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The Effect of Rest on the Swimming Performance of Fatigued Adult Silver Salmon

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Abstract

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Eighteen adult silver salmon (Oncorhynchus kisutch) were subjected to swimming performance tests before and after rest periods of one, two and three hours. The salmon were fatigued by their swimming effort in the first test, and the second test was used to measure the extent of recuperation during the rest period. The experiment was run according to a Latin square design. Using this design each fish was tested before and after each type of rest period. A total of 108 individual swimming tests were run. The three rest-period-treatments were presented to each salmon on three consecutive days. This allowed an evaluation of the fish's recovery after an overnight (18 to 24 hours) rest.

The primary experimental results were: (1) Recovery from an exhaustive swimming effort was found to be 31 percent complete after a one-hour rest, 43 percent complete after a two-hour rest, and 67 percent complete after a three-hour rest. (2) All fish recovered completely after an overnight rest of 18 to 24 hours. (3) A significant swimming performance decrement was associated with pre-test activity, suggesting that salmon are highly susceptible to fatigue.

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Introduction

One of the basic problems in the design of fish ladders is the location number and size of resting pools. Of the many considerations in such design problems, the behavior and swimming ability of the species using the ladder are paramount. The present study was undertaken to obtain information on the resting time necessary for upstream migrant salmon to recuperate after vigorous muscular activity. Recovery time information may also be of considerable interest in other phases of fisheries work. Tagging operations, involving capture and handling, expose the tagged fish to varying degrees of muscular activity. Black (3) recommended holding transported fish at the planting site until the fish have recovered from the effects of muscular activity before releasing them.

The length of time needed by a fish for recuperation after vigorous activity is dependent upon the intensity and duration of the activity. The degree of exhaustion voluntarily experienced by a salmon ascending a fish ladder is an extremely difficult thing to measure. Furthermore, an interaction of external stimuli and the internal motivation might be expected to influence the salmon's activity in the ladder. For these reasons, and in order to avoid some of the ambiguities inherent in the definition of a partially fatigued fish, the salmon used as subjects in this study were forced to swim until they could no longer hold a position in front of an illuminated electrical barrier. This strong motivation was selected in an attempt to produce a state of muscular fatigue exceeding that which might be encountered under natural conditions. A powerful stimulus such as the electrical barrier tends to elicit a response that is relatively independent of individual behavior traits, and thus not only allows more accurate assessment of actual physical capacity but produces replicable measurements (

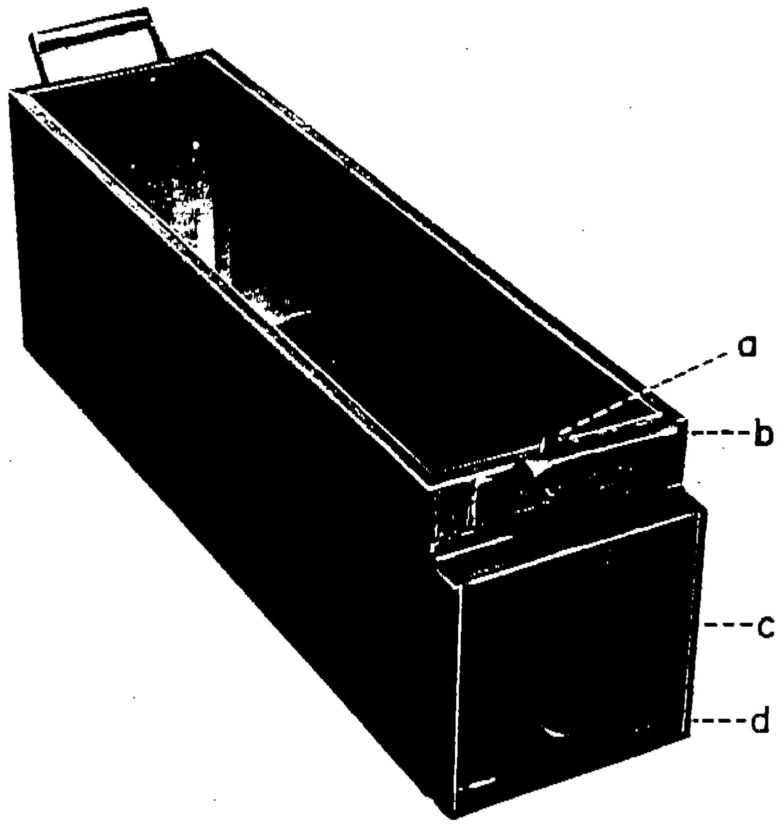
This approach, i.e., the measurement of performance, is somewhat pragmat in the sense that it is an endeavor to find a relationship between work outpu and recovery time without considering what is happening within the fish. Specific tissue conditions within the fish are not necessarily related to ove activity in a straight forward manner (2, 11). However, the usefulness of a concept of the relationship between rest and performance is not negated by want of a reason for the relationship.

Methods and Materials

Eighteen adult silver salmon (Oncorhynchus kisutch) were used in this study. The salmon were obtained at the Washington State Department of Fisheries weir on Soos Creek on November 11, 1955. Soos Creek is a tributary of the Green River which in turn empties into Elliott Bay. The hatchery weir is located about 35 miles above salt water. The salmon were captured in a large seine in regular use by the hatchery staff. As the water was fairly turbid and the fish were confined to a small area of the stream, between two weirs when the sample was taken, it is believed the sample was unbiased with respect to swimming ability and was representative of the population in the stream at that time. The first eighteen fish caught were taken. The sample was made up of silver salmon of both sexes in varying stages of maturity including males which shed milt when handled. The fish were picked up by hand from a small pocket of the net and carried to a waiting truck for transportation to the University of Washington hatchery. Travel time was one hour. Unloading was accomplished by means of a carrying box (Fig. 1) which minimized handling of the salmon.

After the fish had been held at the University for four days they were given a pre-test trial of two minutes duration in the annular tank which is described below. The purpose of the pre-test was to eliminate some of the variability in performance between the fish's first and second experiences within the test apparatus, which was anticipated as a result of previous experiments. Thus, all fish had a two-minute experience with the test situation prior to the collection of the first experimental data. At the conclusion of the pre-test the salmon were marked for later identification by notching one or more fins, and were then placed in either of two rectangu concrete hatchery raceways. The raceways were five feet wide and were divid by heavy wire gratings into four compartments each seven feet long. These outdoor raceways were not covered or shielded in any manner. The water leve in the raceways was maintained at approximately 16 inches. The water temperature varied from 48°F. to 50°F. during the experimental period. The water used in the raceway and in the annular tank was taken from the same source and the temperature difference between the water in the holding ponds and that in the annular tank was always less than 1°F.

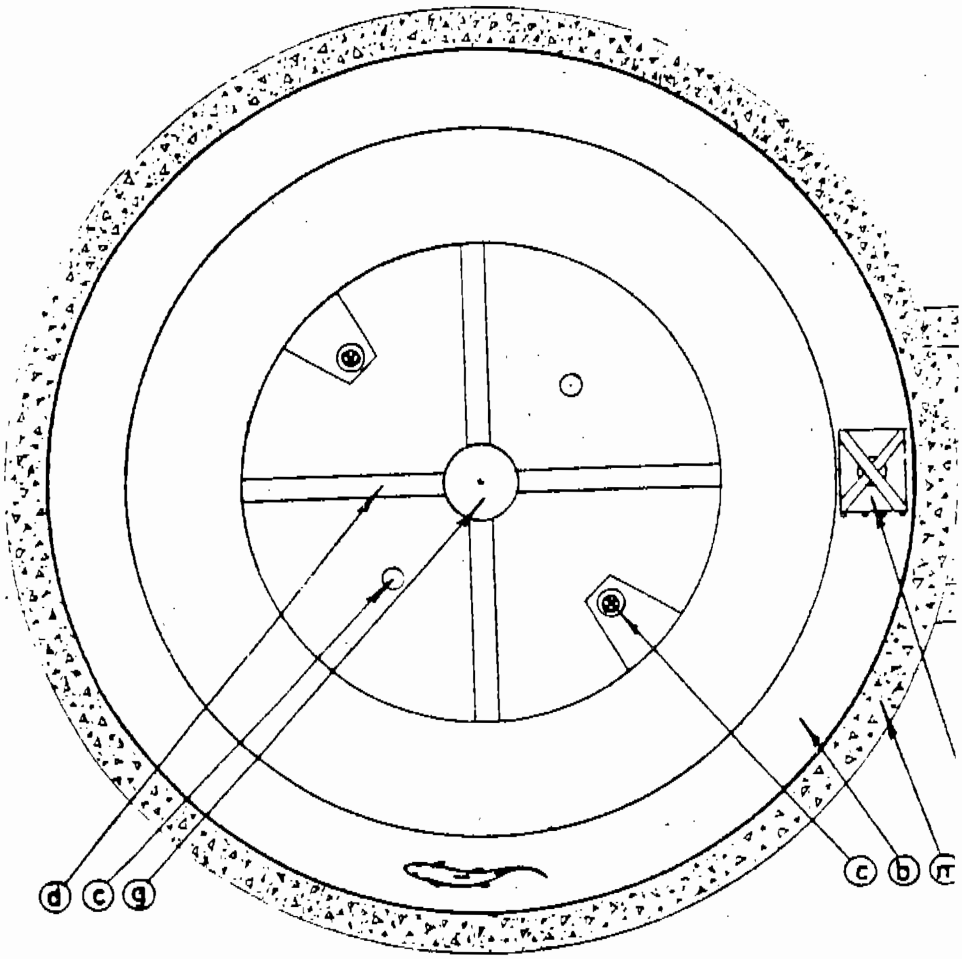
Figures 2 and 3 show the essential features of the revolving annular tank that was used to test the fish at desired water velocities. The tank is constructed entirely of steel. The turntable on which the tank is mounte is supported by a center bearing and twelve rubber casters (Fig. 2). All inside tank surfaces were ground or filled and sand blasted before painting. The importance of eliminating any visible reference points on rotating parts in this type of apparatus is discussed by Gray (9). However, visible stationary objects that could be used as reference points to aid the fish in



CARRYING BOX

a Gate release lever
b Handle
c Water tight gate
d Gate latch

FIGURE 1. Carrying box with cover removed.



ROTARY FISH TANK

b outside channel - 12" width

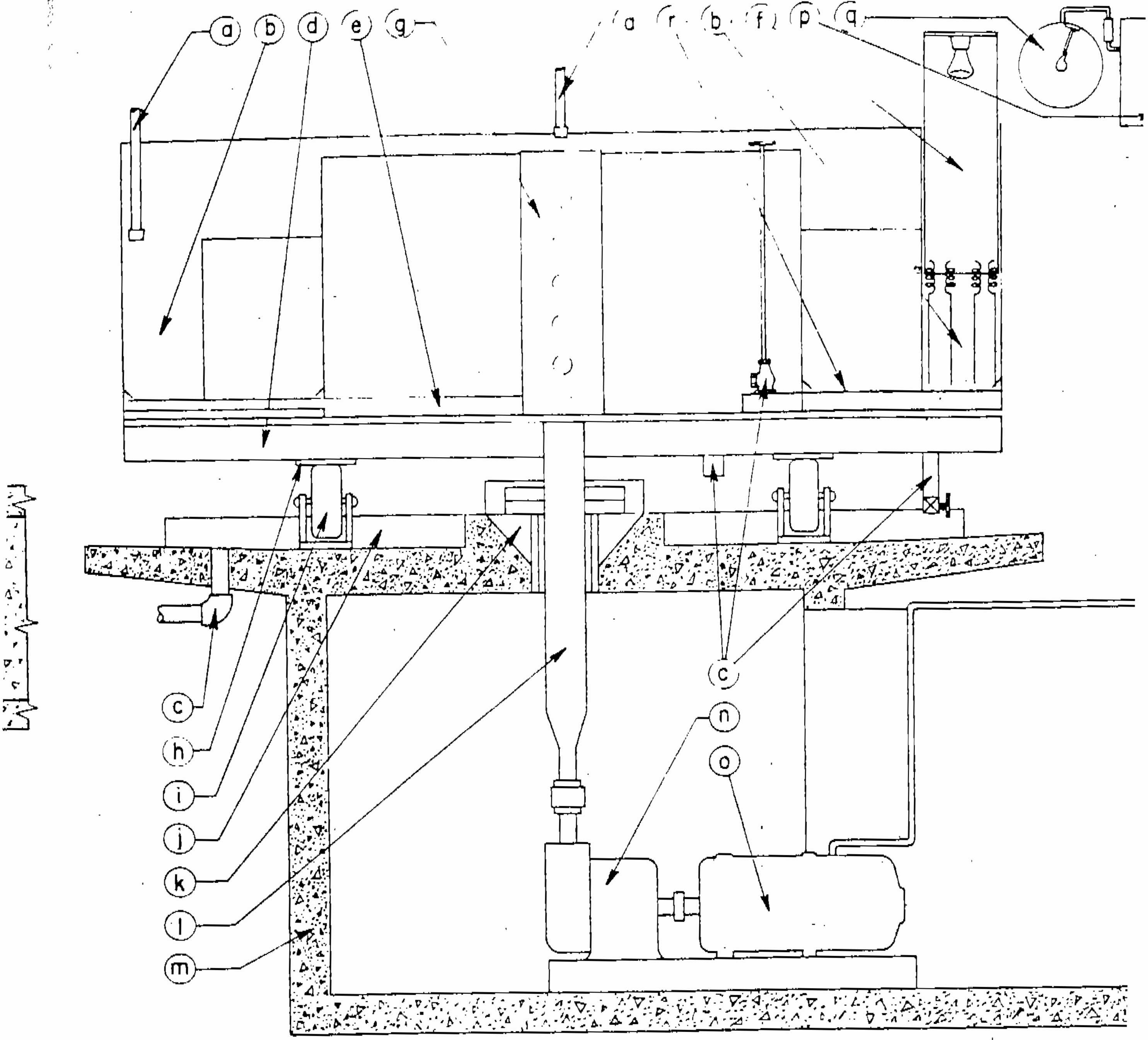
c drains

d channel beam supports

f coil spring electrodes an
barrier

g center spill weir - 12" dian

m concrete support platfor



ROTARY FISH TANK

(a) water inlet
(b) outside channel - 12" width
(c) drains
(d) channel beam supports
(e) 2"x 3" 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 controll
r false bottom

ight

er

FIGURE 3. Rotary Fish Tank (Elevation view)

maintaining spatial orientation were not eliminated. Positive stimuli of this sort were provided by a combined light and electrode barrier and the overhead jet of water which was sprayed directly into the test channel. Water was introduced at the outer edge of the outer channel through inlets concealed behind a continuous circular shield. Water interchange between the test channel and the drain chamber beneath the false bottom was accomplished through 1/8 inch slots in the tank bottom placed intermittently along 6-1/2 feet and 9 feet diameter circles. Black stripes one inch in width were painted along these circles to provide a background against which the slots would be inconspicuous. The remainder of the tank bottom was painted white. All vertical inside tank surfaces were painted black.

Water was circulated continuously at the rate of three gallons a minute during each test day. This rate of circulation held the variation in water temperature throughout the test day to less than $1^{\circ}F$. The water was aerated by the overhead jet, and by incidental turbulence caused by the wake of the electrodes and the activity of the fish. Aeration by incidental turbulence alone was shown by previous experiments to be sufficient to sustain a 7 p.p.m. level of dissolved oxygen.

The water depth in the test channel was maintained at 11 inches by means of the spill weir in the center of the tank and the inside drain valves. At this depth the total volume of water in the complete channel was 460 gallons. In this series of tests the fish were confined to an outer annular division of the total channel. This division was accomplished by the insertion of a circular channel divider. The annular test channel was 12 inches in width and had a center diameter of 10 feet. The relative curvature of this channel in relation to the average size salmon used in this experiment may be seen in Fig. 2.

The tank was rotated in a counterclockwise direction by a five horsepower adjustable-speed electric motor. The speed and pattern of rotation were controlled automatically by a pneumatic-electronic device. This mechanism made possible the replication of exact velocities for any number of successive tests. All tests described in this paper were conducted at a tank speed of 7 r.p.m. At this tank speed the water velocity in the test channel varied from 3.6 f.p.s. near the outer wall of the channel to 3.2 f.p.s. near the inner wall of the channel with a mid-channel velocity of 3.4 f.p.s. Velocity determinations were made with a Steven's midget current meter and also with various types of floats.

A weak electrical field (one volt per inch gradient--60 cycle a.c.) and a powerful beam of light restricted to the immediate area of the electrodes were combined to produce a barrier which would effectively induce the fish to swim against the current without appreciably disturbing the velocity pattern in the test channel. The salmon's natural light avoiding behavior (8) was reinforced with an electric shock when the fish entered the small, intensely lighted area directly beneath the barrier. The source of light was a 300 watt photospot bulb mounted 32 inches above the water. By darkening the rest of the room the demarcation between the brightly lighted area and the remainder of the test channel was accentuated. This sharp demarcation was an important factor in keeping the fish positively oriented into the current. The electrodes consisted of a straight section of steel rod continuous with and suspended by a coil or spring section of the same rod. This coil spring was strong enough to hold the electrode in place against the water current generated by rotation of the tank but was flexible enough to allow the electrode to be brushed aside if contacted by a fish. The distance between the two electrodes was ten inches. The electrodes were one inch away from the test channel walls which were coated with a nonconducting paint.

All experimental events were recorded on a tape recorder during the tes and were later transcribed. All fish were tested individually. In accordar with a predetermined order (see discussion) each fish was returned to its re spective raceway section and left there for a given length of time before be retested. The pickup of the fish from the raceway section was carefully executed in an effort to minimize the fish's activity during this part of the operation. The capture was effected by slowly approaching the fish in the shallow water with the open carrying box turned on its side. By this means the fish was cornered and forced to enter the box. Frequently the fish ent the box of its own volition in an effort to hide. The lid was placed on th box immediately and this action usually served to still the struggles of an fish that was fighting confinement in the box. A subjective estimate of th relative amount of energy expended by each fish while it was being caught f testing was recorded by the experimenters according to the following patter

E. E. No. 0 - No disturbance.

E. E. No. 1 - Slight disturbance, fish unexcited.

E. E. No. 2 - Moderate disturbance, fish swam about section two or three times or struggled slightly in box.

E. E. No. 3 - Considerable disturbance, fish became excited and swam about raceway section or struggled considerabl in box.

E. E. No. 4 - Extreme disturbance, fish struggled violently duri pickup.

The two men carrying the box agreed upon the "energy expenditure" number a recorded it.

The room lights were darkened and the speed of rotation of the tank w recorded. The fish were introduced at a position from 135° to 150° upstream (12 to 14 feet) from the barrier. The carrying box was held just above the surface of the moving water with the exit facing upstream. The exit was then opened, by means of a small catch activated by thumb pressure, spilling the fish and water into the test channel. The majority of fish immediately responded to their release by beginning to swim in an upstream direction. However, those that failed to orient positively were reversed (reoriented into the current) by means of a small knotless nylon net before they contacted the barrier. This was usually achieved with one quick motion and caused virtually no visible expenditure of energy by the fish. Whenever during a test a fish became disoriented it was reversed in this manner as it passed a position about four feet upstream from the barrier. Thus, no fish was allowed to make more than one complete circuit of the tank at any one time facing in a downstream direction. In addition to reversals, the following events were also recorded during each test: Shock - contact with electrical field which was usually followed by an immediate upstream movement of less than two feet; Dart 1 - contact with electrical field followed immediately by swift, continuous upstream movement greater than two feet but less than six; Dart 2 - contact with electrical field followed immediately by swift, continuous upstream movement greater than six feet; Position 1 - fish swimming at inner edge of test channel; Position 2 - fish swimming at center of test channel; Position 3 - fish swimming at outer edge of test channel; Lap Type 1 - fish is swept through barrier while swimming actively and oriented upstream; Lap Type 2 - fish changes orientation after contact with barrier and dashes through barrier headed downstream; Lap Type 3 - fish is disoriented at time of contact with barrier and continues to swim downstream through barrier. The frequency of these happenings was recorded for each

30 second period during the entire test except that Type 1 Laps were recorded at the exact second of occurrence.

The test for a fish was arbitrarily ended when the third Type 1 Lap occurred. The assumption that such fish were exhausted or very nearly exhausted at the end of the test was substantiated by changes in body chemistry (11), the common occurrence of the fish losing equilibrium after one or more Type 1 Laps, and the consistent equality of the time interval between the first and second Type 1 Laps and the second and third Type 1 Laps. These time intervals were only slightly longer than the drift time of a free floating object at the same water velocity.

The fish were immediately removed from the test channel after the third Type 1 Lap. A subjective rating of the fish's state of exhaustion was made and the fish was returned to its raceway section. The fish was out of water for 10 to 15 seconds during this transfer. The various states of exhaustion recorded are defined as follows:

No. 1 - No signs of fatigue.

No 2 - Partial fatigue, fish tried to avoid net and struggled when picked up.

No 3 - Complete fatigue, fish made no attempt to avoid capture and was picked up without struggle.

No. 4 - Loss of equilibrium.

The fish were left in the raceway for specified rest periods at the end of which they were retested in the manner just described. When the performance tests were completed the fish were transferred to a holding pen in Lake Washington where they remained undisturbed until death. No attempt was made to ascertain the cause of death.

Discussion

The experimental observations were taken according to a Latin square design. Bliss and Rose (4) and Bacharard (1) have pioneered in the use of this type of design in the field of animal experimentation. This particular arrangement has the advantage of allowing statistical control of the intra-subject and experimentally introduced sources of variation that would ordinarily tend to obscure the treatment effects that are of primary interest. In the case at hand, this is of particular significance as the sample size was small and the silver salmon composing the sample were extremely heterogeneous with respect to size, maturity and physical condition. Data on the individual fish in the sample are given in Table 1. The time between the arrival of the salmon at the University and the death of the salmon varied from that of fish No. 16 which died after testing on the third experimental day (period II - Table 1) to that of fish No. 3 and fish No. 8 which lived at least 21 days after the completion of 3 days of testing (period I).

Table 1 also shows the experimental layout and the original data. There were six experimental units with three fish in each unit. Each fish was tested six times, twice each day for three successive days. Because of a time limitation on the number of tests that could be run during a single day, the experiment was broken down into two three-day experimental periods, November 16, 17 and 18; and November 21, 22 and 23 respectively. The rows in Table 1 represent individual fish, the columns represent one, two and three-hour rest periods. At the conclusion of the pre-test conditioning trials the individual fish were numbered and randomly assigned to the experimental treatments.

The rest periods were selected on the basis of preliminary tests. These tests indicated that changes of an hour in the length of a rest period during the first few hours following a swimming effort which exhausted the salmon would appreciably alter the salmon's swimming performance in a second test. There were indications that a three-hour rest period is sufficient to allow an exhausted silver salmon to nearly regain its original capacity for swimming. As can be seen from Table 1, each fish was tested before and after each rest period and each rest period occurred equally often on each experimental day. Of considerable interest in itself is the overnight recovery of the experimental fish and the possible occurrence of systematic daily changes in swimming ability during the three-day test period for the entire group. The six possible orders in which the treatments could be presented to the individual fish are represented by two 3 by 3 latin squares, each of which was replicated three times to make up the total of 54 observations. The order factor was included in the design to discern whether or not the sequence in which the three rest periods were presented to the salmon influenced the results of the performance tests. For example, a fish that was given a three-hour rest period the first day would have spent considerably longer in the annular tank than a fish which was given a one-hour rest on the first day. This differential experience with the annular tank could possibly have affected the fish's behavior and performance in later tests.

Each day the three salmon which were given a three-hour rest period were the first group tested at the start of the day, the fish that were given a two-hour rest were the second group tested, and the fish that were given a one-hour rest were the third group tested. The groups were retested after the rest periods in reverse order, that is, the group that had rested for one hour was retested first, the group that had rested for two hours second, and group that had rested for three hours third. As all the fish were held in two raceways (each of which was partitioned by wire screens) the pickup and return to the raceway of the fish in the group tested early in the day resulted in a certain amount of commotion which disturbed the fish that were to be tested later. Although it was impossible to make any sort of quantitative estimate of each fish's pre-test activity resulting from these disturbances, it was apparent that the fish's random movement about the raceway increased considerably when the experimenters were working with other fish in the same raceway. Thus, the pre-test fatigue histories differed according to the length of time the fish were to be rested after the first test, with the amount of pre-test activity inversely related to the length of the rest period.

The performance score used in the analysis was the total number of seconds elapsing between the introduction of the fish and the loss of the third Type 1 Lap. The third Type 1 Lap was used because this proved to be the most consistent measure. However, the use of the first Type 1 Lap in the statistical analysis did not affect the results of significance. The validity of these tests of significance (in the Latin square analysis) depends on the assumptions of normality of distributions, common variance, and negligible interactions between factors. In order to satisfy better the first two assumptions it was necessary to transform the original raw scores (total swimming times in seconds). The most suitable transformation to correct for the relationship between the means and variances of the data, grouped by rest periods, was a logarithmic transformation (10). This transformation did not change the conclusions reached using the raw scores in the analysis. A study of the error terms calculated for the individual 3 by 3 Latin squares indicates that the data may not satisfy the third assumption. This would seem to be the consequence of differences in the response of the individual fish to repeated daily testing. A learning effect operating differentially with respect to the physical condition of the individual fish could have been responsible for these heterogeneous error terms. Salmon that were in good condition at the start of the test period might be expected to improve their performances as a result of successive tests in the annular tank, while fish that were in poor condition at the start of the test period were probably weakened by successive tests. To eliminate this interaction between fish and days it would be necessary to start with a group of fish that were alike with respect to stage of maturity and physical condition.

As an aid in discussing the experimental results the terms re-run and first run will be defined and as used hereafter these terms will refer to the definitions given below. First run refers to the swimming performance test given to the salmon before a rest period of one, two or three hours. The first run was always the first of the two swimming performance tests that a salmon was given on an experimental day. The purpose of the first run was to measure the fish's swimming ability after a rest of at least eighteen hours, and to fatigue the salmon to such an extent that it was unable to maintain position in a low water velocity. Re-run refers to the swimming performance test given to a salmon after the salmon had been exhausted in the first run and had rested for one, two or three hours following the first run. The purpose of the re-run was to measure the swimming ability of the salmon after the respective rest periods.

Table 2 gives the results of the analysis of variance using the transformed re-run scores. The swimming performances were significantly affected by the length of the rest period and there was a significant daily increase in

Table 2 Analysis of variance of transformed performance scores of adult silver salmon on re-runs after rest period.

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	Variance Ratio
Order of presentation	0.5178	5	0.1036	2.34
Differences between fish in the same order (pooled)	0.5303	12	0.0442	
Differences between fish (total)	1.0480	17	0.0616	4.35 **
Differences between test days	0.3038	2	0.1519	10.73 **
Differences between length of rest period	1.2425	2	0.6213	43.88 **
Interaction or experimental error	0.4531	32	0.0142	
Total	3.0474	53		

* significant at the 5% level

** significant at the 1% level

swimming performances for the entire group on the average. However, the daily increase seems to be an artifact of design rather than a result of learning or of any other cause. This may be seen by ranking the fish using the total of the swimming performances scores in the first runs over the three test days as the criteria. This seems to be the best available scheme to rank the fish according to their swimming ability at the water velocity used in these tests. It may be seen that five of the six lowest fish on this scale were given a three-hour rest period on the first test day. Since the fish's recovery between the second and third hour of rest was considerable, this has the effect of lowering the first day scores on the re-runs and raising the second and third day scores on the re-runs. Any interpretation of this daily variation should, therefore, be made with extreme caution.

The variance in test scores attributable to the order in which the treatments were presented was tested against the error term associated with the variation between fish in the same order. The order effects were confounded with the two three-day test periods. Orders I, II and III were replicated in the first period but not in the second, while order IV, V and VI were replicated in the second but not in the first period. Although the difference between the periods was not significant, a large interaction between the periods and orders could cause the tests of significance for the order effects to be misleading. Fortunately in this experiment, the order effects appear to be relatively unimportant.

As the data in Table 1 show a clearcut relationship between the fish's performance in the first run and the fish's performance in the re-run (due to individual differences between fish) it becomes necessary to determine if the first run was independent of the particular rest period which followed before accepting the above conclusions. Referring to the discussion on testing sequence, it may be seen that this is in reality a test of the effects of the sequence in which the fish were tested each day. Using the log transformation of the scores attained on the first runs it was possible to test this hypothesis. The results of this analysis are summarized in Table 3. There was a highly significant difference between the first runs of the fish that were designated for the different rest periods. The swimming time scores decreased markedly when the fish were run later in the daily testing sequence. The most logical explanation of this phenomenon would seem to be that the disturbances the fish experienced while waiting for their turn to be tested fatigued them enough to cause a performance decrement. The possibility that this could be due to some sort of metabolic daily cycle was ruled out as the relationship between performance and the sequence of testing seemed to be independent of variations of as much as two hours in the start of testing for the day. The difference between performance scores on the successive test days was not significant and indicates that the salmon were completely recovered after an overnight rest (from 18 to 24 hours).

To adjust the data statistically for this inequality in the lengths of the first runs a covariance analysis technique (5) was used. This test was applied under the assumptions that (1) a linear relationship exists between the transformed scores on the first runs and the transformed scores on the re-runs, and (2) the variances of the transformed scores are constant about the regression lines for the three rest periods. The second assumption was tested by Bartlett's test of homogeneity of variance (5). The results of the test indicated that this assumption was certainly tenable. The first null hypothesis (hypothesis A) tested by the analysis of covariance was that the

Table 3 Analysis of variance of transformed performance scores of adult silver salmon on runs before rest periods.

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	Variance Ratio
Order of presentation	1.7999	5	0.3600	3.21 *
Differences between fish in same order (pooled)	1.3477	12	0.1123	
Differences between fish (total)	3.1476	17	0.1852	8.84 **
Differences between test days	0.0027	2	0.0014	---
Differences between the order in daily testing sequence	0.2219	2	0.1109	5.29 **
Interaction or experimental error	0.6705	32	0.0210	
Total	4.0427	53		

* significant at the 5% level

** significant at the 1% level

three regression lines associated with the rest periods could be represented by one common regression line. The analysis of variance is given in Table 4. This null hypothesis was rejected at the one percent level of significance, demonstrating that significant increases in the recovery of swimming ability were caused by the increment of one hour in the length of time the salmon rested between tests. The second null hypothesis (hypothesis B) was that the slopes of the recovery curves were the same for the three rest periods. The difference between the slopes was significant at the five percent level. As the length of the first run increased, the differences in the percentages of recovery between rest periods became greater.

The equations of the curves shown in Fig. 4 were derived from the transformed data by the method of least squares. The actual performance scores are plotted about the theoretical line for the group that was given a three-hour rest. Letting y stand for the performance time on the re-run and x for the performance time on the first run, the equations for the recovery curves in Fig. 4 are:

One-hour rest period - $y = 31.138\ x^{0.2631}$

Two-hour rest period - $y = 45.811\ x^{0.2526}$

Three-hour rest period - $y = 3.426\ x^{0.7373}$

The three recovery curves are characterized by positive slopes and negative accelerations. The direction of slope infers a positive correlation between the fish's performance in the first run and re-run, i.e., the fish that were superior performers in the first runs would maintain this relative superiority during the re-run. The negative acceleration points out the decrease in percentage recovery as the length of time the fish swam during the first run increases.

Table 4 Analysis of variance for the difference between recovery curves for the one-hour, two-hour and three-hour rest periods.

Hypothesis A: The three recovery curves could be represented by a single curve.

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	Variance Ratio
Differences between curves	1.0244	4	0.2561	12.08 **
Error	1.0173	48	0.0212	
Total	2.0417	52		

Hypothesis B: The slopes of the three recovery curves are the same.

Variation due to	Sum of Squares	Degrees of Freedom	Mean Square	Variance Ratio
Differences between slopes of the recovery curves	0.1790	2	0.8951	4.22 *
Error	1.0172	48	0.0212	
Total	1.1962	50		

** significant at the 1% level

* significant at the 5% level

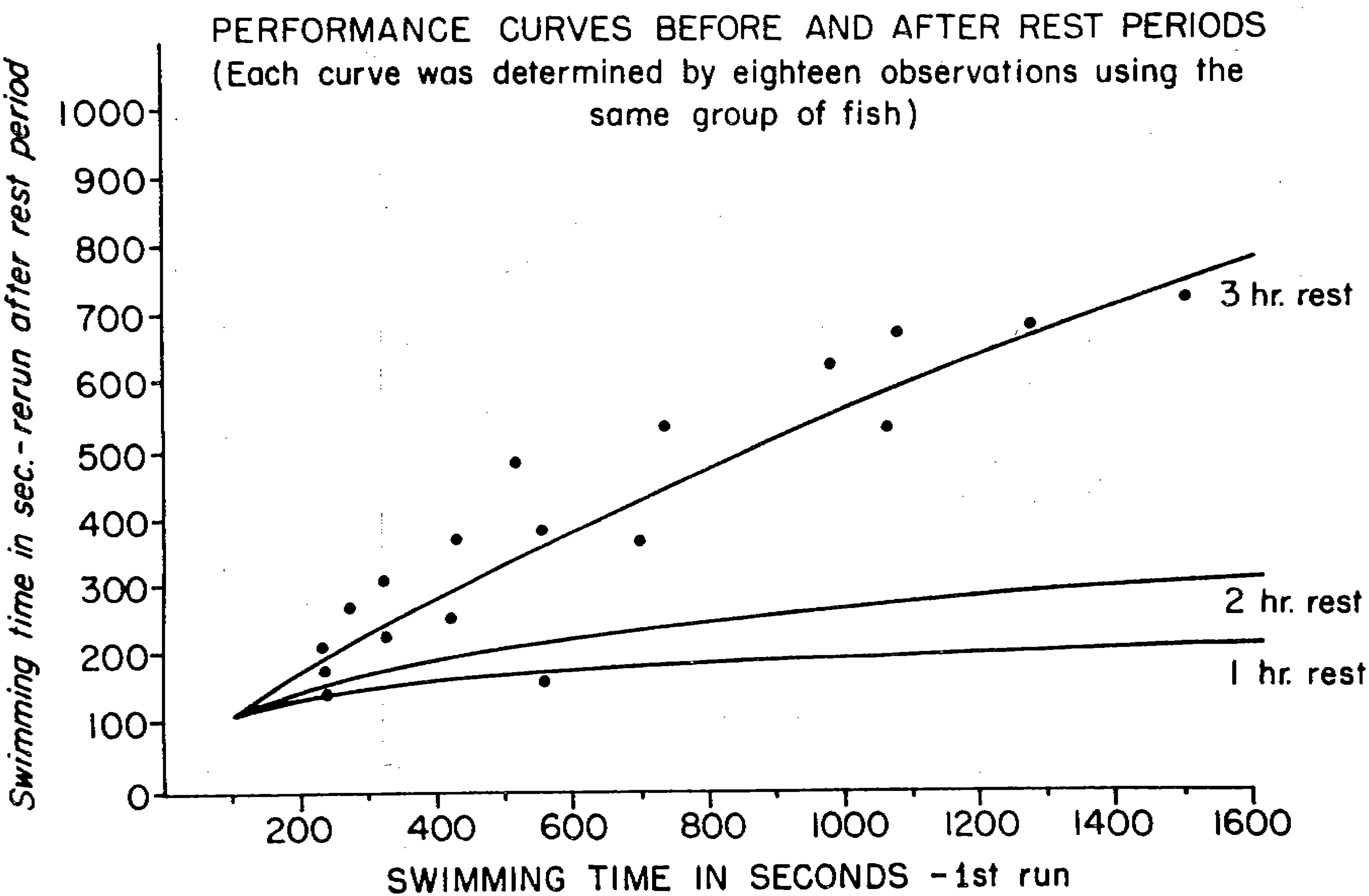


Figure 4. Theoretical recovery curves.

The re-run performances were much higher when the fish were given a three-hour rest rather than a one or two-hour rest. Using the mean first run performance for all tests (515 seconds), the recovery percentages, calculated by multiplying the ratio of the re-run performance to the first performance by 100, for the one, two and three-hour rest periods were respectively: 31%, 43% and 67%.

The lower percentage recovery associated with the longer first performances is in all probability related to the fish's state of exhaustion at the end of the first run, assuming motivation remains constant. If this is so, it was not detected by the brief examination made at the end of each test. The fatigue condition ratings (page 9) were not directly related to the test performances. Nakatani (11) was unable to find any simple correlation between inorganic phosphate levels, which increased markedly after exercise, and the length of time the fish were exercised. Nakatani worked with yearling steelhead. However, a pronounced difference in swimming motion was noted between the high and the low-performance silver salmon. Low-performance fish, as the term is used here, would include fish Nos. 1, 4, 7, 10, 11, 13 and 17 (Table 1). Fish Nos. 3, 5, 8, 9 and 18 would be considered high-performance fish. The oscillatory movements of low-performance fish were of greater amplitude and involved more of the anterior portion of the body than those of the high-performance fish. This difference was most noticeable during the first part of the test. Toward the end of the test, just before the fish lost a Type I Lap, this struggling type of motion was observed, regardless of the length of time the fish had swum. The difference in motion suggests that, although the water velocity was held constant, the total bodily activity necessary to maintain position upstream from the light and electrode barrier varied greatly between individual fish.

Ryan (12), in summarizing the results of a number of experiments involving different types of muscular fatigue, states that humans recover work capacity more rapidly after quick exhaustion than after slower development of fatigue. Results of earlier experiments on recovery time in the annular tank (7) indicate that Ryan's statement would also apply to fish. In those experiments both sockeye and silver salmon were fatigued rapidly by swimming in a steadily accelerating velocity which caused the fish to work at a high rate regardless of capacity. The salmon fatigued by swimming at an accelerating velocity recovered from the swimming effort in a much shorter time than the silver salmon fatigued by swimming at a constant speed of 3.4 f.p.s. The rapid recovery shown by the low-performance silver salmon in the present study may be at least partially explained by the dependence of recovery time on the rate of fatigue.

The 67 percent recovery after a three-hour rest tends to be a minimum estimate of recovery. A performance decrement was shown to be associated with tests that were conducted toward the end of the testing schedule on any given day. This factor would affect the re-runs (the last group tested each day) but not the first runs of the fish that were given a three-hour rest between runs. A comparison of the swimming performances of the fish on the re-runs after a three-hour rest to the performances of the fish on the first run that were exposed to the most pre-test disturbances before the first run (the first runs of the fish that were given a one-hour rest) offers an evaluation of this confounding factor. As each fish was tested under both rest conditions the variation due to differences between fish was separated from the experimental error. This comparison yielded an F value of 1.13 (with

1 and 17 degrees of freedom, an F value of 4.45 is significant at the five percent level) using the transformed data. The respective mean performance times were 442 seconds and 391 seconds for the first runs before a one-hour rest and the re-runs after a three-hour rest.

The fish's total activity during the swimming test is only partially represented by the length of time the fish swam. A number of concomitant observations were recorded during each test (as described in methods and materials section) that are of interest in themselves and because of the possible bias they could introduce in performance time. For example, the fish's position in the test flume would determine the water velocity in which the fish was swimming and therefore influence energy requirements necessary to maintain position. Scores were assigned to the several position readings taken during each test according to the following plan: Inside channel - 1, center channel - 2, and outside channel - 3. Using these scores it was shown that although the individual fish changes position often during a test, the average positions were fairly constant. The average position was not correlated with the length of time the fish swam before becoming exhausted. The salmon did not exhibit any preference for the inside of the channel where the water velocity was slower, even after one or more days of testing. The overall average position, computed by treating the average for each test as a single observation, was 2.24,i.e., slightly to the outside of the center of the channel.

The number of electrical shocks received by a salmon during one test varied from 3 to 95; and the total number of shocks per salmon for the three-day test period varied from 16 to 177. The salmon appeared to differ considerably with regard to the number of shocks necessary to induce swimming.

Little is known about the effect of electric shock on intact organisms, however, there was no performance decrement associated with the number of contacts with the electrical barrier such as might be expected if the shocks were seriously interfering with the salmon's normal muscular contraction and coordination. Survival time was also unrelated to the number of shocks. Analysis of the shock data in the Latin square format (Table 1) yielded a significant difference between fish (at the one percent level) while the day, rest period and order factors were all insignificant.

The number of Type II and III Laps, and reverses was small and highly variable and did not reveal any clear-cut relationship to performance. Of the variables length, sex and survival time, only length was significantly correlated with performance. The length-performance correlation coefficient was -0.52, suggesting that the larger fish were weaker swimmers or were adversely affected by the experimental conditions.

Tagging operations, especially those concerned with estimating speed of upstream migration or passage time for a fish ladder, could be improved by allowing the salmon to rest overnight after being tagged. Fish released in a fatigued condition are unable to continue their journey upstream and may be swept some distance downstream before finding a suitable resting area. These temporarily incapacitated fish would also be more susceptible to predation.

The dependence of recovery time on the degree and type of fatigue is strong evidence of the necessity for adequate resting facilities in a fish pasing device in which water velocities exceed 3-1/2 f.p.s. (e.g., a Denil fishway) for any considerable distance. Lacking information on the relationship of the work and rest pattern to total work accomplished in a given time, it is recommended that facilities should be provided that would allow the salmon to set their own pace. The experimental results indicate that to prevent extensive exhaustion, salmon should not be forced to maintain a strenuous effort for more than a few minutes.

Conclusions

1. Recovery from an exhaustive swimming effort was found to be 31 percent complete for a one-hour rest, 43 percent complete for a two-hour rest, and 67 percent complete for a three-hour rest. The 67 percent recovery figure for the three-hour rest tends to be a minimum estimate.
2. All fish recovered completely after an overnight rest of 18 to 24 hours.
3. A significant swimming performance decrement was associated with pre-test activity, suggesting that salmon are highly susceptible to fatigue.
4. The rate at which the fish were fatigued appeared to affect the length of the recuperation period. The salmon which swam for a longer time before becoming fatigued also required a longer rest period to recover their original swimming ability than the salmon which were fatigued rapidly.

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