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RELATIVE VULNERABILITY OF THERMALLY SHOCKED
JUVENILE SALMONIDS TO PREDATION⁽¹⁾

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ABSTRACT

Thermally shocked juvenile rainbow trout and chinook salmon were found to be selectively preyed upon by larger fishes under controlled laboratory conditions when both shocked and control fish were offered simultaneously. Relative vulnerability to predation increased with time of sublethal exposure to lethal temperatures. Significant increases in predation rates were found at thermal doses above 10% (chinook) and 20% (rainbow) of the doses causing equilibrium loss visible to the investigator. The effects are partly reversible. Quantitative description of observed differences allows their use in designing safe thermal releases to the aquatic environment.

INTRODUCTION

Acute thermal shock can occur to juvenile salmon passing involuntarily through heated industrial discharges in rivers during out-migration. Exposures to lethal high temperature may occur in situations where temperatures are extremely high or where rate of passage through the mixing zone is slow, or both. Often, however, exposures will be of sublethal duration even though the temperature encountered may be within the lethal range established by laboratory thermal resistance testing (e.g., Brett, 1952). The latter appears to be the case in thermal effluents discharged from the plutonium-production nuclear reactors at the U.S. Atomic Energy Commission (AEC) Hanford Works in the Columbia River above Richland, Washington (Jaske et al., in press). Although the effects of high temperature exposure in thermal plumes may not be directly lethal, other factors acting subsequent to thermal shock may induce mortality.

One factor affecting survival of emigrating salmonids under natural conditions is predation by larger fishes (Ricker, 1941; Roos, 1960).

The objective of this study was to determine whether sublethal exposures to elevated temperatures will measurably increase rates of predation.

To assess this question, a method of testing relative performance of prey fish in the laboratory was adopted from Bams (1967), who compared the performance of hatchery-reared and wild sockeye salmon. Measures of absolute performance, and of changes in this performance with variations of an environmental factor such as temperature, must be obtained from accurate measurement and/or rigid control of all factors affecting the predation situation. These complex and interacting factors include predator recognition, energy supply and delivery systems of the prey, predator and prey densities, predator hunger, rate of searching by the predators, and several others. The possible components of functional responses in predation have been described by Holling (1966). Unless tests separated in time are rigidly controlled and performed under near identical conditions, comparison of absolute performance data is difficult. Differences among individual test animals provide additional obstacles to precise comparison of results.

For groups of fish simultaneously available, a simplified procedure was developed by Bams (1967) which accurately measures relative performance. It not only identifies differences between groups in ability to evade predators, if such differences exist, but it quantifies those differences in relative and comparable terms. The procedure involves simultaneous testing of two groups of fish under identical conditions in one tank with the same predators. It does not require accurate control or measurement

of the actual conditions, as long as they are favorable for proper functioning of the predator and prey organisms.

MATERIALS AND METHODS

Juvenile chinook salmon, Oncorhynchus tshawytscha (Walbaum), and rainbow trout, Salmo gairdneri (Richardson), were used as prey fish. They are abundant in the Hanford area annually from April to August (Park, 1969; Mains and Smith, 1964; Becker, in press).

Juvenile chinook for these tests were raised in the Battelle-Northwest hatchery from eggs secured from Priest Rapids Dam. The fish averaged 64.28 mm, standard deviation 9.91, in length from snout to the hypural plate and 3.82 g, standard deviation 1.89, in weight when tests were run in July and August. All were acclimated to 15 °C. Juvenile rainbow were also raised in our hatchery from adult rainbow brood stock maintained for several years. Juvenile rainbows averaged 75.37 mm (standard deviation 9.60) length (Figure 5) and 8.02 (standard deviation 2.67) grams. Rainbow were not acclimated to a constant temperature, but were held in hatchery water pumped directly from the Columbia. Temperatures, which were recorded continuously, ranged from about 17 to about 19 C during the tests.

Predators for preliminary chinook and all rainbow tests were adult rainbow trout more than three years old from the hatchery brood stock. Two-year-old rainbows, which were more agile than older adults, were used as predators for the 1969 chinook tests. Preliminary tests were conducted with adult squawfish obtained by shoreline seining from the river.

Each test was executed according to the flow diagram in Figure 1. Fish were removed from a common stock tank and both groups were

marked by a liquid nitrogen cold brand (Fujihara and Nakatani, 1967). After a minimum of 72 hours for recovery from handling, and for appearance of a strong brand, each of the two groups was transferred to a different tank, one containing heated water, the other containing water at acclimation temperature. The exposure tanks were supplied with flowing water which had been air-equilibrated after heating to avoid additional stress from gas supersaturation. Temperatures were maintained by a control valve (Model PX9700, Automatic Controls Co.) that mixed hot and cold water supplies.

The shock temperatures selected were 28.0 ± 0.05 °C for chinook and 30.5 ± 0.05 °C for rainbow. These temperatures are within the lethal ranges for the test species, with median death times approximately 22 1/2 min and 15 1/2 min, respectively (Coutant and Dean, unpublished). Because of recognized behavioral changes (i.e., loss of equilibrium) at a well-defined point prior to death, different times of exposure were administered that were percentages of this median equilibrium-loss dose, (ELD). The relationship between equilibrium loss and death in chinook and rainbow will be discussed in another paper. The median equilibrium loss dose used as a baseline was redetermined at several intervals throughout the rainbow test series to check for possible changes in acclimation. Figure 2 presents the relationship between doses used in this study and units of time, percent of median death time, and percent of the median equilibrium loss dose.

Upon completion of the timed dose, shocked and control groups were reunited in the acclimation temperature. In tests with no recovery period, the mixed groups were offered within one minute to the predators.

Recovery periods were spent by the mixed groups under acclimation conditions where controls were given the sham dose, followed by simultaneous addition of all live fish to the predator tank.

Predation tests were conducted in 4- or 6-foot diameter (1.2 or 1.8 m), circular fiberglass tanks with water depths of 65 and 80 cm, respectively. A continuous exchange of water was maintained at about 15 liters per min. entering at the perimeter surface and leaving via a double standpipe from the center bottom. The tanks were devoid of structures, other than the inlet pipes, outflow standpipe and the tank walls, which would provide visual protection to the fry. Mossman (1955) discusses the theoretical effectiveness of tank walls as cover (by limiting the angles of attack and necessitating "braking" by the predator to avoid collision); practical concerns limited our compensating for such effects. New predators soon learned to avoid long-range lunges for prey and developed a technique of close approach and short jabs.

After introduction of fry, the predators were allowed a maximum of one-half hour to remove approximately 50% of the prey. The remainder was removed, and test and control fish were counted. Rainbow prey were then placed under refrigeration until length and weight determinations were made. The reason for limiting the level of predation (Bams, 1967) is the change in ratio of prey availability during a test, i.e., the decrease in relative abundance of the preferred group throughout the period of exposure to predation. The measured predation rate of the preferred group, based on the results of the overall test, is lower than the actual instantaneous rate for that group. This feature increases as predation continues within a test. To keep the variation in availability

ratios within reasonable limits and the predation rates thus measured comparable, Bams chose to standardize the overall level of predation. His suggestion was adopted for this study.

Surviving fry were not used in subsequent trials as a precaution against learning or long-term effects of thermal shock. Predators were used repeatedly, however, as often as they were able to consume 25 fish within a half-hour period. A longer predation period was unsuitable due to possible recovery of prey fish from thermal shock effects. Predators required some training to accept living prey readily after years of artificial hatchery feed. Once trained, they generally consumed the required number of fish within 3 to 10 min. There was no indication that predator groups increased their selectivity for a given group of prey after several tests.

The statistic chosen by Bams (1967), and used in this study to express the difference in predation rates upon the two groups of fish is the ratio $d_p = \frac{i_1}{i_2}$, where i_1 and i_2 are, respectively, the instantaneous mortality rates of the first (shocked) and the second (control) group. The determination of i is achieved as follows. If one assumes a constant mortality rate of test (or control) fish from one time interval to another within a test, then loss of fish is proportional to population size at termination of the test. If the time of death for each test fish could be recorded, the data could be fit by regression analysis to get $S = Ie^{-i(t)}$, where S = the number of test fish remaining at completion of the test, I = the initial number of fish, i = instantaneous mortality rate, and t = time. But, if we are only able to determine the number of fish at the end of a test, and we express population size as a percentage

of the initial number of fish, then for the same sequence of fish deaths we would have the equation $s = 1.00 e^{-i(t)}$, where s = survival proportion, $\frac{\text{No. at finish}}{\text{No. at start}}$. When time is set as a unit interval, we get $s = e^{-i}$, or $i = -\log_e s$, as used by Bams. The chi-square analysis was used to test for significance of observed differences in predation rates.

RESULTS

Juvenile Rainbow Trout Prey

The results of predation experiments carried out in 1968, are presented in Table 1. There was no recovery period in one series of tests, while one-half hour recovery was allowed in a second series. Trends in the differences in predation rates (d_p) for different lengths of thermal exposure (both for individual tests and for all tests in a treatment group) are illustrated in Figure 3.

No recovery. Tests for heterogeneity reveal a consistency within each of the treatment groups of this series, which includes 15% through 50% of the equilibrium loss dose. Discussion of treatments, therefore, can be based on the χ^2 on totals ("combined") for each length of thermal exposure. There were no significant differences (95% level) between the numbers of test and control fish consumed after the 15% and 20% exposures. Predators did select significantly more test fish (0.05 or 0.01 levels), however, after the 25%, 30%, 40% and 50% exposures, indicating detriment at these thermal doses.

The trend in d_p ratios for this series (i.e., the calculated measure of difference in the rates of predation between test and control prey) shows an intercept with 1 (no difference) between the 15 and 20% dose

levels (Figure 3). The difference increases steeply, although with a somewhat anomalous decrease at 40%. The pattern is relatively unchanged if one considers a linear regression analysis of, alternatively, the unweighted means of individual d_p 's in the treatment groups or the combined d_p 's, both of which are illustrated. Both regressions are significant (0.05 level) with correlations (relation between dose and d_p) of 0.85 and 0.88, respectively.

One-half hour recovery. Tests for heterogeneity indicated that the 60%, 80% and 100% treatments were homogeneous but that the 50% test was not. Discussion of the latter exposures must be based on individual tests. Taken individually, each test in this treatment indicated no significant difference between consumption of heat shocked and control prey. Based upon χ^2 of totals ("combined"), there were significant differences between predation of test fish and controls at doses of 80 and 100% of the equilibrium loss dose, but no significant difference at 60%.

The group d_p ratios, connected by lines in Figure 3 for clarity, exhibit an apparent trend with an intercept with 1 estimated to be near 50%. There were too few treatments in this series, and too few tests within each of the treatments to allow meaningful regression analysis.

Juvenile Chinook Salmon Prey

Preliminary tests were run in 1968 at exposure levels of 50 and 100% ELD, with no recovery time allowed. These results, which should be considered exploratory, are presented in Table 2.

Tests in 1969 on juvenile chinook are presented in Table 3. No recovery was allowed in the first series; there was one-half hour recovery

in a second series and one set of tests was conducted at 80% ELD with one hour of recovery. Trends in d_p ratios for the "no recovery" and "one-half hour recovery" series are shown in Figure 4A and 4B, respectively.

Preliminary tests, no recovery. Data from four tests on fish exposed to 50% ELD were not consistent. There is strong indication of increased predation on the thermally shocked fish in all but one test, but an insufficient number of fish (14) was consumed in this test to render it a valid representation. Results from the three tests at 100% were homogeneous, and the series indicated strongly different predation rates between experimental and control fish.

No recovery Analysis for heterogeneity indicated that tests within each exposure level of this series (5, 10, 20, 30, and 50%) were consistent, and that discussion can be based upon the combined χ^2 for each exposure treatment. There were significant differences (0.05 level of probability of error) between test and control fish consumed at all doses except 5%.

A clear trend in d_p ratios for this series is evident from Figure 4A. An intercept with 1 (no difference) is suggested near 5 to 10%, with a rapid rise with increasing thermal dose. Linear regression of d_p ratios for combined tests had a high correlation (0.96), but an exponential model may be more appropriate (dashed line). For comparable exposure times, d_p ratios for chinook prey exceed considerably those for rainbow trout prey.

One-half hour recovery. All thermal exposure treatments in this series (20, 40, 50 and 80% of the median equilibrium loss dose) were homogeneous. Only the 80% exposure group yielded a χ^2 on totals that

was significant. Examination of d_p ratios (Figure 4B) reveals a slowly rising trend (in contrast to the steep rise without recovery) with increasing thermal doses. An intercept with 1 is suggested at doses near 20%, although variations from 1 at 40% and 50% are so slight as to be insignificant with the number of tests conducted.

One hour recovery. The results of the four tests were homogeneous, and the χ^2 on totals was significant. Despite one hour recovery time, the surviving fish exposed to 80% of their median equilibrium loss time were eaten at a rate significantly greater than the unexposed control fish.

Predation and Fish Length

Fish performance varies greatly with size, and size differences must be considered in predation tests. However, obtaining accurate individual length and weight measurements, while retaining fish in good physical condition immediately prior to an experiment, proved mutually exclusive. Consequently, size data were taken only on survivors from individual tests with juvenile rainbow trout and from stock fish at periodic intervals (Figure 5). Thorough size data were not collected on juvenile chinook.

Surviving shocked and control fish were never significantly different in length, as indicated by overlapping 0.95 confidence intervals. Both measured considerably different from stock fish in some tests, although the survivors were at times smaller and at others, larger than the stock.

Squawfish Predators

The northern squawfish, Ptychocheilus oregonensis (Richardson), is presumed to be an important predator of juvenile salmonids in the Columbia River system. Because of this, it was the first predator considered for these experiments. Feeding performance of this species in laboratory tanks proved unreliable, however, necessitating selection of an alternate. The few successful tests, at 50 and 100% ELD, yielded results that were within the variation of data obtained with large rainbow predators.

DISCUSSION

Experimental fish were actually subjected to two thermal shocks during the timed thermal dose. The first was an abrupt rise in temperature at the time of transfer to the heated water. The second was an abrupt decrease of similar amount on return to the acclimation temperature. The latter shock induced momentary loss of equilibrium in some fish not showing these symptoms in the heated bath. The independent effects of these two shocks could not be assessed in the experiments, although it is appreciated that "cold shock" may also be important since it occurred just prior to exposure to predators.

Under controlled conditions of the experiments, differential predation remains a function of a number of factors, some of which were identified by Bams. They include discovery rate, attack rate, capture rate, retention, availability, level of predation and relative sizes of predators and prey.

Discovery

A difference in discovery rates by predators between two groups of otherwise simultaneously available fry would constitute a basis for

differential predation. Test containers selected for this study offered few physical barriers to the discovery of fry by predators such as might occur in nature. But, as Mossman (1955) discussed, outlet structures, water surface, and tank walls do provide some cover, at least theoretically. When a prey fish approaches the surface, it limits the directions from which discovery (and attack) can come. Attempts were made to ensure that fish from both sources in an experiment mingled freely in the transfer container (a 9-liter plastic pail) and that they were equally exposed to the predators when dumped quickly into the test tank.

Of probable high significance to discovery is the behavior of shocked fish. At the level of thermal dose sufficient to induce median loss of equilibrium, half of the shocked fish have been rendered unable to swim. Most of these fish regain equilibrium on return to cooler water, but their behavior is abnormal, even to the investigator. Previous studies (Coutant and Dean, unpublished; Tsukuda and Ohsawa, 1958) indicate a visible progression of behavioral changes in water of lethal temperature leading to the well-defined point of equilibrium loss. Such changes involve frequency of bursts of swimming activity, position of fish in the water (e.g., head at the surface, tail angled down), and timing and coordination of fin beating, among others. Such patterns are likely to prompt rapid discovery by a lurking predator. Obviously disoriented prey were, in fact, eaten quickly in these tests. There was also a tendency for prey fish to school, perhaps to avoid predation. Some shocked fish did not join the school as it formed in the predator tank, thus inviting preferential discovery. No separate records of differential discovery rate during predation could be made in these experiments,

since most individual prey fish could not be identified reliably in the flurry of predatory and escape activity.

Parker et al. (1963) suggest that differential recognition requires that the "abnormal" fish be in the minority among the population being tested, and that its abnormality stands out for the predator as a result of the statistical imbalance. Their experiments were designed to capitalize on this assumption. Bams (1967), however, used groups of fish supplied in equal numbers and still found consistent predator preference for one group, as in the present study. Other factors may, therefore, be operative at the discovery stage, such as instinctive or learned ability by the predator to quickly perceive particular visual patterns (e.g., the flashing side of a distressed fish). Whereas Bams considered such knowledge by the predator to be remote when comparing hatchery and wild fish having but minute differences, it is a highly plausible factor when the prey fish is injured with a thermal shock.

Attack

After discovery of the prey, the predator may attack test and control groups at different rates, i.e., exert selection by accepting or rejecting each potential prey on the basis of a characteristic or group of characteristics that it perceives. Fish location may also affect the routes available for the predator to attack. Attack rate is likely important in these experiments. Abnormal prey behavior patterns described above, which may vary in degree from high to low levels of thermal dose can provide more suitable cues for initiating pursuit than would the behavior of unshocked fish. Mossman (1955) cites evidence that suggest provocation

of attacks by sign stimuli associated with weakness of the prey species. One behavioral change evident in fish subjected to high percentages of median equilibrium loss dose was slowness in seeking shelter, however futile this attempt. As with the discovery rate, the basic attack rate parameter could not be established directly in the tests and for the same reasons.

Capture

Once attack is initiated, a difference may occur in the rates of capture between the two groups. Capture is principally dependent upon escape performance of the prey fish, although the confines of the test tank may influence capture ratios if the two prey groups do not mix thoroughly. This performance is a complex interaction of several prey abilities, including ability to detect pursuit, burst swimming capacity, agility in changing swimming direction, and capability for a prolonged series of extreme exertions. None of these could be measured independently in these tests. Thus, the statistic for vulnerability to capture must also derive from the overall predation rate. It seems reasonable, however, to ascribe some of the observed differences in predation rates to a differential capture rate. Fish that have undergone long sublethal thermal doses are obviously less responsive to manual stimulation than are unshocked fish from the same source. This change in responsiveness may be manifested in recognition of predators as well, and may be progressive from very low thermal doses. Herting and Witt (1967) ascribed an observed increase in bowfin predation on starved, diseased or otherwise weakened bluegill sunfish and largemouth bass to sluggishness in swimming of the weakened prey.

Retention

A parameter not mentioned by Bams, yet evident in these experiments (particularly when squawfish were tried as predators) is prey retention. Some prey fish were apparently caught (i.e., they show teeth marks) yet were not retained. This may be the result of a predator deficiency with seizure, of aborted multiple catches, of instinctive reaction of an already gorged fish, or perhaps of a faculty which makes the prey temporarily less palatable. The possibility of retention differences was not recognized sufficiently early in the experiments for correlation with prey source. Unless obviously regurgitated, the rejected fish were considered alive.

Other Factors

The questions of availability and level of predation were discussed above with methodology. Equal numbers of fish from shocked and control sources were introduced initially to all test tanks, and the experiment was terminated as nearly as possible when half of the fish had been dispatched. The latter procedure was difficult to adhere to in practice. Several tests were voided because predation was stopped prematurely or too many fish had been eaten. In general, tests were not considered valid if more than 35 or fewer than 15 fish remained. The results given for a particular test include a bias proportional to the indicated rates of predation and the difference between the total fish remaining and 25. Estimation of this bias is not easily made and it was therefore not carried out.

Experiments by Bams and others have confirmed the hypothesis that fish performance, especially swimming ability, is strongly correlated

with fish length. For proper assessment of differential performance, the groups compared must be of equal size range. It was not possible to determine this precisely for samples drawn from a common stock prior to each test, however, and still retain fish in good condition. The three sets of measurements made (sample of stock, surviving shocked fish, and surviving control fish) provided some assurance of comparability, since surviving shocked and control fish did not differ significantly in lengths. Both surviving groups differed from the stock in some tests, suggesting that inadvertent selection for length occurred, either by predators or by the investigator in choosing fish from the stock, but without regard to fish treatment. This apparent selection was not consistent throughout the tests, for survivors were smaller than the stock in some tests (Nos. 27, 28 and 29) but larger in others (e.g., 59, 60, 61, 63). While the relationship of fish length to observed differences in predation must remain unclear as long as the prey are consumed, the role of length appeared to be minor.

Reversibility of Effects

Whatever the causes for differences in predation rates shown by these experiments, they are clearly reversible to some degree with time. In tests with "no recovery", a maximum of one-half hour was actually allowed for the predation to occur, during which fish not yet eaten could be recovering. In most cases the act was accomplished in less than half that time. The experiments with juvenile chinook were generally over within 5 min. of prey introduction. When a minimum of one-half hour was allotted for recovery prior to introduction of mixed prey, the

thermal dose required to invoke differences in predation rates rose approximately three to four times, from about 20% to about 80% of the equilibrium loss dose. This suggests that further recovery time might erase all demonstrable effects of thermal shock in the range of temperatures used. This appears unlikely without further study because of 1) the significantly greater predation rates in the single series with juvenile chinook at 80% with one hour recovery and 2) the "insignificant" but noticeably unequal predation rates at 40 and 50% with a half hour recovery.

Increased vulnerability of shocked fish to predation without recovery time is strongly correlated with the actual dose received. Following recovery for one-half hour, there is little correlation, however.

These experiments have dealt solely with differing sublethal thermal doses at arbitrarily-selected lethal temperatures. Further study is desirable at a range of lethal and sublethal shock temperatures in order to determine if there is a consistent relationship between thermal dose causing significantly increased vulnerability to predation and percentage of the equilibrium loss or death doses.

In conclusion, it is apparent that small, sublethal exposures to potentially lethal high temperatures incapacitate juvenile salmonids to an extent that they are more vulnerable, at least temporarily, to being eaten by predators. The differences in predation rates can be described quantitatively and thus they can be included in scientific design of safe mixing zones for thermal releases to the aquatic environment.

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TABLE 1. Results of Predation on Juvenile Rainbow Trout by Adult Rainbow Trout. Acclimation temperature, 17-19 C; shock temperature, 30.5 C. Number of fish in each group at start of predation was 25, unless noted. [$i = -\log_e$ (survival proportion); $d_p = \frac{i \text{ shocked}}{i \text{ control}}$]

Percent Equilibrium Loss Dose	Number Surviving		Chi Square (1 d.f.)	i		d_p
	Shocked	Control		Shocked	Control	
No Recovery						
15	9	11	0.200	1.021	0.820	1.244
15	16	9	1.960	0.446	1.021	0.436
15	23	16	1.256	0.083	0.446	0.186
Combined Heterogeneity χ^2	48	36	0.857 1.559	0.446	0.734	0.608
20	22	15	1.324	0.127	0.510	0.250
20	20	22	0.095	0.223	0.127	1.745
20	14	20	1.058	0.579	0.223	2.598
20	14	17	0.290	0.579	0.385	1.503
20	13	14	0.037	0.653	0.579	1.127
20	14	9	1.086	0.579	1.021	0.567
20	10	13	0.391	0.916	0.653	1.401
20	9	13	0.727	1.021	0.653	1.562
Combined Heterogeneity χ^2	116	123	0.205 4.793	0.544	0.486	1.120
25	9	13	0.727	1.021	0.653	1.562
25	6	14	3.200	1.427	0.579	2.461
Combined Heterogeneity χ^2	15	27	1.714 2.213	1.204	0.616	1.954
30	11	17	1.285	0.820	0.385	2.128
30	14	23	2.189	0.579	0.083	6.953
30	10	20	3.333	0.916	0.223	4.106
Combined Heterogeneity χ^2	35	60	6.579 0.028	0.761	0.223	3.412
40	13	18	0.806	0.653	0.328	1.990
40	8	18	3.846	1.139	0.328	3.468
40	19	21	0.100	0.274	0.174	1.574
40	11	18	1.689	0.820	0.328	2.499
Combined Heterogeneity χ^2	51	75	4.571 1.870	0.673	0.287	2.340

TABLE 1 (Continued)

Percent Equilibrium Loss Dose	Number Surviving		Chi Square (1 d.f.)	i		d p
	Shocked	Control		Shocked	Control	
50	8	20	5.142	1.139	0.223	5.106
50	5	18	7.347	1.609	0.328	4.899
50	1	20	17.190	3.218	0.223	14.425
50	1	19	16.200	3.218	0.274	11.729
50	2	12	7.142	2.525	0.733	3.441
Combined Heterogeneity χ^2	17	89	48.905 5.076	1.995	0.339	5.873
Half-Hour Recovery						
50	16 ¹	23	1.256	0.446	0.083	5.352
50	9 ¹	3	3.251	0.980	2.120	0.462
50	7 ¹	16	3.165	1.232	0.446	2.760
50	16 ¹	10	1.641	0.405	0.916	0.442
Combined Heterogeneity χ^2	48	52	0.0613 9.25	0.703	0.653	1.075
60	11 ⁴	23	2.423	0.646	0.083	7.755
60	17 ²	17	0.059	0.302	0.385	0.783
Combined Heterogeneity χ^2	28	40	0.866 1.61	0.451	0.223	2.025
80	4 ¹	21	10.881	1.791	0.174	10.276
80	13	16 ⁵	0.310	0.653	0.446	1.465
80	11	24 ⁵	4.828	0.820	0.040	20.111
80	14	18	0.500	0.579	0.328	1.765
Combined Heterogeneity χ^2	42	80	11.457 5.67	0.857	0.223	3.842
100	12 ³	20	1.113	0.606	0.223	2.716
100	6 ³	17	3.966	1.299	0.385	3.368
100	15 ¹	19	0.321	0.470	0.274	1.712
Combined Heterogeneity χ^2	33	56	3.914 1.49	0.723	0.292	2.474

¹24 fish at start of predation

²23 fish at start of predation

³22 fish at start of predation

⁴21 fish at start of predation

⁵No fish eaten, but one assumed eaten for purposes of calculation

TABLE 2. Results of Predation on Juvenile Chinook Salmon by Adult Rainbow Trout. Acclimation temperature, 15 C; shock temperature, 28 C. Number of fish in each group at start of predation was 25. No recovery. Column headings are explained in Table 1.

Percent Equilibrium Loss Dose	Number Surviving		Chi Square (1 d.f.)	i		d _p
	Shocked	Control		Shocked	Control	
50	5	17	6.545	1.609	0.385	4.173
50	15	21	1.000	0.510	0.174	2.929
50	1	24 ¹	21.160	3.218	0.040	78.851
50	3	13	6.250	2.120	0.653	3.242
Combined Heterogeneity χ^2	24	76	27.040 8.908	1.427	0.274	5.200
100	5	16	5.761	1.609	0.446	3.450
100	1	21	18.181	3.218	0.174	18.461
100	2	23	17.640	2.525	0.083	30.291
Combined Heterogeneity χ^2	8	60	39.764 1.819	2.238	0.223	10.029

¹No fish eaten, but one assumed eaten for purposes of calculation

TABLE 3. Results of Predation on Juvenile Chinook Salmon by 2-year-old Rainbow Trout. Acclimation temperature, 15 C; shock temperature, 28 C. Number of fish in each group at start of predation was 25, unless noted. Column headings are explained in Table 1.

Percent Equilibrium Loss Dose	Number Surviving		Chi Square (1 d.f.)	i		d _p
	Shocked	Control		Shocked	Control	
No Recovery						
5	8	10	0.222	1.139	0.916	1.243
5	9	13	0.727	1.021	0.653	1.562
5	11	14	0.360	0.820	0.579	1.415
5	9	14	1.086	1.021	0.579	1.762
5	13	13	0	0.653	0.653	1.000
5	8	8	0	1.139	1.139	1.000
5	15	12	0.333	0.510	0.733	0.695
Combined Heterogeneity χ^2	73	84	0.770 1.96	0.874	0.733	1.191
10	3	22	14.440	2.120	0.127	16.586
10	10	19	2.793	0.916	0.274	3.338
10	13	16	0.310	0.653	0.446	1.465
10	14	22	1.777	0.579	0.127	4.535
10	9	22	5.451	1.021	0.127	7.992
10	8	13	1.190	1.139	0.653	1.742
Combined Heterogeneity χ^2	57	114	19.000 6.96	0.967	0.274	3.525
20	6	18	6.000	1.427	0.328	4.344
20	3	24	16.333	2.120	0.040	51.939
20	8	21	5.827	1.139	0.174	6.535
20	7	23	8.533	1.272	0.083	15.266
Combined Heterogeneity χ^2	24	86	34.945 1.75	1.427	0.150	9.462
30	3	23	15.384	2.120	0.083	25.428
30	1	22	19.173	3.218	0.127	25.180
30	2	22	16.666	2.525	0.127	19.757
30	1	23	20.166	3.218	0.083	38.604
Combined Heterogeneity χ^2	7	90	71.020 0.37	2.659	0.105	25.239
50	1	24	21.160	3.218	0.040	78.851
50	1	24	21.160	3.218	0.040	78.851
Combined Heterogeneity χ^2	2	48	42.320 0.000	3.218	0.040	78.851

TABLE 3 (Continued)

Percent Equilibrium Loss Dose	Number Surviving		Chi Square (1 d.f.)	i		d p
	Shocked	Control		Shocked	Control	
Half-Hour Recovery						
20	11	14	0.360	0.820	0.579	1.415
20	10	14	0.666	0.916	0.579	1.580
20	15	14	0.034	0.510	0.579	0.881
20	12	16	0.571	0.733	0.446	1.644
20	11	11	0	0.820	0.820	1.000
20	12	12	0	0.733	0.733	1.000
Combined Heterogeneity χ^2	71	81	0.657 0.97	0.747	0.616	1.213
40	5	10	1.666	1.609	0.916	1.756
40	10	14	0.666	0.916	0.579	1.580
40	10 ₁	14	0.666	0.916	0.579	1.580
40	9 ¹	14	0.892	0.980	0.579	1.691
Combined Heterogeneity χ^2	34	52	3.588 0.30	1.068	0.653	1.634
50	12 ¹	20	1.687	0.693	0.223	3.106
50	12 ²	11	0.043	0.733	0.820	0.894
50	8 ²	16	2.045	1.056	0.446	2.366
50	9 ¹	11	0.126	0.980	0.820	1.194
Combined Heterogeneity χ^2	41	58	2.267 1.63	0.850	0.544	1.561
80	9	17	2.461	1.021	0.385	2.649
80	5 ²	21	9.846	1.609	0.174	9.230
80	9 ²	20	3.311	0.938	0.223	4.204
80	8 ¹	12	0.645	1.098	0.733	1.496
Combined Heterogeneity χ^2	31	70	13.898 2.36	1.140	0.356	3.198
One Hour Recovery						
80	9 ²	16	1.422	0.938	0.446	2.102
80	12 ³	14	0.004	0.606	0.579	1.045
80	3 ²	16	7.858	2.036	0.446	4.564
80	7 ⁴	15	0.911	0.944	0.510	1.848
Combined Heterogeneity χ^2	31	61	5.820 4.38	1.020	0.494	2.064
¹ 24 fish at start of predation						
² 23 fish at start of predation						
³ 22 fish at start of predation						
⁴ 18 fish at start of predation						

FLOW DIAGRAM, PREDATOR TESTS

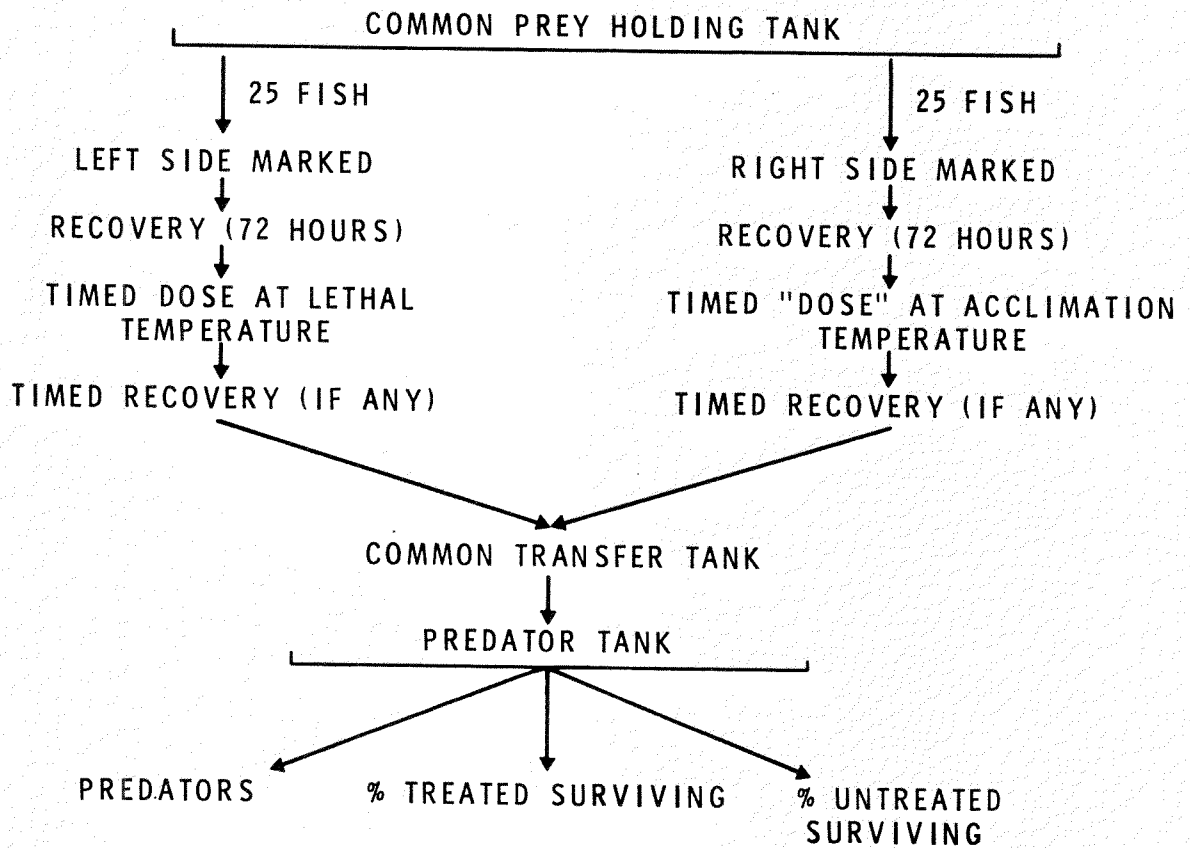


Figure 1. Flow diagram for differential predation tests.

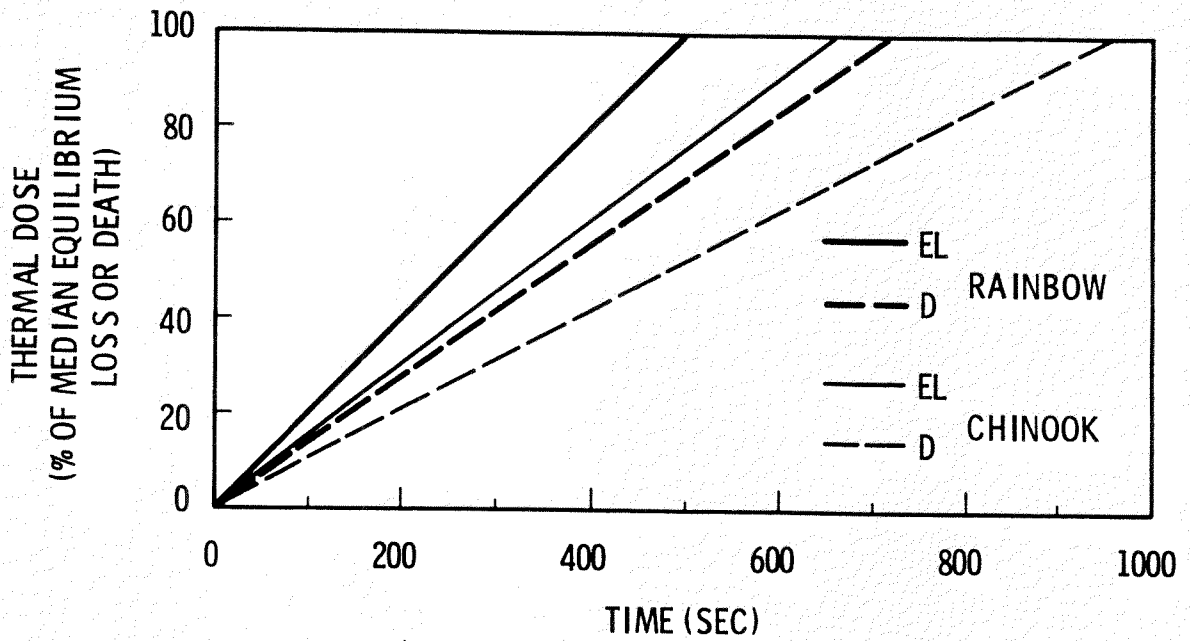


Figure 2. Relationships between thermal dose used in the text (percent of the median equilibrium loss dose) and (1) median time to equilibrium loss (EL), (2) median time to death (D), and (3) percent of median death dose. (Derived from unpublished data, Coutant, C. C. and J. M. Dean).

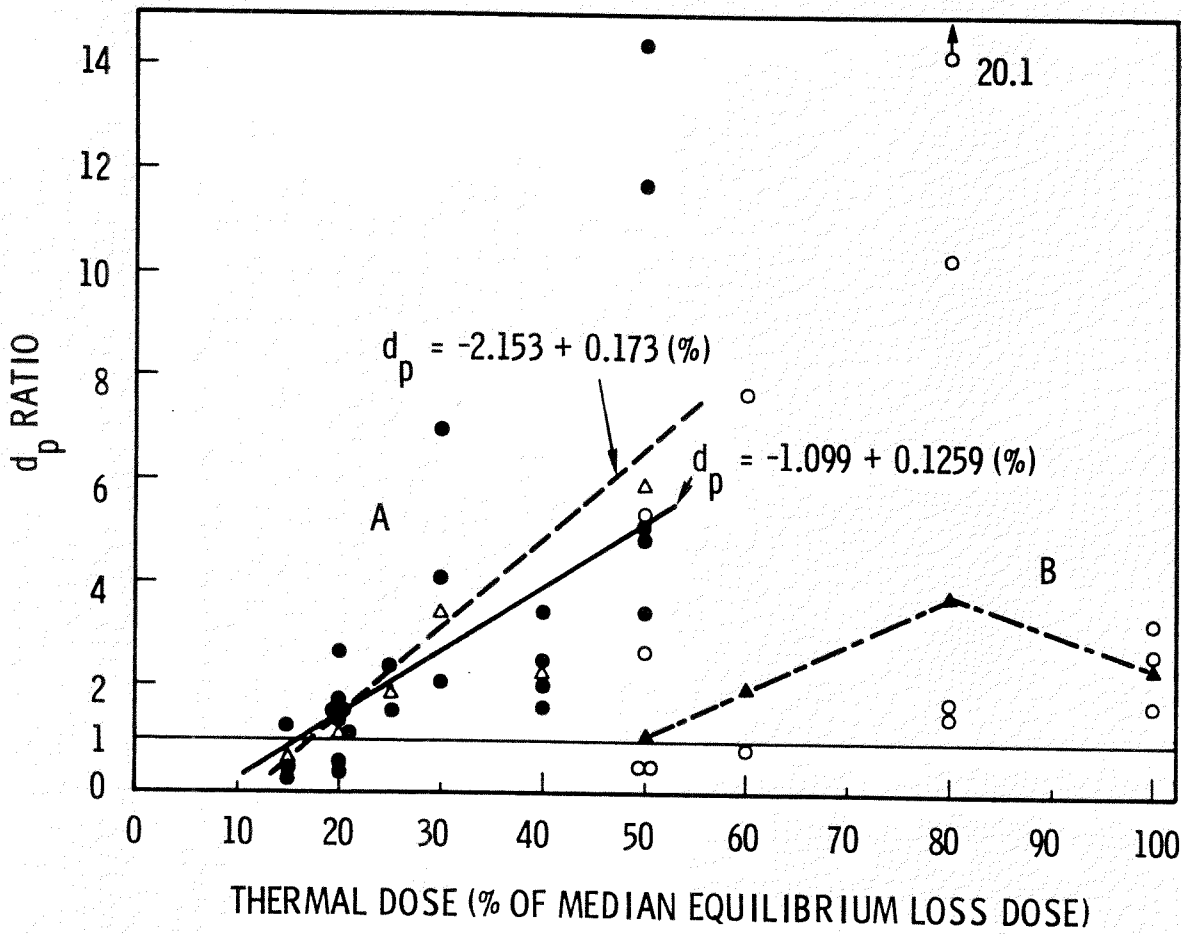


Figure 3. Pattern of d_p ratios with increasing thermal doses, juvenile rainbow trout with (A) no recovery, and (B) one-half hour recovery. Ratios for individual tests and the "combined" ratio are shown to reach exposure time.

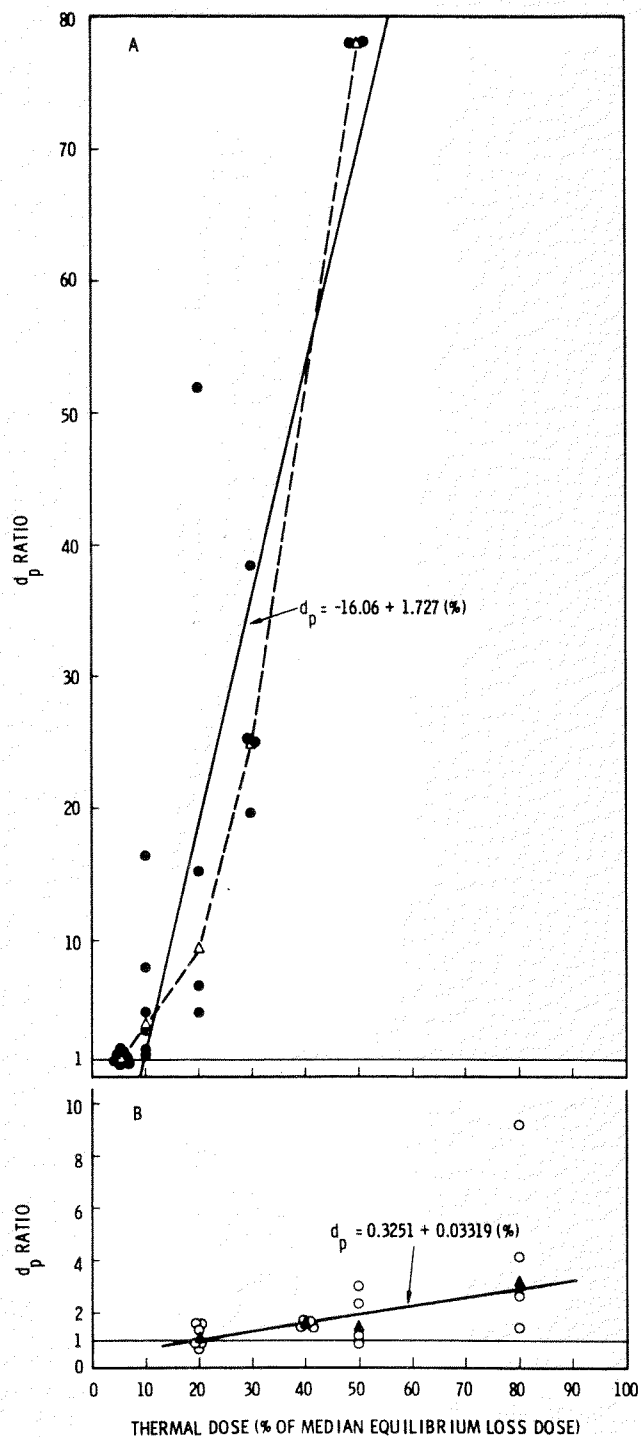


Figure 4. Pattern of d_p ratios with increasing thermal doses, juvenile chinook salmon with (A) no recovery, and (B) with one-half hour recovery. Scale of A is twice that of B and Figure 3. Ratios for individual tests and the "combined" ratio are shown to reach exposure time.

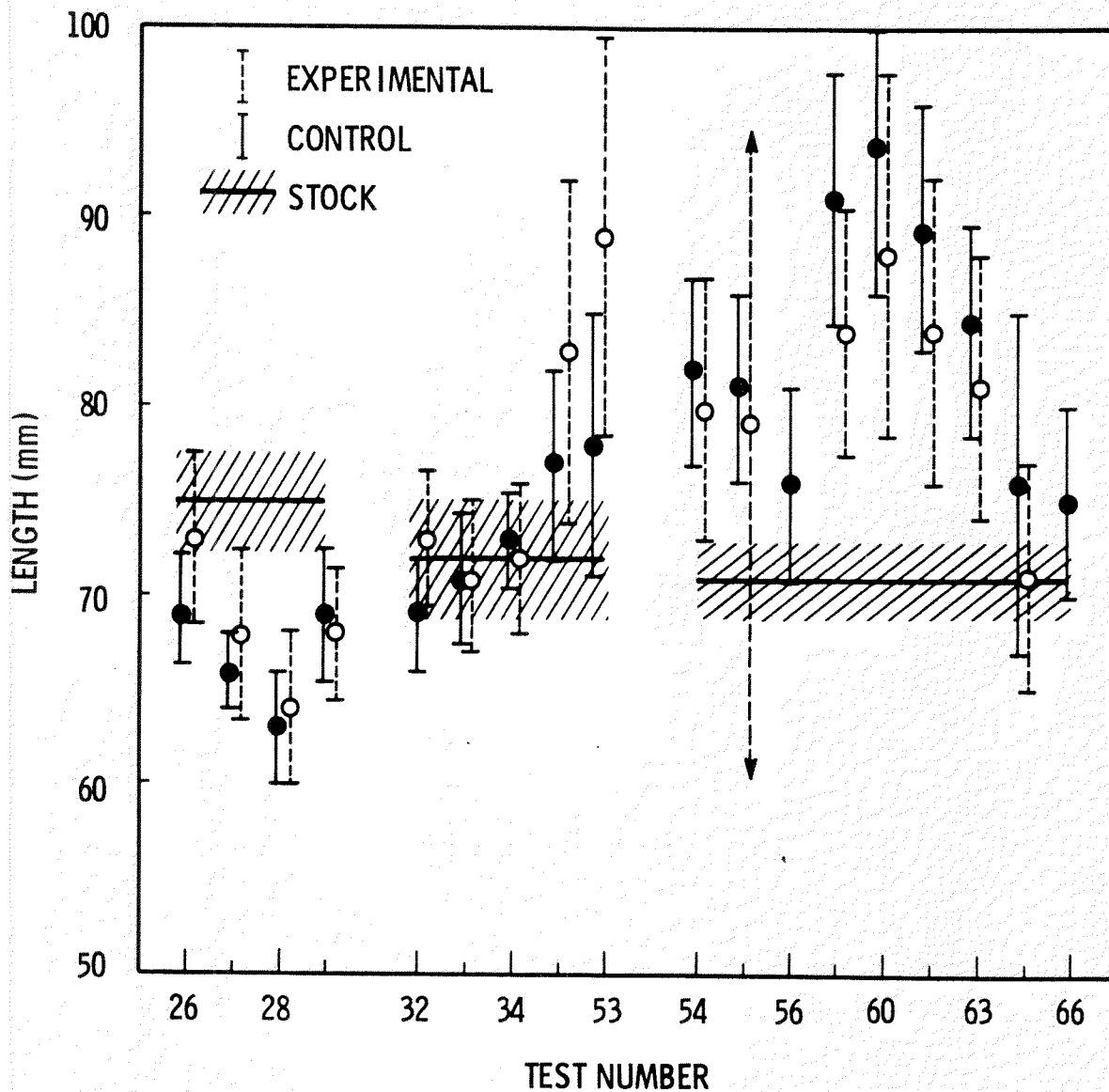


Figure 5. Lengths of rainbow trout from stock, surviving shocked, and surviving control groups (mean and 95% confidence intervals) in representative tests.