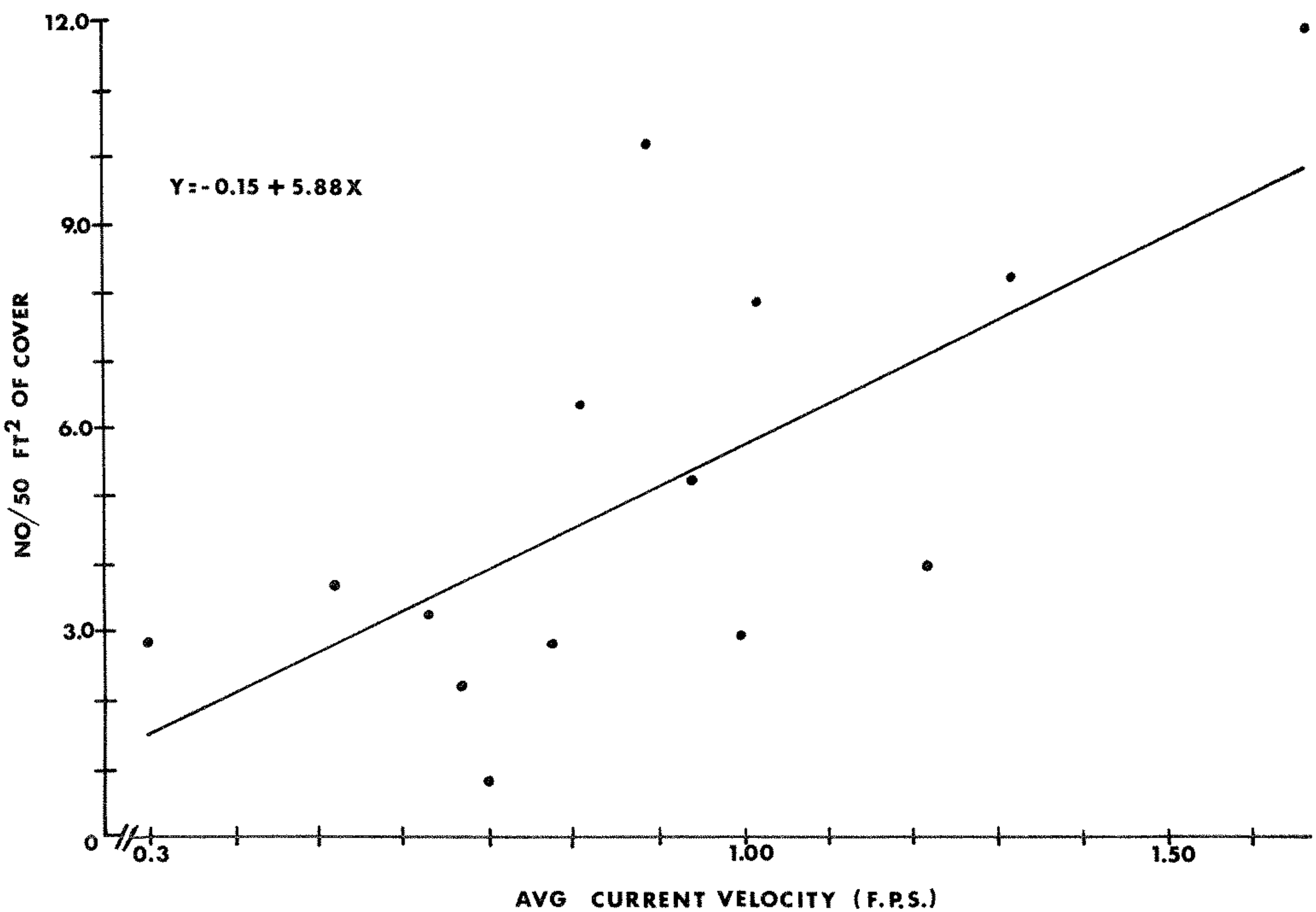

Figure 7. Cover quality, relationship of current velocity to number of trout per 50 square feet of cover showing fitted regression line.

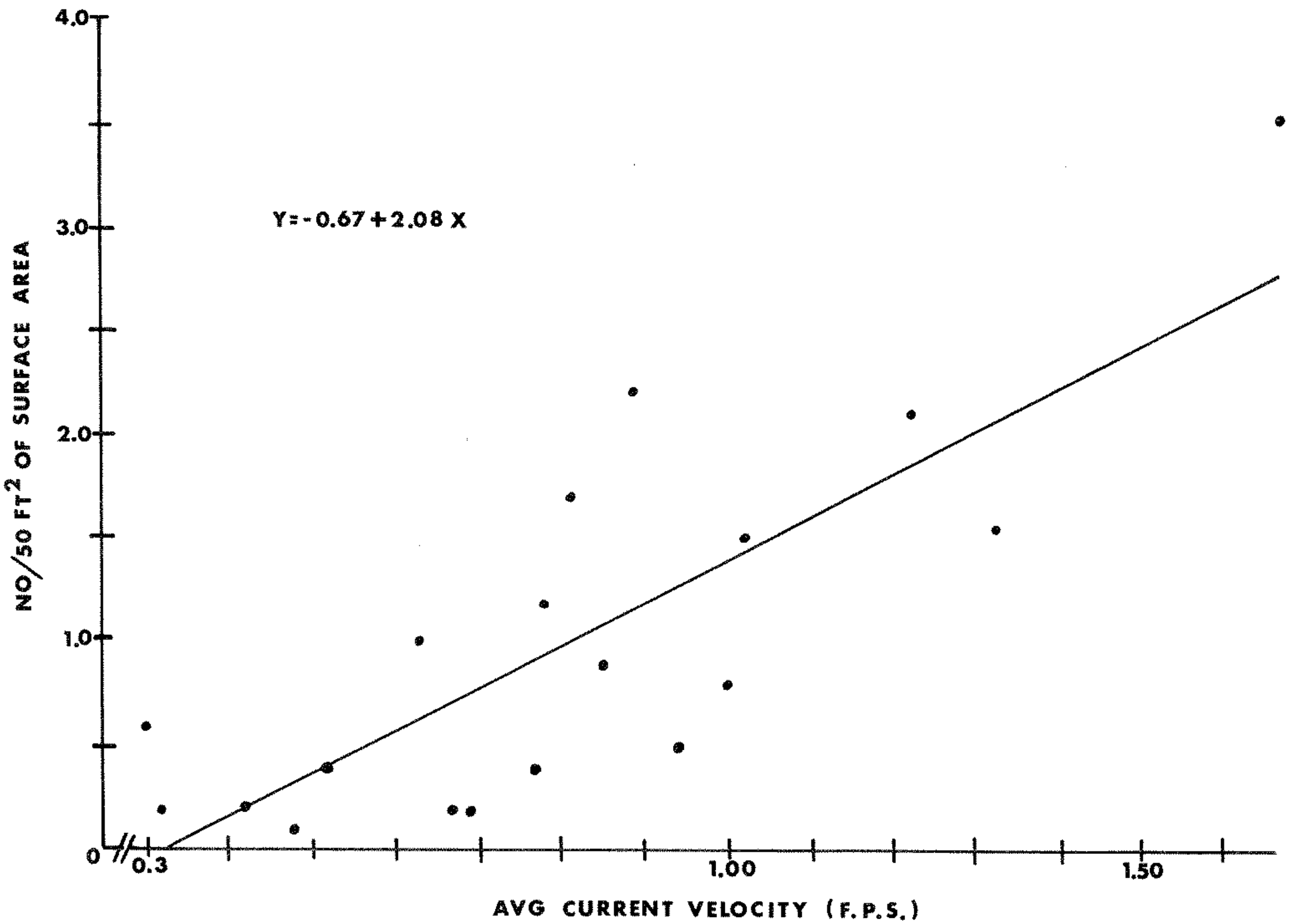

Figure 8. Pool quality, relationship of current velocity to number of trout per 50 square feet of pool surface area showing fitted regression line.

turnover. The losses observed from one summer to the next were due to natural mortality, unknown angler mortality or movement. The extent of movement was unknown since no systematic effort was made to recover fish above and below the pools.

The annual stability of whitefish and sucker populations was very low. Only 2 of 46 whitefish (4 percent) and 3 of 152 suckers (2 percent) were recovered in the pool where tagged. The low stability of suckers appears to be due to movement. Tag returns indicated a general upstream movement in the spring and a gradual downstream drift throughout the summer. A similar pattern was observed by Stefanich (1951) on lower portions of the same stream.

Seasonal population stability was studied in the stability area. Riffles made up 80 percent of the length of this stream section and were from 150 to 340 feet long. From 70 to 80 percent of the water in the riffle areas was shallow-fast with depths averaging 0.6 to 0.7 feet. Cover was sparse in the riffles ranging from 30 to 98 square feet. The three pools in the area (numbers 17, 18 and 19) had physical characteristics that were not associated with high annual population stability. A total of 87 trout longer than 6.9 inches was collected in the area August 3, 1965. There were 53 brown trout, 31 rainbow trout and 3 brook trout.

Twenty-seven brown trout and 13 rainbow trout were tagged in the 3 pools August 3, 1965. Sixteen or 40 percent were found in the home pools December 20, 1965, but by the following summer home pool returns had dropped to 18 percent. Brown trout in the pools had higher seasonal population stability than rainbow trout. During the three seasonal sampling periods (December 20, 1965; April 1, 1966; and July 19, 1966) 44 recaptures of fish originally tagged in the pools were made in the area. Of these 44, 27 or 61 percent were in home pools and 17 or 39 percent were in other pools or riffles of the area. Of the 17 recaptures involving movement within the area, 8 moved upstream a maximum of 340 feet while 9 moved downstream a maximum of 710 feet. The stability and pattern of movement was very similar for trout tagged in the riffles. These data suggest a limited home territory for at least a portion of the trout in this section of stream and correspond with the findings of Miller (1957) and Stefanich (1951). No systematic attempt was made to recover fish above and below the area.

Sampling done in the stability area also yielded information on the seasonal importance of pools to trout longer than 6.9 inches. Of those collected August 3, 1965, 49 percent were found in the riffles and 51 percent in the pools. However, on December 20, 1965, 70 percent were found in the pools. The distribution was similar both summers. The pattern of seasonal distribution was the same for brown trout and rainbow trout. A greater use of pools during the winter is in contrast with the findings of Logan (1963) who reported greater use of riffles during the winter due to cover provided by surface ice. However, shelf ice did not form in the riffles of the stability area due to shallow-fast water. The ice that did form at the riffle margins reduced the amount of cover available.

Sixty-eight percent of the trout (4.0 to 6.9 inches long) collected in the stability area were found in the riffles during both summers. Only 5 of the 50 collected on August 3, 1965, were found during the winter sampling period. This represented a drop of 90 percent and suggested a large winter mortality in this group. However, by the following summer recruitment (primarily rainbow trout) had increased the number by 48 percent over the previous summer.

DISCUSSION

The population density of trout in pools is determined to a great extent by the physical environment, especially cover and current velocity. The value of cover is probably related to security and the photonegative response of trout causing them to seek out overhead cover (Gibson and Keenleyside, 1966; McCrimmon and Kwain, 1966). Population increases associated with high current velocity may be rheotactic responses, but most probably are related to feeding relationships and the territorial concept. Chapman (1966) refers to this as the space-food convention. Müller (1953) and Nilsson (1957) found that organism drift is the major food source in streams, and in areas of faster current velocity the supply of drift would be greater. Thus, in swifter areas of the stream, fish require less space to obtain needed food, territory size is reduced and population densities can be greater (Chapman, 1966). Kalleberg (1958) found smaller territories for juvenile Atlantic salmon and brown trout in higher current velocities relating this to visual isolation. These concepts may explain the greater densities of trout per unit area of cover and per unit of pool surface area found in the fast-water pools studied.

The importance of current velocity to rainbow trout and cover to brown trout may be the result of actual habitat preference or species segregation due to inter-specific competition. Newman (1956) states that dominance is based on size and since brown trout were larger than rainbow trout the habitat preference of rainbow trout may have been obscured if behavioral interaction was a factor. In the absence of brown trout, rainbow trout may have utilized cover in slow-water pools to a greater degree.

There were other factors not measured that could account for some of the unexplained variation in trout numbers. Foremost among these is food which may be considerably more abundant in one pool than another partially depending on the extent of riffle immediately above the pool. Another factor may be light intensity under the cover. In view of the photo-negative response of trout denser cover that allows less light penetration may be more attractive to trout. Angler mortality of fish was also a possible source of error since some of the pools studied were more accessible to anglers than others. Of 354 trout tagged in all areas from August 3, 1965, to April 1, 1966, 37 tags or 11 percent were returned as of November 30, 1966. The percent return for brown trout and rainbow trout was about the same. These figures are minimal as no effort was made to recover tags.

The results of this study may not apply to different types of streams, larger rivers or similar streams with different species composition. The relationships found apply only to low summer water conditions since the relative importance of physical factors may change seasonally. Chapman (1966) speculates that in spring, summer and early fall the space-food convention may be most important, but in winter space alone may govern density. Thus, during the winter other pool types may become more important.

APPENDIX

Table 5. Multiple regression analyses for total trout

Analysis	Independent variables X_i	Partial regr coef	T	F	Multiple R	R^2
1	Surface area(ft^2)	+ 0.0649	+1.57	6.00**	0.87	0.75
	Volume(ft^3)	- 0.0276	-1.61			
	Depth(ft)	+16.0309	+1.01			
	Current vel (f.p.s)	+20.5790	+3.23**			
	Total cover (ft^2)	+ 0.0290	+0.79			
	Percent cover	+ 0.0821	+0.26			
Regression line: $Y = -48.64 + 0.06X_1 - 0.03X_2 + 16.03X_3 + 20.58X_4 + 0.03X_5 + 0.08X_6$						
2	Depth(ft)	- 4.7020	-0.91	10.34**	0.82	0.67
	Current vel (f.p.s.)	+12.7521	+2.70*			
	Total cover (ft^2)	+ 0.0457	+3.93**			
Regression line: $Y = 4.98 - 4.70X_1 + 12.75X_2 + 0.05X_3$						
3	Current vel (f.p.s.)	+15.1191	3.85**	15.25**	0.81	0.66
	Total cover (ft^2)	+ 0.0481	4.28**			
Regression line: $Y = -6.66 + 15.12X_1 + 0.05X_2$						

** Significant at 0.01 level.
* Significant at 0.05 level.

Table 6. Multiple regression analyses for brown trout

Analysis	Independent variables X_i	Partial regr coef	T	F	Multiple R	R^2
1	Surface area(ft^2)	+ 0.0200	+0.74	6.77**	0.88	0.77
	Volume(ft^3)	- 0.0091	-0.81			
	Depth(ft)	+ 1.1558	+0.11			
	Current vel (f.p.s.)	+11.0441	+2.68*			
	Total cover (ft^2)	+ 0.0500	+2.12			
	Percent cover	- 0.2085	-1.03			
Regression line: $Y = -8.47 + 0.02X_1 - 0.01X_2 + 1.16X_3 + 11.04X_4 + 0.05X_5 - 0.21X_6$						
2	Depth(ft)	- 2.4490	-0.69	10.00**	0.82	0.67
	Current vel (f.p.s.)	+ 6.3629	+1.96			
	Total cover (ft^2)	+ 0.0365	+4.59**			
Regression line: $Y = 1.80 - 2.45X_1 + 6.36X_2 + 0.04X_3$						
3	Current vel (f.p.s.)	+ 7.5957	+2.85*	15.26**	0.81	0.66
	Total cover (ft^2)	+ 0.0378	+4.96**			
Regression line: $Y = -4.26 + 7.60X_1 + 0.04X_2$						

** Significant at 0.01 level.
* Significant at 0.05 level.

Table 7. Multiple regression analyses for rainbow trout

Analysis	Independent variables X_i	Partial regr coef	T	F	Multiple R	R^2
1	Surface area(ft^2)	+ 0.0319	+1.77	4.77*	0.84	0.70
	Volume(ft^3)	- 0.0130	-1.74			
	Depth(ft)	+11.4509	+1.66			
	Current vel (f.p.s.)	+ 9.1651	+3.31**			
	Total cover (ft^2)	- 0.0175	-1.10			
	Percent cover	+0.2549	+1.88			
Regression line: $Y = -32.20 + 0.03X_1 - 0.01X_2 + 11.45X_3 + 9.17X_4 - 0.02X_5 + 0.25X_6$						
2	Depth(ft)	- 1.1480	-0.50	7.45**	0.77	0.60
	Current vel (f.p.s.)	+ 7.2781	+3.47**			
	Total cover (ft^2)	+ 0.0084	+1.63			
Regression line: $Y = -0.20 - 1.15X_1 + 7.28X_2 + 0.01X_3$						
3	Current vel (f.p.s.)	+ 7.8560	4.59**	11.60**	0.77	0.59
	Total cover (ft^2)	+ 0.0090	1.83			
Regression line: $Y = -3.04 + 7.86X_1 + 0.01X_2$						
4	Current vel (f.p.s.)	+ 7.5739	4.16**	17.38**	0.71	0.51
Regression line: $Y = -1.41 + 7.57X$						

** Significant at 0.01 level.
 * Significant at 0.05 level.

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