Abstract

Paulik, Gerald J., and Allan C. DeLacy. Swimming Abilities Of Upstream Migrant Silver Salmon, Sockeye Salmon And Steelhead At Several Water Velocities. School of Fisheries, University of Washington, June 1957, Technical Report No. 44.[1]

The terminal water velocities at which adult sockeye and silver salmon and steelhead were no longer able to maintain position in an accelerating flow were determined in this study. Fifteen sockeye salmon, nine silver salmon and ten steelhead were used in the accelerating velocity tests. Twenty-two additional silver salmon were each tested at two starting velocities in the accelerating flow. These tests demonstrated that the terminal speed attained is dependent on the acceleration pattern and therefore accelerating velocity tests cannot be used to measure a fish's absolute maximum swimming speed.

A number of bounding speed experiments were conducted using silver salmon. The maximum speed recorded over a distance of one foot in these tests was 12.2 f.p.s.

Two groups of silver salmon, one of 8 fish and one of 14 fish, and 21 steelhead, were tested to determine the length of time they were able to swim at constant water velocities of 3, 4, 5, 6, 7, 8, 9 and 10 f.p.s. before becoming exhausted. A total of 218 individual constant velocity tests were run. Seven of the steelhead were tested six hours after they had been fatigued in a swimming performance test. They were able to repeat their initial performance in the second test.

It is recommended that the capacity of the lower pools of a fish ladder should be increased at installations where high water velocities may be present immediately downstream from the ladder entrance.

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[1] This report is part of a series initiated in July 1953 for research in connection with the Fisheries Engineering Research Program of the U. S. Army, Corps of Engineers and is part of a study under U. S. Government Contract No. DA 35-026-eng-20800 between the University of Washington and the Corps of Engineers.

Introduction

During the past half century there has been a considerable amount of research conducted on the locomotion of fish. The purpose of most of the past work has been to determine how fish are able to propel themselves through the water and the amount of chemical and mechanical energy expended in propulsion. A complete hydrodynamic theory for flexible bodies of approximately the same density as the surrounding medium and which utilize oscillation for a means of propulsion has not yet been developed. Since an engineering solution to the problem is dependent on such a theory, this approach must await the bridging of several gaps in the existing basic theory. Some of the major contributors who have advanced the basic theory in this area are Harris (10), Richardson (15), Denil (3), Parry (12), Gero (7), and Gray (8). The functional and comparative aspects of fish locomotion have been investigated by Breder (1), Gray (8) and Harris (9), among others. The large body of field observations might be considered as a third phase of the locomotion research. This third phase contains, at present, the most useful information concerning swimming ability of salmon when migrating upstream. However, because of the nature of the problem and the interest of the investigators, most of the information is limited to the maximum performance of fish over short distances. Stringham (20) and Denil (4, 5) are a few of the many contributors of observations pertinent to the problems of salmon migration.

While obviously, those agencies charged with the responsibility of providing access for upstream migrant salmon to spawning areas, need information on the length of time these particular fish are able to swim at given water velocities before becoming fatigued. The ability of adult salmon and steelhead to surmount obstacles and pass through regions of high water velocity is generally dependent on the length of time the fish can sustain a certain swimming speed. Little

specific mention of fatigue and the extent to which it limits performance, can be found in the literature.

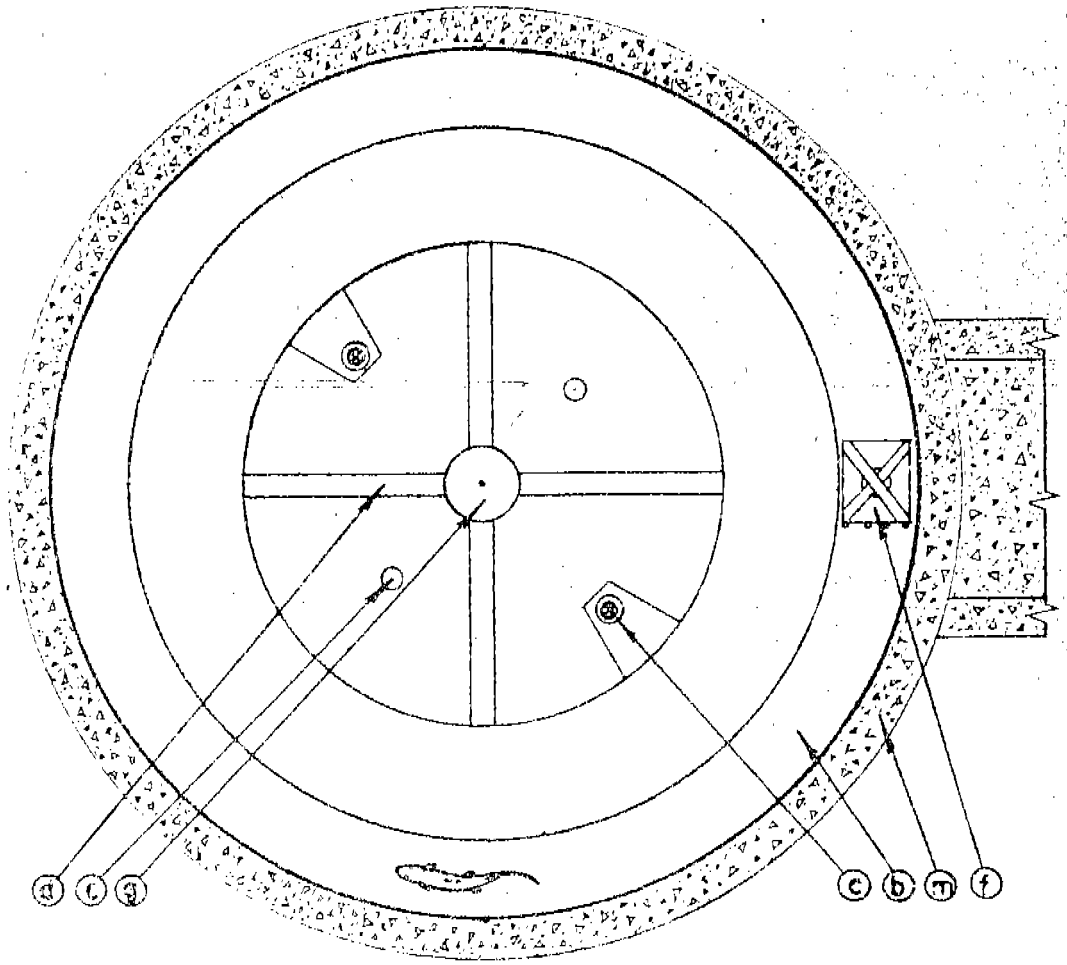
The purpose of this investigation is simply to find how long adult salmon and steelhead trout will swim at different water velocities under strong motivation A brief summary of a number of preliminary experiments, which were not expressly designed to measure swimming ability but nevertheless contain useful information on the subject, is included in this report.

Methods and Materials

A wide variety of equipment was employed in the exploratory work which is briefly reviewed in the first part of this report. The description of special equipment used for only one experiment is, therefore, postponed until the particular experiment is reviewed. Any modification of either the "standard" equipment or methods described in this part of the paper will also be noted in the appropriate place. In all of the constant speed tests reported upon in the last section of this paper only the standard equipment and methods described below were used.

Since a detailed description of the basic equipment employed in the majority of these studies is available in Technical Report No. 31 (13), only major changes made since the publication of that report will be covered in detail here.

The major piece of equipment used in these experiments was an eleven-foot diameter annular tank (Figs. 1 and 2). The rotation of this tank can be easily controlled by a servo-mechanism so as to produce any water velocity up to 20 f.p.s. in the center of the outer twelve-inch channel to which the fish were confined. This tank was employed as a "treadmill", in which the fish were forced to swim at any given water velocity by means of a light-electrode barrier. Previous work has shown that the fish will swim to maintain a position upstream



ROTARY FISH TANK

b outside channel - 12" width

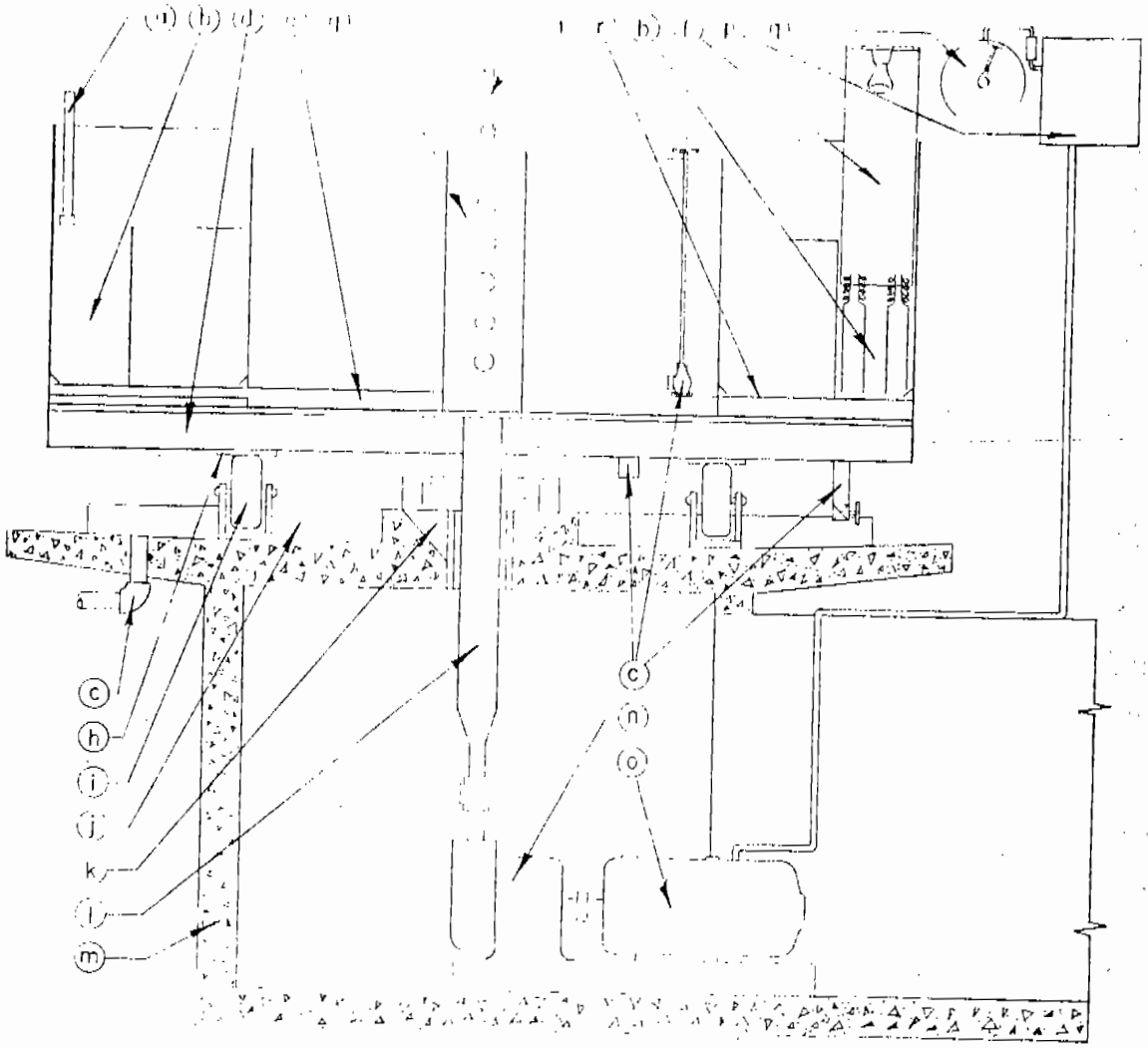
c drains

d channel beam supports

f coil spring electrodes and light barrier

g center spill weir - 12" diameter

m concrete support platform



ROTARY FISH TANK

(a) water inlet
(b) outside channel - 12" width
(c) drains
(d) channel beam supports
(e) 2"x3" supply channel
(f) coil spring electrodes & light barrier
(g) center spill weir - 12" diameter
(h) caster track
(i) 1000 lb load swivel caster
(j) drain trough
(k) 3000 lb load thrust bearing
(l) drive shaft - 6" diameter
(m) concrete support platform
(n) right angle gear reducer
(o) 5hp ac motor
(p) electronic control box
(q) pneumatic speed controller
(r) false bottom

from this barrier until they are exhausted.

One noteworthy change has been made in the actual testing apparatus since the publication of Technical Report No. 31 (13). The number of coil spring electrodes on the barrier was increased from two to four, in order to produce a more uniform electrical field. The distance between any two electrodes in the four electrode field is three and one-third inches. The outer electrodes are one inch from the insulated inner and outer walls. Positive and negative electrodes are placed alternately to produce the field. It has been shown (13) that pre-test activity has a definite effect on a fish's test performance and therefore should be uniform for a given group of fish. The holding facilities and pickup techniques were consequently modified from those described previously (13). Each raceway was subdivided into 16 compartments by plywood inserts. The individual compartments were 39 inches long, 32 inches wide, and 24 inches deep. Thirty holes of one-half inch diameter were drilled in both the upstream and downstream ends of the boxes to provide entrance and exit for the water continually circulated through the raceway at the rate of 12 g.p.m. Oxygen readings taken with the raceway at full capacity (16 fish), during the summer when the water temperature was 60 degrees, showed that the O_2 level in the compartments at the tail-end of the raceway was maintained at 9.0 p.p.m.

This type of holding facility has the following advantages: (1) The abrasions suffered during the holding period are reduced by confining the fish in a smooth-walled compartment. (2) The fish is held in a uniform darkened environment where it is not disturbed by the usual activity about a hatchery. (3) Previous work[1] has also demonstrated that an avoiding response to a light barrier was significantly greater in fish that have been dark adapted for at least 50 minutes. (4) The need

[1] Progress Report No. 10 as of April 30, 1955, to Investigate the Effects of Fatigue and Current Velocities on Adult Salmon and Steelhead Trout, Contract No. DA 35-026-eng-20800 with the University of Washington.

for marking the fish in any manner is eliminated by providing each fish with an individual compartment. (5) Capture of the fish for transfer to the testing apparatus is facilitated.

The carrying box previously described (13) was modified for use with the individual holding boxes. The lid was replaced by a sliding door which could be controlled with a small latch on the side of the box (Figure 3). To pick up a fish from a holding compartment, the carrying box was first turned on its side and the sliding lid for the box opened and fixed in the open position by means of the latch. Two tongs were then used to lower the box into the compartment housing the fish. When the carrying box was completely submerged in the compartment, it effectively restricted the available area, so that the fish was forced to enter the box when it was slowly moved across the compartment (Figure 3). As soon as the fish entered the box, the sliding lid was dropped, closing the box. The box was then removed from the raceway, and the fish was introduced into the annular tank in the usual manner.

A tape recorder was used to record all experimental protocols. A complete description of the events recorded is given in (13). A Type I Lap occurred when the fish was swept through the barrier while swimming actively and oriented upstream. Each swimming test was arbitrarily ended when the second Type I Lap occurred.

Accelerating velocity tests

In many of the early experiments using the annular tank, the test fish were introduced into a low starting water velocity which was then accelerated steadily according to a fixed pattern (Figure 4). The water velocity at which the fish lost the third Type I Lap was recorded as the end of the test. At this terminal water velocity the fish was no longer able to swim against or maintain a fixed

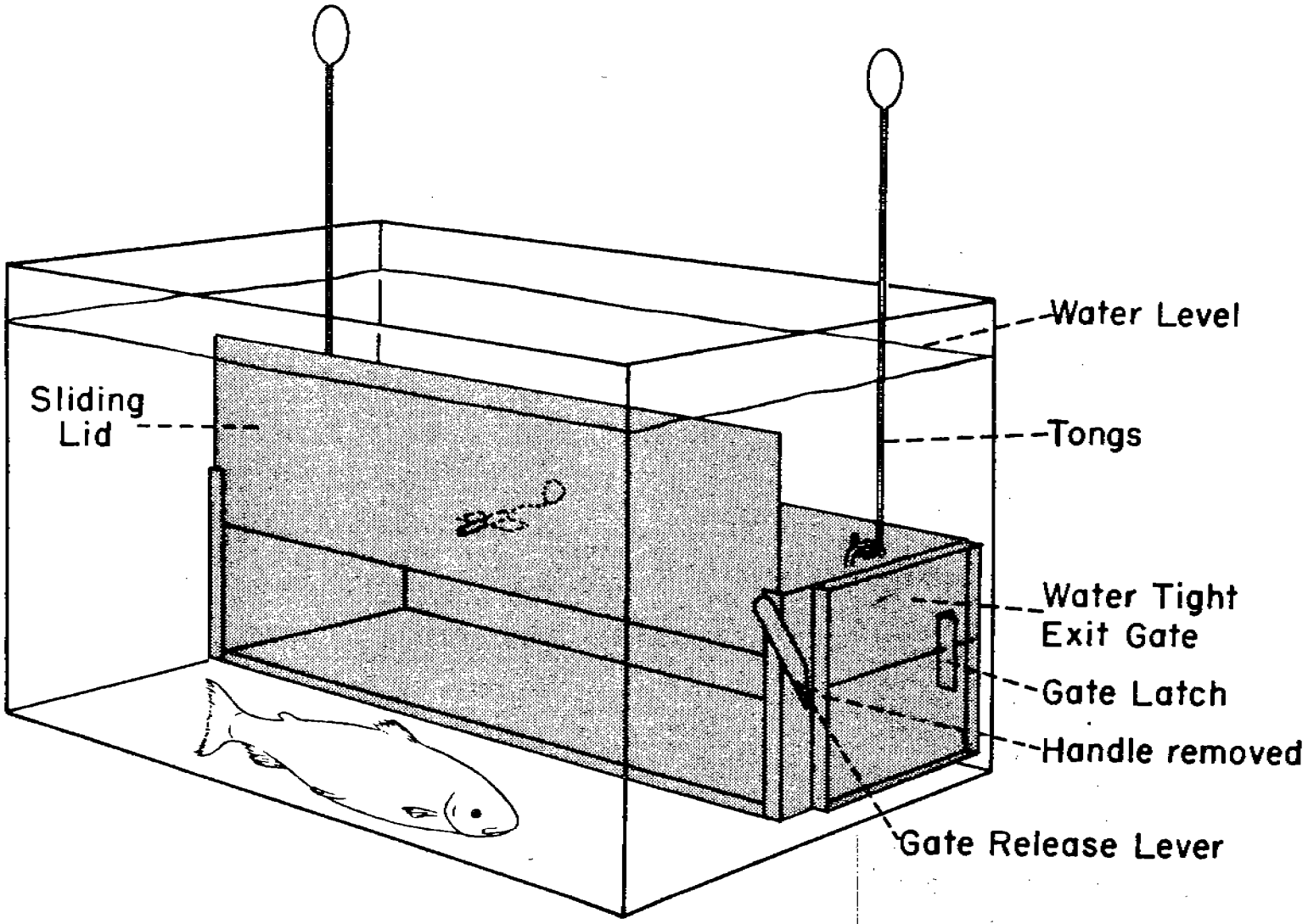


Figure 3. Removal of fish from holding compartment by means of the carrying box.

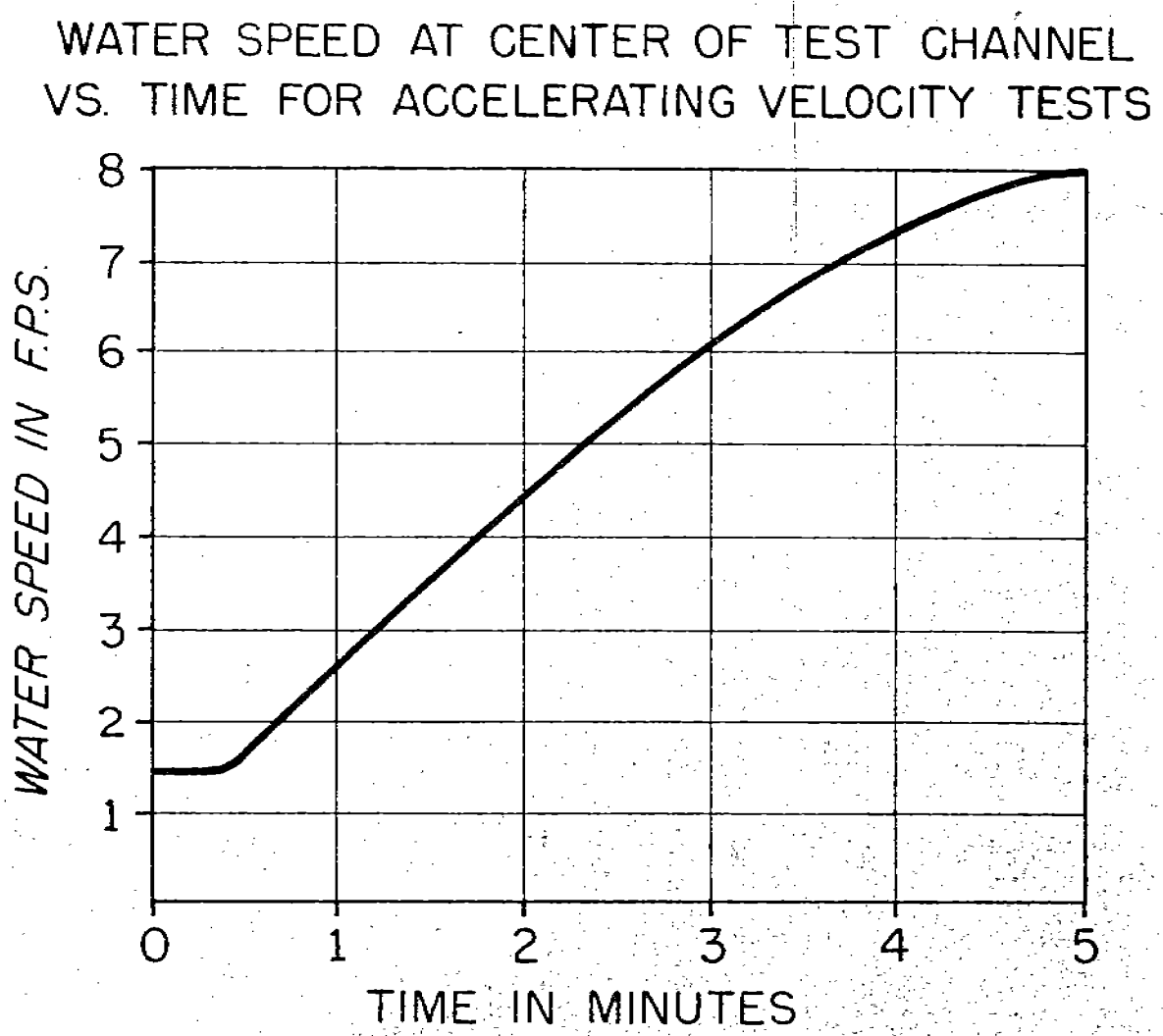


Figure 4. Water velocity acceleration pattern.

position in the current. This type of a test is considerably different from the constant velocity type of test in which the water velocity was held constant from the time of introduction, until the fish was no longer able to maintain position upstream from the light-electrode barrier.

Two groups of sockeye, obtained from the Washington State Department of Fisheries weir on Issaquah Creek, were used in a series of tests in which the water velocity was accelerated according to the pattern shown in Figure 4. The first group of fish was obtained on September 6, and the second on September 22, 1955. The second group was largely made up of fish which arrived at the weir site at the same time as the first group but were held at the weir for an additional 16 days. The length and sex of these fish are given in Table 1. The sockeye were held in an uncovered raceway which was subdivided into four sections. Two fish were held in each section. The electrodes in the light-electrode barrier used during these tests, were constructed of stainless steel with an airfoil cross-section. Two of these electrodes were used in place of the four coil spring electrodes described earlier. Table 1 gives the water velocities at which the individual tests were terminated. Because of malfunctioning of the tape recorder and death of some of the fish during the test period, the number of swimming tests recorded varies between fish. These tests were conducted on consecutive days beginning 10 days after the fish has been transported to the University of Washington for the September 6 group and 5 days after arrival for the September 22 group. The pooled variance associated with repeated performances by the same fish and the variance between fish for both groups are given in Table 2.[2] The variance between fish is not significantly greater than the variation between repeated tests of the same fish for the September 6 group, whereas in the September 22 group, the

[2] See (19) p. 264, Section 10.14 Samples within samples. Model II, for description of statistical analysis used.

variation between fish is highly significant when compared to the within fish variance. This non-significance of the between fish variation in the September 6 group is in all probability a result of handling techniques which had not been completely standardized at that time and increased the variability between repeated tests of the same fish.

Table 1 Maximum speed attained by adult sockeye salmon in accelerating velocity tests

First group of sockeye taken from Issaquah Creek, September 6, 1955

Fish no.	Speed attained (f.p.s.) in tests conducted on four consecutive days					Fork-length (inches)	Sex
	Maximum				Mean maximum		
1	3.7	6.1	5.8	6.0	5.40	25-1/4	M
2	6.1	5.9	5.8		5.93	24	M
3	5.7	6.0	6.0	6.0	5.92	26	M
4	5.9	6.0			5.95	23	M
5	6.0	6.2	6.0	6.2	6.10	25-1/4	M
6	6.2	7.0	7.1	6.8	6.78	29-3/4	M
7	5.1	5.8	5.8	5.9	5.65	25-3/4	M
8	5.2	5.8	6.2	6.2	5.85	25	M
Water temperature - 58 to 58-1/2°F.							
Second group of sockeye taken from Issaquah Creek, September 22, 1955							
9	4.9	5.5	5.3	4.9	5.15	27-1/2	M
10	5.8	5.5	5.8		5.70	24-3/4	M
11	6.2	6.3	6.5		6.33	24-1/2	M
12	5.9	6.1	5.9		5.97	25-1/2	M
13	5.8	4.9	5.3	5.1	5.28	21-1/2	F
14	5.7	6.0			5.85	23-1/4	F
15	5.2	5.4	5.2		5.27	27	M
Water temperature - 57-1/2 to 58-1/2°F.							

By using the pooled between fish variance for an error term, it is possible to test the significance of the decrease in performance between the first and second groups. This test yields an F value of 2.94 (with 1, 13 degrees of freedom) which is too low to demonstrate a significant difference between the two groups. By treating the mean performance of each fish as a single observation, the overall mean velocity for the combined groups of sockeye is 5.81 f.p.s. (with a 95% confidence interval from 5.33 f.p.s. to 6.29 f.p.s.).

Table 2 Analysis of variance for Issaquah Creek sockeye

Source of variation	Degree of freedom	Mean square	F value
September 6, 1955 Group			
Between fish	7	0.631	2.35 (N.S.
Repeated test of same fish	21	0.268	
September 22, 1955 Group			
Between fish	6	0.621	9.84 **
Repeated test of same fish	15	0.063	
Comparison between groups			
Between Sept. 6th Group and Sept. 22 Group	1	1.840	2.94 (N.S
Between fish (pooled)	13	0.626	

N.S. - Not significant

** - Significant at 1% level

Swimming performance tests of silver salmon in an accelerating flow, similar to the tests with sockeye, were conducted on December 6, 7, and 8, 1955. The rigid steel electrodes used in the sockeye tests had been replaced by two coil spring electrodes before the silvers were tested. The silvers were held at the University of Washington for six days before the start of the tests. In all other respects these tests were comparable to those with sockeyes. Length and

sex data are given in Table 3 for nine silver salmon captured at the Washington State Department of Fisheries weir at Soos Creek November 30, 1955. Soos Creek is a tributary of the Green River which empties into Elliott Bay, Puget Sound. The hatchery weir is located about 35 miles above salt water. The performance of the nine silver salmon in tests conducted on the three consecutive days are also contained in Table 3. The statistics computed from these data are summarized in Table 4. The variation between fish was significantly greater (1% level) than the variation between repeated tests of the same fish. The overall mean swimming performance of the silver salmon was 6.24 f.p.s. (with a 95% confidence interval from 5.53 f.p.s. to 6.95 f.p.s.).

Table 3 Maximum speeds attained by adult silver salmon in accelerating velocity tests

Fish no.	Speed attained (f.p.s.) in tests conducted on three consecutive days				Fork-length (inches)	Sex
	Maximum			Mean maximum		
1	6.3	5.5	5.6	5.80	21-1/2	M
2	5.9	6.3	7.1	6.43	26-1/2	M
3	6.0	5.6	6.1	5.90	26-1/4	M
4	6.1	6.2	6.5	6.27	22	F
5	5.4	5.3	5.1	5.27	22-1/4	F
6	6.5	6.3	6.2	6.33	20-1/4	F
7	6.4	6.8	7.0	6.73	22-3/4	M
8	7.0	7.2	7.0	7.07	20-1/2	M
9	7.0	5.5	6.6	6.37	17-1/2	F
Water temperature - 50 to 50-1/2°F.						

Table 4 Analysis of variance for Soos Creek silver salmon

Source of variation	Degrees of freedom	Mean square	F value
Between fish	8	0.843	5.30 **
Repeated tests of same fish	18	0.159	

** Significant at 1% level

Ten adult male steelhead were each given a single accelerating velocity test on February 11, 1956. These tests were conducted in exactly the same manner, and the same equipment was employed as described above in the tests with silver salmon The steelhead were obtained, on February 4, 1956, from the Washington State Fish and Game Department's Hatchery weir on Chambers Creek. The test results and lengths of the steelhead are given in Table 5. The mean termination velocity for the tests was 6.98 f.p.s. The 95% confidence limits for this mean are 6.67 f.p.s. and 7.29 f.p.s. There is a significant difference at the one percent level between the performances of the steelhead and the two species of salmon tested.

Table 5 Maximum speed attained by Chambers Creek steelhead in accelerating velocity tests

Fish no.	Maximum speed attained (f.p.s.)	Fork-length (inches)
1	7.0	23-1/8
2	7.3	26-1/8
3	6.1	26-3/4
4	7.2	25-1/4
5	7.2	24-1/2
6	6.9	23-1/4
7	7.4	24-3/4
8	7.3	26-1/2
9	7.1	26-1/4
10	6.3	24-3/4
Water temperature - 44-1/2 to 45°F.		

A pertinent question regarding these accelerating velocity tests is whether the maximum velocity a fish can attain in this type of test is the maximum velocit at which this fish can swim. If this is true, it means that swimming during the period when the velocity is being accelerated until the terminal speed is reached, does not seriously fatigue the fish or affect the ultimate terminal speed attained in any manner. An experiment was designed to determine if the terminal speed was independent of fatigue incurred during the time that it takes the water velocity to become swift enough to displace the fish. Eighteen silver salmon taken from Soos Creek on November 30, 1955 were used in this test. The fish were randomly assigned to two groups. One group was tested in the usual manner (introduced at time zero or into 1.5 f.p.s. - Figure 4), and the second group was introduced into the tank after the water velocity had accelerated for two minutes and reached 4.4 f.p.s. On the next day, these treatments were reversed between the two groups, so that the maximum swimming speed of each fish was determined for both introductic velocites. Each day the fish from each group were tested alternately so that no two fish from any one group were tested successively. Possible bias that could arise from the order of testing or time of day was thus reduced or eliminated. The test results and the length and sex for the silver salmon are presented in Table 6. It is evident from the analysis in Table 7, that the velocity at the time the fish was introduced definitely affected the ultimate velocity attained. Swimming during the two minutes required for the velocity to accelerate from 1.5 to 4.4 f.p.s. lowered the maximum speed attained. This demonstrates that an accelerating velocity test does not measure a fish's maximum swimming speed and that the maximum speed attained is dependent on the the acceleration pattern. This also illustrates the manner in which fatigue may affect a salmon's ability to pass through an area of high velocity. The velocity conditions immediately downstream from the area of highest velocity may be equally as important as the

Table 6 Maximum attainable swimming speed for silver salmon introduced into an accelerating flow at 1.5 f.p.s. and 4.4 f.p.s.

Fish no.	Maximum speed attained		Length (inches)	Sex
	Intro. into 1.5 f.p.s.	Intro. into 4.4 f.p.s.		
1	5.3	6.7	22-1/4	F
2	6.1	7.0	21-1/2	M
3	6.0	6.1	24-3/8	F
4	7.0	6.9	20-1/2	M
5	5.4	5.9	26-3/4	M
6	5.5	6.3	17-1/2	M
7	6.2	6.8	19-1/2	M
8	6.0	6.6	20-1/4	F
9	5.0	6.6	17-1/2	M
10	5.6	6.7	19	M
11	6.4	5.8	—	F
12	6.5	6.4	22-3/4	M
13	6.2	6.5	17-1/2	F
14	6.4	7.0	26-1/2	M
15	5.0	6.0	26-1/2	M
16	5.9	5.9	25-5/8	M
17	5.3	5.7	25-1/4	F
18	5.5	7.0	20-1/4	F
19	6.1	6.5	14	M
20	5.5	6.5	26-1/4	M
21	6.6	6.2	22	F
22	6.0	6.2	24	F

Water temperature - 50°F.

velocity conditions in the area of highest velocity for determining the success of passage of salmon.

Table 7 Analysis of variance of maximum speed attained by silver salmon introduced at two different velocities during acceleration.

Source of variation	Degrees of freedom	Mean square	F value
Introduction velocity	1	3.161	27.02 **
Fish	21	0.274	2.34 *
Interaction (error)	21	0.177	

* Significant at 5% level

** Significant at 1% level

Work reported upon earlier has shown that performance decrements were associated with handling and with pre-test activity (13). These previous results and the finding that the fish's maximum attainable speed is influenced by the acceleration pattern indicate that salmon are highly susceptible to fatigue. Considering this susceptibility to fatigue as well as the long recuperation period required (13), one possible weakness in the design of the present pool and weir type ladder becomes apparent. If a salmon must swim through an area of high but passable water velocity to reach the entrance to a ladder, it enters the ladder with a reduced capacity for performance. The salmon will then have to rest sooner (quite possibly in the lower pools of the ladder) thus altering its activity pattern so that the length of time spent in the lower pools of the ladder increases to compensate for the fatigue incurred before entering the ladder. The pools in the lower part of the ladder may reach their capacity long before the pools in the middle or upper part of the ladder and may interfere with the entrance of additional fish into the ladder. In an installation where high attraction flows are necessary, increasing the capacity of the lower pools of a

ladder may alleviate possible crowding problems.

Bounding Speed Experiments With Adult Silver Salmon

Reports in the literature on the maximum swimming speed which salmon can attain range from 10 f.p.s. to 20 f.p.s. The majority of these figures were obtained either by observations of the fish swimming in natural currents or by observations of the salmon jumping. Using the latter technique, some characteristics of the salmon's leap from the water are measured and the velocity at which the salmon left the water is determined by back-calculation. A comprehensive discussion of this technique is given by Denil (4). He used the following formula[3] to calculate the bounding speed of salmon.

$$y = x\tan\alpha - \frac{gx^2}{2Vo^2 \cos^2\alpha}$$

(where x and y are the abscissa and ordinate respectively of a rectangular coordinate system with the origin at the point the fish leaves the water, α is the angle of the path of the leap with respect to the water, and v_o is the fish's velocity at the start of the leap).

However, whether the salmon could attain this velocity if it remains immersed is open to question. The salmon may accelerate its velocity considerably as it is leaving the water at the beginning of the leap. The water would be used somewhat as a "spring board" in this maneuver. As the fish goes from the more dense to the less dense medium the resistance associated with any given velocity is the result of entirely different forces. In water, the salmon is confronted with resistance to movement from friction, form drag and induced drag arising from the oscillatory swimming motion (7). In air, the salmon must overcome the force of gravity and air-resistance. At velocities of this magnitude, air resistance is

[3] Derivation and applications of this formula may be found in any calculus book; e.g., see (18) section 245, Projectiles, p. 263.

practically negligible. Due to the lack of information concerning the magnitude of the resistance forces that the salmon encounters in water it is not possible to establish a usable relationship between these two types of resistance. Gero (7) used the leap of a porpoise starting from a "dead stop" in a vertical nose-up position to compute tail thrust. For the reasons stated above, it is felt that some of the swimming velocities attributed to salmon as a result of their observed jumping ability may be too high.

Table 8 below, was prepared as a summary of some of the existing information on the maximum swimming speeds fish can maintain for "short distances". The values contained in this table were obtained by different methods and under different conditions, and thus are not strictly comparable, but they do serve as a useful guide to the upper limit of a salmon's swimming speed.

Table 8 Sustained maximum swimming speeds over short distances[4]

Source:	Stringham (20)					Jackson (11)
Observer:	Stringham	Lavolle	Denil	Bayer	Napier	Jackson
Fish:	alewife	salmon	salmon	—	sockeye	chinook
Speed: (f.p.s.)	11.8	9.9	10.3	10.0	8.8 to 10.3	12.5 to 14.5 *

Source:	Gray (8)			Rounsefell and Everhart (16)	
Observer:	Gray	Lane	Kreitman	Frischholz	McLeod and Nemenyi
Fish:	salmon	trout	trout	good-swimming species	trout
Speed: (f.p.s.)	10.3 to 11.8	29.4	13.2	6.3 to 8.6	7.0

* Sockeye were unable to swim at this velocity.

With the exception of the 29.4 f.p.s. maximum speed reported for trout by Lane, there is fairly close agreement between the entries in the table.

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[4] The term "short distances" is believed to have reference to distances of less than 100 feet in all instances and probably refers to distances of less than 50 feet for most of the entries in the table. Additional information on distances may be found in the sources cited.

Of Lane's estimate, Gray (8) says " ..., although Lane has recorded the speed at which various 'sporting' fishes are reported to have run out line from a reel..... Without knowing the precise conditions under which such observatio are made, these conclusions must be accepted with some reserve."
The sustained maximum swimming speeds reported for salmon are between 10 f.p.s. and 15 f.p.s.

During December 1956, high speed motion pictures were taken of the swimming performances of five male silver salmon in the annular tank. Four of these salmon were wild fish captured at the Washington State Department of Fisheries trap on White River just below Mud Mountain Dam. The other silver salmon was hatchery reared and had been transferred from the salt-water aquarium at the University to the fresh water in the holding raceway twelve days before the test. The coloring of the silvers from White River and later examination of the gonads indicated that these fish were in an advanced stage of maturity at the time these tests were conducted. Otherwise, they appeared to be in excellent physical condition. The silver from the salt-water aquarium appeared to be weak and apparently had been adversely affected by the sudden transfer to fresh water. Further information concerning these fish is in Table 9.

Markers, spaced at intervals of one foot, were placed just above the surface of the water in the outer channel of the annular tank. The motion picture camera was focused on the outer channel and mounted on one end of a boom which pivoted on a point directly above the center of the tank. This arrangement made it possible for the photographer to keep the salmon in focus regardless of its speed or location in the tank. Figure 5 shows a frame taken from the film of these tests. By counting the number of frames that a fixed point on the salmon took to move between any two markers (a known distance), the swimming speed over the distance was computed by multiplying the frames/second by the distance/frame.

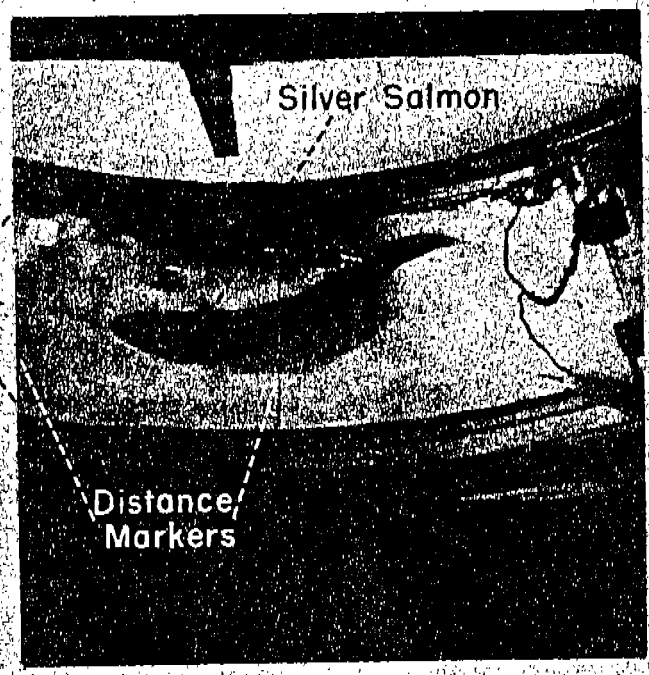

Figure 5. Frame from film of bounding speed tests in annular tank.

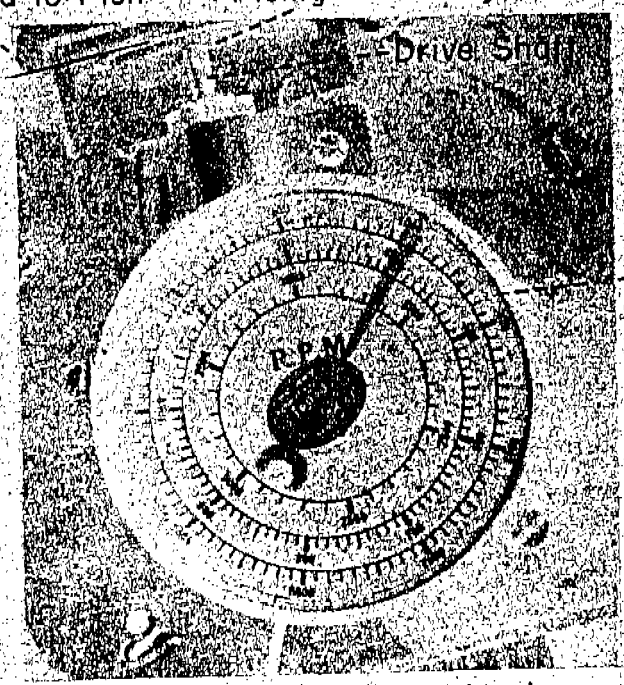

Figure 6. Frame from reversal film showing centrifugal tachometer used to measure speed at which line was pulled off reel.

During each of the tests, the test fish made at least eight sustained bursts of speed for distances from two to ten feet. The fish were stimulated when they entered the electric field set up by the electrode-light barrier and the usual response of the fish was to move away from the barrier with a quick burst of speed. The illumination provided for the photography seemed to excite the fish and cause a higher number of darts than would be otherwise expected. The maximum speed attained during a dart usually occurred at a distance of two or three feet from the spot where the dart started. The speed for each salmon as given in Table 9 is the maximum recorded over a distance of one foot during the entire swimming test. All figures were corrected for the salmon's position in the channel with respect to the center of the tank. The average speed over the entire length of a dart was much lower than the fastest velocity which was maintained for a distance of one foot during the dart. Also the average of the maximum velocities maintained for one foot for all the darts that a fish made during the test was considerably lower than the maximum velocity recorded for the fish in Table 9. During these bursts of speed, the salmon usually swam at the outside of the channel and may have been hindered to some extent by the curvature of the tank particularly over a distance of several feet.

The presence of a salmon in the channel causes a restriction of the availabl area and a corresponding increase in the water velocity about the body of the fis This increase is directly proportional to the salmon's maximum cross-sectional area. A correction for the bias caused in our measurement by this area restrict may be easily made by use of the continuity relation[5] if we assume the increased velocity to be uniform about the circumference of the fish. Estimated maximum cross-sectional areas for the test fish determined by measurement for other silve salmon of approximately the same size as the test fish, are listed in Table 9.

[5] See (21) section 16. Equation of Continuity, p. 64.

Table 9 Maximum speeds attained by adult silver salmon over a distance of one foot.

Fish no.	Maximum speed (f.p.s.)		Distance from start of dart that maximum was attained (feet)	Estimated cross-sectional area (sq. inches)	Fork-length (inches)
	Measured	Corrected for area restriction			
1	9.8	10.5	2 to 3	8-1/2	21
2	9.8	10.7	1 to 2	10-1/2	26
3	11.2	12.2	4 to 5	9-1/2	23
4	9.8	10.9	3 to 4	12	30
5*	6.7	7.2	2 to 3	8	20

* Salmon from salt-water aquarium.

Using the 12 square inch figure (fish No. 4) to illustrate the use of this correction the actual velocity about the fish's body can be computed by multiplying the observed velocity by 121/109 where the denominator is the cross-sectional area of the channel reduced by the presence of the test salmon and the numerator is the unrestricted cross-sectional area. Actually this correction has a tendency to be somewhat too high, as both the numerator and denominator of the above fraction refer to the available cross-sectional area when the tank is at rest. When the tank is revolved, and the water is forced to the outside of the tank by centrifugal force, this ratio decreases considerably, depending of course, on the speed of rotation.

As can be seen by comparing Tables 8 and 9, the maximum speeds measured in these tests agree fairly well with those previously reported.

An effort was made to measure the darting ability of a salmon in an unrestricted area during October 1956. One technique used was simply to clock the salmon over a measured distance in a raceway which was five feet wide and thirty feet long. Observers with stop watches were stationed at markers twenty feet apart. A portable electric shocking device was used to "chase" the salmon over the measured distance. To eliminate the acceleration period, the salmon was allowed to swim five feet before

it entered the measured distance. However, the behavior of the fish and the rapidity with which they were fatigued, combined with a sizeable variation in the measurements attributable to observer reaction time, caused the discontinuance of these tests after only a small number of fish were tested. In two successful tests, both a male and a female silver salmon of 27-1/2 inches and 30 inches fork-length respectively were able to swim the twenty foot distance in 2.05 seconds for an average speed of 9.8 f.p.s.

The second method tried consisted of attaching a line to the salmon and measuring the rate at which the salmon was able to pull the line off a spool. The line was looped over a small plexiglass pulley attached to the shaft of a centrifugal tachometer. The spool and tachometer were mounted on a base which was free to revolve in any direction. A high-speed motion picture camera was used to record the movements of the needle on the dial of the tachometer. A frame from the film is shown in Figure 6. The line was fastened to the salmon at the base of the dorsal fin. Several tests were conducted with this equipment, however, the salmon could not be induced to make any sustained runs at high speeds with the attached line. The highest speed recorded was 10 f.p.s. and was maintained for only a fraction of a second. This speed was attained by a male silver salmon with a fork-length of 25-1/4 inches.

Constant speed tests

A number of swimming performance tests were conducted during the fall and winter of 1956 for the express purpose of determining how long salmon and steelhead are able to swim at a particular water velocity. One group tested was selected from sixteen silver salmon captured at the Washington State Department of Fisheries Hatchery weir on Soos Creek, October 23, 1956. These fish were from the early part of the fall run. The sample of sixteen fish was selected with regard to condition and size. Extremely large or small fish were not taken.

Salmon with obvious serious injuries or which appeared to be within a few days of spawning were similarly excluded from the sample.

Upon arrival at the University hatchery, the fish were placed in individual holding compartments. After one day of rest, each fish was given two pre-test conditioning trials on successive days. These pre-test trials were conducted in the same manner as the usual swimming tests with the exception that the pre-tests were terminated after one Type I Lap. The water velocity was 4 f.p.s. during the pre-tests. Two further selections were made at this point. Four fish were discarded from the test group because of eye injuries or open wounds that were previously undetected. The eight test fish were selected from the remaining 12 fish on the basis of the orientation to the current during the second pre-test. The salmon which oriented into the current immediatel upon introduction and required the fewest number of reversals (reorientation into the current) during the pre-test were used as test animals. The purpose of the selection was to increase the accuracy of the estimate of the relationship between velocity and swimming time by testing those salmon for which total swimming time was the best measure of total activity in the annular tank. In particular, this selection represents an attempt to reduce a potential source of error associated with reversals at high velocities. At high water velocities, reversing the fish with a net causes a certain amount of turbulence and temporarily lowers the water velocity. This disturbance may last several seconds and thus introduce a non-trivial error in swimming times of less than a minute. Observations showed that these fish and others tested later consistently maintained orientation at higher velocities regardless of their behavior at lower velocities.

The test sample selected in the manner described above may not be truly representative of the population from which it was selected with respect to swimming ability. However, no significant correlation was found between

swimming time and any of the measures of orientation recorded (reversals, Type II Laps and Type III Laps (13)) for silver salmon tested at 3.5 f.p.s. (13) or sockeye salmon tested at 4.3 f.p.s. (14).

The plan of the experiment using the eight silver salmon selected in the manner described above is shown in Table 10. The observations on the first four days were taken according to a 4 by 4 Latin Square design which was replicated once.[6] The factor of primary concern was the water velocity at which each test was conducted. The day factor was included simply to balance out any possible bias it might cause in the salmon's performance at the different water velocities. The experiment was conducted in the following manner: the tank mechanism was regulated to produce a given water speed at the center of the channel; as soon as the water velocity was stabilized at the desired speed, the salmon from replicate I that was to be tested at this water velocity was introduced into the channel; upon completion of the swimming test and removal of the first salmon from the tank the salmon from replicate II that was to be tested at the same water velocity was introduced into the tank. When the second test at the given velocity was finished and the salmon had been replaced in its holding compartment, the water speed in the test channel was changed to the next velocity. This sequence of events was continued until all eight fish had been tested. The order in which the pairs of fish were tested on any test day was randomly determined.

At the conclusion of the fourth test day it was apparent that the salmon could be successfully tested at higher water velocities. The seven surviving salmon, which, with the exception of fish Number 6, appeared to be in good condition were tested at 7 and 8 f.p.s. on the next two days. The standard method of analysis for the Latin Square design is not applicable because some of the tests at 3 f.p.s. were too lengthy to complete and because one of the test fish died during the

[6] See (6) for further discussion of this type of design.

Table 10 Performance scores (swimming time in seconds) of upstream migrant silver salmon in water velocities from 3 to 8 f.p.s.

Replicate I

Fish no.	Water velocity in f.p.s. Test date 10/28	10/29	10/30	10/31	Performance Score in seconds 10/28	10/29	10/30	10/31	Sex	Length (inches)
1	4	3	6	5	343	486	210	184	M	22-1/8
2	3	6	5	4	685	174	187	370	M	22-3/4
3	6	5	4	3	81	110	240	*	F	24-1/4
4	5	4	3	6	174	462	4560**	192	F	24-3/4
Replicate II										
5	4	3	6	5	307	759	125	184	F	21-3/8
6	3	6	5	4	897	116	139	240	F	20-1/2
7	6	5	4	3	85	163	312	6720**	M	20-1/2
8	5	4	3	6	130	156	320	145	F	24-7/8

Fish no.	Test date 11/1	11/2	Score in seconds 11/1	11/2
1	7	8	130	85
2	7	8	150	162
3	7	8	*	*
4	7	8	183	143
5	7	8	129	80
6	7	8	29***	40***
7	7	8	70	55
8	7	8	163	53

Water temperature - 54 to 56°F.

* Fish No. 3 died after testing on 10/30.

** Tests were terminated before fish was exhausted.

*** Fish No. 6 had fungus growth on caudal peduncle and caudal fin which appoared to interfer with its swimming during the tests on 11/1 and 11/2.

experimental period. The swimming times at 3 f.p.s. are clearly much longer than the swimming times at 4 f. p.s. or higher. Using the Friedman two-way analysis of variance by ranks,[7] it can be easily shown that there are highly significant differences between the swimming times of the salmon at 4, 5, and 6 f.p.s. At 3 f.p.s. the behavior of the fish during the test is critical. The salmon seemed to be able to swim at this velocity with little exertion. Several of the salmon, after swimming easily at this velocity for several minutes, darted rapidly about the tank or reversed their orientation and attempted to swim downstream. In two of the tests at this velocity it was necessary to terminate the tests and return the salmon to the raceway before they were exhausted. Recordings of these two tests showed that both of the salmon swam at a steady pace.

Figure 7 shows the curvilinear regression line computed for the data by the method of least squares. An exponential curve seemed to fit the data fairly well for water velocities from 4 f.p.s. to 8 f.p.s. The selection of this curve was arbitrary and may be used as only a first approximation to the actual relationship between these variables. Because of the large increase in the length of time the fish were able to swim at 3 f.p.s. and the previously mentioned difficulti. encountered in testing the salmon at this velocity the curve was not extended to 3 f.p.s.

Of further interest are the relative abilities of the fish in relation to one another at the different water velocities. In particular, if the salmon are ranked with respect to their swimming ability at any particular water velocity, do they tend to retain the same rank at a different water velocity? Kendall's coefficient of concordance (17) is a measure of agreement between sets of ranks.

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[7] A discussion of this test is available in (17) Chapter 7, pp. 166-173.

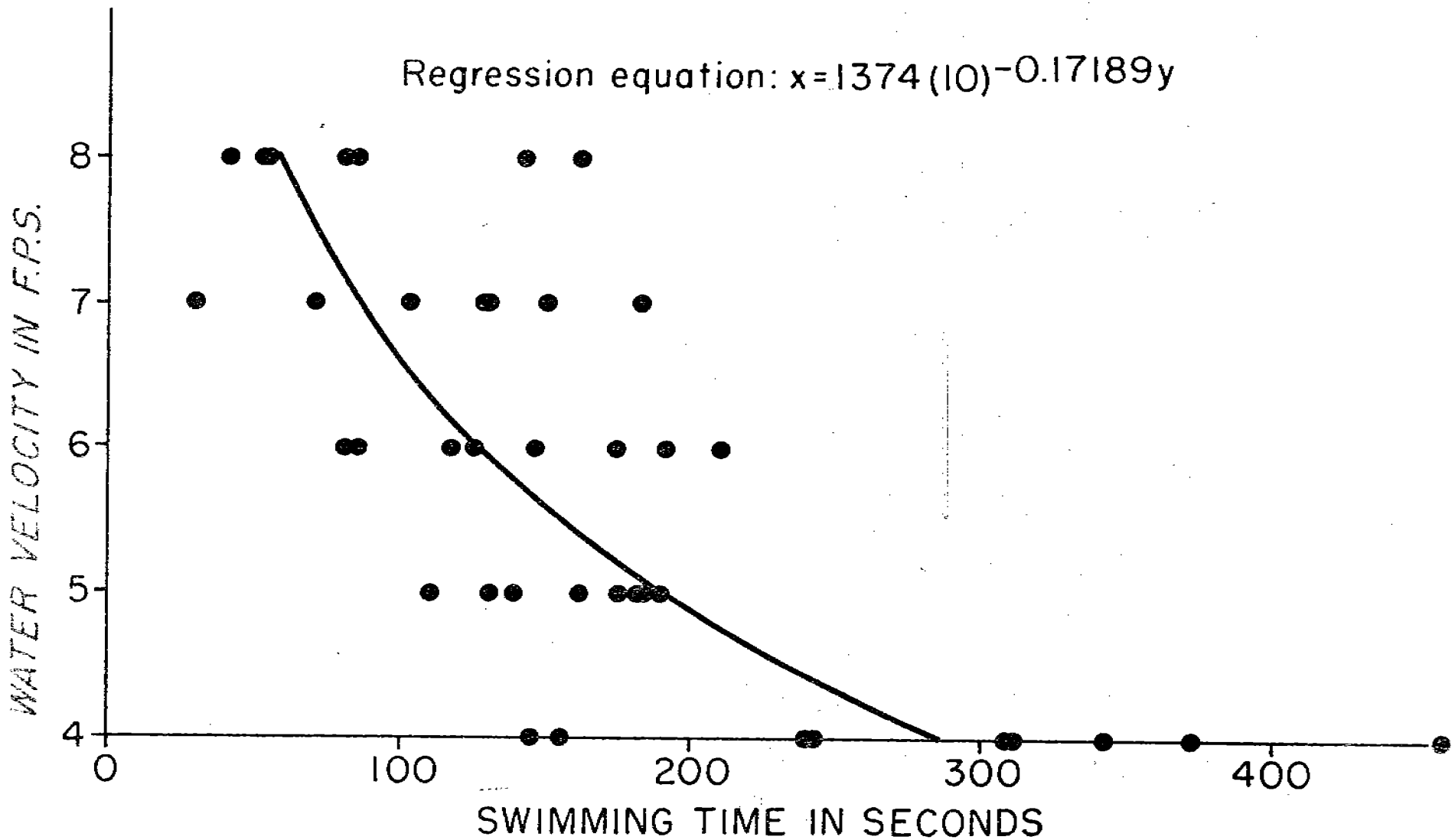

Figure 7: Swimming performance curve for adult silver salmon taken from Soos Creek on October 23, 1956.

The coefficient of concordance for these data was computed at 0.593 which rejects at the 1% level of significance the null hypothesis that there is no agreement between the ranks of the salmon according to swimming ability at different water velocities. It may be concluded from this that fish which are relatively strong or weak swimmers at one water velocity also tend to remain relatively strong or weak swimmers at other water velocities.

A second sample from the Soos Creek run of silver salmon was taken on November 19, 1956. The fall run was at its peak at the time this sample was taken. Twenty-five fish were selected on the basis of size, physical condition and maturity in the same manner as the October 23 sample. These salmon were held in individual holding compartments at the University hatchery during the course of the experiment. The day after the salmon had been unloaded at the University they were given a pre-test trial of two minutes duration in the annular tank at 4 f.p.s. (all the salmon were able to swim at 4 f.p.s. for this length of time). Fourteen were then selected according to their behavior in this pre-test for use in the velocity tests.

The velocity tests were conducted according to a Youden Square design.[8] The fourteen test fish were randomly assigned to the rows of two identical Youden squares. The experimental procedure employed was similar to that used for the October 23 group, i.e., two salmon, one from each replicate were tested successivel at the same water velocity before the velocity was changed. The 7 by 4 Youden Square arrangement of treatments that was used and the results of the swimming tests are shown in Table 11. The random order in which the velocities were tested is given in Table 11 for the four test days. The primary advantage of this design over the Latin Square type of design previously used (13) is that the number of test days (or replicates in the notation of Cochran and Cox) can

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[8] See (3) Chapter 13, Incomplete Latin Squares (Youden Squares) p. 370-375.

Table 11 Performance scores (swimming time in seconds) of upstream migrant silver salmon in water velocities from 4 to 10 f.p.s.

Fish no.	Water velocity in f.p.s. Test date 11/21	11/22	11/23	11/24	Performance Score in seconds 11/21	11/22	11/23	11/24	Sex	Length (inches
Replicate I										
1	6	8	9	10	75	73	66	45	M	29-5/8
2	7	9	10	4	72	30	30	360	M	18-3/4
3	8	10	4	5	31	18	226	81	F	25-5/8
4	9	4	5	6	43	149	81	75	F	26-3/8
5	10	5	6	7	27	162	153	90	M	19-1/4
6	4	6	7	8	117	64	42	35	M	20-3/8
7	5	7	8	9	215	88	43	40	F	21-7/8
Replicate II										
8	6	8	9	10	85	44	21	31	F	25-3/8
9	7	9	10	4	110	45	35	160	F	22-3/4
10	8	10	4	5	65	30	210	78	M	19-5/8
11	9	4	5	6	34	176	107	128	M	26-7/8
12	10	5	6	7	8	120	97	114	M	27-1/8
13	4	6	7	8	145	85	154	58	F	26-5/8
14	5	7	8	9	105	70	40	27	F	25

Order in which velocities were tested

11/21 f.p.s.	11/22 f.p.s.	11/23 f.p.s.	11/24 f.p.s.
9	6	10	6
8	5	9	9
7	8	5	8
4	4	8	5
5	9	7	4
6	7	6	10
10	10	4	7

Water temperature - 50 to 51-1/2°F.

be less than the number of treatments. Whereas a group of adult salmon may be reasonably expected to survive an experiment lasting four days, if the same experiment were to last seven days some of the salmon could be expected to incur injuries or die during the course of the experiment.

In order to complete the analysis of the data it is necessary to assume that the observations are normally distributed, have a common variance and that there are no interactions. Previous experience with performance tests has indicated that there is a positive relationship between the mean and the variance of swimming performances for a given treatment. To eliminate this relationship and to satisfy better the assumptions of the test the swimming times were transformed to logarithms before carrying out the analysis.[9] Table 12 gives the results of the analysis of variance and the adjusted mean swimming times at each water velocity. This adjustment, which corrects the mean performance times for differences between fish, was necessary as each fish was tested at only four water velocities. The validity and usefulness of this type of correction rests on the assumption that there is no interaction between fish and water velocity. The positive correlation between the ranks of the silver salmon ranked according to swimming ability at different water velocities for the October 23 group indicates that this assumption is reasonable.

It may be seen in Table 12 that the difference in the average performances of the group between test days was insignificant, indicating that the behavior and physical condition of the group were fairly constant during the four-day experimental period. There is a highly significant difference between the average performances

[9] A complete analysis was also made using the swimming time in seconds as the random variable. The results of this analysis were almost identical with the results obtained by using the logarithms of the swimming times as the random variable.

Table 12 Analysis of variance in transformed performance scores of silver salmon taken from Soos Creek November 12, 1956 on velocity tests.

Variation due to	Sum of squares	Degrees of freedom	Mean square	F value
Differences between test days	0.04145	3	0.01382	0.1701 (N.S.)
Differences between fish (uncorrected for treatment)	0.63899	12		
Differences between water velocities	2.20203	6	0.36701	4.5183**
Interaction of experimental error	2.76172	34	0.08123	
Total	5.64419	55		

Adjusted mean swimming times

Water velocity	4 f.p.s.	5	6	7	8	9	10
Swimming time in seconds	189.8	114.6	93.2	86.9	48.4	34.1	23.8

N.S. - not significant

** - significant at 1% level

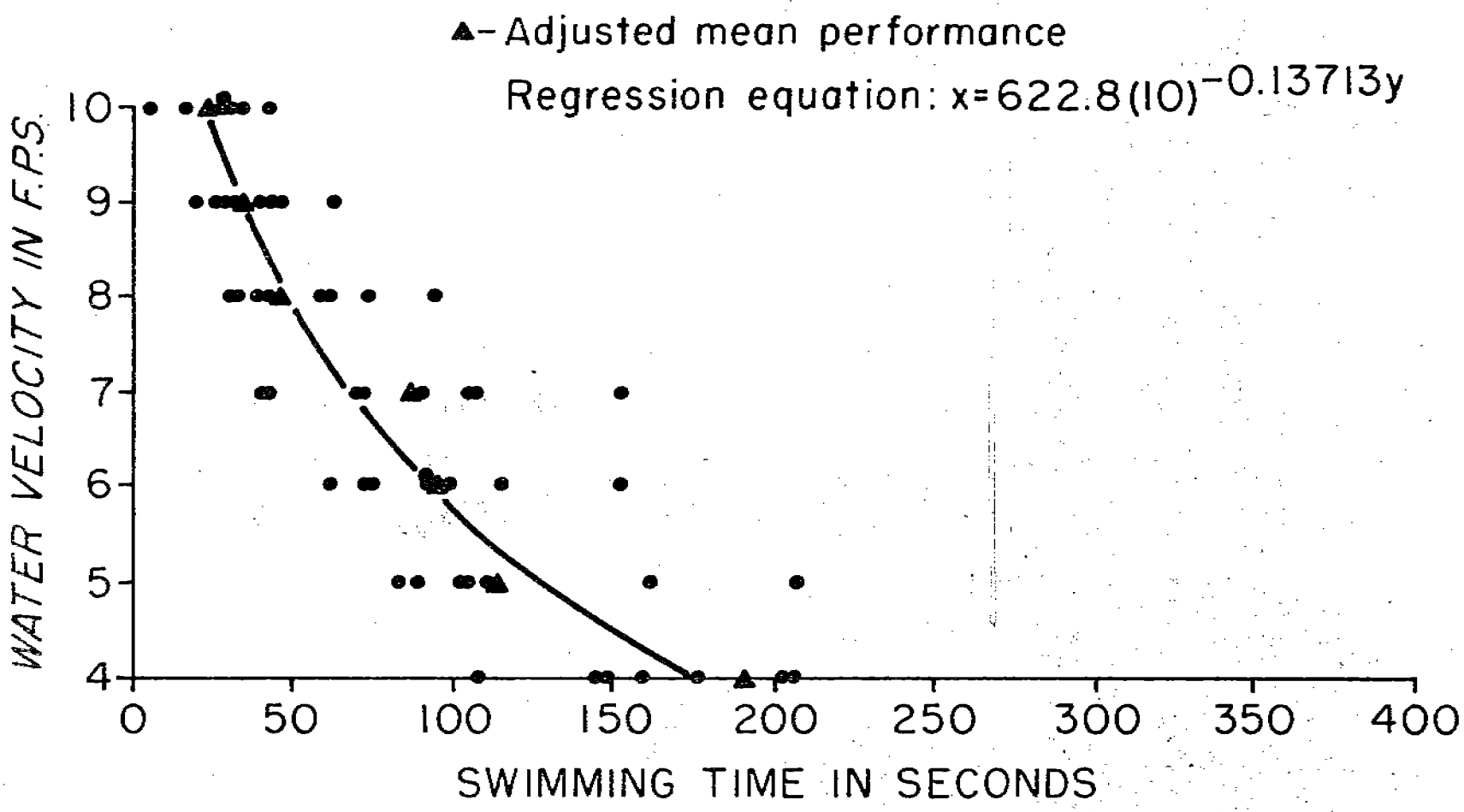

Figure 8: Swimming performance curve for adult silver salmon taken from Soos Creek on November 19, 1956.

Table 13 Performance scores (swimming time in seconds) of upstream migrant steelhead in water velocities from 4 to 10 f.p.s.

Fish no.	Water velocity in f.p.s. Test date 12/31	1/1	1/2	1/3	Performance Score in seconds 12/31	1/1	1/2	1/3	Sex	Length (inches)
Replicate I										
1	6	8	9	10	267	134	74	83	F	24
2	7	9	10	4	253	130	107	332	M	25-1/4
3	8	10	4	5	120	89	175	183	F	29-1/2
4	9	4	5	6	86	218	182	155	M	24-3/4
5	10	5	6	7	55	174	176	155	F	26-3/4
6	4	6	7	8	420	246	277	187	M	27-1/8
7	5	7	8	9	228	179	139	117	M	26-3/8
Replicate II										
8	6	8	9	10	104	120	74	69	F	30-3/4
9	7	9	10	4	190	86	86	286	M	24-3/4
10	8	10	4	5	105	54	109	129	F	32-1/4
11	9	4	5	6	83	330	193	202	M	26
12	10	5	6	7	73	205	187	207	F	25-5/8
13	4	6	7	8	440	404	234	128	F	25-5/8
14	5	7	8	9	147	187	160	91	F	27-1/8
Replicate III										
15	6	8	9	10	50	20	17	15	M	17-3/4
16	7	9	10	4	165	94	66	237	M	24-3/4
17	8	10	4	5	35	25	133	122	F	21-5/8
18	9	4	5	6	43	286	67	62	M	19-7/8
19	10	5	6	7	73	125	153	232	M	30-1/4
20	4	6	7	8	162	229	128	72	F	26-3/8
21	5	7	8	9	165	150	113	89	F	24

Water temperature - 50 to 53-1/2°F.

necessitated a slight modification of the experimental procedure previously described for the two groups of silver salmon. The seven steelhead in replicate I were the first seven fish tested each day; the water velocity was changed at the end of every test. At the conclusion of the seventh test the steelhead from replicates II and III were tested in pairs at each of the water velocities. After the steelhead from replicate I had rested for six hours, they were re-tested. The order in which the tests were run is shown in Table 14.

The last column (Jan. 3) of replicate I was repeated on January 4. This series of tests was conducted approximately eighteen hours after the conclusion of the re-tests on January 3.

Table 15 contains the analysis of variance using the transformed performance scores for the combined replicates I and II and for replicate III which was treated separately. The variation between the average performances of both groups on different test days is, as for the silver salmon, extremely small. The variation in average performance attributable to water velocity is highly significant for both groups. The mean performance times, adjusted to compensate for the varying abilities of the fish tested at each water velocity, are given for the combined replicates I and II and for replicate III in Table 15. The adjusted mean performance times clearly demonstrate the superior swimming ability of the selected sub-sample (replicate I and II).

Examination of the performances of the seven steelhead in replicate III shows that the physically incapacitated fish, Nos. 15, 17, 18, and 20 were weaker swimmers than the fish which were excluded from replicates I and II on the basis of behavior (Nos. 16, 19, and 21). The "least-squares" performance curve for the fourteen steelhead in replicates I and II is shown in Figure 9. For purposes of comparison the performance curve for replicate III is also represented in this graph. Both curves have the same general form; the only difference between them

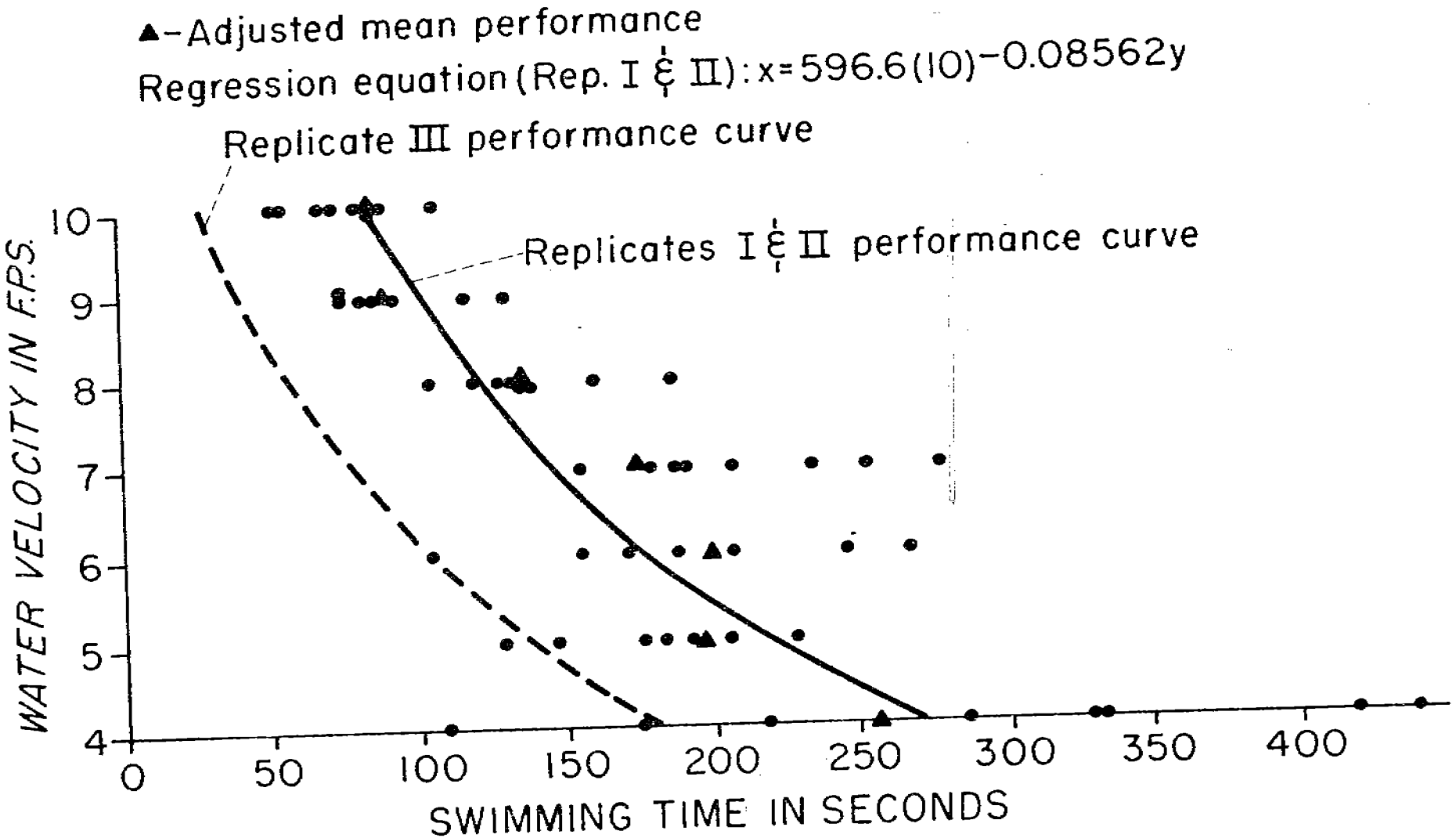

Figure 9: Swimming performance curve for adult steelhead (Replicates I & II) taken from Soos Creek on December 26, 1956.

Table 14 Performance scores (swimming time in seconds) of steelhead in tests before and after a six-hour rest period and testing schedule

Fish no.	Water velocity in f.p.s. Test date 12/31	1/1	1/2	1/3	Score in seconds on first test 12/31	1/1	1/2	1/3	Score in seconds after 6 hr. recovery period 12/31	1/1	1/2	1/3	Repeat of 1/3 vel. 1/4
1	6	8	9	10	252	134	74	83	245	93	111	64	80
2	7	9	10	4	253	130	107	332	240	120	84	350	502
3	8	10	4	5	120	89	175	183	121	49	185	175	174
4	9	4	5	6	86	218	182	115	100	205	217	153	153
5	10	5	6	7	55	174	176	155	65	206	154	179	156
6	4	6	7	8	420	246	277	187	308	234	235	74	188
7	5	7	8	9	228	134	74	83	246	194	136	108	114

Test Order Replicate I (First test)

12/31 Fish no.	12/31 Water vel. f.p.s.	1/1 Fish no.	1/1 Water vel. f.p.s.	1/2 Fish no.	1/2 Water vel. f.p.s.	1/3 Fish no.	1/3 Water vel. f.p.s.	1/4 Fish no.	1/4 Water vel. f.p.s.
6	4	5	5	4	5	5	7	5	7
2	7	7	7	5	6	1	10	1	10
7	5	2	9	6	7	7	9	7	9
1	6	6	6	7	8	3	5	3	5
4	9	1	8	2	10	4	6	4	6
5	10	3	10	1	9	2	4	2	4
3	8	4	4	3	4	6	8	6	8

Replicate II and III

13 20	4	12 19	5	11 18	5	12 19	7
9 16	7	14 21	7	12 19	6	8 15	10
14 21	5	9 16	9	13 20	7	14 21	9
8 15	6	13 20	6	14 21	8	10 17	5
11 18	9	8 15	8	9 16	10	11 18	6
12 19	10	17 10	10	8 15	9	9 16	4
10 17	8	18 11	4	10 17	4	13 20	8

Replicate I (re-test)

6	4	5	5	4	5	5	7
2	4	4	4	5	6	1	10
7	5	2	9	6	7	7	9
1	6	6	6	7	8	3	5
4	9	1	8	2	10	4	6
5	10	3	9	1	9	2	9
3	8	4	4	3	4	6	8

being that the curve for replicates I and II is simply translated to the right or may be thought of as operating at a higher level of performance. The injuries suffered by the fish in replicate III seem to have a constant deleterious effect on the performance of the steelhead regardless of the water velocity.

Table 14 contains the results of the original tests and the re-tests six hours later for the seven steelhead in replicate I on the four test days and the results of the one series of tests conducted on the fifth day. It is obvious from a comparison of the regression lines plotted in Figure 10 that the steelhead were able to recover completely, performance-wise, from the effects of fatigue experienced in the first test during the six-hour rest period. Although, in some cases, there was a sizable variation of random nature between two performances of the same fish on the same day, the performance curves for the two groups are nearly identical. The adjusted mean performances (see Fig. 10) also show the same close agreement with only random variation. The results of the repetition of the January 3 tests on January 4 tend to substantiate the reliability of the performance measurements. The swimming time of 502 seconds at 4 f.p.s. for fish No. 2 on January 4 was considerably longer than the two performances of 332 and 350 seconds by this fish at the same velocity on January 3. However, the large variance which has been previously mentioned as being associated with the longer performance times may be responsible for this difference. It is of interest to note that no daily decrease in performance was experienced by the seven steelhead in replicate I, in spite of the testing twice a day. These fish did not appear to differ, at the end of the experimental period, from the steelhead in replicate II which were fatigued only once a day.

At the end of the testing period the silver salmon and steelhead used in the constant velocity tests appeared to be in good physical condition in spite of the severe muscular exertion experienced. They were subsequently returned to Soos

Table 15 Analysis of variance for transformed performance scores of steelhead, taken from Soos Creek on December 26, 1956, on velocity tests

Replicates I and II

Variation due to	Sum of squares	Degrees of freedom	Mean square	F value
1. Differences between test days	0.02505	3	0.00835	0.2928 (N.S.)
2. Differences between steelhead (uncorrected for treatment)	0.92091	12		
3. Difference between water velocities	0.72820	6	0.12137	4.2556**
4. Experimental error or interaction	0.96981	34	0.02852	
5. Total	2.64397	55		

Replicate III

1. Differences between test days	0.01628	3	0.00543	0.2220 (N.S.)
2. Differences between steelhead (uncorrected for treatment)	1.96513	6		
3. Difference between water velocities	1.16017	6	0.19336	7.9052**
4. Experimental error or interaction	0.29349	12	0.02446	
5. Total	3.4507	27		

Adjusted mean performance times

Replicates I and II							
Water velocity	4 f.p.s.	5 f.p.s.	6 f.p.s.	7 f.p.s.	8 f.p.s.	9 f.p.s.	10 f.p.s.
Swimming time in seconds	253.6	195.2	198.5	174.8	136.7	89.4	81.8
Replicate III							
Swimming time in seconds	190.7	103.1	118.5	112.0	57.0	54.3	41.3

Adjusted mean performance: first test – ▲

: retest – ●

Regression equations: first test – $x = 573.9(10)^{-0.08045y}$

: retest – $x = 651.9(10)^{-0.09006}$

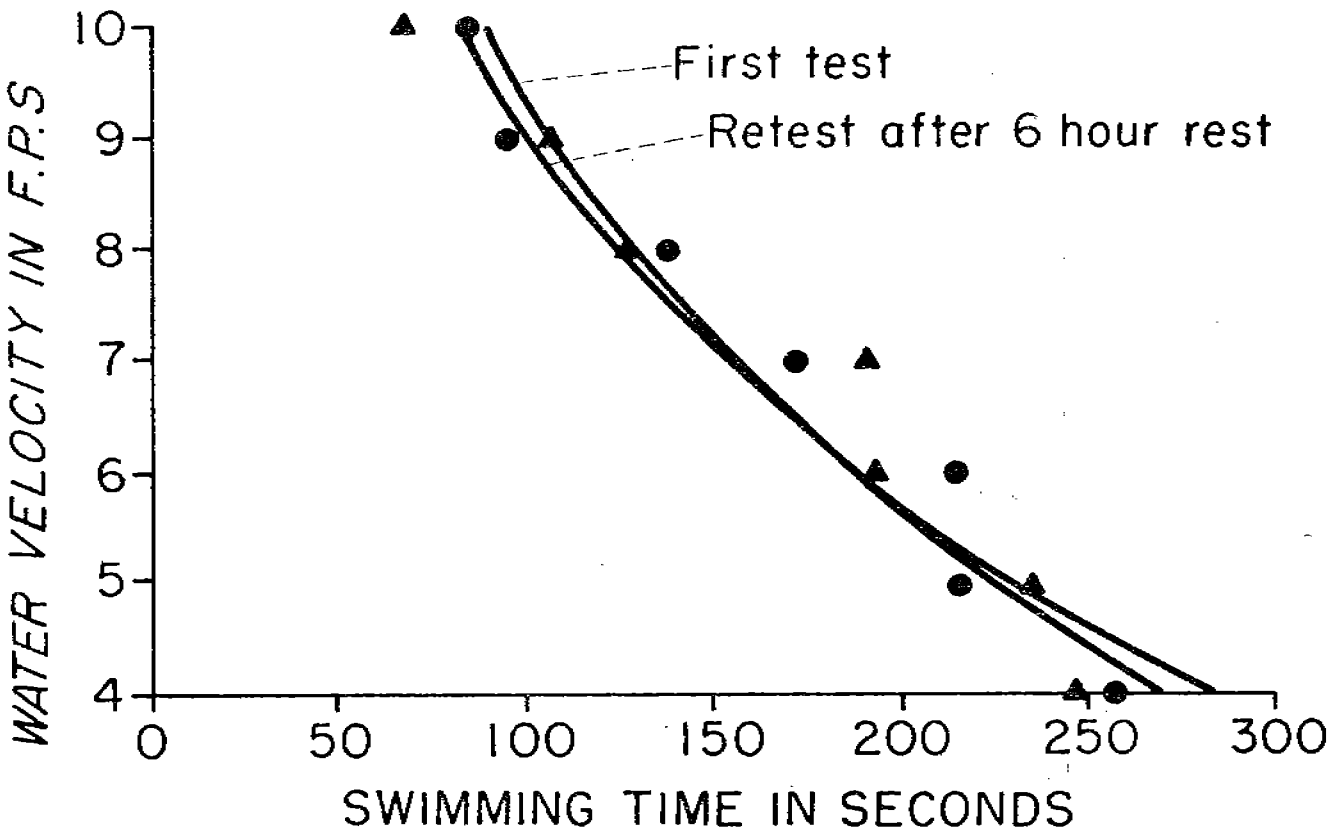

Figure 10: Swimming performance curves for adult steelhead (Replicate I) before and after 6 hour rest period.

Creek and released.

The performance curves for the two groups of silver salmon and the "normal" steelhead are presented in Figure 11. Considering first the two groups of silver salmon and extrapolating the October 23 performance curve from 8 f.p.s. to 10 f.p.s., the difference between the early and mid-run silvers appears to be a function of the water velocity. At higher water velocities the two curves approach one another asymptotically while they diverge markedly at the lower velocities. Thus the differences in swimming ability between the silvers taken from the early part of the run and those taken from the peak of the run become more pronounced as the rate of energy expenditure decreases.

The performance curve for the steelhead (replicates I & II) has the same form as the performance curve for the November 19 group of silver salmon but operates at a higher performance level. The steelhead swimming times at 4 f.p.s. are comparable to the swimming times of the October 23 group of silver salmon at this velocity. Although these two performance curves intersect at 4 f.p.s., the decrease in swimming time per unit increase in velocity is more rapid for the silver salmon than for the steelhead. As more silver salmon were available when the samples were taken, any bias arising from the method of selection would result in a relative increase in the swimming times of the silver salmon. Therefore it would seem safe to conclude that steelhead are considerably stronger swimmers than silver salmon at higher water velocities.

Any extrapolation of the performance curves given in Figure 10 in either direction is not permissible. At 3 f.p.s. a much larger increase in swimming times was observed for the October 23 group of silver salmon than would have been predicted by extending the performance curve. At least two of the fish appeared to be approaching a rate of energy expenditure which could be maintained for an

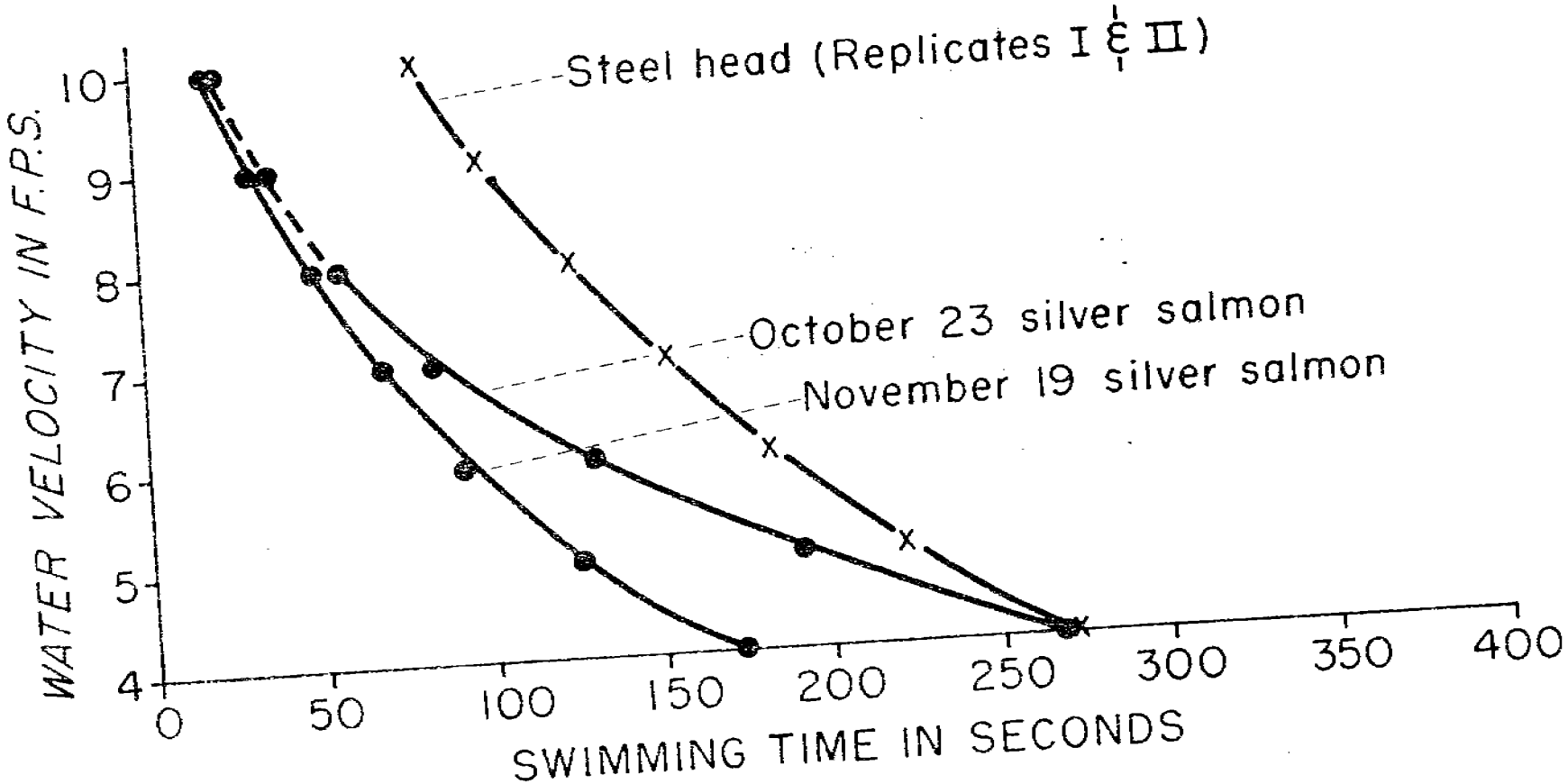

Figure 11. Swimming performance curves for October 23 and November 19 groups of silver salmon and Replicates I & II of the December 26 group of steelhead.

extended period of time at this water velocity. The accuracy of the predicted performances at velocities above 10 f.p.s. was examined by testing two of the steelhead, numbers 2 and 6, at 12 f.p.s. While the predicted performance was 45 seconds, the observed performances were 30 and 31 seconds respectively, indicating that performances drop off more rapidly than would be expected on the basis of performance curves obtained for velocities from 4 f.p.s. to 10 f.p.s.

Performance tests conducted in an experimental laboratory can not be expected to yield results which can be used directly without modification to predict the performance of a fish in a normal field situation. As soon as the fish is removed from its natural environment any inferences concerning its performance have to be restricted to a particular set of conditions. The logical starting point for performance studies is to determine the fish's performance under extremely strong motivation, and if possible this motivation should be at least equal in strength to any motivation that the fish would experience naturally. If it can be assummed that the fish were so motivated during the tests in the annular tank (13), performances of the fish in these tests can be used to construct a reference frame of the fish's capabilities. Such a reference frame would be an aid in recognizing the occurrence of limiting conditions in field situations.

Generally speaking, the length of time the fish could swim at any given velocity as recorded in the annular tank is lower than the length of time the fish might be expected to swim in a river or stream at the same water velocity under the same motivation because of the experimental conditions. The physical restriction imposed by the size and curvature of the test channel has the mechanical effect of increasing the resistance the fish must overcome at a given water velocit It is also possible that the annular tank may have adverse effects of a biological

or physiological nature. The increase in velocity due to the reduced area in the channel about the body of the fish has already been discussed. Other, but less obvious effects of this area restriction are the alterations in the nature of flow about the fish's body and an increase in shearing or frictional stress.[10] A change in the nature of the flow affects the total drag coefficient as defined by Gero (7).[11] The magnitude of the increased resistance that the fish must overcome in order to swim is proportional to the extent that the fish's body restricts the available area in the channel. Experiments carried out to measure the magnitude of this bias using rigid fish forms (frozen sockeye and silver salmon) with fork lengths of 20 to 23 inches indicate that the bias in performance times caused by changes in flow characteristics and shearing stress imposed by the restricted dimensions of the test channel is not serious for fish of this size.

Since these experiments were conducted in a rotating device the effects of centrifugal force must also be considered. During a test the water velocity is stabilized at the desired test speed before the fish is introduced into the test channel. With four electrodes in the channel the water velocity stabilizes at from 73% of the tank velocity at 3 f.p.s. to 90% of the tank velocity at 10 f.p.s. As the fish must swim to maintain its position ahead of the stationary light-electrode barrier it may be thought of as essentially a stationary object of approximately the same density as the water. The fish is subjected to one force acting normal to its median-vertical plane and directed toward the outside of the tank. This force, which acts on the right side of the fish (assuming the

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[10] See (21) Section 5. Viscosity, p. 11.

[11] See (7), p. 3-14, for discussion of drag acting on fish's body as it moves through water.

tank is being rotated in a counterclockwise direction and the fish is oriented into the current), is the sum of centrifugal force plus the force exerted by the water column above the fish's right side. However, an opposing force directed toward the inside of the tank of magnitude equal to the sum of these two forces is imposed by the water column above the fish's left side. Therefore, as long as the fish maintains its position, centrifugal force has no mechanical effect. The possible physiological effect of centrifugal force is not known. The parabolic shape of the water's surface during rotation causes a weak counter current to be set up in the test channel. Because this current is extremely slight its effects are thought to be negligible.

The variation in swimming performances between the individual fish in any of the groups tested during this series of experiments was rather large. Although purely energistic considerations cannot be used to account for all the variations in performance this does not imply that the variation observed in the annular tank experiments is any the less real or absent in nature. The spread or range in abilities of a group of salmon migrating upstream is equally as important as the mean swimming ability of the group. For the same group of salmon or steelhead, a wide difference would be expected to exist between the water velocity which would not interfere with the upstream migration of the group and the water velocity which would stop or block the upstream migration of the group. Consider for example the November 19 group of silver salmon from Soos Creek (Fig. 7). To allow all eight of the salmon tested at any of the velocities between 4 f.p.s. and 10 f.p.s. to pass a 500 foot reach, the water velocity in the reach should be reduced to less than 5 f.p.s.; on the other hand, to prevent the passage of all eight salmon in the same reach a 10 f.p.s. flow would be required.

The variations in ability between groups of fish may also be quite large; compare, for example, the steelhead and silver salmon performances reported in Figure 11, the October 23 sample to the November 19 sample of silver salmon, Soos Creek silvers to Columbia River sockeye (14), or groups of sockeye salmon taken from the Columbia River at various distances from salt water (14). The magnitude of these variations in ability between species, between salmon from different areas, and between the same fish at different stages of maturity during their upstream migration, indicates that the efficient design of fish passage facilities is dependent upon knowledge of the capabilities of the particular fish that will use the facilities.

Conclusions

1. The length of time silver salmon and steelhead are able to swim in the annular tank until exhausted was determined at water velocities from 4 f.p.s. to 10 f.p.s. (see Figs. 7, 8, 9).

2. Steelhead recovered (performance-wise) from an exhaustive swimming effort in six hours.

3. Differences in swimming ability at low water velocities were found between early and mid-run silver salmon.

4. A salmon's maximum swimming speed cannot be determined by an accelerating velocity test. Swimming during the time the water is being accelerated affects the maximum speed attained.

5. Steelhead are stronger swimmers than either silver salmon or sockeye salmon.

6. Two steelhead were able to swim at 12 f.p.s. in the annular tank for 30 and 31 seconds respectively.

7. The maximum swimming speed recorded for a silver salmon over a distance of one foot was 12.2 f.p.s.

8. It is recommended that the capacity of the lower pools of a fish ladder should be increased at installations where high water velocities may be present immediately downstream from the ladder entrance.

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