Stream Pollution

EXPERIMENTS ON THE DISSOLVED OXYGEN REQUIREMENTS OF COLD-WATER FISHES[*]

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The dissolved oxygen requirements of the salmonids have been investigated more thoroughly than those of any other group of fishes, but specific knowledge of these requirements is still quite limited. The level to which these fishes can reduce the dissolved oxygen content of water when confined in sealed vessels, before dying, or losing equilibrium, sometimes has been determined as a measure or lower limit of their tolerance (1). Several investigators have exposed the experimental animals to more or less constant low oxygen concentrations, achieved and maintained in various ways (2) (3) (4) (5) (6). Minimum concentrations tolerated by resting fish for one day or longer have been evaluated in this manner.

In order to succeed in their natural environment, fishes must be able not only to tolerate the most adverse conditions to which they may be occasionally exposed for short periods, but also to maintain at other times normal activity—resisting currents, seeking food, and escaping enemies. They must grow and be able to reproduce successfully. Dissolved oxygen concentrations necessary for the maintenance of varied, healthy fish populations probably are much higher than the concentrations which barely can be tolerated for limited periods by resting fish even of the most sensitive kinds. Field studies of fish distribution in relation to dissolved oxygen, especially in polluted waters (7) (8), as well as some experimental data and theoretical considerations have led to this conclusion.

Observations made in the field are not sufficiently instructive, however, and the validity of conclusions concerning minimum oxygen levels necessary for the maintenance of normal fish populations can be seriously questioned as long as these conclusions are based mostly on such observations. It is not clear to what extent the absence or scarcity of desirable fishes in many waters polluted with oxygen-depleting organic wastes is due to dissolved oxygen deficiency. The lack of fishes may be referable often to other pollutional effects of these wastes, which can upset the ecology of receiving waters in various ways, as by stimulating growth of benthic bacterial "slimes" and other periphyton which may interfere with the production of bottom-living fish-food organisms. Furthermore, field studies rarely have provided sufficiently complete and accurate information concerning the past history of the fish populations sampled. The observed environmental conditions may not always represent average conditions and are rarely indicative of the most adverse conditions that may have occurred in the past. Besides, fish can move about in response to changing conditions.

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A number of experiments have been reported on the influence of reduced oxygen concentrations on the respiratory metabolism, activity, and development of fishes, on the effects of acclimatization and other factors which influence resistance to low oxygen concentrations, and on the avoidance reactions of fishes to oxygen deficiency. Nevertheless, there is still not enough reliable information concerning minimum oxygen concentrations compatible with prolonged survival, normal performance, successful development, and general well-being of fishes. The variations of resistance to oxygen deficiency due to environmental and other factors also need further investigation. Accordingly, a comprehensive cooperative study of the influence of dissolved oxygen on the survival, development, food consumption, growth, activity potential, and movements of fishes has been undertaken. A factual basis will thereby be established for judgment as to the minimal oxygen concentrations that are compatible not only with brief survival of certain fishes, but also with their ordinary activities and their continued prosperity under varying conditions encountered in nature.

In this paper are collected the results of some exploratory work preliminary to the more detailed studies which are to be reported in future publications. From a large accumulation of test results, those data deemed most instructive have been selected and are briefly reported here, though some of the experiments are not considered entirely satisfactory, and some of the findings need verification. Subjects considered here are (a) the influence of temperature on the minimum oxygen concentrations necessary for the survival of fasting juvenile coho salmon, *Oncorhynchus kisutch*, for moderately prolonged exposure periods; (b) the long-term survival, food consumption, and growth of juvenile coho salmon at low oxygen concentrations and moderately high temperatures; (c) the influence of sulfite-process pulp-mill waste, in concentration well above that ordinarily encountered in receiving streams of the Pacific Northwest, on the resistance of coho salmon to oxygen deficiency; and (d) the resistance for periods of one to five days of the sculpin *Cottus perplexus* to low oxygen concentrations at summer temperatures (18 to 19°C).

Material and Methods

Most of the experiments were performed at the Yaquina Bay Fisheries Laboratory of Oregon State College, located near Newport, Ore. The water supply is obtained by filtering the soft water from a small spring-fed stream, which is naturally of high quality.

History and Feeding of Fish

The fish used in most of the experiments were wild juvenile coho salmon, *Oncorhynchus kisutch* (Walbaum), 40 to 109 mm in total length, seined from the headwaters of Beaver Creek in Lincoln County, Ore. Presumably they were all one year old or younger. Freshwater sculpins, *Cottus perplexus* (Gilbert and Evermann), 40 to 67 mm in total length, collected in Oak Creek, Benton County, also were used in one series of experiments.

The fish ordinarily were held for periods of one to eight weeks in outdoor tanks supplied with running water, where they were fed raw liver every other day. Before use in experiments, they were acclimatized for at least four days to a temperature (usually 20°C) differing by not more than 4°C from the test temperature. Thereafter, the fish were held in the test vessels at the test temperature for 24 hr before the dissolved oxygen content of the water was reduced. They were not fed for one day before being placed in the vessels, nor during the experiments, except during tests of long duration (i.e., more than five days). In a prolonged experiment on the influence of reduced oxygen concentrations on the food consumption and growth of coho salmon, feeding once every two days was continued throughout the tests. One hundred uniform pieces of liver, with a total weight of 5 g, then were dropped, five pieces at a time, into each test vessel containing 10 fish, and the number of pieces consumed by each group of test animals was noted. Unconsumed food was withdrawn by means of a siphon immediately after the feeding, and excrement was removed daily in the same manner.

The experiments on the influence of sulfite waste liquor on the dissolved oxygen requirements of juvenile coho salmon were performed at Corvallis, Ore., using filtered, untreated river water supplied to the laboratory from Marys River. The salmon for these experiments were collected from the headwaters of the Yaquina River, Lincoln County, Ore. In the laboratory stock-tanks they were fed a prepared mixture of ground beef liver and fish, with dried meal supplements.

Apparatus

An apparatus essentially similar to those used is diagrammed in Figure 1. Shown in Figure 1 is one of several units used simultaneously, all receiving water from a common temperature-control and distribution system, which is also pictured. Each unit consists of a test vessel, a glass column in which oxygen is removed from the water by means of nitrogen, and other components. Unlike the column described by Fry (9), each column used for reducing the oxygen content of the water is capable of delivering at one time water of only one oxygen concentration, so that a separate column must be used with each test vessel. A single vessel receiving water with dissolved oxygen near the saturation level is provided for performing a control test concurrently with each series of tests at reduced oxygen concentrations.

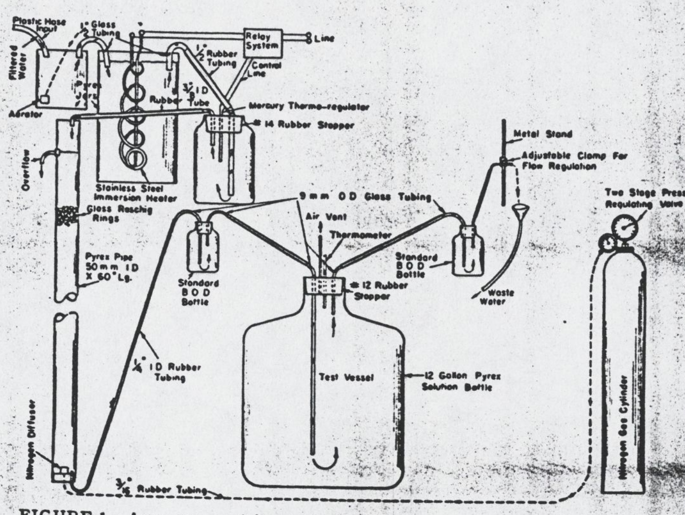

FIGURE 1.—Apparatus used for studies of the effects on fishes of reduced dissolved oxygen concentrations.

The vessels in which the fish are held during tests are "Pyrex" glass solution bottles of 5- or 12-gal capacity, fitted with No. 12 rubber stoppers. Inserted into each stopper are an inlet tube (9 mm OD glass tubing) extending nearly to the bottom of the bottle, a screened outlet tube extending about 3 in. into the neck of the bottle, a thin glass tube which serves as an air vent, and a thermometer.

Operation Pattern

The water supplied to the test vessels is filtered and then heated to the desired temperature by means of a thermostatically controlled, stainless steel, tube-type immersion heater suspended in a 10-gal Pyrex glass jar. The water flows into this jar through a connecting siphon from another jar which is always filled to overflowing, so that a constant water level is maintained. The mercury thermoregulator which controls the water temperature is inserted into the rubber stopper of a tightly stoppered wide-mouth glass jar, to which the heated water is delivered through a siphon tube, and from which it is distributed to the glass columns through several other tubes passing through the stopper.

Each of the columns is a vertically placed, 5-ft section of 2-in. Pyrex glass pipe, stoppered at the bottom, filled with Raschig rings, and having an overflow at the top. Water enters the column at the top, at a rate sufficient to keep the column full to overflowing, the small amount of overflow going to waste. Dissolved oxygen is removed from the downward flowing water by passing through it a stream of rising nitrogen bubbles released several inches above the bottom of the column from a gas disperser which is connected to a cylinder of compressed nitrogen. The water leaves the column at the bottom through a tube inserted into the stopper, and flows successively through a sampling bottle (300-ml standard BOD bottle), the test vessel, another sampling bottle, and an adjustable tube discharging into a drain funnel. The discharge tube can be raised or lowered as necessary to adjust the rate of flow through the system.

The water flows through each glass column and test vessel at a uniform rate of 300 ml/min or more. The dissolved oxygen content is adjusted by regulating the flow of nitrogen to each column by means of a two-stage pressure-reducing gas regulator with needle valve. Samples for chemical analysis of the water flowing into and out of each test vessel are obtained by removing the sample bottles, after withdrawing their stoppers, and immediately substituting other sample bottles.

When it was necessary to add waste sulfite liquor continually to the water flowing into a test vessel, the liquor was injected by means of a low-capacity chemical pump into the inlet tube through a glass T located between the influent sample bottle and the test vessel. The influent water thus could be sampled for determination of the dissolved oxygen content before it had been contaminated with the liquor.

Test Procedure and Conditions

Dissolved oxygen concentrations were determined usually by the unmodified Winkler method (10) at the Yaquina Bay laboratory, and by the Alsterberg (azide) modification of the Winkler method (10) at the Corvallis laboratory.

The oxygen content of the water in the experimental vessels was reduced to the desired levels gradually, during a period of about 6 to 8 hr. The recorded duration of exposure of the test animals to the tested oxygen concentration is in every case necessarily only approximate, as the moment when this concentration was achieved could not be precisely determined, and the fish then had already been exposed for some time to only slightly higher concentrations. The dissolved oxygen content of the effluent from a test vessel, determined several times during the first day of a test and at least twice daily thereafter, was considered to be the concentration to which the test animals in the vessel were exposed at the time of sampling. When the oxygen concentration in the effluent had become nearly stable, it differed by not more than a few tenths of a milligram per liter from the oxygen content of the influent water. In experiments in which the fish were fed in the test vessels, the flow of water through the vessels was interrupted briefly at the time of each feeding. The numbers of fish surviving were noted and recorded at regular intervals, and dead fish were removed promptly. Data were discarded from experiments during which any control fish died in the well-oxygenated water.

Excepting experiments in which sulfite waste liquor was added to Marys River water, the recorded free carbon dioxide concentrations of water leaving the test vessels did not exceed 3.5 mg/l and were usually much lower, and the recorded pH values were between 7.0 and 7.9.

Experimental Results

Influence of Temperature

Some results of tests of the lethality to juvenile coho salmon of low dissolved oxygen concentrations at five different temperatures ranging from about 12 to 23.5°C, all performed in the fall of 1953, are presented in Table I. Five-gallon test vessels were used, with water renewed at the rate of 300 ml/min. The test temperatures did not deviate from the stated average values by more than 0.5°C. The individual tests have been grouped and the recorded percentages of fish surviving at approximately the same mean dissolved oxygen concentrations and temperatures have been averaged for the sake of brevity and to facilitate the derivation of comparable indexes of tolerance, which are plotted in Figure 2.

TABLE I.—Survival for One Day of Juvenile Coho Salmon at Different Temperatures and Low Dissolved Oxygen Concentrations in Fall

Date (1953)	Temperature (°C)	No. of Tests	No. of Fish	Dissolved Oxygen Concentration (mg/l)			Percentage of Fish Surviving
				Over-all Range	Range of Test Means	Mean of Test Means	
12/13	12	3	30	1.05–1.2	1.12–1.13	1.12	17
12/13	12	2	20	1.3 –1.4	1.35–1.37	1.36	95
11/15	16	2	20	1.05–1.25	1.12–1.18	1.15	50
11/15	16	4	40	1.2 –1.45	1.30–1.35	1.33	90
11/29	16	3	30	1.5 –1.6	1.53–1.60	1.57	100
10/7	20	3	30	1.35–1.45	1.35–1.42	1.39	67
9/28	20	1	10	1.65 only	1.65 only	1.65	100
9/28	20	3	30	1.8 –2.0	1.83–1.90	1.88	100
10/14	22	2	20	1.5 –1.6	1.52–1.55	1.54	85
10/14	22	4	40	1.8 –1.9	1.82–1.87	1.85	100
10/25	23.5	2	20	1.8 –2.0	1.90–1.92	1.91	35*
11/5	23.5	3	30	2.05–2.2	2.12–2.15	2.13	97†

* Percentage surviving after about 16 hr, when the tests were prematurely interrupted.

† The same result (97 per cent survival) was obtained also in 3 tests performed on October 26 with DO means averaging 2.12 mg/l, but ranging widely from 2.03 to 2.23 mg/l (over-all DO range, 1.95 to 2.3 mg/l).

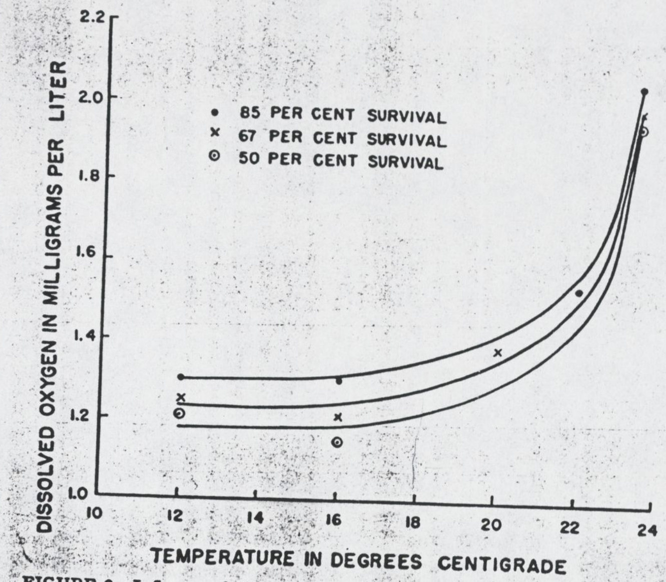

FIGURE 2.—Influence of dissolved oxygen and temperature on 24-hr survival of juvenile coho salmon in the fall season.

Table I shows the mean percentages of test animals surviving after exposure to the experimental concentrations of dissolved oxygen for about one day only. Most of the tests were continued for longer periods, however, and it was noted that fish surviving at a given oxygen concentration for one day usually survived at that concentration for the longer exposure periods up to five days. Of the 35 tests recorded in Table I (including the second footnote), 15 continued for 5 days, 9 for 4 days, and 6 for 2 days. In 12 of the 30 tests which were continued for 2 days or longer, one or more of the 10 test animals died within the first day. The number of fish dying within one day in these 12 tests was 30 (25 per cent), and in none of them did the mortality during the first day exceed 50 per cent. Yet, only 1 additional death occurred in these same 12 tests and only 4 deaths occurred in all of the 30 extended tests after the first day. Had all the tests been continued for 2 days, and even for 4 or 5 days, it is apparent that the final results (survival percentages) would not have been markedly different from the 1-day test results reported in Table I. Gradual acclimatization to reduced but not rapidly lethal oxygen concentrations, which has been demonstrated in experiments with brook trout (5), evidently occurs also in coho salmon. In one experiment at 18°C, 9 juvenile coho salmon were held for 5 days at concentrations near 2 mg/l, and the oxygen concentration was then further reduced gradually. These fish died at concentrations (0.9 to 0.7 mg/l) averaging about 0.2 mg/l lower than the corresponding lethal concentrations (1.1 to 0.9 mg/l) for 10 unacclimatized fish. The latter fish had been held in well-aerated water before the oxygen content was gradually reduced within 8 to 10 hr to the rapidly lethal levels.

Development and Interpretation of Curves

Estimates of the dissolved oxygen concentrations that are lethal to 85, 67, and 50 per cent of the test animals at the different experimental temperatures, derived from the data presented in Table I, are plotted in Figure 2. Most of these values were obtained by graphical interpolation, after plotting the experimental data on probability paper, with mean survival percentages laid off on the probit scale and mean oxygen concentrations on an arithmetic scale. A straight line was drawn through two points representing in this graph oxygen concentrations lethal to some but not to all of the test animals at a given temperature. The points at which this line intersects the coordinate lines representing 85, 67, and 50 per cent survival then were located, and the corresponding oxygen concentrations were plotted against the temperature in Figure 2. The estimates for the test temperature of 23.5°C are based on the assumption that all fish which at this temperature could not tolerate for one day oxygen concentrations averaging 1.90 and 1.92 mg/l had died at these concentrations when the tests were prematurely discontinued after 16 hr. No serious error can result from this assumption, since the estimates would have been only slightly higher even had it been assumed that nearly all the fish (95 per cent) would have died within one full day at the test concentrations in question. In other tests the death of fish after more than 16 hr was relatively infrequent.

The available data did not make possible estimation by the interpolative method described above of dissolved oxygen concentrations tolerated by 85 and 50 per cent of the test animals at 20°C, and by 67 and 50 per cent of test animals at 22°C. Estimates of these concentrations can be derived, however, from Figure 2. The curves in Figure 2 were fitted for this purpose by inspection to the plotted points to obtain the best possible fit while maintaining a logical or congruous relation among the three curves. These curves do not necessarily represent accurately the true relation between temperature and the dissolved oxygen requirements of fully acclimatized juvenile coho salmon of uniform age and history. Nevertheless, it seems safe to conclude that the minimum oxygen concentrations tolerated by the fish for one day, after gradual reduction, are little different at varying temperatures between 12 and 20°C, but rise markedly at temperatures approaching the upper limit of thermal tolerance of young coho salmon, which has been reported to be near 25°C (11).

1953 Summer Tests

The results of experiments performed during the summer of 1953 were somewhat erratic. During this period heavy mortality occurred frequently among controls held in well-oxygenated water. In experiments in which controls survived, coho salmon tested in July at temperatures of 17.5 to 18°C proved nearly as resistant to low oxygen concentrations as those tested in November at temperatures near 16°C (Table I). However, at 20°C the fish proved somewhat more susceptible in early July than in the fall, requiring apparently at least 0.1 or 0.2 mg/l more oxygen for survival; and at 22°C fish tested in August appeared to be far more sensitive than those tested in October. Most of the fish tested in August at 22°C succumbed within a day at oxygen concentrations between 2.0 and 2.2 mg/l, though not at higher concentrations. The significance of the latter observations is not entirely clear.

Food Consumption and Growth

The results of an experiment wherein three groups of recently captured yearling coho salmon were held for 30 days in winter at a uniform temperature near 18°C and at dissolved oxygen concentrations averaging 2.0 mg/l, 2.9 mg/l, and 9.0 mg/l (controls) are presented in Table II. A group of 10 fish, which had been weighed at the beginning of the test, was held in each of three 12-gal bottles in which the different oxygen concentrations were maintained. The water in the bottles was replaced at the rate of 500 ml/min. Each group of fish was offered 100 pieces of liver, averaging 0.05 g in weight, every other day, in the manner already described. The numbers of pieces of liver taken by the fish within each of four successive depth intervals into which each bottle was divided, as well as the total food consumption, were noted and recorded from the 14th to the 28th day of the experiment (last 8 feedings) only. The percentages of offered food particles consumed during this period by the different groups of fish are shown in Table II. With the exception of one fish which died on the 30th day of the test in the bottle with dissolved oxygen averaging 2.0 mg/l, all of the experimental fish lived for the duration of the 30-day test. The total weight of the fish in each bottle, including the weight of the single dead fish, was determined at the conclusion of the test. Table II shows the change in weight of each group of fish in the course of the entire test.

It will be noted that the fish held at oxygen concentrations averaging 2.0 mg/l consumed only a small fraction of the food offered, and they lost weight during the experiment. They seemed to be consuming somewhat more food during the first few days of the test, when no determinations and records of food consumption were made, but their appetite was soon markedly affected. The fish held at oxygen concentrations averaging 2.9 mg/l consumed nearly all of the food offered and gained weight, as did the control fish held in water with dissolved oxygen content near the saturation value. However, the weight gain of the fish at the reduced oxygen concentration was somewhat less than that of the controls. Unfortunately, their total initial weight was considerably greater than that of the controls, so that the results obtained with these two groups of fish are not entirely comparable. Had the control fish been larger, they perhaps

TABLE II.—Effects of Low Oxygen Concentrations on the Food Consumption and Growth of Yearling Coho Salmon Held for 30 Days at 18°C in Winter (Jan.–Feb. 1954)

Dissolved Oxygen (mg/l)		Number of Fish	Fish Surviving (per cent)	Food Taken* (per cent)	Total Weight of Fish (g)		Change in Weight of Fish	
Mean	Range				Initial	Final	Grams	Per Cent
2.0	1.8–2.4	10	90	21	55.9	52.2†	− 3.7	− 6.7
2.9	2.4–3.2	10	100	97	56.3	72.1	+15.8	+28.1
9.0	8.8–9.2	10	100	97	46.0	65.3	+19.3	+42.0

* Food taken from the 14th to the 28th day of the experiment (at the last 8 feedings) only.
† Includes the weight of the single dead fish, which died on the 30th day of this test.

would have gained less weight than they did, while consuming nearly all the available food, and the weight gain expressed as a percentage of the initial weight almost certainly would have been less than the reported gain.

The control fish took the proffered food more promptly than did those held at low oxygen concentrations. When the pertinent observations were made, the controls consumed, on the average, 87 per cent of the food particles before these had descended 5 in. below the water surface, and 94 per cent before the particles had fallen 10 in. The corresponding percentages for fish held at 2.9 mg/l average dissolved oxygen were 76 and 89 per cent. Almost all of the food particles consumed by both of these groups of fish were taken before they had fallen 15 in., whereas nearly one-fourth of the small amount of food eaten by the fish exposed to 2.0 mg/l DO was taken at greater depths, less than half (9 per cent of all the food offered) having been consumed before the food had fallen 5 in. from the surface. The total depth of the water in each test vessel was about 20 in., the neck of the bottle having been emptied before feeding commenced.

Summary of Additional Data

The results of the preliminary experiments just presented, obtained with yearling coho salmon in winter, may be somewhat misleading. They may create the erroneous impression that dissolved oxygen concentrations even as low as 3 mg/l can have little if any adverse influence on the survival, food consumption, and growth of juvenile coho salmon in general. In order to ensure against such misinterpretation of the data, pertinent additional data now available are briefly summarized here. These results of numerous experiments performed during the years 1955 and 1956, as well as the methods employed, have been fully reported by Herrmann (12).

With certain exceptions to be noted, the experiments were performed in the summer and fall, at a constant temperature of 20°C, with coho salmon in their first year of life. Ten fish of uniform size were used in each test at a given oxygen concentration. The fish were fed live marine amphipods (beach fleas) twice daily, in quantity always exceeding the amount consumed, and the excess was not immediately removed. It is believed, therefore, that neither the amount of food consumed by the fish nor their growth was limited by food availability in these experiments. Each group of test fish was weighed at the beginning and at the end of an experiment. The food supplied to each group and the uneaten excess removed were weighed daily. The duration of an experiment was about three to four weeks. Of 80 controls held at oxygen concentrations near the air-saturation value, only one fish died.

The survival of fish held at oxygen concentrations below 4 mg/l proved highly variable. In three tests at concentrations averaging 2.1 to 2.3 mg/l performed in 1956, mortality within 20 to 28 days ranged from 100 per cent (in May) to 0 per cent (in late November and early December, at 18°C). The fish lost weight in every case.

At oxygen concentrations averaging 2.7 to 3.3 mg/l, all fish died within two weeks in three tests performed in late July and August of 1955, and in a fourth test only 30 per cent remained alive after 19 days, when the test was discontinued. In each of these tests, the fish lost much weight (up to 32 per cent), while controls grew rapidly. Yet, in a test begun on October 15, 1956, the fish not only lived for 21 days at an oxygen concentration averaging 3.1 mg/l, but also showed a 48 per cent gain in weight. Controls at this time showed a weight gain of 103 per cent.

In May 1956, 18 of 20 salmon in their first year of life lived for 21 days

at oxygen concentrations averaging 3.1 mg/l and showed a weight gain of 13.4 per cent, while 19 of 20 controls lived and showed a weight gain of 100 per cent. At the same time, all of 10 yearling fish succumbed at the same mean oxygen concentration, as well as at a concentration of 2.4 mg/l. There were no yearling controls. It is possible that the susceptibility of yearling fish to low oxygen concentrations increases about the time of their seaward migration.

With very few exceptions (3 fish only), the juvenile coho salmon lived for the duration of the experiments (21 to 27 days) at oxygen concentrations averaging about 4, 5, 6, and 8 mg/l, in five tests at each concentration, performed in 1955 (July 21 to September 22) and 1956 (July 29 to November 4), each group of fish gaining weight. The mean weight gains of surviving fish at these four oxygen concentrations in the five experiments were found to be 56, 68, 88, and 92 per cent, respectively. The amounts of food consumed per gram of initial weight of the fish averaged 3.15, 3.44, 4.10, and 4.27 g, respectively. Increases in weight of the fish per gram of food consumed averaged 0.168, 0.188, 0.216, and 0.220 g, respectively.

Thus, under the conditions of these experiments, the rate of growth, the food consumption, and the efficiency of conversion of food to body weight generally decreased materially when the oxygen concentration was reduced to values below 6 mg/l, and they seem to have been somewhat depressed even at this concentration. They varied widely in different tests at the same oxygen concentration (especially at a concentration below 6 mg/l), but were always less for fish held at oxygen concentrations near 4 mg/l than for controls held at the same time at concentrations near 8 mg/l.

The fish proved more susceptible to the adverse effects of reduced oxygen concentration in experiments performed in 1955 than in experiments performed in 1956 at the same time of year. In both years these effects on juvenile coho salmon in their first year of life were most pronounced in the early tests, and became less marked later in the year, as the fish grew older.

Sulfite Waste Liquor Tests

Results of some comparative tests of the resistance of juvenile coho salmon to reduced oxygen concentrations in the presence and in the absence of calcium-base, sulfite-process pulp-mill waste liquor, performed with Marys River water in the fall of 1954, are presented in Table III. The concentration of sulfite waste liquor, which was added to the water after reducing its oxygen content to the desired level, was in every instance 1,200 mg/l liquor of 10-per cent solids content. Twelve-gallon test vessels were used, and the water was renewed at the rate of 550 ml/min. The dissolved oxygen content of the nitrogen-treated water (without waste liquor) flowing to each experimental vessel was determined repeatedly, as was also that of the effluent from each vessel receiving no waste liquor. The oxygen content of the effluents from bottles receiving the diluted sulfite waste liquor could not be reliably determined by chemical test, because of chemical interference by liquor constituents. However, it can be assumed that the decrease of the oxygen content of the water during passage through the test vessels was not usually greater when the water contained no waste liquor than when the liquor was present. Presumably, if there was any consistent difference, the greater reduction occurred when the water contained waste liquor, because of the oxygen demand (immediate and biochemical) of the liquor.

The data in Table III show, therefore, that the addition of 1,200 mg of sulfite waste liquor (with 10-per cent solids content) per liter of river water

TABLE III.—Survival of Juvenile Coho Salmon at Low Dissolved Oxygen Concentrations in the Presence and Absence of Sulfite Waste Liquor (1,200 mg/l Liquor of 10-Per Cent Solids Content)

Dates (1954)	Mean Temperature (°C)	Sulfite Waste Liquor	Dissolved Oxygen Concentrations (mg/l)				Percentage of 10 Test Animals Surviving[*]	
			Influent		Effluent			
			Mean	Range	Mean	Range	1 Day	2 Days
10/22–24	16	Absent	1.70	1.5–2.0	1.53	1.3–2.0	90	90
10/22–24	16	Present	1.82	1.5–2.0	—	—	90	80
11/12–14	18	Absent	1.67	1.6–1.8	1.41	1.3–1.6	80	50
11/12–14	18	Present	1.72	1.6–1.8	—	—	90	30
11/19–20	18	Absent	1.64	1.6–1.8	1.53	1.5–1.6	30	—
11/19–20	18	Present	1.72	1.7–1.8	—	—	50	—
12/19–21	16	Absent	1.76	1.5–2.1	1.62	1.4–1.9	50	40
12/19–21	16	Present	1.73	1.2–1.9	—	—	50	50
12/22–24	16	Absent	1.78	1.5–2.0	1.65	1.5–1.8	40	40
12/22–24	16	Present	1.74	1.5–2.0	—	—	60	40
Mean[†]	—	—	1.71	—	1.55	—	58	55
Mean[‡]	—	—	1.75	—	—	—	68	50

[*] In each of two control tests with well aerated water, with and without sulfite waste liquor, performed concurrently with every experiment reported, all of 10 fish survived.

[†] For tests excluding sulfite waste liquor.

[‡] For tests including sulfite waste liquor.

did not materially increase the dissolved oxygen requirements of the fish. The mean oxygen content of the influent water for all of the five reported tests of partially deoxygenated water without sulfite waste liquor and the corresponding value for the five comparable tests of water with waste liquor added are nearly equal (1.71 and 1.75 mg/l, respectively). The mean percentages of test animals surviving for one or two days in the water without waste liquor and in the water with waste liquor also are not markedly different. Any considerable increase of the dissolved oxygen requirements of salmon exposed to diluted sulfite waste liquor should have resulted in markedly lower mean percentages of survival of these fish.

TABLE IV.—Survival of Sculpins, *Cottus perplexus*, Exposed to Various Concentrations of Dissolved Oxygen at Temperatures of 18 to 19°C, During Late Summer (Aug. 12–Sept. 11, 1954)

Dissolved Oxygen (mg/l)		No. of Tests	No. of Fish	Percentage of Fish Surviving				
Mean	Range			1 Day	2 Days	3 Days	4 Days	5 Days
1.18[*]	1.1 –1.25	3	30	0	0	0	0	0
1.27	1.2 –1.35	1	10	40	10	0	0	0
1.38	1.25–1.5	1	10	90	40	20	20	20
1.49	1.4 –1.6	1	10	100	90	80	60	60
1.64	1.55–1.7	1	10	100	100	100	100	100
2.31	1.7 –2.4	1	10	100	100	100	100	100
3.05	3.0 –3.25	1	10	100	100	100	100	100
Controls	—	5	50	100	100	100	100	100

[*] Mean of three test means.

Tests with Sculpin

Table IV shows the results of a series of tests of the resistance of the sculpin *Cottus perplexus* to low oxygen concentrations at temperatures of 18 to 19°C, performed at the Yaquina Bay laboratory in the summer of 1954. Twelve-gallon test vessels were used, and the water in them was renewed at the rate of about 400 ml/min. The duration of each test was 5 days, and the numbers of fish surviving were recorded at daily intervals. It is apparent that the dissolved oxygen requirements of the sculpins at the stated temperatures are not very different from those of juvenile coho salmon at the same temperatures. It is noteworthy, however, that a large majority of the sculpins which succumbed at lethal or critical oxygen concentrations above 1.2 mg/l died only after exposure for more than one day to these low dissolved oxygen levels, and that several deaths occurred after more than 2 days. The oxygen concentrations tolerated for one day by only 50, 67, and 85 per cent of the test animals, estimated by interpolation in the same manner as were the corresponding values for coho salmon plotted in Figure 2, were found to be about 1.29, 1.32, and 1.36 mg/l, respectively. The median tolerance limit for an exposure period of 4 days has been estimated to be about 1.46 mg/l; and the corresponding 5-day value appears to be the same.

Discussion

Temperature Effects

The data of Burdick *et al.* (1) show that for trout of three species (brook, rainbow, and brown) the mean "lethal oxygen concentrations" (i.e., actually concentrations at which the fish turned over when confined in sealed vessels) increased by at least 40 per cent, and in some cases by more than 50 per cent, when the experimental temperature was increased from 12 to 20°C. The highest temperatures at which the experiments with trout were performed by these investigators were 20 to 22°C. They stated that "In all species studied, within the temperature ranges covered, the mean lethal oxygen concentrations plotted on the logarithmic scale against the temperatures on the arithmetic scale appear to form a straight line on semi-logarithmic graph paper." Graham's data (4) suggest a similar relationship in brook trout over a wide range of temperatures (3.5 to 23°C), but her estimates of lethal oxygen levels for trout placed in continually renewed (running) water, partially deoxygenated by means of nitrogen, were based on experiments with very few fish. A corresponding relationship between temperature and the minimum oxygen concentrations tolerated for one day by juvenile coho salmon is not suggested by the data reported here.

The curves plotted in Figure 2 suggest that critical oxygen concentrations for the salmon may increase by only about 10 per cent with a rise of temperature from 12 to 20°C, and may be almost independent of temperature when the temperatures are below 16°C, but there is a marked increase at much higher temperatures, particularly temperatures above 22°C. These curves are not deemed entirely reliable, for the tests at different temperatures were not performed simultaneously, and the fish probably were not yet completely adjusted to some of the test temperatures.

The influence of thermal acclimatization on the respiratory metabolism of fishes and their resistance to lack of oxygen has been long established (13) (14). Recent exposure of the salmon tested at 16°C to a somewhat higher temperature (20°C), and of those tested at 12°C to a somewhat lower temperature, could have resulted in their failure to exhibit a difference of resistance which they might have shown after complete acclimatization to the test temperatures and consequent stabilization of metabolic rates. Nevertheless, there can be little doubt that the influence of temperature on the minimum oxygen levels tolerated by juvenile coho salmon under the experimental conditions described is very different from its influence on the tolerance limits of trout as determined by Burdick *et al.* under their somewhat different experimental conditions. It is not clear to what extent this disparity is ascribable to differences between the species, and how much of it may be attributable to differences of experimental conditions or methods of tolerance evaluation.

Downing and Merkens (6) have reported that the resistance of rainbow trout to reduced oxygen levels, to which the fish were suddenly exposed in running water which had been treated with nitrogen, decreased markedly with rise of temperature from 10.6 to 16.4°C, but not with a further rise of temperature from 16.4 to 19.9°C. Other species of fish tested by these authors did not yield corresponding results. Mirror carp seemed to require more oxygen than the rainbow trout for survival for a period as long as one week at the temperature of 19.9°C, but at the lower test temperatures they proved much more resistant to low oxygen levels than the trout. Even at 19.9°C they withstood for short periods (less than 2 days) levels much lower than those tolerated by the trout. Lozinov (15), in reviewing several other investigations with various fishes, has noted that the data reported in the literature appear to be somewhat contradictory or variable. He remarked that in some instances a marked increase of the threshold concentration of dissolved oxygen with increasing temperature has been reported, whereas in other instances there was almost no change, or else pronounced increases occurred only at temperatures near the upper limits of thermal tolerance (i.e., as reported here for coho salmon).

Variability of Tolerance

With regard to the critical levels of dissolved oxygen at low temperatures, there is good agreement between the experimental results reported here and the comparable published data of other investigators who have tested the resistance of coho salmon fingerlings to oxygen deficiency in flowing water at temperatures of 10.9 to 12.7°C (2) (3). The published data on the resistance of other salmonid species are variable and are not often closely comparable with the data presented here, because of differences of experimental conditions and methods. Some of the data based on flowing-water tests of comparatively long duration such as those reported here (2) (4) (5) (6) suggest that young brook trout (*Salvelinus fontinalis*) and rainbow or steelhead trout (*Salmo gairdneri*) may be somewhat more sensitive than the juvenile coho salmon. Even results of some tests of relatively brief duration, such as those of Burdick *et al.* (1), indicate that dissolved oxygen concentrations above 2.0 mg/l can be rapidly disabling to brook trout and brown trout (*Salmo trutta*) at moderately high temperatures below 20°C. The relatively high resistance shown by the coho salmon at these temperatures in experiments reported here may be ascribable partly to more favorable experimental conditions (e.g., the spacious test vessels, the gradual reduction of dissolved oxygen only after the fish have been held in the vessels at high oxygen concentrations for one day, etc.).

The average resistances of the juvenile coho salmon to low oxygen concentrations did not prove uniform even in similar experiments at like temperatures. Fish from Beaver Creek, tested in 1953 in spring water at the Yaquina Bay laboratory, appeared to be more resistant in the fall than in summer at relatively high temperatures only. At

somewhat lower test temperatures (16 to 18°C), they proved consistently more resistant than were the Yaquina River fish tested at the same temperatures at Corvallis in the fall of 1954, using Marys River water. As Table III shows, only 58 per cent of the latter fish survived for one day in the test vessel receiving no sulfite waste liquor and with dissolved oxygen in the effluent water averaging about 1.55 mg/l. On the other hand, oxygen concentrations averaging about 1.3 mg/l were tolerated by more than 80 per cent of the Beaver Creek fish tested at the Yaquina Bay laboratory in November and July of 1953 at corresponding temperatures (about 16 to 18°C). At 20°C the susceptibility of the latter fish to oxygen deficiency in the same laboratory in July 1953 approached that of the Yaquina River fish tested at Corvallis in the fall of 1954 at temperatures of 16 to 18°C. However, other results (16) have shown mean oxygen concentrations greater than 1.8 mg/l to have been necessary in July 1955 for survival of more than 50 per cent of juvenile coho salmon from the Yaquina River drainage basin for one day in filtered Marys River water at temperatures near 20°C. It must be concluded that the resistance of juvenile coho salmon to oxygen deficiency varies considerably not only with temperature, but probably also with the season or with the age of the fish, and with other factors or variables such as the source, history, and condition of the animals and perhaps the quality of the water.

Sulfite Waste Liquor

The observation that the addition of 1,200 mg of sulfite waste liquor (or about 120 mg of sulfite waste liquor solids) per liter of Marys River water did not cause any material increase of the dissolved oxygen requirements of coho salmon indicates that these requirements are not necessarily affected markedly by such impurities in the water. It is not regarded as conclusive evidence, however, that sulfite waste liquor in the tested concentration cannot have an effect on the oxygen requirements of salmonid fishes, since wastes from different pulp mills vary considerably in their composition. Townsend and Earnest (3) reported a demonstrable but variable effect. Townsend and Cheyne (17) suggested that the variability of the results may have been due to variations of the pH of waste samples and dilutions, these authors having observed increased susceptibility of coho salmon to low oxygen concentrations in water with reduced pH. The influence of pH and of free carbon dioxide concentration on the dissolved oxygen requirements of juvenile coho salmon has been further investigated (16). The results of these studies are to be reported in a future publication.

Non-Lethal Effects of Low DO

While the yearling coho salmon in winter lived for 30 days at oxygen concentrations averaging 2.0 mg/l and temperatures near 18°C, their sluggish behavior, reduced appetite, and consequent loss of weight clearly showed the oxygen concentrations to be inadequate when they persist for long periods. Dissolved oxygen concentrations averaging 2.9 mg/l have not been shown to be markedly detrimental to the yearling coho salmon by the results of the experiments reported (at 18°C). The fish held under these conditions did not grow as much as the controls held in well-oxygenated water, but it has been noted already that the difference could have been due, at least partly, to the smaller initial size of the controls, which presumably required less food for maintenance. The quantities of food consumed by these two groups of fish apparently were equal. It is noteworthy, however, that, had more food been available, both groups probably

[1981]

Oxygen Requirements for Growth of Young Coho (*Oncorhynchus kisutch*) and Sockeye (*O. nerka*) Salmon at 15°C

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BRETT, J. R., AND J. M. BLACKBURN. 1981. Oxygen requirements for growth of young coho (*Oncorhynchus kisutch*) and sockeye (*O. nerka*) salmon at 15°C. Can. J. Fish. Aquat. Sci. 38: 399–404.

The growth rate and food conversion efficiency of young coho and sockeye salmon on a full ration were determined in freshwater at oxygen concentrations ranging from 2 to 15 mg/L (15°C). The data, and a reanalysis of selected published records for bass, carp, and coho, were examined critically in relation to the Limiting Factor hypothesis. It was concluded for all species that above a critical level ranging from 4.0 to 4.5 mg O_2/L, growth and conversion efficiency were not limited when tested for relatively short periods (6–8 wk) under the pristine conditions of laboratory tanks. A slight but significant trend to exhibit higher hematocrits at lower oxygen levels revealed the possible presence of an adaptive mechanism for improved respiratory capacity at subcritical oxygen concentrations.

Key words: limiting oxygen, growth rate, blood hematocrits, salmon tolerance

BRETT, J. R., AND J. M. BLACKBURN. 1981. Oxygen requirements for growth of young coho (*Oncorhynchus kisutch*) and sockeye (*O. nerka*) salmon at 15°C. Can. J. Fish. Aquat. Sci. 38: 399–404.

Les auteurs ont déterminé, dans de l'eau fraîche à des teneurs en oxygène variant de 2 à 15 mg/L (15°C), le taux de croissance et l'efficacité de conversion des aliments chez de jeunes saumons coho et nerka exposés à un plein régime. On a examiné de façon critique les données et une réanalyse d'un choix de données publiées sur l'achigan, la carpe et le saumon coho, en regard de l'hypothèse du facteur limitatif. On a conclu que, chez toutes ces espèces, au-dessus d'un niveau critique variant de 4,0 à 4,5 mg O_2/L, la croissance et l'efficacité de conversion des aliments ne sont pas limitées lorsque testées pendant des périodes relativement courtes (6–8 semaines), dans les conditions intactes des réservoirs du laboratoire. Une tendance, légère mais significative, vers des hématocrites plus élevés aux niveaux inférieurs d'oxygène indique la présence possible d'un mécanisme d'adaptation en vertu duquelle la capacité respiratoire s'améliore aux concentrations d'oxygène subcritiques.

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THE effect of reduced environmental oxygen on the growth rate of fish has been the object of a number of studies (see reviews by Doudoroff and Shumway 1970; Davis 1975). In most cases laboratory experiments were designed to determine the incipient threshold level of oxygen that would just support maximum growth rate. In the manner of a true Limiting Factor (Fry 1947, 1971), it was hypothesized that oxygen concentrations above such a threshold would not improve either growth rate or food conversion efficiency (Brett 1979). However, growth responses in some species were sufficiently variable that an oxygen threshold was not always apparent, leading more than one author to propose an optimum level of oxygen requirement in the vicinity of the atmospheric saturation point. Higher, supersaturated levels could impair growth (Herrmann et al. 1962; Stewart et al. 1967; Adelman and Smith 1970).

Because of these differences, and recognizing that in the case of fish hatcheries acceptable oxygen concentrations would likely be influenced by the presence of accumulated excretory products (Willoughby 1968; Westers 1970; McLean and Fraser 1974), it was proposed to examine the case for two species of Pacific salmon, firstly under conditions of virtual elimination of any possible interaction with metabolic wastes, and secondly to determine the level of nitrogenous excretion that interacted with low oxygen to reduce maximum growth rate.

This study reports on the initial step of the proposal, setting the "baseline" relation (without contaminants) between growth rate and oxygen concentration for young coho (*Oncorhynchus kisutch*) and sockeye (*O. nerka*) salmon. A temperature of 15°C was chosen — the approximate optimum

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temperature for growth of Pacific salmon. The case for oxygen as a strict Limiting Factor is examined in the light of the present findings and a reevaluation of some pertinent, earlier literature.

In addition to recording growth responses, samples of blood and gill filaments were taken at the start and finish of the experiments to examine some other indicators of potential stress from low oxygen.

Materials and Methods

FISH

The first experiments were performed with coho salmon in the fall of 1977. Mean initial weight was 5.6 ± 0.2 g. Because of their natural agressive behavior, the extent of variability in growth rates within and between tanks required further experimentation, spanning a slightly wider range of oxygen concentrations. Additional tests were, therefore, conducted with coho (6.6 ± 0.1 g) in the fall of 1978. These included a series with young sockeye salmon (mean initial weight 14.9 ± 0.4 g), a naturally schooling species in which growth variation tends to be less than in territorial coho. By adding the supplementary tests on coho, and including a species less subject to variability in growth rate, the target of precise definition of threshold oxygen levels was considered possible.

The stocks of coho were obtained from Rosewall Creek hatchery, Vancouver Island, B.C., where the water temperature was fairly constant at 7–8°C. The sockeye had originated in Babine Lake, B.C., but were also cultured from the egg stage at Rosewall Creek. In the laboratory all fish were acclimated for a period of 2 wk to 15°C before the start of growth tests. They were held on a normal declining photoperiod (fall season) throughout the acclimation and experimental periods; no preacclimation to subsaturated oxygen levels was applied. When ready, fish were immersed directly into the prescribed environmental O_2-concentration.

EXPERIMENTAL CONDITIONS AND FEEDING

From a selected sample in which the size range was within the mean weight ± 1 SD of the cultured hatchery stock, 30 fish were assigned by random numbers to each of 10 tanks. The prescribed oxygen concentrations in 1977 were 3, 4, 5, 6, 7, 8, and 10 mg O_2/L, with replicates at 3, 5, and 7 mg O_2/L. These were intended to cover effectively the dependent and independent segments of the relation between growth rate and O_2-concentration (see Fig. 1). The additional series performed a year later included 2, 3, 7, and 10 mg O_2/L for coho, and 2, 3, 4, 5, 7, 10, and 15 mg O_2/L for sockeye.

Each experimental tank held 180 L of freshwater which was flushed with oxygen-controlled water at a rate of 360 L/h. A recirculation pump served to keep the water well mixed and produced an average velocity within the oval tanks of 6–8 cm/s; this, in turn, helped to remove rapidly any fecal matter through a central standpipe. Temperatures were recorded and adjusted each day to within ± 0.1 of 15.0°C.

The fish were hand-fed with Oregon moist pellets four times per day on weekdays (Monday through Friday) and a similar number of times by automatic feeders on weekends (Saturday and Sunday). During the weekdays the amount of food was carefully monitored to produce an estimated 5% in excess of satiation, i.e. 5% of pellets were seen to swirl around the tanks untouched. The daily consumed amount was apportioned to automatic feeding for the weekend on the assumption that the determined daily rate during the week applied throughout the whole week.

Conversion efficiencies were calculated on the basis of dry weight gain to dry weight fed.

OXYGEN CONTROL AND MONITORING

Each tank was equipped with a gas stripping column, 10 cm in diameter and 122 cm long, packed with porcelain saddles. In the standard manner for gas stripping, nitrogen was bubbled up the column in counter-flow to temperature-adjusted water flowing down the column. The large amount of desaturated water required to flush each tank twice each hour necessitated correspondingly large amounts of nitrogen. This was provided from two 150 L, low-pressure liquid nitrogen tanks using a regulator and distribution manifold with gas flow-meters for each stripping column. For precision control of oxygen levels it was important to keep the full length of the column free from any flooding with water, and to maintain a close watch on the O_2-concentrations by frequent recordings (see Tables 1, 2).

All 10 tanks were monitored by two remote oxygen electrodes and meters (Electronic Instruments Ltd., model 15A) and continuously recorded on two strip chart recorders (Hewlett Packard 7100B). Tanks 1–5 were monitored by one electrode and tanks 6–10 by the second electrode, periodically flushed by the discharge water from each tank. This was accomplished by a system of solenoid valves controlled by a 10-unit time switch: for 15 min water from tank 1 flowed over the electrode, then tank 2 was recorded for 15 min, and so on — to the 5th tank in each set and back to 1. In this way the O_2-level in each tank was recorded every 75 min throughout the day. The system was calibrated every 2 d by Winkler titrations of water siphoned carefully from three tanks: a high O_2 tank, a low O_2 tank, and a middle-level O_2 tank. Then both recorders were adjusted to give accurate, equivalent, and linear responses. Calibration usually involved only a minor adjustment in recorder levels. Homogeneity of O_2-concentration within each tank and the discharge water was checked and found to be consistently high.

AMMONIA AND pH LEVELS

To confirm that the flushing rates were indeed keeping potentially inhibiting waste products well below any critical level, samples of water from the inlet and from three tanks with low oxygen were analyzed for ammonia and pH. Total ammonia, determined at a mean level of 0.04 mg/L in the tanks, was approximately double that of the inlet water. Since the pH levels at each sampling point were not significantly different (range 7.13–7.22), the un-ionized ammonia was also about twice the inlet level, at 0.17 µg/L. Toxicity of ammonia is mainly ascribed to the unionized fraction. The recorded tank level was consequently less than 1/100 of the

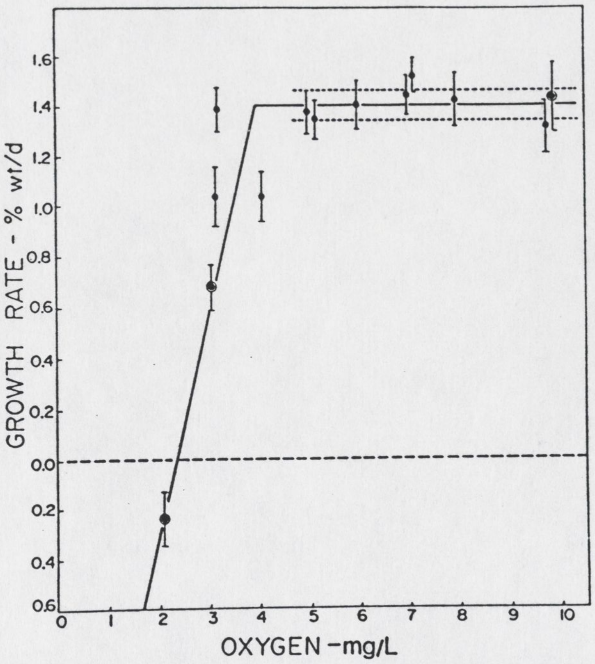

FIG. 1. Specific growth rates (±SE) of fingerling coho salmon (5–10 g) in relation to oxygen concentration at 15°C. Results of second experiment (1978) shown as circled points. Values (8) obtained at and above 5 mg O_2/L had a mean growth rate of 1.41% wt/d, shown as horizontal solid line with 95% confidence limits as dotted lines. Sloped line is the zone of dependence (drawn by eye). Replicates performed at ~ 3, 5, 7, and 10 mg O_2/L.

incipient toxic level (Environmental Protection Agency 1976) and 1/10 of the most conservative safe level (Burrows 1964).

HEMATOCRITS

Blood was collected from 20 fish at the start of the experiment and from 12 fish from each tank at the end of the experiment. The fish were dried of surface moisture, their tails cut off, and blood collected in heparinized microhematocrit tubes. These were spun for 10 min in an I.E.C. model M.B. centrifuge, and then read.

GILL CONDITION

Gill arches were dissected from an initial random sample of 10 stock fish and from a final sample of 3 fish per tank at the end of the experiment. They were fixed in Bouins fluid. Five micrometres paraffin sections were cut to show the lamellae; these were stained with hematoxylin and eosin. The slides were examined for clubbing of the lamellae, swelling or damage to surface cells, and any edematous fluid between cells.

Results and Discussion

COHO GROWTH RESPONSE

The results from the 1977 and 1978 experiments with coho (Fig. 1, Table 1) indicated a marked dependence of growth on environmental oxygen at concentrations below 5 mg/L. Using this level as a provisionary threshold concentration, all growth rates at or above 5 mg O_2/L were pooled to provide a mean value of 1.41% wt/d ± 0.02 SE. Of the five tests performed below 5 mg O_2/L, four were significantly lower in growth rate ($P < 0.01$, Table 1) than the independent rates. However, in one particular case (the 1977 coho in tank 10 at 3 mg O_2/L) the mean growth rate was even slightly higher than that for the 1977 tank 5 at 10 mg O_2/L. It had been observed during the acclimation period that the coho in tank 10 were a remarkably ravenous group. Their intensive feeding activity persisted into the controlled oxygen period when they were assigned (by random number) to a target concentration of 3 mg O_2/L. Despite this low level of oxygen they were able to maintain a normal growth rate with correspondingly high conversion efficiency. The extent of the chance variability in response among samples of this species shows up in the use of replicated tanks where a difference of 0.12%/d in growth rate occurred at the air-saturated level (~ 10 mg O_2/L) and 0.35%/d at 3 mg O_2/L.

One growth record, 0.87% wt/d at 7 mg O_2/L (Table 1, 1978 fish) was discarded as being aberrant when compared with all growth rates above 5 mg O_2/L $P < 0.01$). It was one-third less than expected and had a conversion efficiency (13.3%) much below average (21.8%). The 2-weekly incremental growth rate fell off markedly in the latter part of testing, possibly indicating incipient disease.

The construction lines drawn through the coho points in Fig. 1 are in keeping with the concept of Limiting Factors (Fry 1947, 1971). The dependent zone rises from zero growth at the intercept at 2.3 mg O_2/L reaching the mean maximum growth at the interpolated threshold level of 4.0 mg O_2/L, defining the level of the plateau for the independent zone.

SOCKEYE GROWTH RESPONSE

The sockeye data (Table 2) lend strong support for the basic interpretation of the coho response. Displaying somewhat less variability between 5 and 10 mg O_2/L, their obvious zone of independence (Fig. 2) adds confirmation to the Limiting Factor concept. By iterpolation in the zone of dependence, the intercept at zero growth occurred at 2.6 mg O_2/L reaching a plateau (zone of independence) at 4.2 mg O_2/L. The single set of growth rates determined above the air-saturated oxygen level, at 15 mg O_2/L, was not significantly different from that at air saturation (10 mg O_2/L); its mean fell just within the 95% confidence limits for the means of the four determinations at and above 5 mg O_2/L.

SOME COMPARISONS

A selection of three, well-documented cases has been made from the literature, examining the published data in relation to the Limiting Factor hypothesis, i.e. to test if the concept of a threshold plateau could be disproved.

Herrmann's coho — The results of experiments performed by Herrmann et al. (1962) on coho salmon at 20°C are mostly comparable with those recorded in the present study. A strong inflection (downward) in growth rate occurred between 4 and 5 mg O_2/L; however, at higher oxygen concentrations Herr-

TABLE 1. Record of oxygen levels, weights, growth rates, conversion efficiencies, and hematocrits of fingerling coho salmon tested in the fall of 1977 and 1978. Mean ±SE given. Temperature maintained through the 6-wk-growth period at 15 ± 0.1°C. Number of fish per tank = 30. Starting hematocrit was 39.8 ± 1.1% (1977) and 38.4 ± 0.4% (1978). Significant differences (t-test; $P < 0.01$) in growth rate from mean values at and above 5 mg O_2/L shown with double asterists (**) — highly significant. Statistical reference: Steel and Torrie (1960).

Target O_2 (mg/L)	Actual O_2 (mg/L)	Start weight (g)	Final weight (g)	Growth rate (% wt/d)	Conversion effic. (%)	Final hematocrit (%)
			1977			
10	9.79±0.02	5.67±0.16	9.86±0.35	1.32±0.11	21.2	40.3±0.4
8	7.99±0.04	5.58±0.18	10.21±0.21	1.43±0.11	21.2	37.0±1.5
7	7.08±0.03	5.53±0.14	10.31±0.19	1.53±0.07	22.2	39.3±0.5
7	7.00±0.05	5.61±0.16	10.04±0.20	1.45±0.08	22.7	40.7±0.7
6	6.04±0.02	5.54±0.14	9.65±0.33	1.41±0.10	21.5	40.4±0.6
5	5.15±0.06	5.68±0.13	9.78±0.24	1.35±0.08	21.8	42.3±0.8
5	5.10±0.05	5.42±0.17	9.56±0.28	1.38±0.09	21.2	39.7±0.6
4	4.10±0.02	5.33±0.15	8.30±0.27	1.04±0.10**	17.8	41.7±0.7
3	3.20±0.07	5.64±0.15	10.05±0.28	1.39±0.09	21.2	41.5±0.8
3	3.17±0.06	5.70±0.16	8.82±0.34	1.04±0.12**	19.0	46.8±1.3
			1978			
10[a]	9.77±0.02	6.54±0.13	9.90±0.32	1.44±0.14	19.7	35.7±0.6
7	7.07±0.02	6.69±0.15	9.44±0.26	0.87±0.09**	13.3[c]	40.2±0.6
3	3.06±0.02	6.72±0.14	8.91±0.27	0.68±0.09**	13.5	39.5±1.0
2[b]	2.10±0.02	6.55±0.12	6.33±0.14	−0.24±0.11**	−4.4	41.0±0.5

[a] Four-week duration.

[b] Two-week duration.

[c] Conversion efficiency significantly different ($P < 0.01$) from values for 5 mg O_2/L and above.

TABLE 2. Similar records to Table 1, for sockeye tested in 1978. Note that initial weights were about twice that for coho, resulting in generally lower growth rates. Starting hematocrit = 37.0 ± 0.9%. Temp = 15 ± 0.1°C.

Target O_2 (mg/L)	Actual O_2 (mg/L)	Start weight (g)	Final weight (g)	Growth rate (% wt/d)	Conversion effic. (%)	Final hematocrit (%)
15[a]	15.05±0.05	16.67±0.58	22.19±1.02	1.03±0.21	21.3	34.4±0.4
10	9.76±0.01	14.19±0.32	21.34±0.57	0.96±0.08	19.7	39.9±1.6
7	6.93±0.03	15.16±0.36	22.81±0.65	0.93±0.08	21.7	35.6±1.1
5	5.15±0.02	14.69±0.37	21.88±0.62	0.91±0.09	19.8	40.5±0.9
4	4.05±0.03	15.25±0.37	21.25±0.80	0.74±0.11**	20.9	41.6±1.2
3	3.06±0.02	14.18±0.31	17.47±0.43	0.45±0.07**	13.6	38.0±0.6
2[b]	2.19±0.03	14.16±0.35	13.59±0.36	−0.29±0.09**	−13.3	40.7±0.4

[a] Four-week duration.

[b] Two-week duration.

mann believed that a gradual positive slope, rather than a plateau, characterized the "upper" growth rates. The contention was supported by a similar interpretation of the plotted relation between feeding rate and O_2-concentrations above 5 mg/L. However, a comparison of both the growth rates[1] and feeding rates grouped around the experimentally selected O_2-levels of 5, 6, and 8.5 mg/L shows no significant difference in growth rate when means of the grouped points are compared (ANOVA). Insufficient account was taken of the variability in growth and the fact that chance alone would account for the presumed incline. The feeding rates naturally correlate with and reflect the higher growth rates; so the likeness in distribution cannot be used as a supporting argument. Conversion efficiency would be expected to remove the natural bias of feeding rate correlated with growth rate. Indeed, this is what Herrmann displays in his fig. 3 (p. 162), relating food conversiion ratio to O_2-concentration; a plateau characterizes the distribution of points from 5 mg O_2/L and above, not an incline. The use of food conversion efficiency as a sensitive indicator of sublethal stress was demonstrated by Webb and Brett (1972, 1973) when studying the effects of toxic solutions of a pulpmill effluent and a herbicide (sodium pentachlorophenate). In physiological terms, this index can be taken as reflecting a normal capability to digest, absorb, metabolize, and retain essential food components. It can be considered a wide spectrum indicator of an organism's functional capability. Thus, the sustained food conversion efficiency of Herrmann's coho at 5 mg O_2/L and above can be

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[1] Only the 1956 data are considered because of some possibility of leached toxicity from rubber tubing in the 1955 experiments.

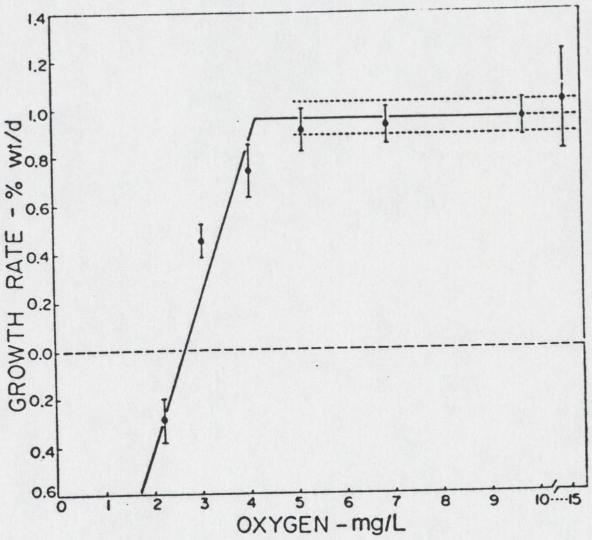

FIG. 2. Specific growth rates (±SE) of fingerling sockeye salmon (14–23 g) in relation to oxygen concentration at 15°C. Values (4) obtained at and above 5 mg O_2/L had a mean growth rate of 0.96% wt/d, shown as horizontal solid line with 95% confidence limits as dotted lines. Point for oxygen concentration (15 mg O_2/L) above air-saturatiion level plotted on a truncated axis. Sloped line in the zone of dependence drawn by eye.

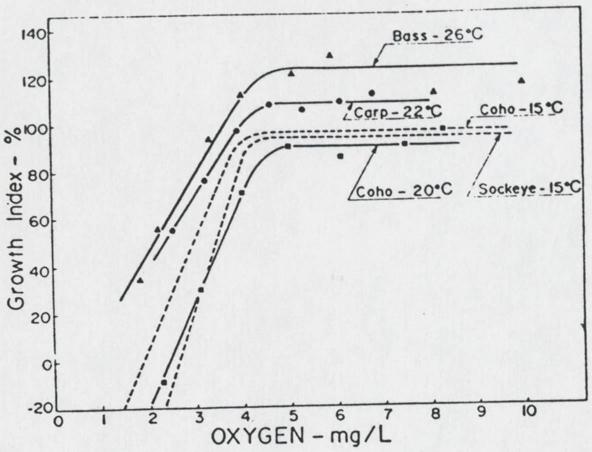

FIG. 3. Relation of oxygen concentration to growth rate expressed as a percentage of the "growth index" developed by each author. Data for bass (*Micropterus salmoides*) from Stewart et al. (1967), for carp (*Cyprinus carpio*) from Chiba (1966), and for coho at 20°C from Herrmann et al. (1962). Coho and sockeye lines (broken) transcribed as a percentage of mean maximum growth rates determined in this paper. The vertical positioning by species has no relative significance. (Adapted from Brett 1979.)

interpreted as confirming the general absence of any stress affecting growth.

Stewart's bass — At the same laboratory similar studies to those on coho were preformed on largemouth bass (*Micropterus salmoides*) by Stewart et al. (1976). At a temperature of 26°C, oxygen concentrations ranging from 1.6 mg/L to as high as 24.1 mg/L were used, both as fixed exposures (mostly 15 d) and as fluctuating daily concentrations. Only the data for the former are considered. Some difference in mean initial weights of fish naturally occurred for the 7-mo period over which experiments were conducted. On the whole, however, these were remarkably similar falling between means of 2.6 g and 4.2 g for five of the six experiments; one had a mean weight of 6.7 g. The authors chose to express growth as % gain in weight for each experimental time, which was not a uniform period in all cases. For purposes of analysis here, the specific growth rates as % gain in dry weight per day were calculated, omitting the one case of larger fish because of the lack of comparability that size imposes.

The data were split into three groups: (1) a low group between 1 and 5 mg O_2/L, (2) an intermediate group between 5 and 10 mg O_2/L, and (3) an upper group from 15 to 25 mg O_2/L. These were tested first for association between O_2-concentration and growth rate, and second (where no significant correlation existed, $r^2 = 0.4$ or less) for significant differences in mean growth rate. As is obvious to expect from the original data plots, there was a highly significant correlation for group 1, in the dependent O_2-zone ($r = 0.90$). Above 5 mg O_2/L there was no correlation within a group nor any significant difference between groups (t-test). The natural variability, noted through the use of replicates in the present coho–sockeye series, is quite sufficient to explain the distribution of observed values, i.e. growth rate independent of O_2-concentration above 5 mg/L, and, therefore, without an optimum. The Limiting Factor hypothesis is not negated. Indeed, the authors appear to have been influenced by one particularly low value determined in September at 24.1 mg O_2/L (their exp. 5 and fig. 2). The food conversion determinations display a clear plateau at and above 5 mg O_2/L.

Chiba's carp — Chiba (1966) exposed juvenile carp (*Cyprinus carpio*) to various oxygen concentrations from 2.2 mg/L to 7.2 mg/L at temperatures in the range of 20–23°C. The smallest fish, weighing about 0.6 g, were tested for only 5 d; the largest fish at a mean weight of 3.2 g and 3.4 g were exposed for 21 and 35 d, respectively. The considerable variability reported in observed growth rate no doubt reflected variability arising from size and time differences as well as that from biological variability and any imprecision of oxygen control. By grouping the results in divisions of 0.5 cm^3 O_2/L, mean responses were determined for each interval from 1.5 to 5.0 cm^3 O_2/L (~ 2–7 mg O_2/L). Chiba's fig. 2 shows these means above 4.0 mg O_2/L to fall approximately on a straight line that is not significantly different from a plateau, i.e. a definite zone of oxygen independence occurs above 4.3 mg O_2/L (our estimate).

These three cases were discussed in less detail in Brett (1979). They have been analyzed further here for comparison with the coho–sockeye series. The combined information has been plotted in Fig. 3, including the derived data points from the above-mentioned three cases. It is of interest that within the range of temperatures (15–26°C) and four species involved, the inflection from oxygen dependence to independence occurs between 4 and 5 mg O_2/L. Precise inflection points are difficult to set because of the greater variability that accompanies transition zones. Despite differences of species and temperature the common nature of the response is most apparent.

HEMATOCRIT AND GILL CONDITION

The percent volume of compressed cells in a centrifuged sample of whole blood (hematocrit) has been considered normal for a clinically healthy salmonid when the value ranges between 32 and 52 (Wedemeyer and Chatterton 1971). All 177 coho samples fell well within this range, not dropping in mean value below 35% and, in one instances, raching 47%. Within this span there was a significant negative correlation between hematocrit level (y) and O_2-concentration (x) ($y = 44.1 - 0.63x$, $r = -0.61$, $P < 0.05$). From an interpolated estimate at 38% at 10 mg O_2/L the hematocrit level rose on the average to 43% at 2 mg O_2/L. This is viewed as a natural adaptive response to increase the blood-carrying capacity for oxygen as the availability decreases, not unlike the effect of increasing altitude on the hematocrit of some higher vertebrates.

The sockeye data showed a similar relation ($r = -0.67$). Although the values were all normal, the slight but indicative trend developed over only 6 wk of exposure to various oxygen levels strongly suggests that prolonged exposure would incerase the strength of the adaptive response.

The generally healthy state of all fish (only those from the 1977 experiment were examined) was confirmed from gill examination. Histological inspection revealed no trace of clubbing or swelling to suggest any form of respiratory distress down to 3 mg O_2/L when exposed for 6 wk.

CONCLUDING STATEMENT

It has not been the purpose of this study to seek evidence on the acceptable level of oxygen in nature (or, for that matter, in salmon hatcheries). This subject is fraught with problems of environmental complexity involving all life stages and functions, the necessary levels of activity to survive in a competitive world, and the interaction of water quality (or lack of it) with varying oxygen concentrations (see Davis 1975). It has been the purpose to define how oxygen acts on the activity of growing in the pristine environment of highly controlled laboratory conditions. It is concluded from the data of these experiments and supported by analysis of selected, substantial experiments of others, that oxygen acts as a strict Limiting Factor. Excessively high, supersaturated levels have not been examined extensively; almost any environmental factor can be increased to a debiliating level. The defined critical inflection from oxygen dependence to independence occurs at 4.0–4.2 mg O_2/L for coho and sockeye at 15°C. This is equivalent to an O_2-saturation of about 43%.

Acknowledgments

We express appreciation to Mr J. E. Shelbourn for his willing undertaking of any statistical analyses. The excellent support of the engineering staff of the Pacific Biological Station under Mr P. Vogt should not go unmentioned for their reliable supply of high-quality, temperature-controlled water.

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Fish Physiol. v. 4 Randall

p. 283: change 10° – 20° w/ goldfish increases standard oxygen uptake by 254% (3.5×)
increase temp. – increase cardiac output & ventilation.

Fry, v. 6 – acclimation – process of adapting to change – acclimatization – 'preadaptation' ex. seasonal rhythym – anticipates change.
– lethal factor
– controlling factor ex. temp. – influence change metabolic M
– limiting factor O_2 & growth
– Masking factor

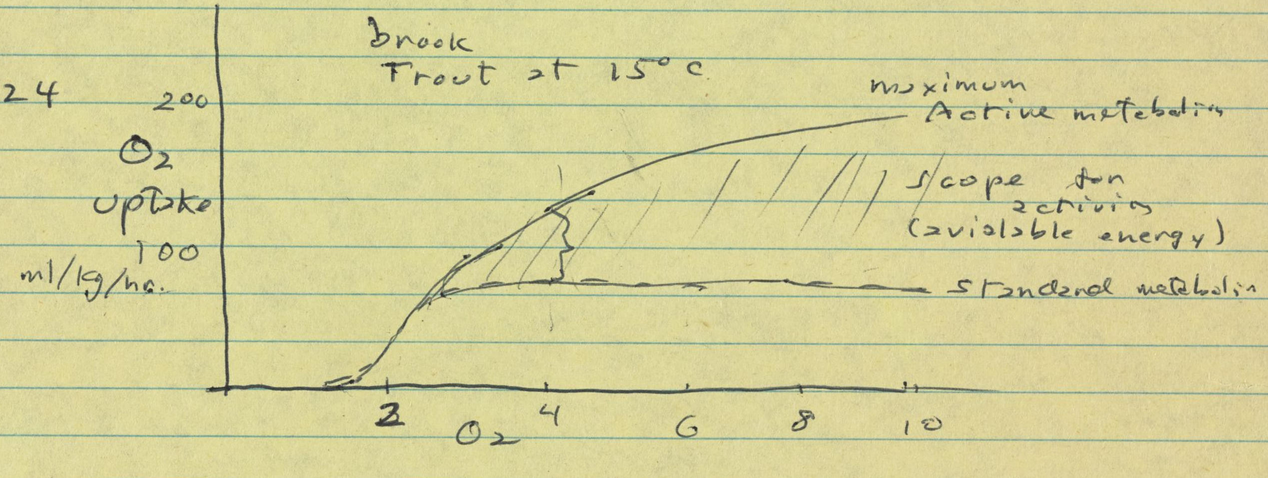
* but note compared w/ nongame fish

Table II · sockeye

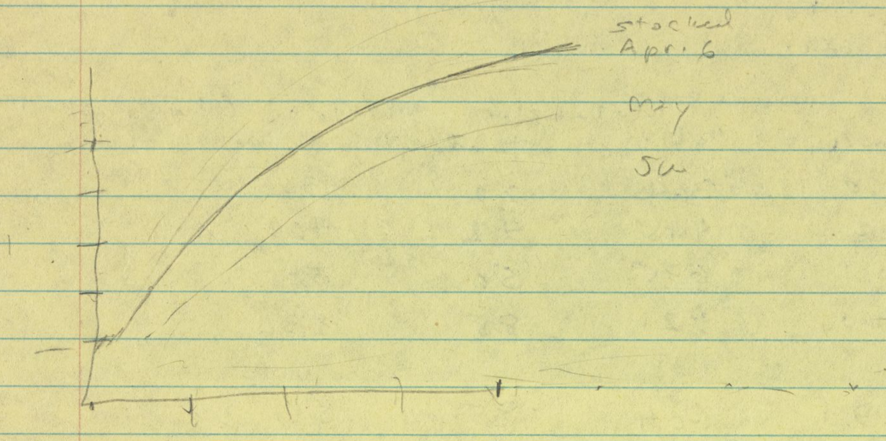
Temp.	O_2 mg/l	Metabolism ml/kg./hr. (O_2 uptake) Active	Standard	Scope
5	12.8	364	29	335
10	11.2.	445	42	403
15	10.1	635	50	585
20	14.0	921	85	836
20	9.1	604	85	519
24	8.5	601	139	462

acclimation to low O_2 – 160-200 hrs = 4-8 days

Fig. 24



CO_2 levels – partial pressure effect. O_2-CO_2 -


stocked
April 6
May
Jun

—overhead

GROWTH OF RAINBOW TROUT STOCKED IN LAKE OGALLALA

Date	April 7 Stocked	June 1 Two Months	August 1 Four Months	October 1 Six Months	April 1 year
Length	280 mm (11 in)	320 mm (12.6 in)	371 mm (14.6 in)	421 mm (16.6 in)	573
Weight	235 g (1/2 lb)	382 g (5/6 lb)	565 g (1 1/4 lb)	749 g (1 2/3 lb)	1300
C.F.	1.1	1.2	1.1	1.0	0.7

$$K \quad \frac{W \times 10^5}{L^3}$$

W in grams

L in mm

Actual Fish

1987

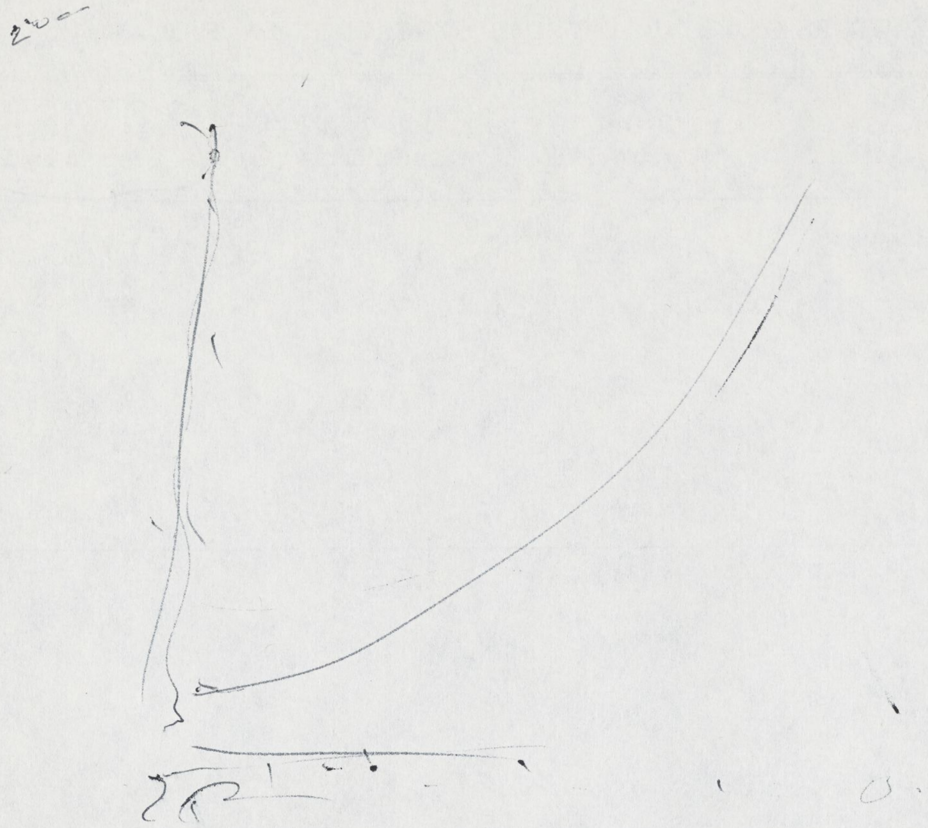
L	W	k
390	660	1.1
370	485	.9
385	675	1.2
395	520	.8
390	620	1.0
420	820	1.1
383	750	1.3
400	660	1.0
406	690	1.0
440	870	1.0

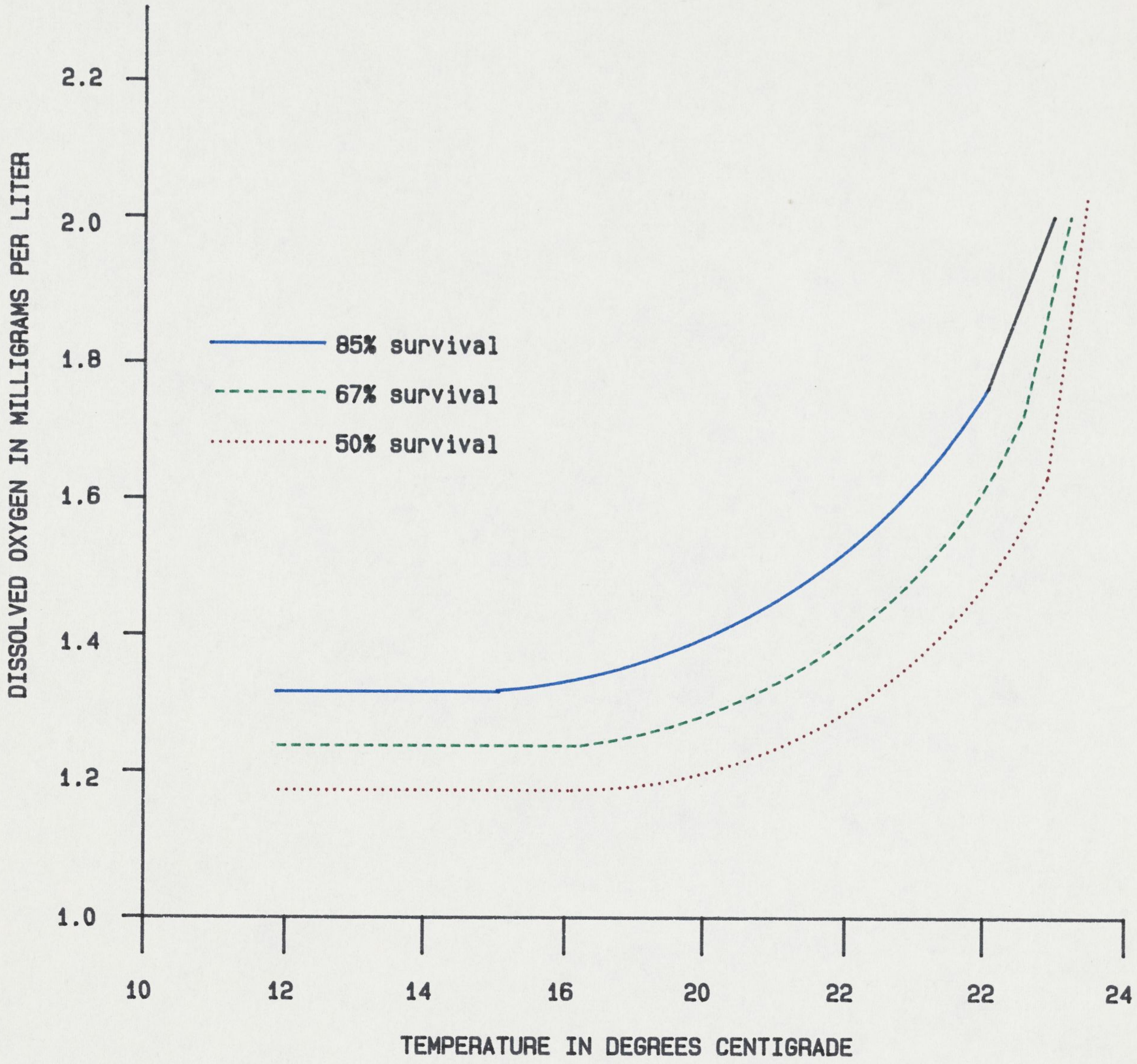
1986

L	W	K
469	1100	1.1
420	1010	1.4
360	500	1.1
455	1100	1.2
473	1200	1.1

CONDITION FACTORS OF RAINBOW TROUT STOCKED IN LAKE OGALLALA

Cohort	At Plant	Before July 15	July 15 to September15	After September15	No.
April	1.0	1.0	1.1	1.0	(1)
May	1.1	1.1	1.1	1.1	(2)
June	1.1	1.1	1.2	1.1	(4)
July	1.1	1.1	1.2	1.2	(1)
August	1.0	--	1.1	1.1	(6)


200

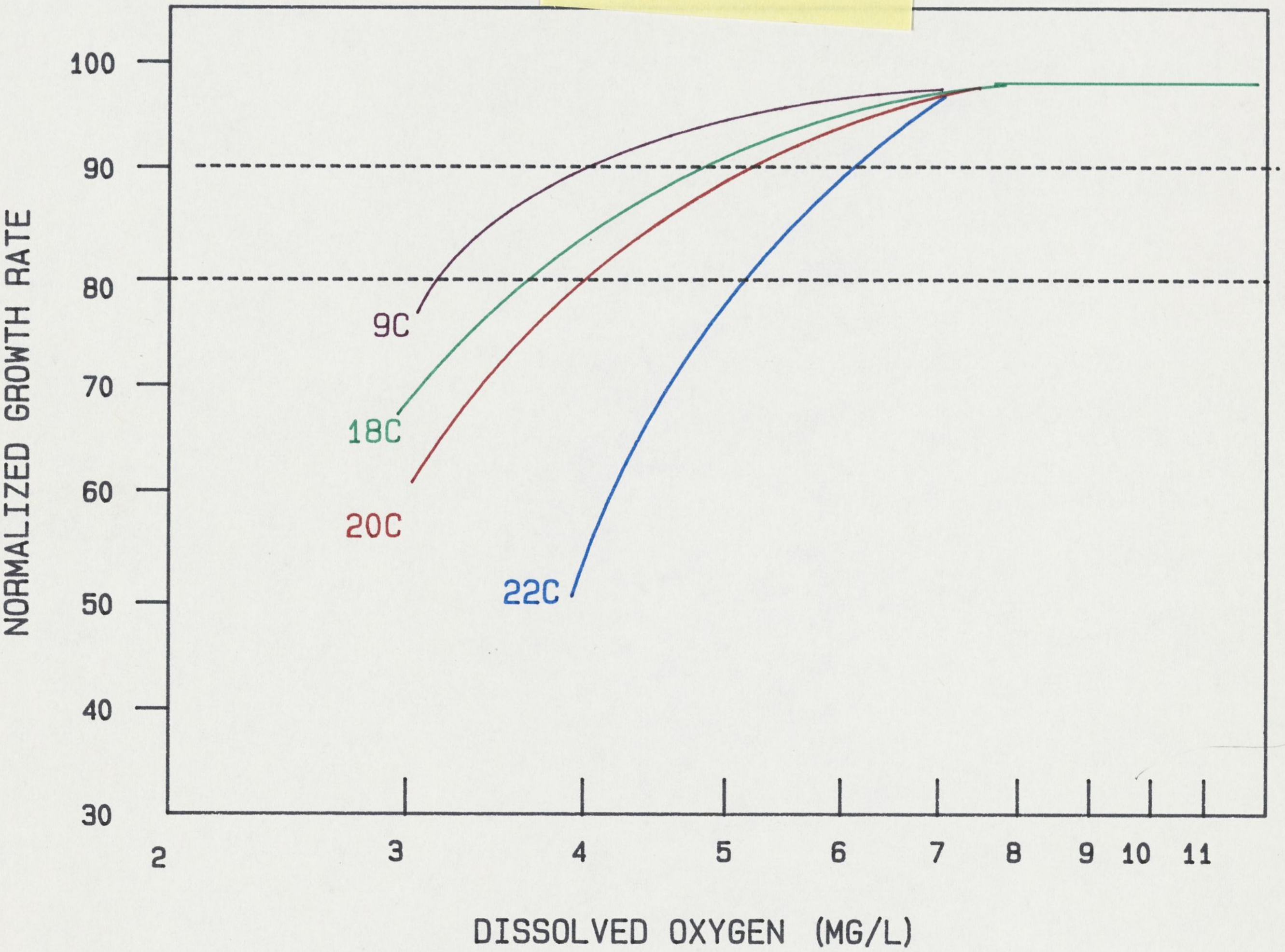


Influence of temperature and oxygen on survival of juvenile Coho Salmon

(from Davison, et al. 1959)

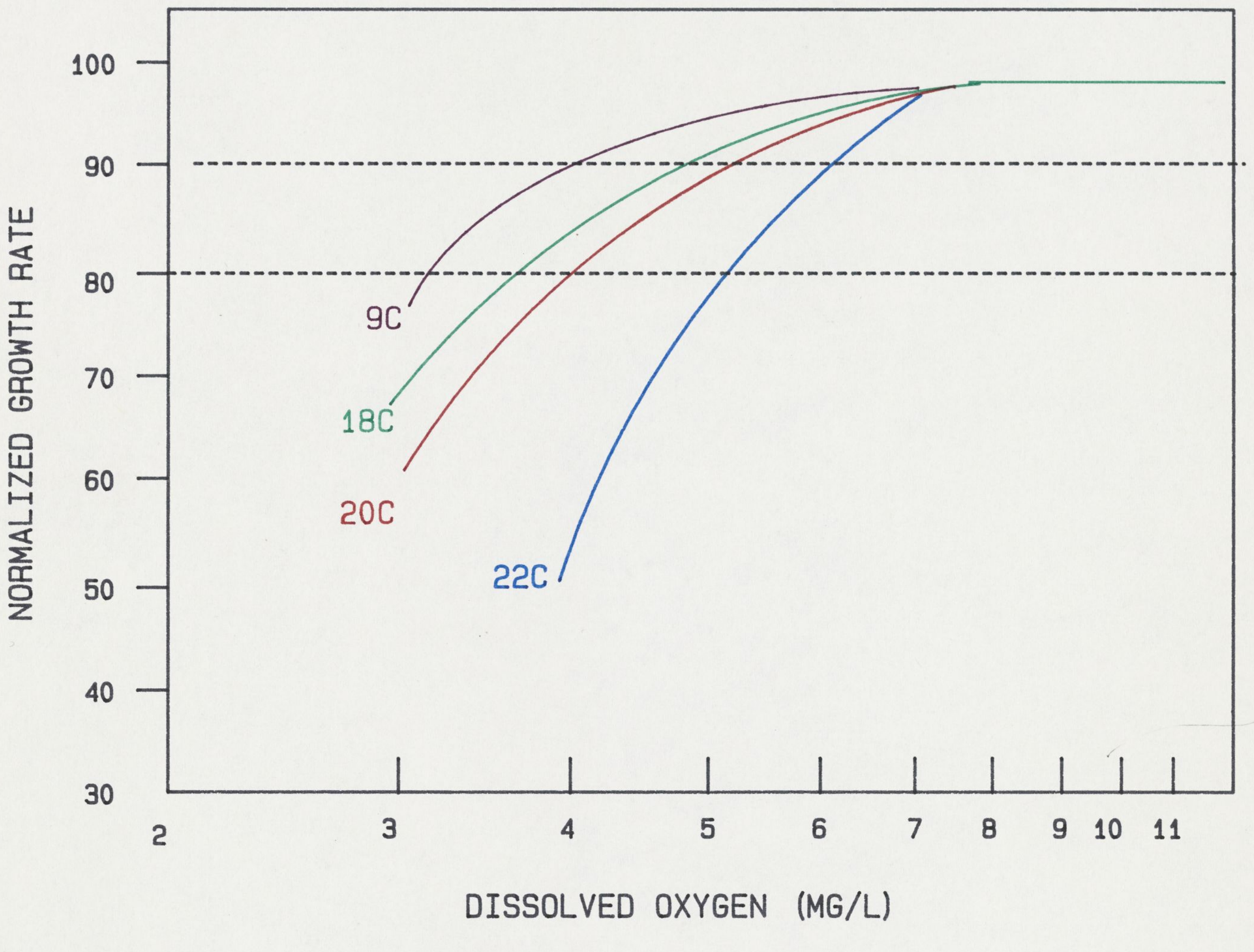
24 hr.?

Fg 6



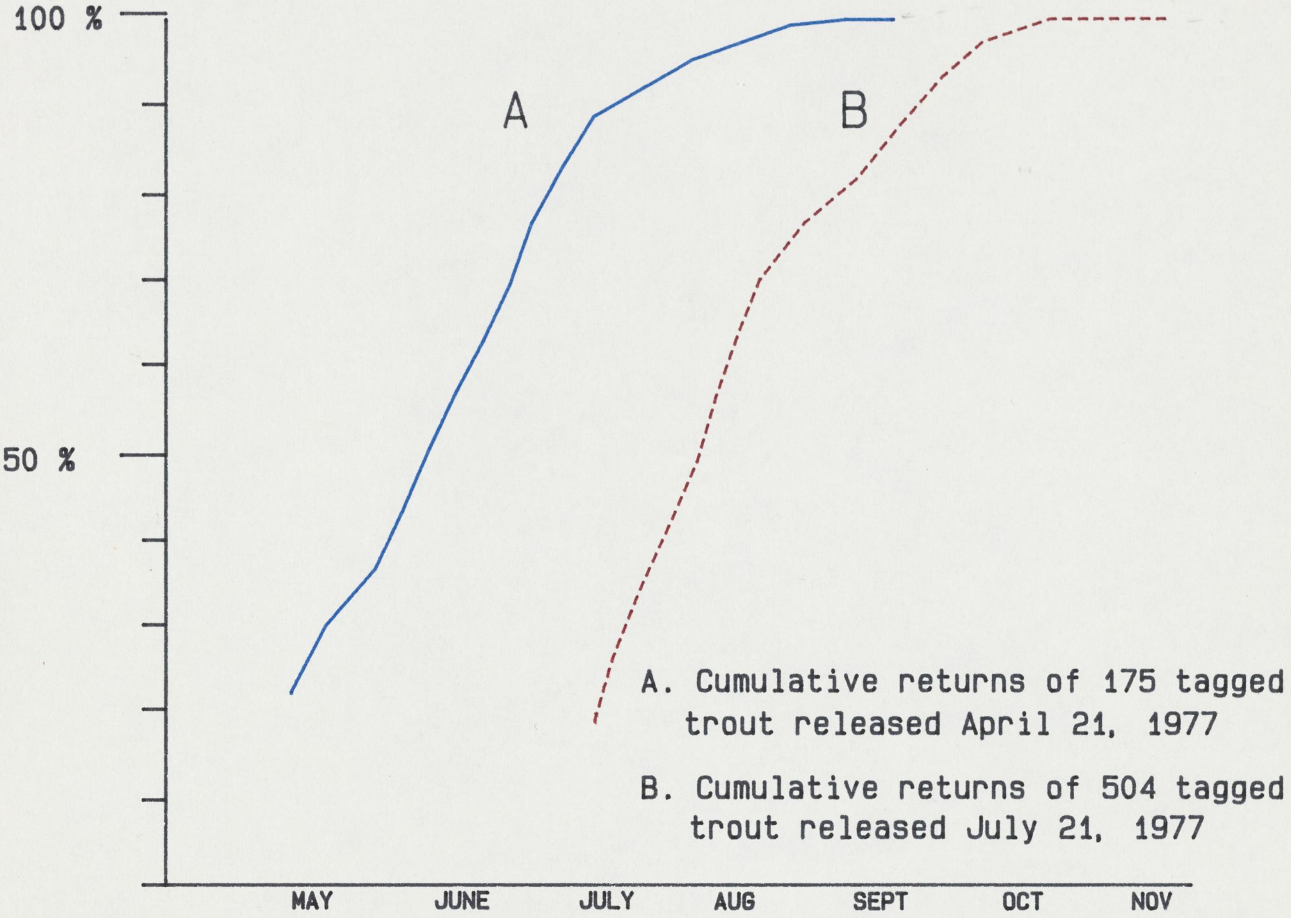
Growth of juvenile Coho Salmon

(from Warren, Doudoroff and Shumway 1973)



Growth of juvenile Coho Salmon

(from Warren, Doudoroff and Shumway 1973)



A. Cumulative returns of 175 tagged trout released April 21, 1977

B. Cumulative returns of 504 tagged trout released July 21, 1977

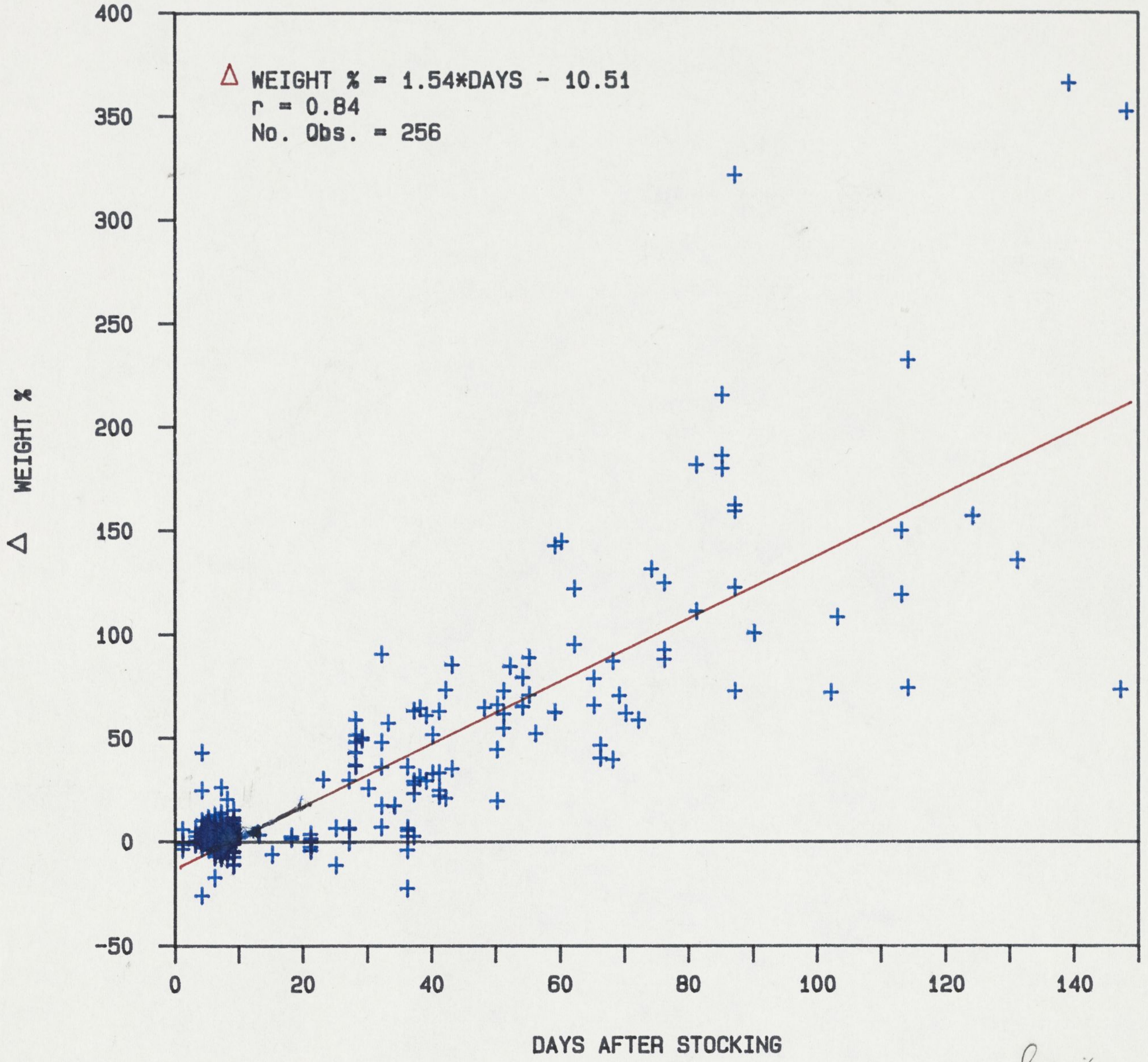
Fg 3

~~how Know~~
100%
return?
None ~~of~~ Apr. trial
return Sept Oct
- none. July?
Oct Nov.

Lake Ogallala

GROWTH OF STOCKED RAINBOW TROUT

TOTAL PLANT - 1987



This is not quite complete

Lake Ogallala

GROWTH OF STOCKED RAINBOW TROUT

APRIL PLANT - 1987

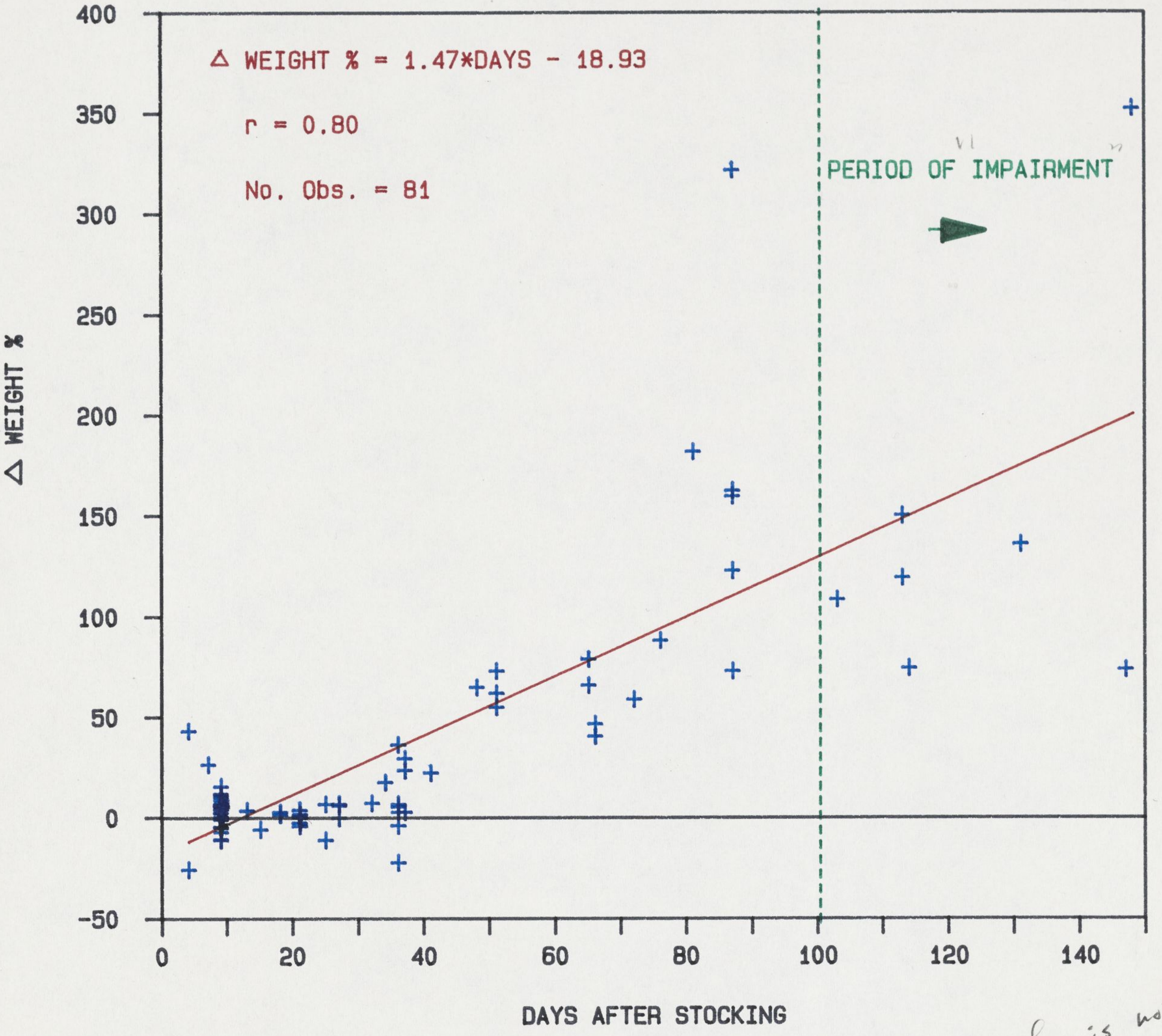


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Fig. 2

LAKE OGALLALA

Buoy Line D.O. – Hourly Values

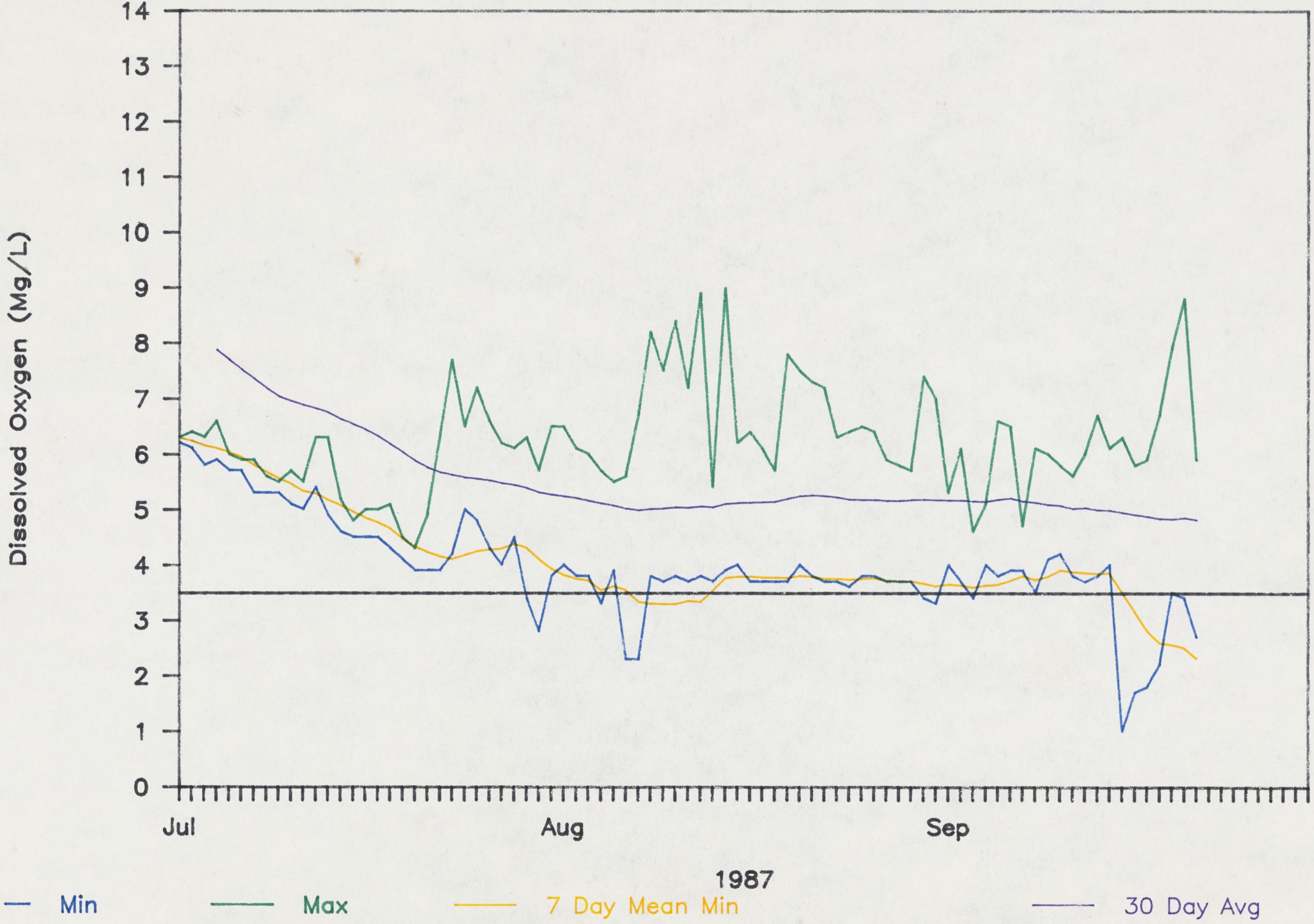
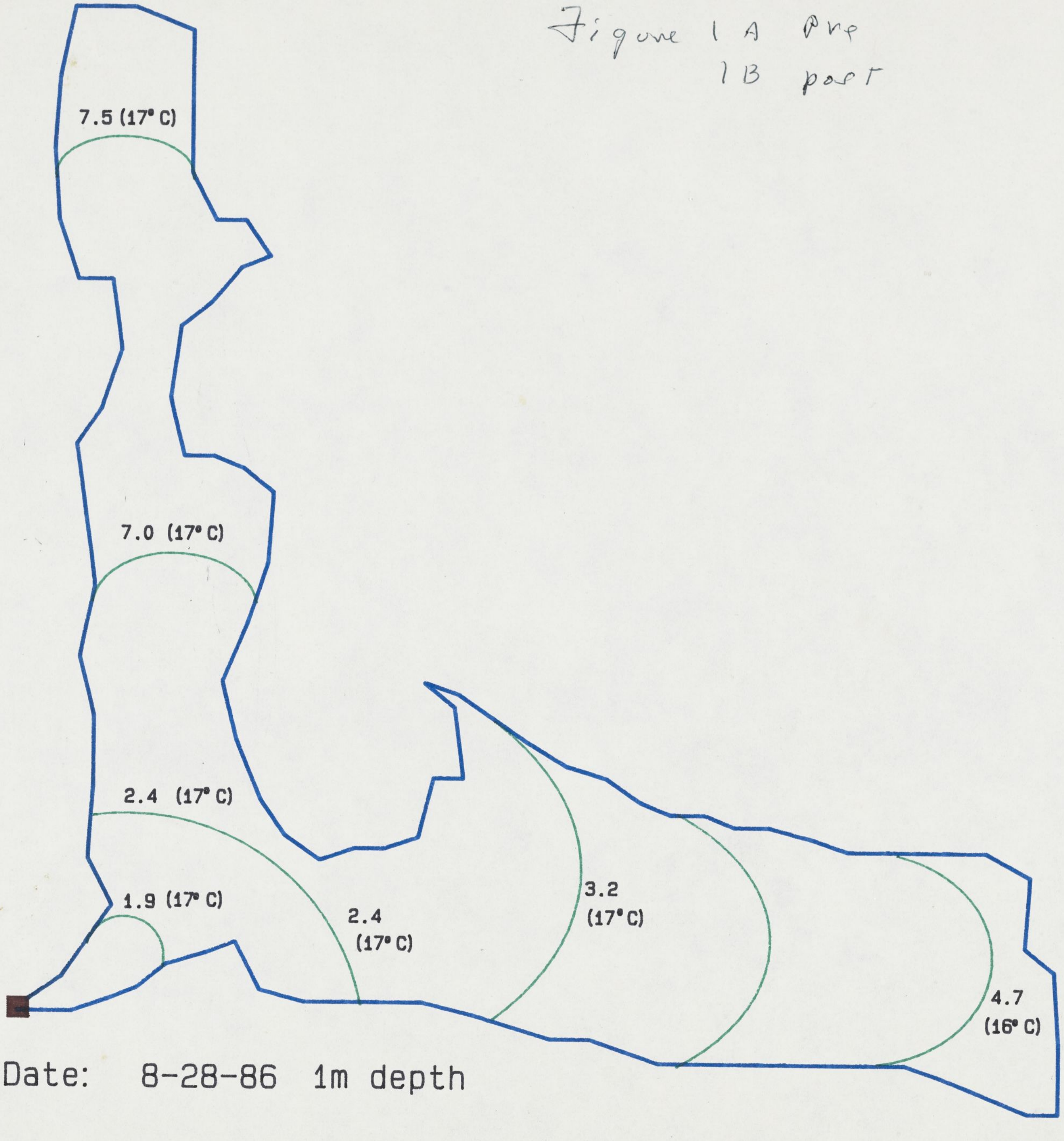


Figure 1A pre
1B post

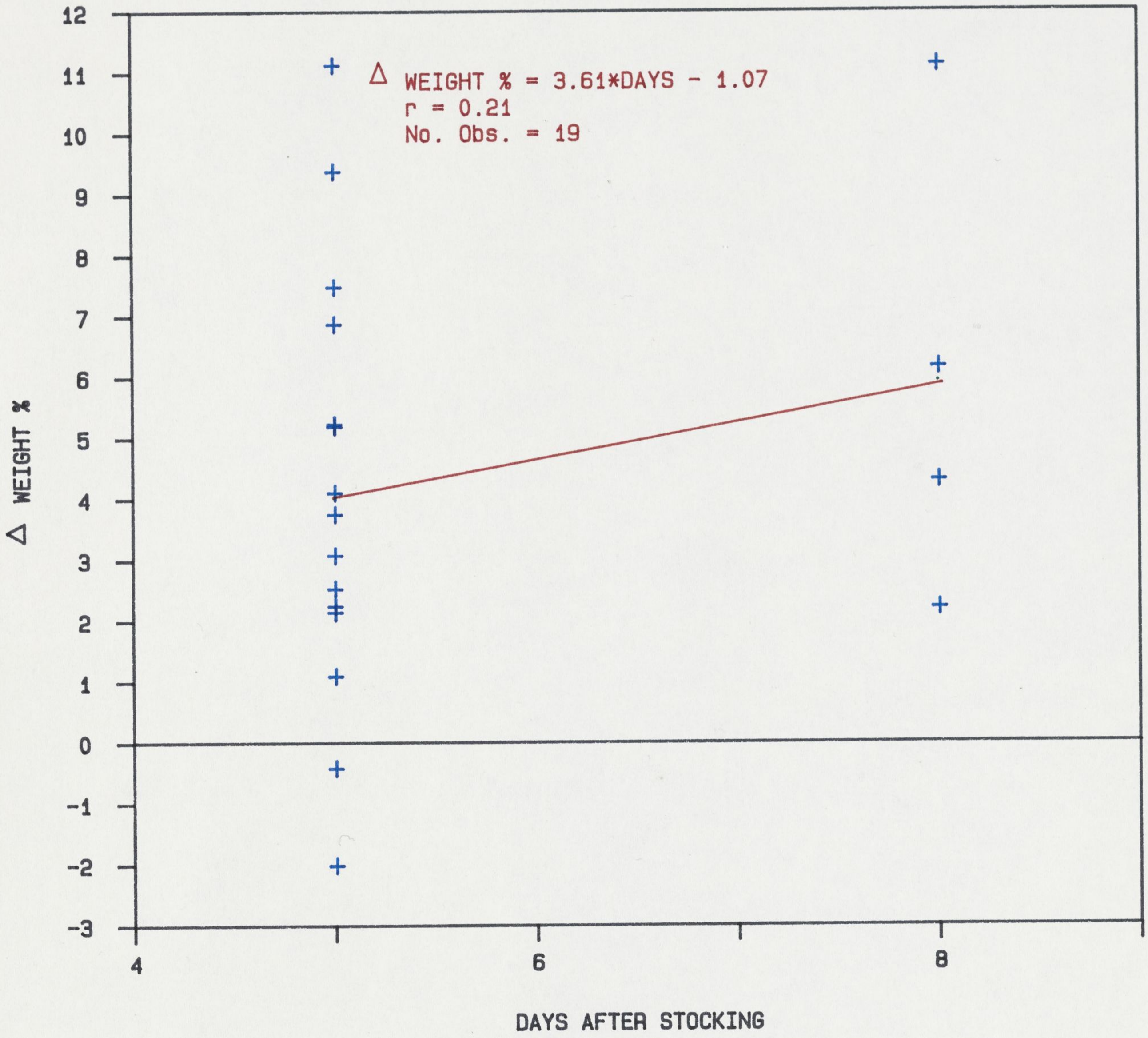


Date: 8-28-86 1m depth

Lake Ogallala

GROWTH OF STOCKED RAINBOW TROUT

OCTOBER PLANT - 1987



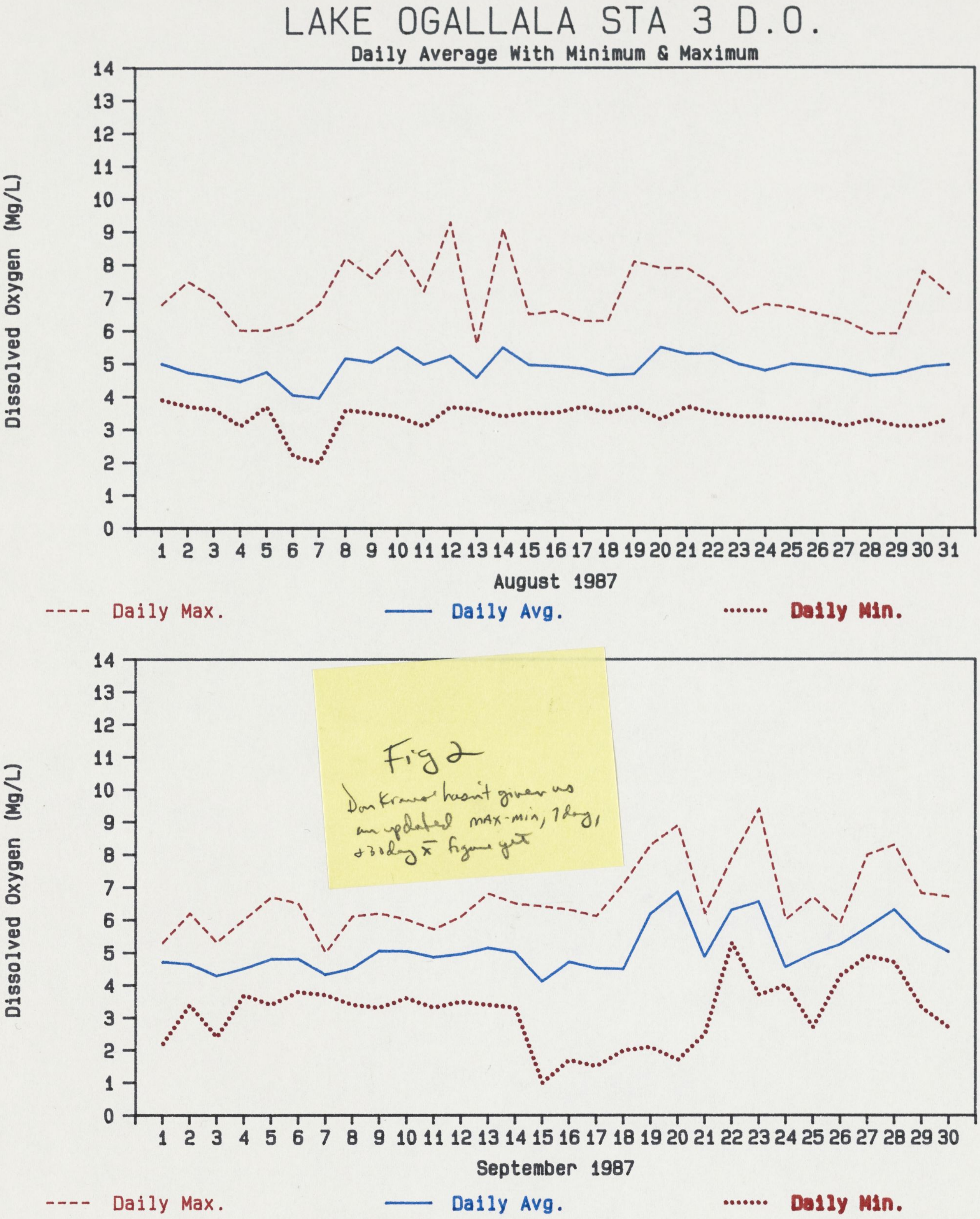


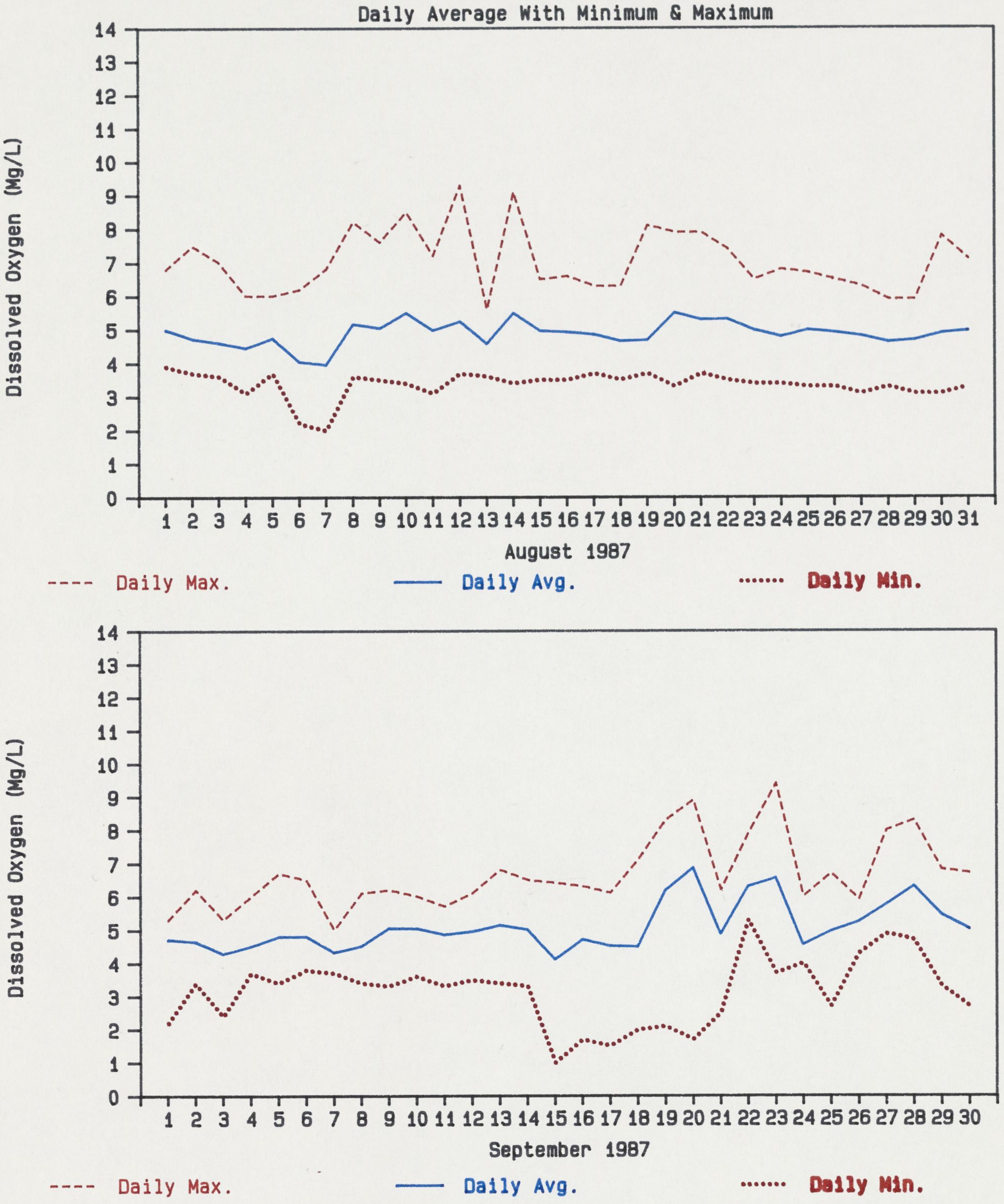
Fig 2

Don Kramer hasn't given us an updated MAX-MIN, 7 day, & 30 day $\bar{x}$ figure yet

Dissolved oxygen at the bouy line

during the August - September "critical period"

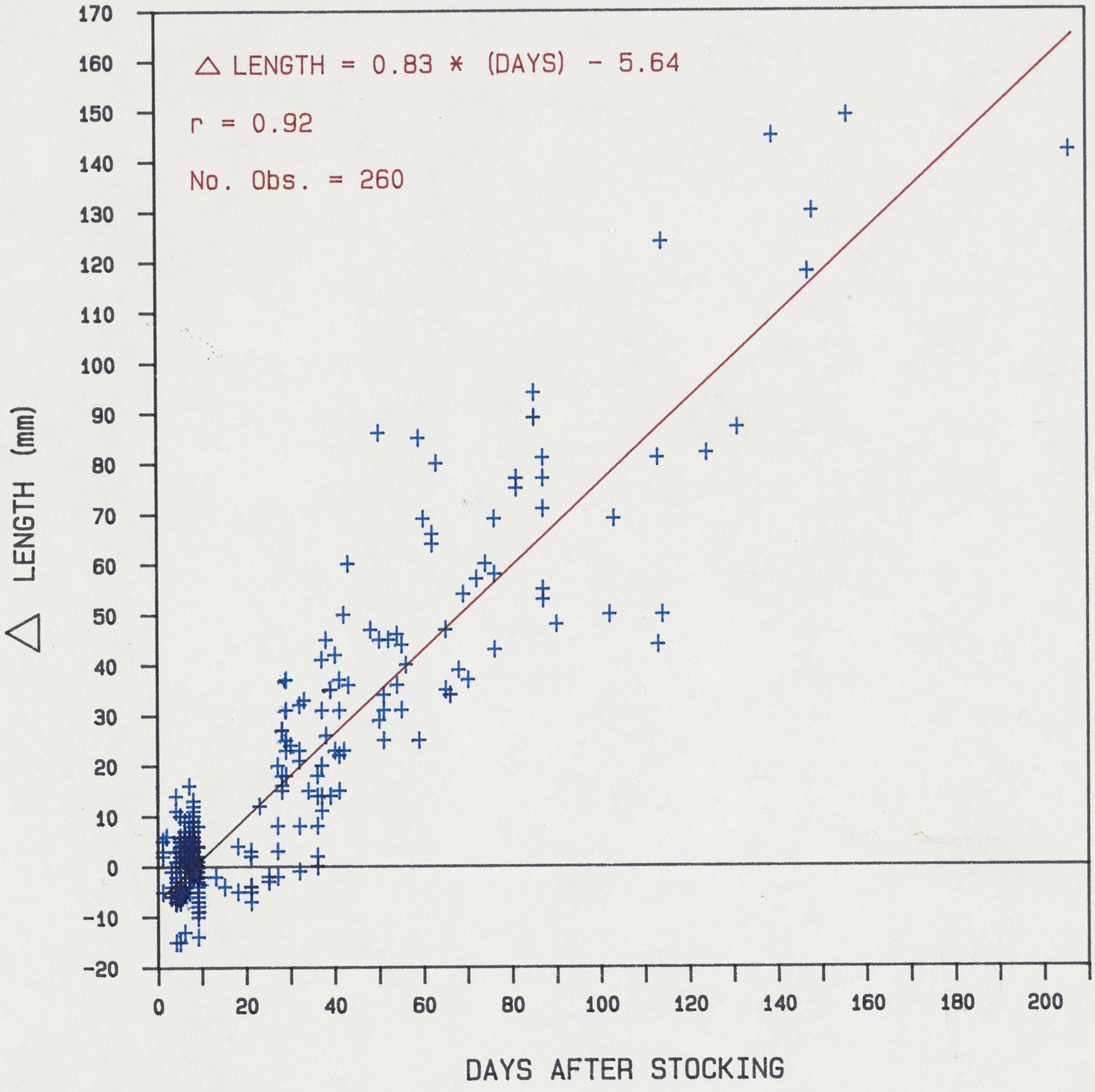
LAKE OGALLALA STA 3 D.O.



Dissolved oxygen at the bouy line

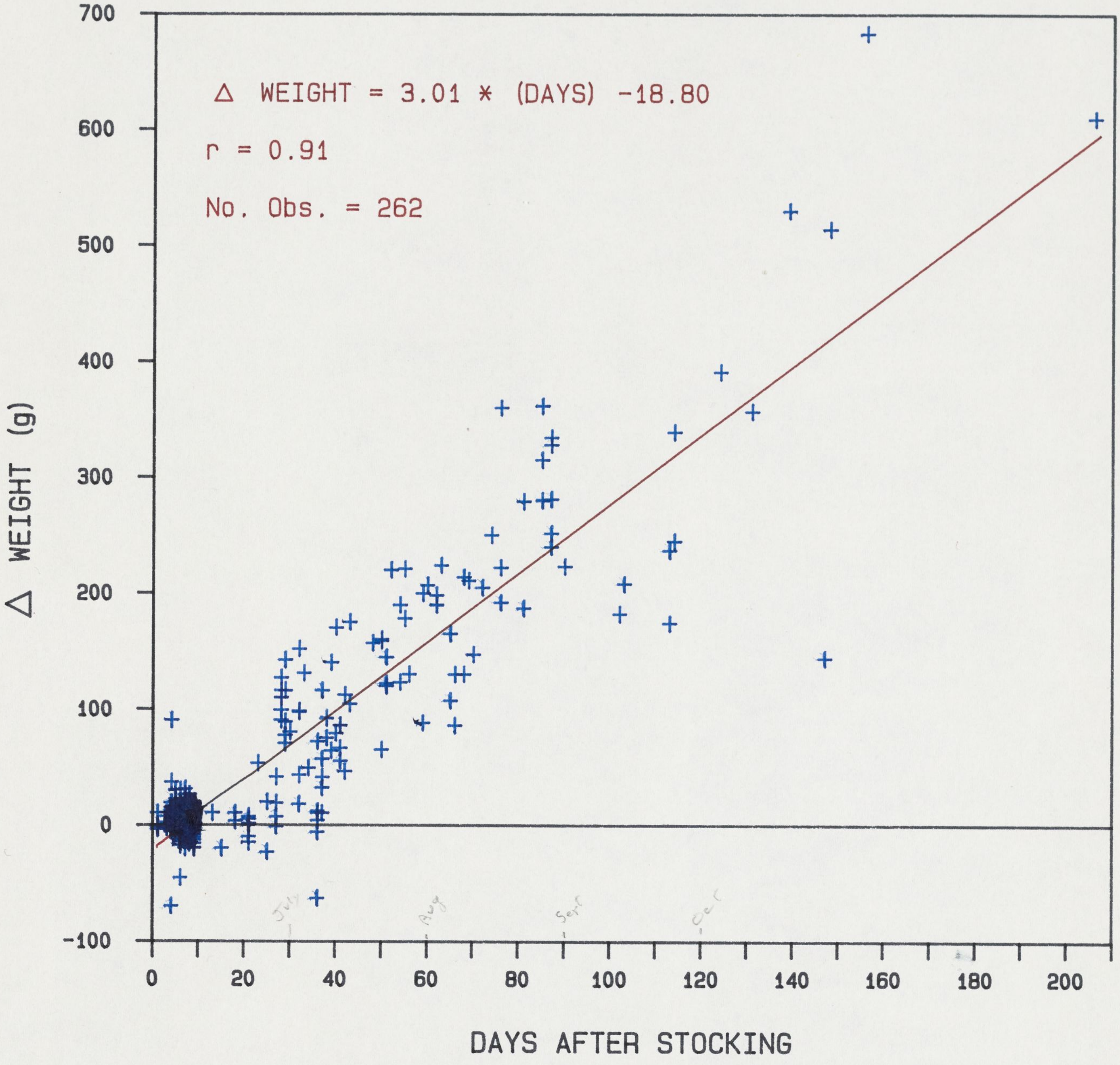
during the August - September "critical period"

LAKE OGALLALA
GROWTH OF STOCKED RAINBOW TROUT - BY LENGTH
TOTAL PLANTS - 1987



LAKE OGALLALA

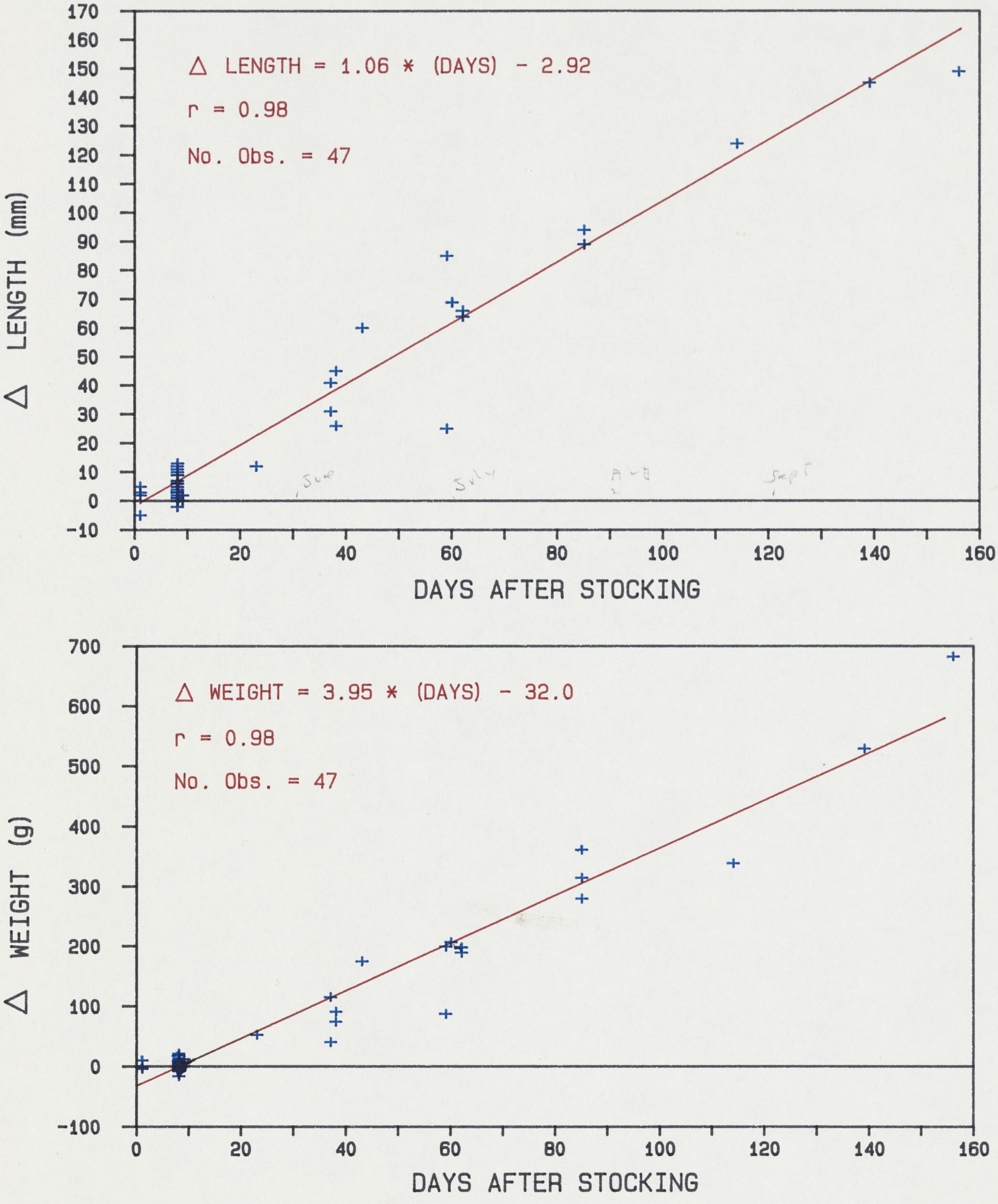
GROWTH OF STOCKED RAINBOW TROUT - BY WEIGHT
TOTAL PLANTS - 1987



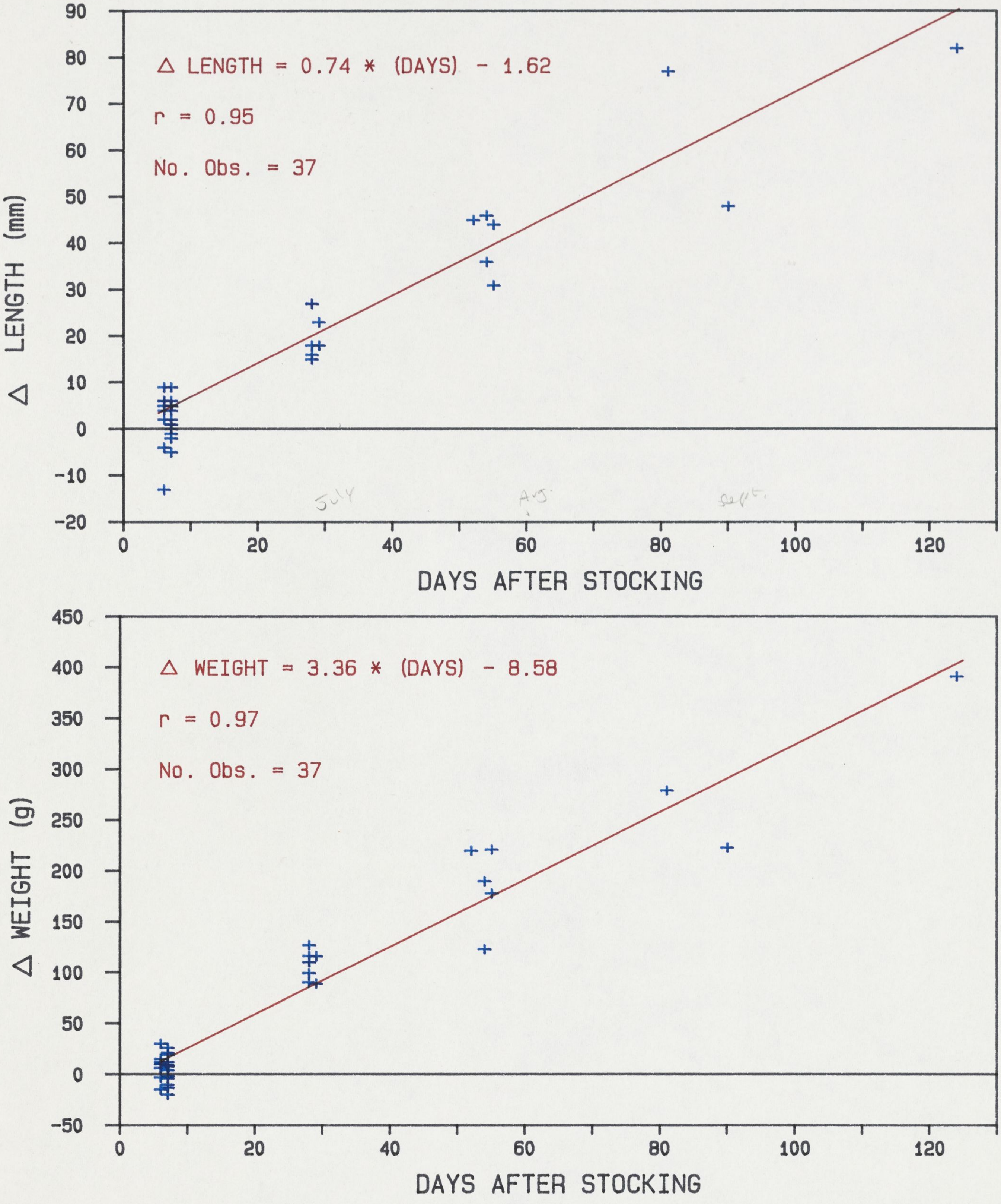
LAKE OGALLALA

GROWTH OF STOCKED RAINBOW TROUT

MAY PLANTS - 1987



LAKE OGALLALA
GROWTH OF STOCKED RAINBOW TROUT
JUNE PLANTS - 1987



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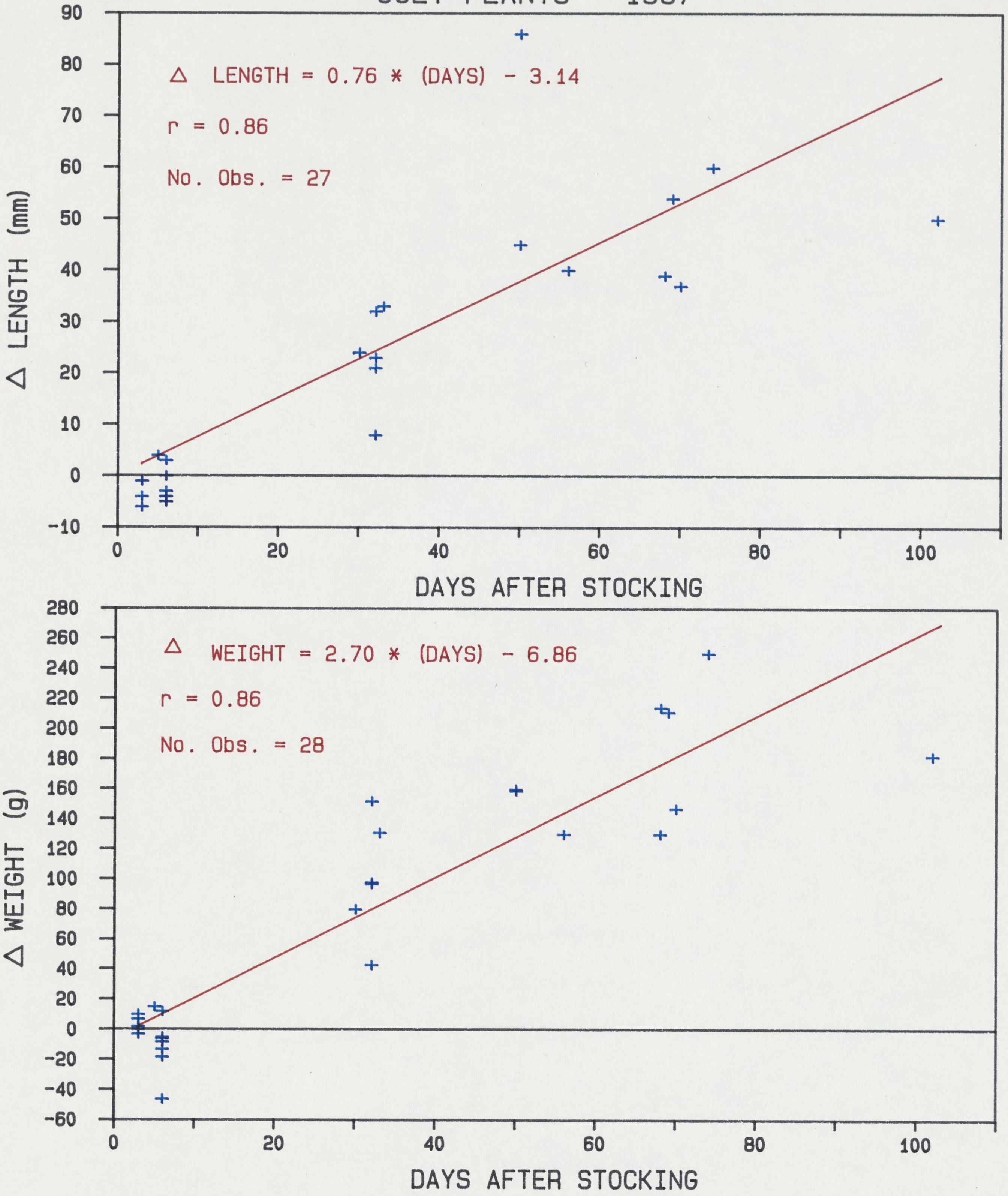
GROWTH OF STOCKED RAINBOW TROUT
JULY PLANTS - 1987



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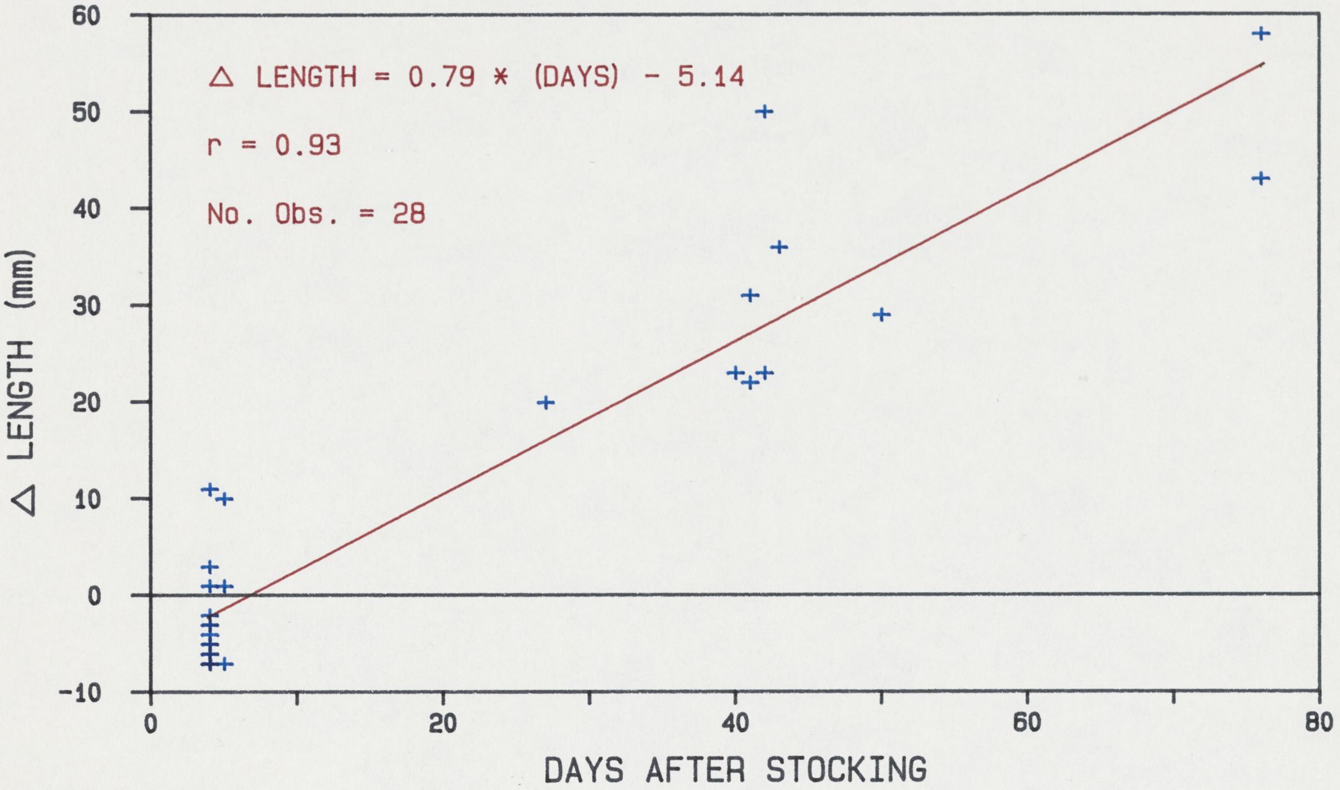
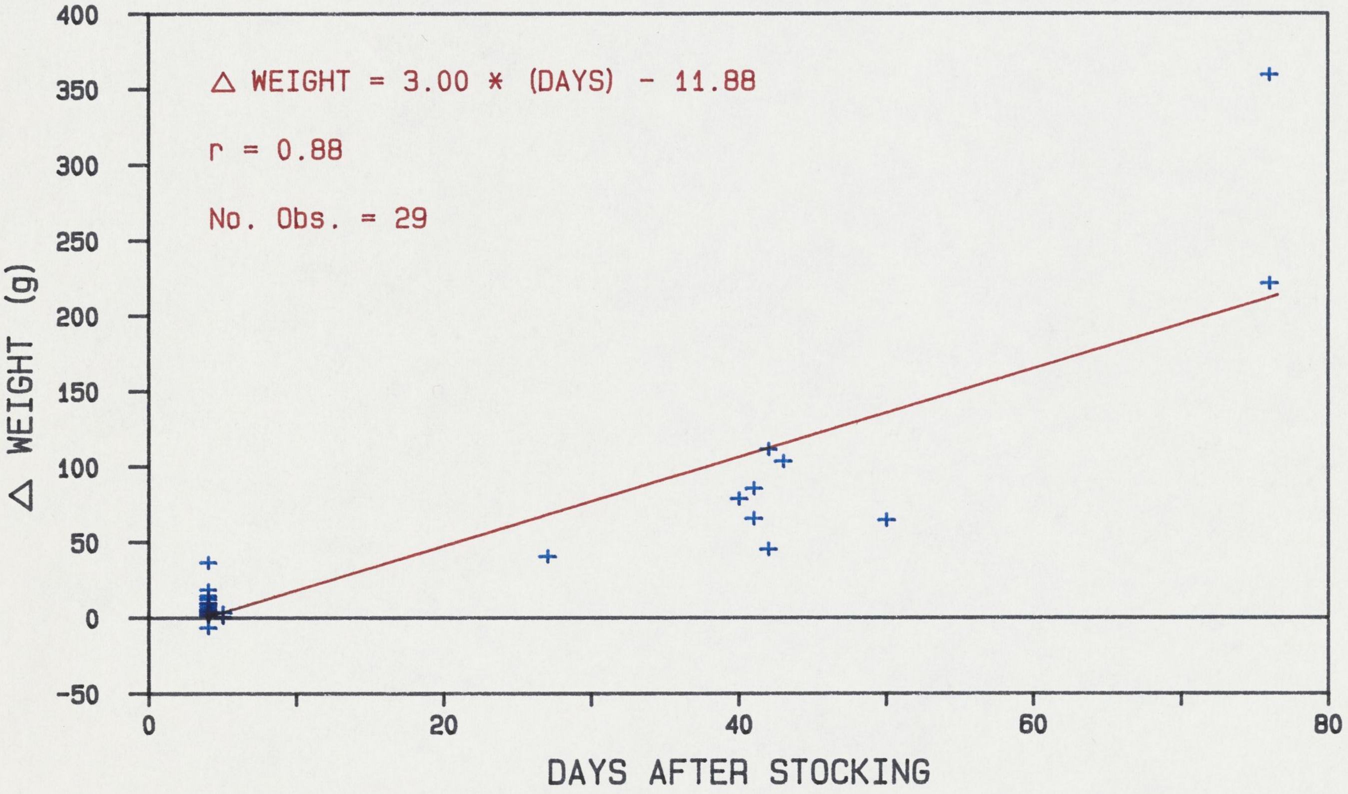
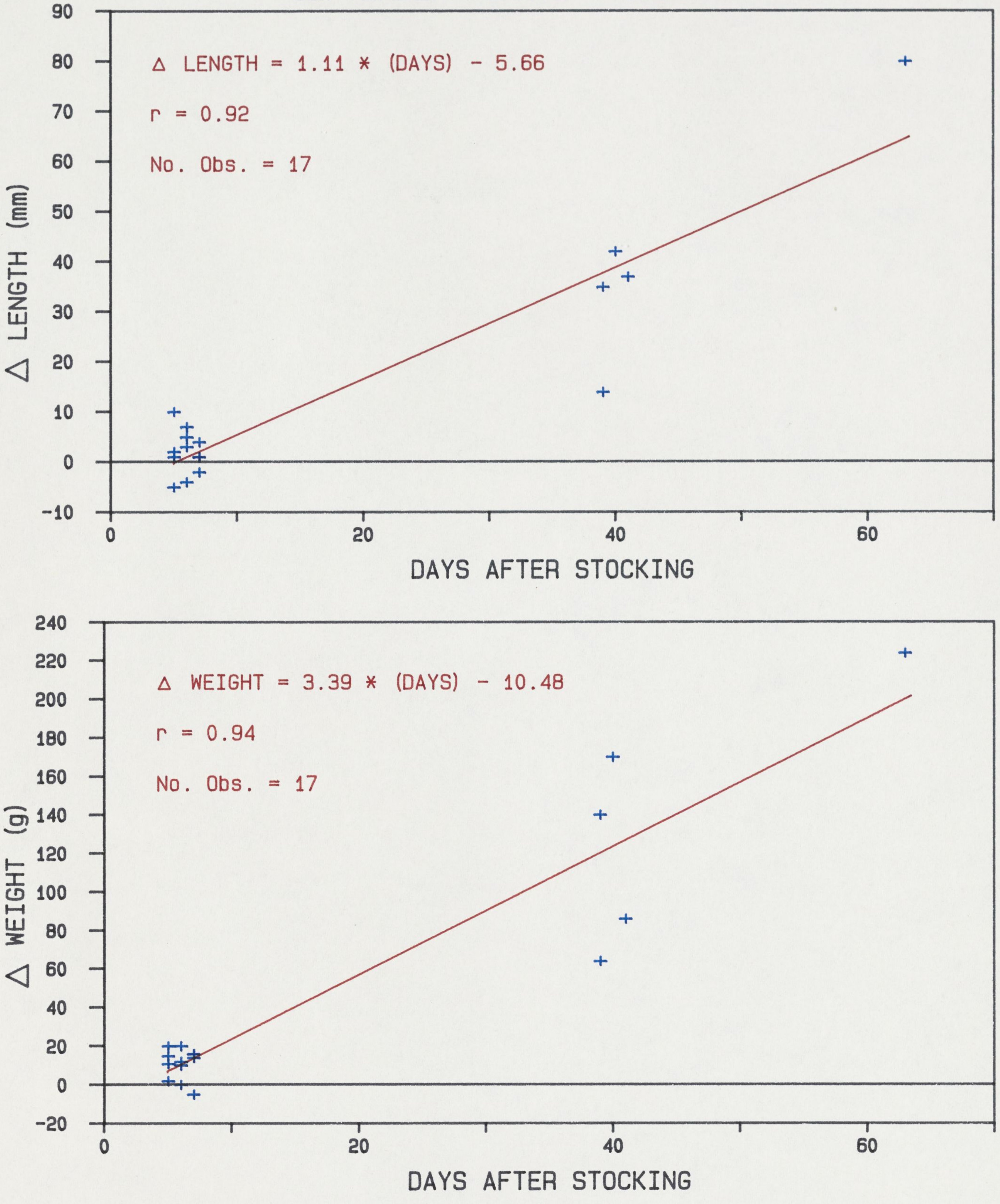
GROWTH OF STOCKED RAINBOW TROUT
AUGUST PLANTS - 1987

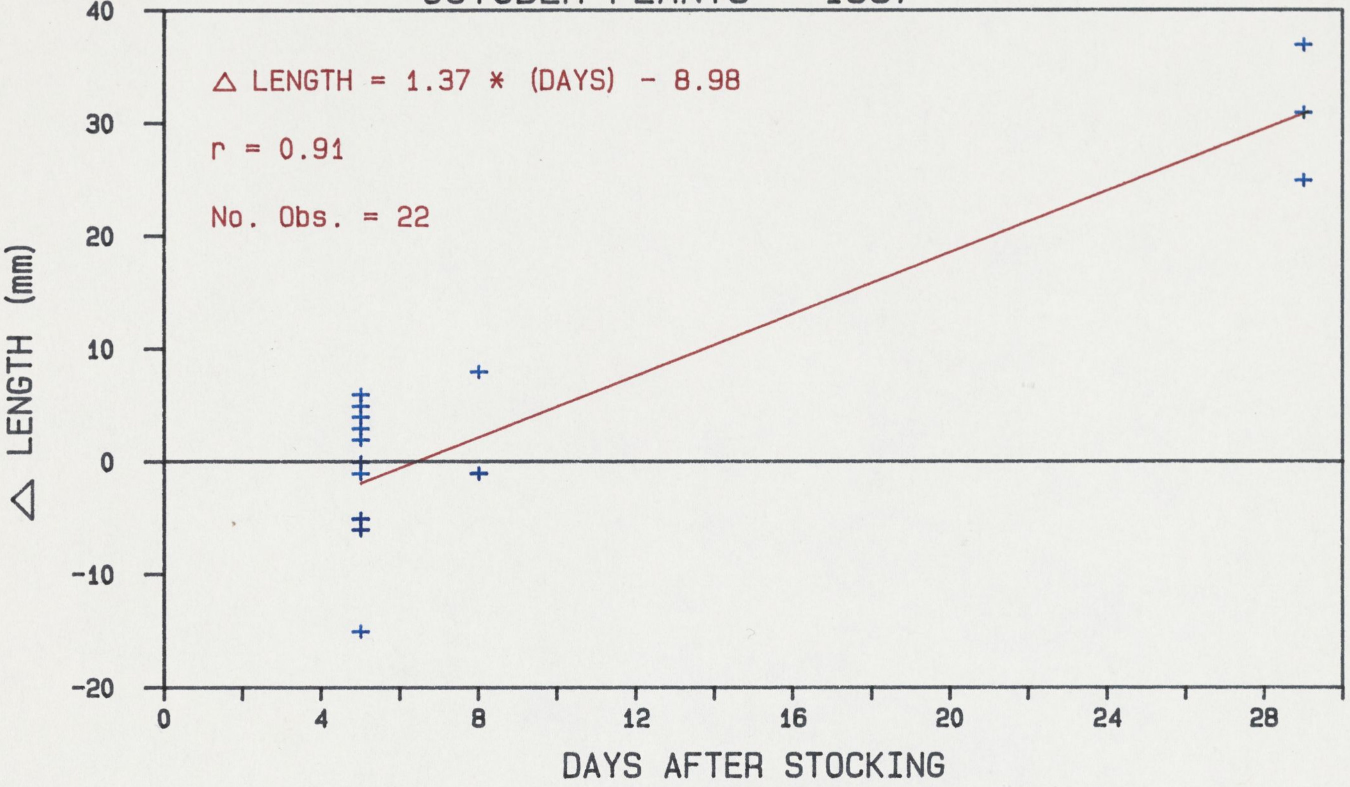


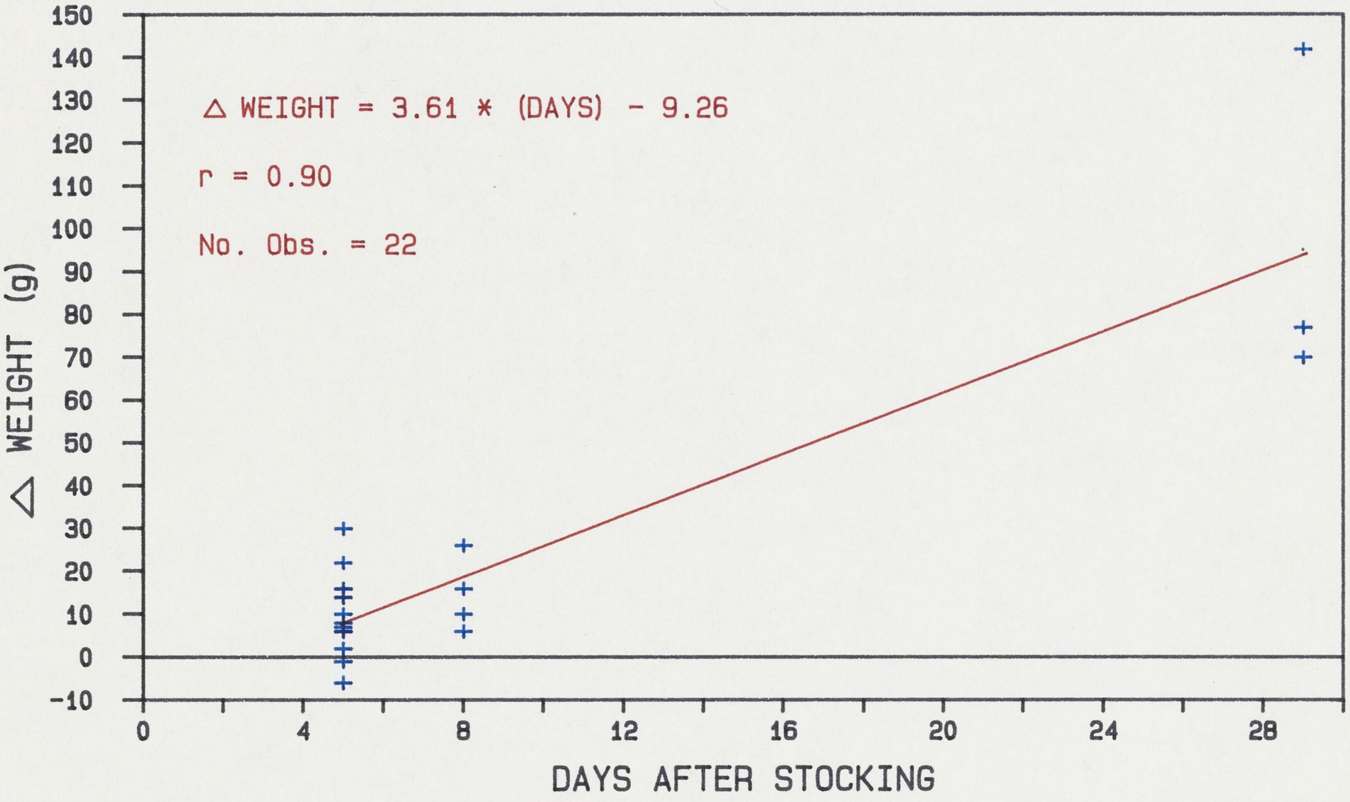


LAKE OGALLALA
GROWTH OF STOCKED RAINBOW TROUT
SEPTEMBER PLANTS - 1987



LAKE OGALLALA
GROWTH OF STOCKED RAINBOW TROUT
OCTOBER PLANTS - 1987





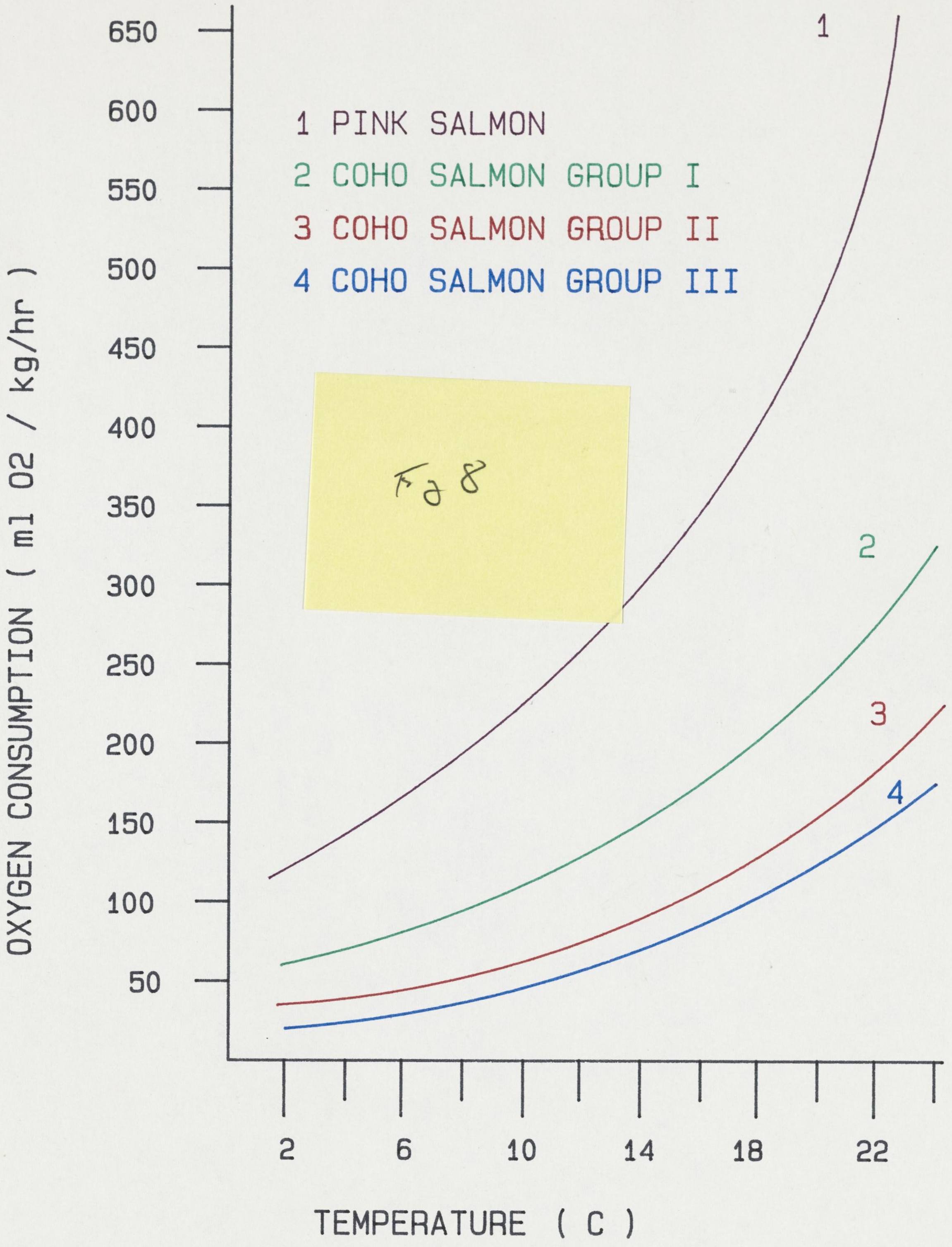
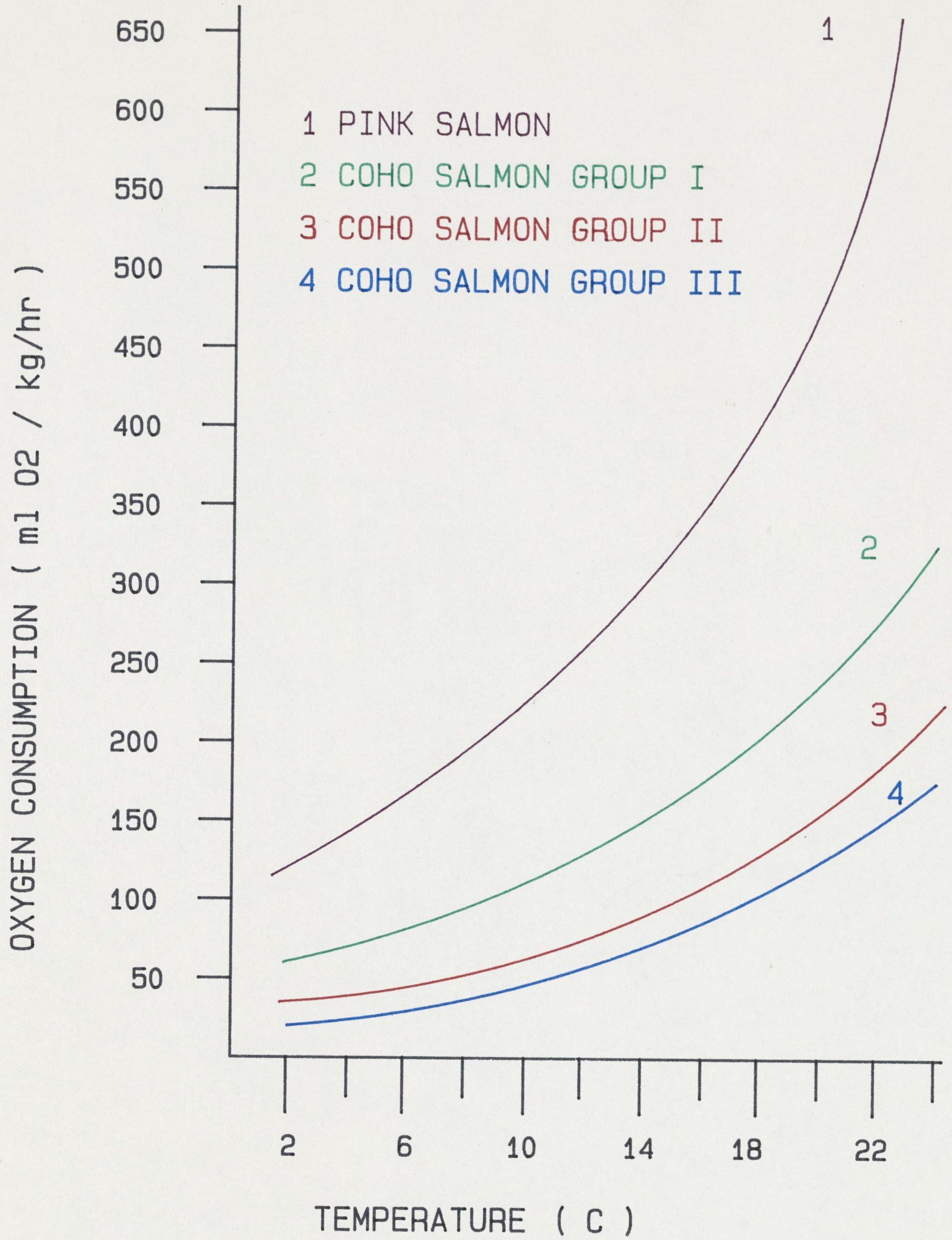
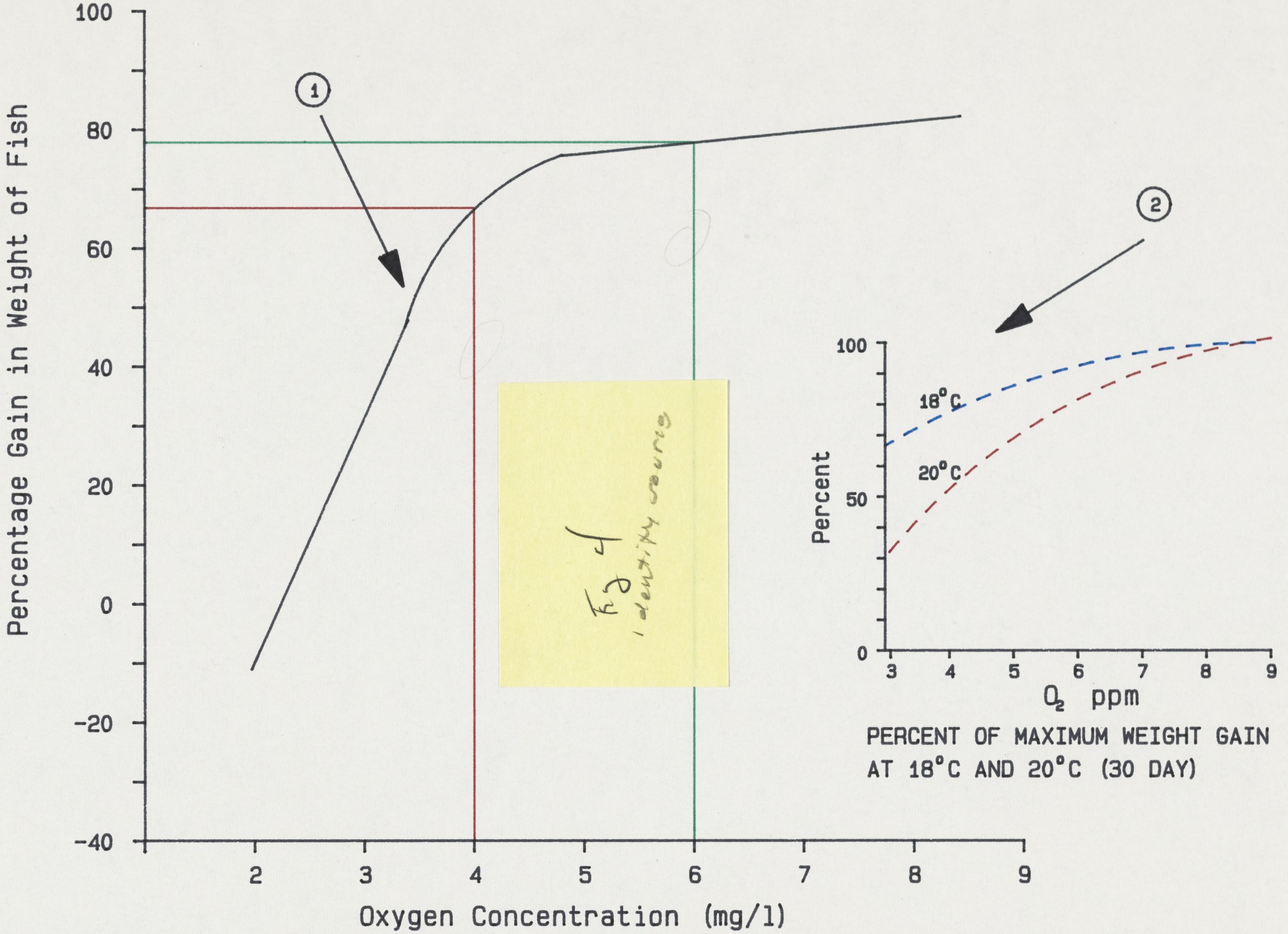


Fig 8

Relationship between oxygen consumption and temperature for Pink Salmon and Coho Salmon (from Smirnov et al. 1987)



Relationship between oxygen consumption and temperature for Pink Salmon and Coho Salmon (from Smirnov et al. 1987)



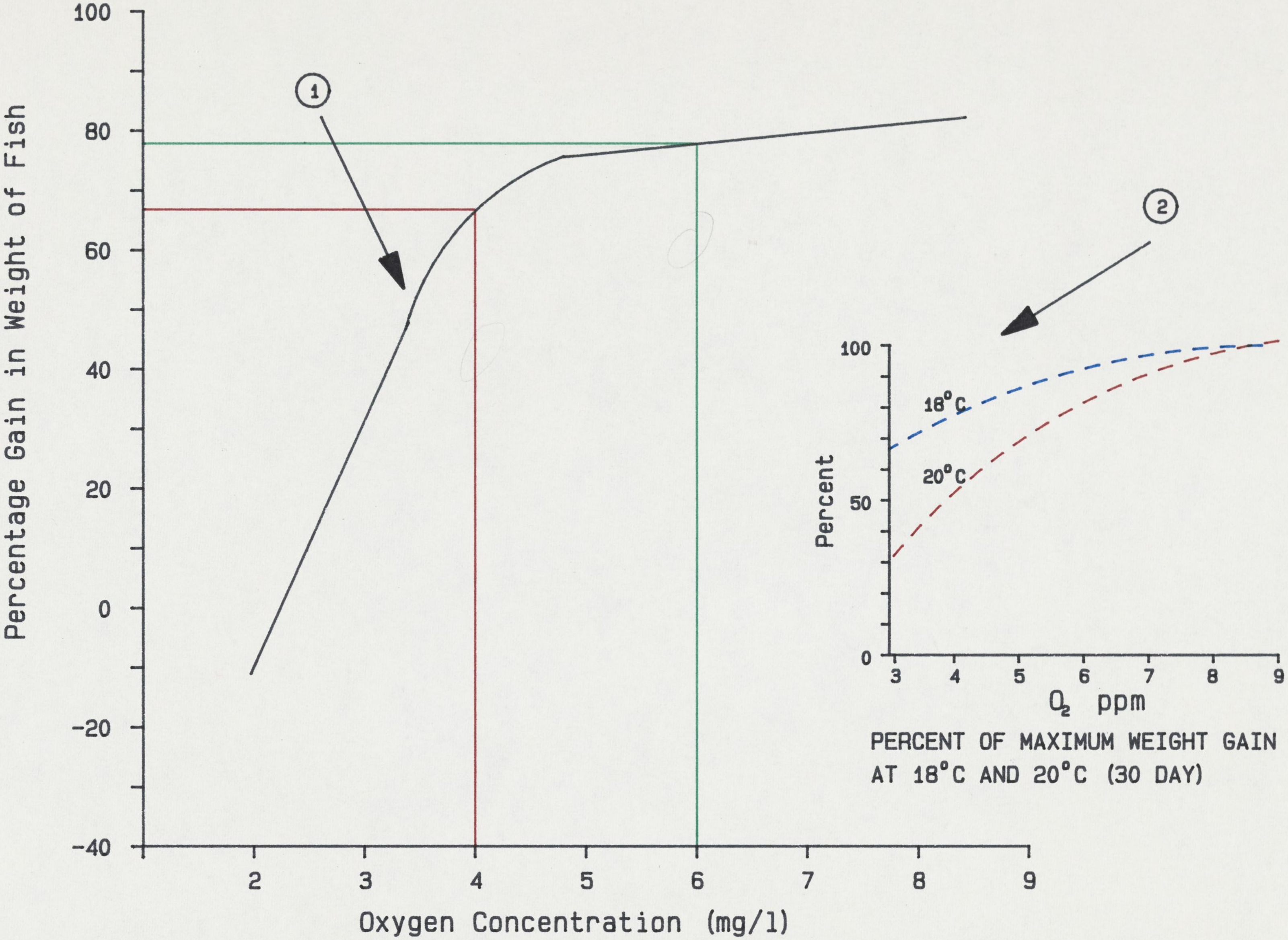
PERCENT OF MAXIMUM WEIGHT GAIN
AT 18°C AND 20°C (30 DAY)

Fig 4
identify source

Growth of yearling Coho Salmon (19 and 28 day trials at 20 ° C)

① GROWTH INCREASED WHEN MIN. 3mg/l O_2 FLUCTUATES DAILY, IN COMPARISON TO GROWTH AT CONSTANT 3mg/l.

② Impairment is less at lower temperatures



PERCENT OF MAXIMUM WEIGHT GAIN
AT 18°C AND 20°C (30 DAY)

Growth of yearling Coho Salmon (19 and 28 day trials at 20 °C)

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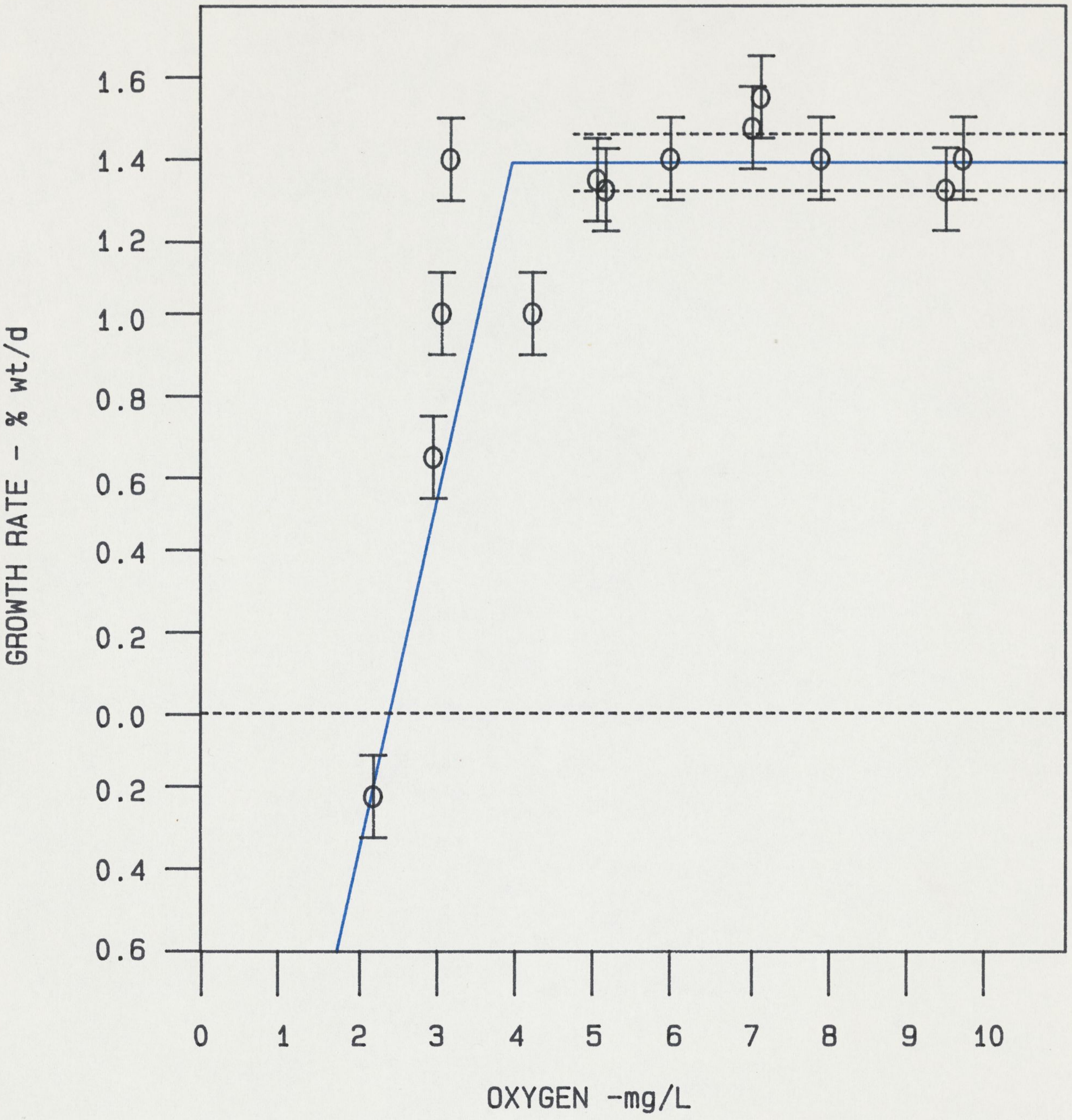


Specific growth rate of fingerling Coho Salmon

(from Brett & Blackburn 1981) at 15°C

May 4, 1984

Dear Dr. Behnke,

Thanks for your prompt reply (12/7/83) + sorry for my tardiness. Your C.S.U. fishery student field trip to Wyoming last June sounded great - only wish it could have happened several years earlier. As I recall, the wildlife students took a similar trip. I was looking through past theses' here at Oak Creek only to discover that Allen Binns earned his MS here in '65 working on a Green River - rotenone project. What do you think of the HQI system? I think it's about the best available but, like anything else, is apt to respond poorly in various situations. I understand that several of Bjornn's students applied the HQI ~~in~~ to several Idaho streams + had mixed results. His students presented a paper at the Idaho AFS meeting in Feb. '84 + I'm trying to find Proceedings.

Binns has all major habitat determinants (flow, cover, food) & is quite [illegible] but quantif. niche by [illegible] - the spp. life hist. stage etc. Warren seeks "p[illegible] classification" but only philosoph. rambling.

The ODFW group working on the White River project planned to use the HQI but the BPA didn't want them fooling around w/ that sort of "nonsense". Neither was BPA interested in our classification scheme - they only want numbers of fish - cold, hard facts. We also attempted to become involved with ODFW's stream habitat improvement project + help by using the classification system but, again, BPA said no thanks. (BPA is funding ODFW). Next week we'll be meeting with ODFW's head of fishery research, Jim Lichatowich, to discuss a possible chinook salmon project. The Oregon stocks

[illegible] tiny ones worth test [illegible] used by government or advocacy groups IFG - FWS.

meet So Ore bal: ~50% repeat spawns

of chinook south of the Umpqua River seem to remain near their home rivers, whereas the stocks north of + including the Umpqua, migrate long distances at sea. South coast chinook are harvested pretty heavily by both sport + commercial fisheries. Small river stocks are managed as one w/ large river stocks thus small river stocks are very vunerable. What we might attempt would be to look at different life history patterns + classify south coast streams + rivers based upon chinook life histories. This would allow us to determine such things as what type of land use practices are permissable on certain rivers. I think that classification has some potential uses but still needs to be worked on. Regarding your question of changing flow regime, it would certainly present some problems w/ "classification," as 'productive capacity' is constantly changing. I'd sure appreciate any feedback or ideas you have because even though I'm learning, I'm not totally sold on the classification. Wonderful theory but I too have a difficult time understanding any realistic application. Rome wasn't built in a day and, as you say, it's good to keep an open mind. Too many people close their minds to such ideas + get nowhere fast.

see p. 41

I've made my first contact to bring funding into the lab. While researching the acid rain problem in the P.N.W. I talked to a fellow w/ the USGS who was very interested in our model streams work. We recently built 8 new streams + are planning to model 8 more. We are thinking of studying potential acid rain problems here in the PNW by modeling streams that now recieve low pH precipitation. Watersheds in this region are extremely susceptible to acid precip. + are becoming a real concern, especially in areas east of Portland + Seattle. So, the U.S.G.S. was very excited + asked if we would be interested in recieving some funding to model streams east of Portland to study future acid precip. Needless to say I replied in the affirmative! I hope to write a proposal + learn all about that part of research. Will know more in several months.

Planning a fishing trip to the Deschutes later in May + then over to the Henry's Fk. of the Snake in late June. J.V. Ward often fishes the Henry's Fork - Should be easy to locate in tweeds! A friend of mine fishes the Henry's Fork regularly so I've got a guide. I hear from Dave Propst occasseonally + he's doing fine.

-Silver City
married
FWS
Phoenix

About all for now - Take care.

Best,

Charlie

P.S. - Had a baby girl in January - Megan Elizabeth!

RP2046-1

ARTIFICIAL STREAMS FOR ECOSYSTEM TOXICITY STUDIES

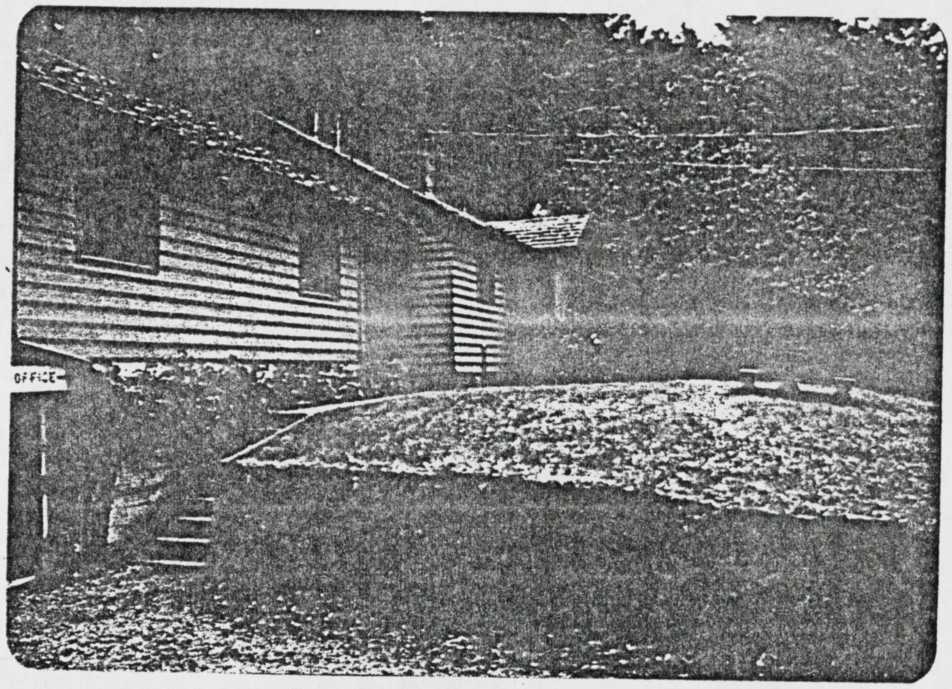
A Progress Report Submitted
For Evaluation Purposes
By or on Behalf of

THE ELECTRIC POWER RESEARCH INSTITUTE

By

THE OAK CREEK LABORATORY OF BIOLOGY
OREGON STATE UNIVERSITY

May 15, 1984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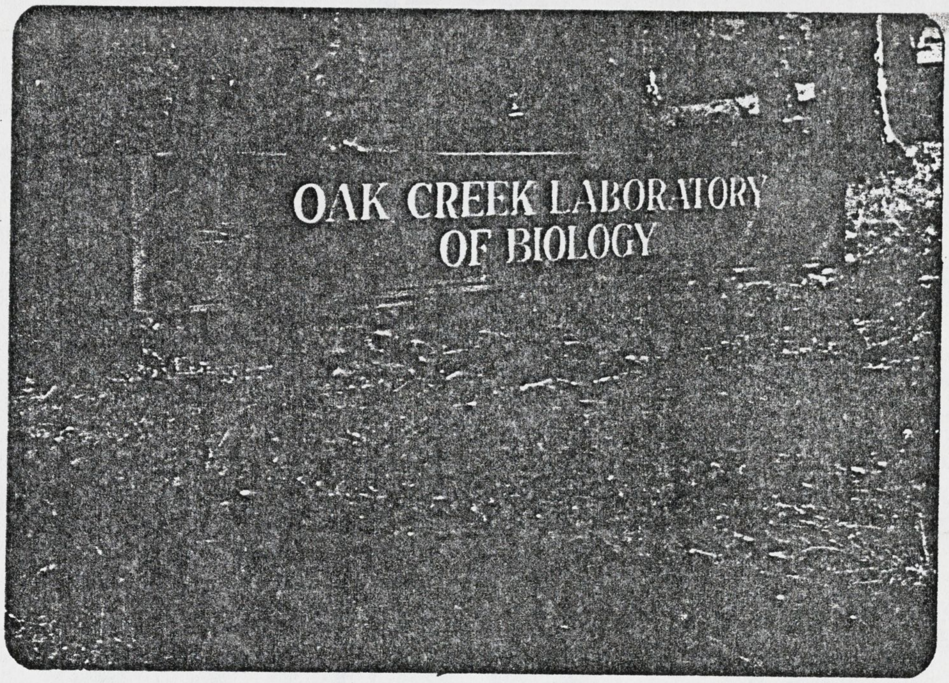
OAK CREEK LABORATORY
OF BIOLOGY

ARTIFICIAL STREAMS FOR
ECOSYSTEM TOXICITY STUDIES

A Progress Report Submitted
for Evaluation Purposes
by or on Behalf of

THE ELECTRIC POWER RESEARCH INSTITUTE

Project Period: June 1, 1982 through May 31, 1985
Report Period: June 1, 1982 through May 15, 1984

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ABSTRACT

The Oak Creek Laboratory of Biology has undertaken research intended to develop, demonstrate, and evaluate the application of laboratory stream ecosystems in dealing with problems of toxic substances, this research being supported by the Electric Power Research Institute for the period June 1, 1982 through May 31, 1985. This report presents the initial objectives and justification of this research, summarizes the progress we have made in the first two years, presents a preliminary evaluation of the results of our work, and indicates needed future emphases.

The objectives guiding this research entailed: (1) Provision and demonstration of classification systems for watersheds and streams and toxic substances; (2) Provision and demonstration of a theory and multisteady-state models making more effective the design and application of laboratory stream ecosystem studies of toxic substances; (3) Provision and demonstration of empirical laboratory stream ecosystem approaches to the study of toxic substances; and (4) Evaluation of the possible roles of laboratory stream research in dealing with problems of toxic substances.

We have largely completed work in the theory and classificaton system for watershed and stream systems, and we are now beginning work on the theory and classification system for toxic substances. Studies of natural streams have been conducted to illustrate the classification system and as a basis for designing laboratory stream ecosystems. These laboratory streams have been developed to model different classes and states of natural streams. And the effects of toxic substances on the organization and development of laboratory stream communities have been studied. We have, in addition, studied the behavior and effects of toxic substances in simpler laboratory microcosms and in individual organisms. Multisteady-state isocline models of toxic behavior and effects have also been developed.

It is our general impression that our continuing laboratory stream studies should emphasize demonstration of theoretical principles relating stream physical conditions to the organization and development of stream communities and the effects of toxic substances. Our classification system for watershed and stream systems, which is based on these theoretical principles, should be demonstrated on moderately large systems of watersheds and streams. For we believe that it is through the application of such a classification system that watershed and stream science and management can come to deal more effectively with our pervasive problems of toxic substances.

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I. INTRODUCTORY PROSPECTUS

The electric power industry, other of our enterprises public as well as private, and indeed our society as a whole face an unprecedented problem of resource utilization, the dimensions of which have hardly been discussed publicly. Indeed, it is to be doubted that any among us fully comprehend the nature, magnitude, interaction, and significance of these dimensions. Leaving for the moment the profound economic and social changes entailed, let us simply note some of the environmental changes associated with the way our culture develops and utilizes resources.

Three decades ago our society began to attack environmental pollution on a broad scale. Then the need was seen to be the correction of sources of pollution having mainly local influences. But though there were local improvements in air and water quality, general solutions continued to escape us. For water, air, and soil problems have become not simply isolated problems of particular industrial or domestic activities at particular geographic locations and times (if they ever were this), but problems of a culture, a way of life, interpenetrating and changing in every way the resources upon which it depends.

There are, to be sure, points in space and time from which environmental change spreads. But there are so many of these, their environmental interactions so complex, and their involvement in the economy and society so deep, it is indeed a very general problem our society faces. The source of water pollution may be land use practices or the use we make of airsheds as well as watersheds. Of direct concern to the electric power industry are acid precipitation, extensive development of low-head hydro-electric power, thermal pollution, strip mining, and various other toxicity problems. But such general problems are not peculiar to the electric power industry. Agricultural and forestry practices have brought about equally general environmental changes. And urban development and transportation are among our most general problems of environmental pollution.

All this cannot be taken as reasons for inaction, as it too often has, in particular instances known to be contributing to the general problem. But it should force us to see that our society is facing what amounts to a major social crisis -- an incoherence between societal expectations and societal possibilities, at least within present understanding and practices. There is a very general cultural-resource crisis.

Now this is a general concern that has been stated by many others in perhaps better ways. But what has not been a general concern, what apparently few recognize or are willing to acknowledge, is that our expectations for resource science and management as generally practiced are incoherent with their possibilities. There is a crisis in the Newtonian-Baconian mechanism of resource science and management. Even were general economic and societal conditions more favorable, resource science and management practices would fall far short of our needs. Nowhere is this more apparent than in watershed and stream science and management. And this is of immediate concern to us here.

To take what is here our most immediate concern -- watershed and stream science and management -- we need to be able to deal with watershed and stream problems on very large scales of space and time as well as more local scales. And we need to be able to deal with stream problems in the ways in which they are coupled to land, air, and culture. Moreover, the changes brought about in watershed and stream systems must be understood in terms of the inherent dynamics of the systems themselves -- those spacio-temporal changes underlying the outcomes of human interactions. Finally, watershed and stream science must provide understanding and information in forms that make it possible to better manage our resources.

For these needs the prevailing approaches are simply not adequate -- neither the approaches of foresters, agriculturalists, or others emphasizing mainly the land aspects of watershed systems nor the approaches of fisheries scientists and stream ecologists emphasizing the aquatic aspects. It is, for example, no overstatement to say that the approaches of stream ecologists have usually been much more suited to their own research interests and needs than to the needs of those concerned with the management of watershed and stream resources, including protection from deleterious environmental change. It is not that such studies are in anyway illegitimate or that aspects of them may not prove to be useful. It is simply that, as they have generally been conceived, they do not fulfill our need for approaches adequate to deal with watershed and stream phenomena on a large scale, do not adequately couple watershed, stream, and cultural phenomena, do not deal adequately with watershed and stream dynamics, and do not provide understanding and information in forms adequate to deal with problems of concern.

However adequate may be the foregoing analysis of the crisis in watershed and stream science and management, however correct our assessment of the needs, and however much we may be able to contribute to their satisfaction, our research proposal to the Electric Power Research Institute had the essential elements in its objectives and approaches.

That is: (1) A classification system hierarchically embedding stream systems in watershed systems and in principle dealing with all their properties, (2) A theory of watershed and stream systems along with appropriate multisteady-state models, (3) Approaches to field studies that are theoretically as well as empirically adequate, (4) Laboratory studies including the use of laboratory stream ecosystems, (5) Classification, theory, models, and laboratory studies of toxic substances more adequate to deal with ecological as well as physiological problems, and (6) A very critical evaluation of the possibilities as well as the results of the integrated application of such approaches.

It was the intention of the Electric Power Research Institute that ways of employing laboratory stream ecosystems in determining the effects of toxicants be developed and evaluated. It was and continues to be our conviction that this can be well done only in the context of classification, theory, models, field studies, and other laboratory studies just noted. We have now nearly reached the half-way mark in these studies. And we find that it is not only time for a preliminary evaluation of results and possiblities of watershed and stream studies, but also to render to those concerned and interested some accounting of our progress. Morever, it is already time to provide some indication of the direction of studies that should be supported in the future. Our position on this is no doubt already apparent: Future studies simply must provide an adequate basis for watershed and stream science and management. We do not now have this. But we do believe we have begun its development.

In the next ten pages of this progress report, we are reprinting without change the Objectives and the Expected Results and Benefits sections from our original research proposal to the Electric Power Research Institute. These, as will become aparent in succeeding sections of this report, we have followed very closely. This report makes no attempt to present all of our data, analysis, and other work including classification and theory, as it could hardly do this, and nearly all work is still in progress. In some areas, we have done more work than originally anticipated. This is especially so in the area of watershed and stream system classification and field studies. These we believe should be emphasized even more in the future, for they offer the most promise for dealing with the problems that concern us all. We will conclude this report with a preliminary evaluation of the results and possibilities of watershed and stream studies, especially as related to toxicity problems, and with some indication of the future direction of this research.

II. OBJECTIVES

(Reprinted from EPRI research proposal 12/1/81)

A. General Objective

The general objective of the research herein proposed is to PROVIDE THEORETICAL UNDERSTANDING AND EMPIRICAL APPROACHES NECESSARY FOR MAKING LABORATORY STREAM ECOSYSTEM STUDIES USEFUL IN SOLVING PROBLEMS OF TRANSPORT, FATE, AND EFFECTS OF TOXIC SUBSTANCES IN NATURAL STREAM ECOSYSTEMS.

Industry, government, science, and indeed society as a whole are faced with an unprecedented problem of evaluation and control of toxic substances entering the environment as a result of perhaps most human activities. The problem is of such technical, social, and natural complexity that one may well wonder by what means and then how adequately it can be managed. While the problem of transport, fates, and effects of toxic substances in the environment is by no means simply a scientific problem, scientific evaluation, explanation, and understanding of the overall problem and its particulars are necessary.

But no one clearly understands, even in terms of general approaches that would be adequate, how even the scientific problem alone is to be handled. Scientific toxicology has until relatively recently been concerned mainly with the effects of toxic substances on individual organisms and their life processes. And even at the individual organism level, we do not have any general theory to deal with the interaction of several toxicants or even with nontoxic environmental conditions. Even so, approaches to individual organism and suborganismic toxicology are the only well established ones we have. And there is a serious need for general approaches to the study of transport, fates, and effects of toxic substances in natural ecosystems, which include biological communities together with their physical-chemical environments.

In recent years there has been increased interest in the use of laboratory microcosms of various designs to evaluate the behavior and effects of toxic substances in ecosystems. Although some interesting work has been done, several general problems remain in the way of developing microcosms including laboratory stream ecosystems into approaches very useful in dealing with the behavior and effects of toxic substances in natural systems. The research here proposed is intended to be a very general attack on the most important and the most difficult of these problems.

The four explanatory objectives that follow articulate in general terms the major thrusts of our approach to solving these problems. Achievement of these objectives will amount to accomplishment of the general objective stated for this research at the beginning of this section. The explanatory objectives address the problems of adequate classification of watershed and stream systems as well as toxic substances, the problems of adequate theory and models, the problems of how laboratory stream ecosystems are to be designed and employed so as to be useful, and how all the above is to be evaluated.

After the explanatory objectives, we articulate, for each of them, several operational objectives. These are to make clear what is intended to be involved in achieving each explanatory objective. The operational objectives serve as a bridge between the general and explanatory objectives and the methodological approaches that will be taken and that are generally described in later sections. We have presented our objectives in this extended hierarchical way to define as clearly as possible the work we are proposing to undertake.

B. Explanatory Objectives

1. PROVIDE CLASSIFICATION SYSTEMS FOR STREAM ECOSYSTEMS AND FOR TOXIC SUBSTANCES AND DEMONSTRATE THE NEED FOR AND USE OF THESE IN DETERMINING THE DESIGN AND CONDUCT OF LABORATORY STREAM ECOSYSTEM STUDIES OF TOXIC SUBSTANCES AND THE INTERPRETATION AND APPLICATION OF RESULTS.
2. PROVIDE AND DEMONSTRATE A THEORY AND MULTISTEADY-STATE MODELS ARTICULATING UNDERSTANDING OF THE DEVELOPMENT, ORGANIZATION, STRUCTURE, OPERATION, AND PERSISTENCE OF STREAM COMMUNITIES OF DIFFERENT CLASSES AND OF THE TRANSPORT, FATES, AND EFFECTS OF DIFFERENT CLASSES OF TOXIC SUBSTANCES, SO AS TO MAKE MORE EFFECTIVE THE DESIGN AND CONDUCT OF

LABORATORY STREAM ECOSYSTEM RESEARCH AND THE INTERPRETATION AND APPLICATION OF RESULTS.

3. PROVIDE AND DEMONSTRATE EMPIRICAL LABORATORY STREAM ECOSYSTEM APPROACHES TO INVESTIGATION OF THE TRANSPORT, FATES, AND EFFECTS OF DIFFERENT CLASSES OF TOXIC SUBSTANCES IN RELATION TO THE DEVELOPMENT, ORGANIZATION, STRUCTURE, OPERATION, AND PERSISTENCE OF STREAM COMMUNITIES OF DIFFERENT CLASSES.

4. PROVIDE SOME DEMONSTRATION THAT LABORATORY STREAM ECOSYSTEMS, AS DESIGNED, INTERPRETED, AND APPLIED THROUGH CLASSIFICATION AND THEORY, USEFULLY MODEL NATURAL STREAM ECOSYSTEMS AND THE TRANSPORT, FATES, AND EFFECTS OF TOXIC SUBSTANCES.

C. Operational Objectives

1. Attainment of Explanatory Objective 1--pertaining to provision and demonstration of classification systems for stream ecosystems and toxic substances--will entail accomplishing the following operational objectives.

a) Selection of major classes of streams according to the biogeoclimatic watershed and stream classification system proposed by Warren (1979).

b) Abstract from these major classes of streams their gradient, substrate, hydrological, chemical, and energy and material determinates as a basis for designing laboratory stream ecosystems representative of the different stream classes.

c) Develop a classification system for toxic substances based on their capacities for different transport, fate, and effect performances in different biogeoclimatic watershed and stream classes.

d) Demonstrate both theoretically and empirically how the capacities according to which stream ecosystems and toxic substances are to be classified jointly determine the transport, fates, and effects of toxic substances and thus how classification can facilitate the design of laboratory stream research and the interpretation and application of results.

2. Attainment of Explanatory Objective 2--pertaining to the provision and demonstration of a theory and multisteady-state models making more effective the design and application of laboratory stream ecosystem studies of toxic substances -- will entail accomplishing the following operational objectives.

a) Relate the theory and models to the classification systems by employing as theoretical concepts the watershed, stream, and toxicant capacities on which the classifications were based, so as to increase the universality of the theory and facilitate its use in the design and application of results of laboratory stream ecosystem studies of toxic substances.

b) Articulate the simplest and most universal set of theoretical generalizations adequate to subsume relevant theoretical and empirical knowledge and achieve the objectives set for the theory, these theoretical generalizations conforming to the conceptual framework articulated by Warren, Allen, and Haefner (1979).

c) Articulate and employ multisteady-state models that relate individual organism life history responses to toxic substances to population development and evolution and to community structure and organization.

d) Apply the multisteady-state isocline models of Booty (1976), Liss (1977), and Warren and Liss (1977) for systems of populations to facilitate the interpretation and application of results on transport, fates, and effects of toxic substances at the population and systems of population levels.

e) Articulate and employ multisteady-state models of stream communities, the parts of which become systems of populations, so as to be able to deal with the dynamic and steady-state behavior of communities as wholes and the behavior and effects of toxic substances.

3. Attainment of Explanatory Objective 3--pertaining to the provision and demonstration of empirical laboratory stream ecosystem approaches to the study of toxic substances--will entail accomplishing the following operational objectives.

a) Design and construct sets of laboratory stream ecosystems that model different major classes of stream ecosystems.

b) Design and conduct laboratory stream ecosystem experiments according to the conceptual framework, theory, classification systems, and isocline and other models, so as to make the design and results of these experiments of the greatest possible interest and relevance to problems of toxic substances in natural streams.

c) Determine differences in the development, organization, structure, operation, and persistence of the different classes of communities that will develop in these different classes of laboratory stream ecosystems when colonized from a known species pool.

d) Determine and demonstrate how transport, fate, and effects of major classes of toxic substances in laboratory stream ecosystems are to be effectively studied, interpreted, and applied to problems of toxic substances in different classes of natural stream ecosystems.

4. Attainment of Explanatory Objective 4--pertaining to provision of some demonstration that laboratory stream ecosystems can usefully model natural stream ecosystems and the transport, fates, and effects of toxic substances--will entail accomplishing the following operational objectives.

a) Habitat structures of the laboratory stream ecosystems will be based on observation of classes of natural stream ecosystems and watersheds to which the laboratory streams will be related.

b) Community structure and development in laboratory stream ecosystems will be compared to the structure and development of communities in natural streams of the classes modeled, differences in the species pools of the natural and laboratory systems being taken into account.

c) Transport, fates, and effects of toxic substances in the laboratory stream ecosystems, as made understandable by classification, theory, and models, will be evaluated on the basis of whether or not more adequate explanation and understanding of reported observations on toxic substances in natural stream ecosystems are achieved.

III. EXPECTED RESULTS AND BENEFITS

(Reprinted from EPRI research proposal 12/1/81)

Our explanatory objectives, as stated in Section II B, can be taken as a summary statement of the results we expect from the proposed research. These objectives require that we (1) provide classification systems for stream ecosystems and toxic substances, (2) provide and demonstrate a theory and multisteady-state models articulating understanding of stream communities and toxic substances, (3) provide and demonstrate empirical laboratory stream ecosystem approaches to investigation of toxic substances, and (4) provide some demonstration that laboratory stream ecosystems usefully model natural stream ecosystems and the transport, fates, and effects of toxic substances. Before we further develop these expected results and consider their significance and associated benefits, it may be helpful to consider briefly three aspects of the general value of the work as a whole.

First, the research we are here proposing will not provide simply some single approach or design for laboratory stream ecosystem research coupled with some particular model or way of modeling. This can never be generally adequate, because the different kinds of experiments and models we employ must be as diverse as are our objectives and the nature of the natural systems of concern. Rather, what we are intending to provide and demonstrate is a conceptual framework, classification, and theoretical basis for determining and designing whatever laboratory stream ecosystems and kinds of formal or simulation models different objectives, natural systems, and toxicant problems require. Only something like this can begin to meet our needs for research of this sort, now and in the future.

Second, with the discovery that simple communities of plants and animals can be maintained in the laboratory, there has come a proliferation of microcosm designs and techniques with little concurrent critical evaluation or even awareness of possible constraints on the meaning and utility of such work (Warren and Davis 1971, Warren and Liss 1977). There is a pressing need for ways to reliably investigate the transport, fates, and effects of toxic substances in natural ecosystems. There is a good possibility that laboratory stream ecosystems and other sorts of microcosms can play some useful role. But on this, the jury is not in as yet.

Indeed, it has hardly considered the critical evidence. Part of the reason for this, beyond early enthusiasm for new approaches, is that any such consideration or evaluation of approaches presupposes some framework for evaluation, "instructions to the jury," as it were. It is our intention to provide a conceptual and empirical framework for evaluation as well as design of laboratory stream ecosystem research.

And third, it is our intent to further understanding of natural stream ecosystems as well as provide understanding of the theoretical relationships between laboratory stream ecosystems and natural stream ecosystems and so of how we study either. The Electric Power Research Institute has expressed the need to "assess potential environmental effects" of power development and production. Any such assessment, to be reliable, must be based on fundamental understanding, which it is the role of science to provide, not simply to provide approaches, laboratory stream ecosystems or whatever.

One cannot speak universally--generally and invariantly--about the transport, fates, and effects of toxic substances in natural stream ecosystems. Toxic substances have different capacities and thus different performances, even in the same environment. And the same toxic substance will have different performances in different environments. Natural stream ecosystems also differ in their capacities and thus in their performances. And there is an indefinite number of kinds of stream ecosystems and toxic substances. Any rational investigation of the transport, fates, and effects of toxic substances in natural stream ecosystems ought to begin, we would think, with some classification of streams and toxic substances, at least an informal one. But this has generally not been done. This leaves the generality of work on toxic substances in laboratory stream ecosystems in considerable doubt.

We are now demonstrating through classification of watersheds and stream ecosystems, a hierarchical land-water classification system developed at our laboratory (Warren 1979). This classification will allow us to design our laboratory stream ecosystems to represent major classes of natural stream ecosystems, thus helping to clarify at the outset the relation between laboratory models and natural systems. We are now beginning to develop a classification of toxic substances based on their capacities. The results of laboratory stream ecosystem studies on substances representative of known classes of toxicants can then be generalized at least over the appropriate domain of stream and toxicant kinds. Provision and demonstration of such classification systems will then be of value not only in the design of future laboratory stream ecosystem research but also in the interpretation and application of results.

Stream ecosystems, because they are so fully open and fluctuate so dramatically, are among the most difficult to study and understand. This has led some stream ecologists to articulate a "continuum concept" of stream systems. Certainly stream communities and ecosystems, like their terrestrial counterparts, exhibit a continuum aspect in their behavior. But emphasis on this aspect alone has led some stream ecologists to postulate an absence of stream succession or a sort of continuous quasi-equilibrium in time, even if the stream environment--the watershed--is in a state of directional succession or change. This, of course, cannot be. No system can reach or even approach steady-state in a changing environment. A more adequate theoretical view of stream systems must be articulated and demonstrated. In Section IV B, we outline such a view. An important part of the proposed research will be to more fully and formally articulate this theory of stream systems. This is very important because theory determines the form of laboratory models and the meaning of their results. It also determines the form of other sorts of models, which really model some theoretical construct, not nature directly. Without an adequate theory of stream systems, little can be expected from models and empirical work.

We will emphasize multisteady-state models that incorporate individual organism life history responses into population behavior, systems of populations, and, finally, community structure and behavior. Our emphasis on multisteady-state models derives from our theoretical and empirical work making clear that under different environmental conditions organismic systems can best be understood as tending toward different possible steady states. Associated with each steady state would be its characteristic life history patterns, population structures, community structure, and rate terms. So long as a community were changing in structure, all rate terms would be changing. But even though rate terms would theoretically be constant at a particular steady state, there would be a different steady state for each set of environmental conditions and thus an indefinite number of steady states. No rate terms can be assumed to be constants, independent of community structure and environmental conditions (Warren and Liss 1977).

To a very considerable extent, laboratory ecosystem studies now seem mainly to focus on two related matters: the validation of simulation models and the estimation of various coefficients of transfer, accumulation, or degradation of toxic substances. The implicit recognized need for models is, we think, quite appropriate. For the relation between laboratory result and natural problem is an indirect one, perhaps through models. But we are very uncomfortable with the notion that simulation models can be validated by means of laboratory ecosystems, which can never be general and which themselves only palely represent natural ecosystems. Secondly, we are aware of no theoretical or empirical evidence supporting the notion of constant coefficients, estimatable from laboratory ecosystems and generally applicable through models. On the contrary, we believe the theoretical and empirical evidence, such as it is, is against there being such constant coefficients. Much delay, harm, and needless expense can be occasioned in our efforts to deal with toxic substances in the environment, if the emphasis of research is wrongfully placed on the search for nonexistent ideal coefficients. In the proposed research, we intend to provide a sound basis for clarification of this entire matter.

It is partly for this reason, and partly for others, that we intend to work with at least 16 laboratory stream ecosystems. This will allow us to model different classes of streams, to expose these streams to different environmental conditions including toxicants, and to have replication of each different treatment. Insofar as coefficients of interest can be estimated, we should be able to show however much or little universality and interest they may have.

We will be especially interested in community development and organization occurring in laboratory streams of different classes colonized from the same species pool. The ways in which we intend to achieve this will help to insure that the community organization, performances, and processes we study will be as near to natural ones as is achievable in the laboratory under more or less controlled conditions. We think this is important. For, among other matters, we believe the transfer, fates, and effects of toxic substances to be determined to a very considerable extent by the organization and thus the capacity of the community. We are saying, in effect, that toxicant behavior is a property of the community as well as of the toxicant. We think our work will be important in showing just how this is so.

From all the above, it follows that the design of laboratory stream ecosystems will determine our results with particular toxicants just as much as do the inherent properties of the toxicants. And because our theories determine how we design our experiments, there is not the generally assumed independence between theory or model and empirical result. And thus there cannot be easy confirmation or falsification of theoretical constructs by empirical observation. Philosophy of science, even if belatedly, has now generally come to recognize this. Evaluation or demonstration of a theory, a model, or an empirical approach comes through its successful use and evidence of its heuristic power.

Still, there continues to be the need for critical evaluation of our theories, models, and empirical approaches. We intend to evaluate our own work by comparative studies of natural stream systems and of the stream and toxic substance literature. Only insofar as our classification, theoretical, and laboratory work illuminate this other work to a greater extent than does other systematic work, only then will we consider its evaluation to be positive. But, for present needs, this alone is not enough. There is a need for a general framework for evaluating laboratory ecosystem research. Provision of such a framework will be a contribution of our work.

IV. WATERSHED AND STREAM SYSTEM THEORY AND MODELS

A. Introduction and Significance

Theories and models together with systems of classification aid in perceiving problems and suggest approaches, including design and interpretation of empirical work in both the laboratory and the field. The provision and demonstration of adequate theoretical perspectives and empirical approaches for understanding watersheds and streams is perhaps the most significant aspect of our work, for these perspectives and approaches can be used in confronting any environmental problems involving watershed and streams systems. Our theoretical perspectives are somewhat difficult to explicate in a few pages, but we will attempt to do so here . Later in this report empirical aproaches based upon these perspectives will be considered.

A theory we take to be a set of theoretical generalizations defining, ordering, unifying, and providing heuristic power over some scientific domain (Warren and Liss 1983). As such, a theory is a way of symbolizing, partially articulating (or talking about), and providing a perspective or way of viewing total relevant experience of the domain. Theories can be understood to come out of even higher level, more universal conceptual constructs such as world views (Pepper 1942) and conceptual frameworks (Warren et al. 1979). The evaluation of theory is not on the basis of simple validation or falsification, but rather on the basis of its utility for understanding. Thus theory evaluation and application occur together.

Models also symbolize and provide a perspective on experience, but in much more limited and particular ways than theory. Unfortunately, in natural resource science and management, theoretical knowledge has all too often been thought to reside only in mathematical models. This has led us to expect far more from models than they are capable of delivering. We think that models are simply other ways of communicating our experience and ought not to be considered apart from other conceptual constructs.

B. Watershed and Stream System Theory

A contextualistic theory of watershed and stream systems, articulated as a set of generalizations, is given in Table 1.

The performance at any time of a watershed, stream, or any other system can be understood to be jointly determined by the realized capacity and the environment of the system at that time. Under different sets of environmental conditions, a system with a given realized capacity will exhibit different performances under different sets of environmental conditions. Thus the realized capacity of a system can be thought of as all possible performances in all possible environments. The way that a system is organized at a particular time determines its realized capacity to perform.

As a system develops, its organization, realized capacity, and performances change. A system's pattern of development, that is, the particular sequence of organizations, realized capacities, and performances the system manifests from its origin to its end, can be understood to be determined by the system's potential capacity and its developmental environment. A system with a given potential capacity will develop differently in different environments. Thus potential capacity can be understood as all possible system developmental patterns in all possible environments.

A stream system can be understood to be composed of a biological community and its habitat. The stream system is embedded in a watershed, which forms the environment of the stream (Generalization 1). The environment of a watershed is a geographically-organized system of interpenetrating watersheds. A watershed with a given potential capacity will develop differently in different environments (Fig. 1). Each developmental pattern of the watershed can be understood as a change in watershed organization, realized capacity, and performances that occurs in conformity with some particular pattern of change in the organization, realized capacity, and performances of the system of watersheds forming its environment. Similarly, a stream system with a given potential capacity will develop in conformity with the development of its watershed environment (Generalization 3, Fig. 2).

Table 1. A General Theory of Watershed and Stream Systems

Generalization 1. A stream system is incorporated in a watershed that is its coextensive and codetermining environmental system.

Generalization 2. A watershed and stream system is incorporated in a system of interpenetrating and concordant watershed and stream systems of different classes and in different developmental states, together forming a spaciotemporal mosaic or polyclimax.

Generalization 3. Any watershed or stream system or subsystem develops through a series of realized capacities and performances according to its potential capacity and its incorporating environment.

Generalization 4. The capacity of any watershed or stream system or subsystem is determined by its organization, or the way in which it incorporates the environments and capacities as well as the performances of its concordant and interpenetrating subsystems.

Generalization 5. The potential capacity, organization, and development or change in capacity and organization of each incorporated and incorporating watershed or stream system or subsystem are relative to its spaciotemporal extent.

Generalization 6. Stream community organization and development are determined by stream habitat organization and development and by the pool of species available for colonization in the system of watershed and stream systems.

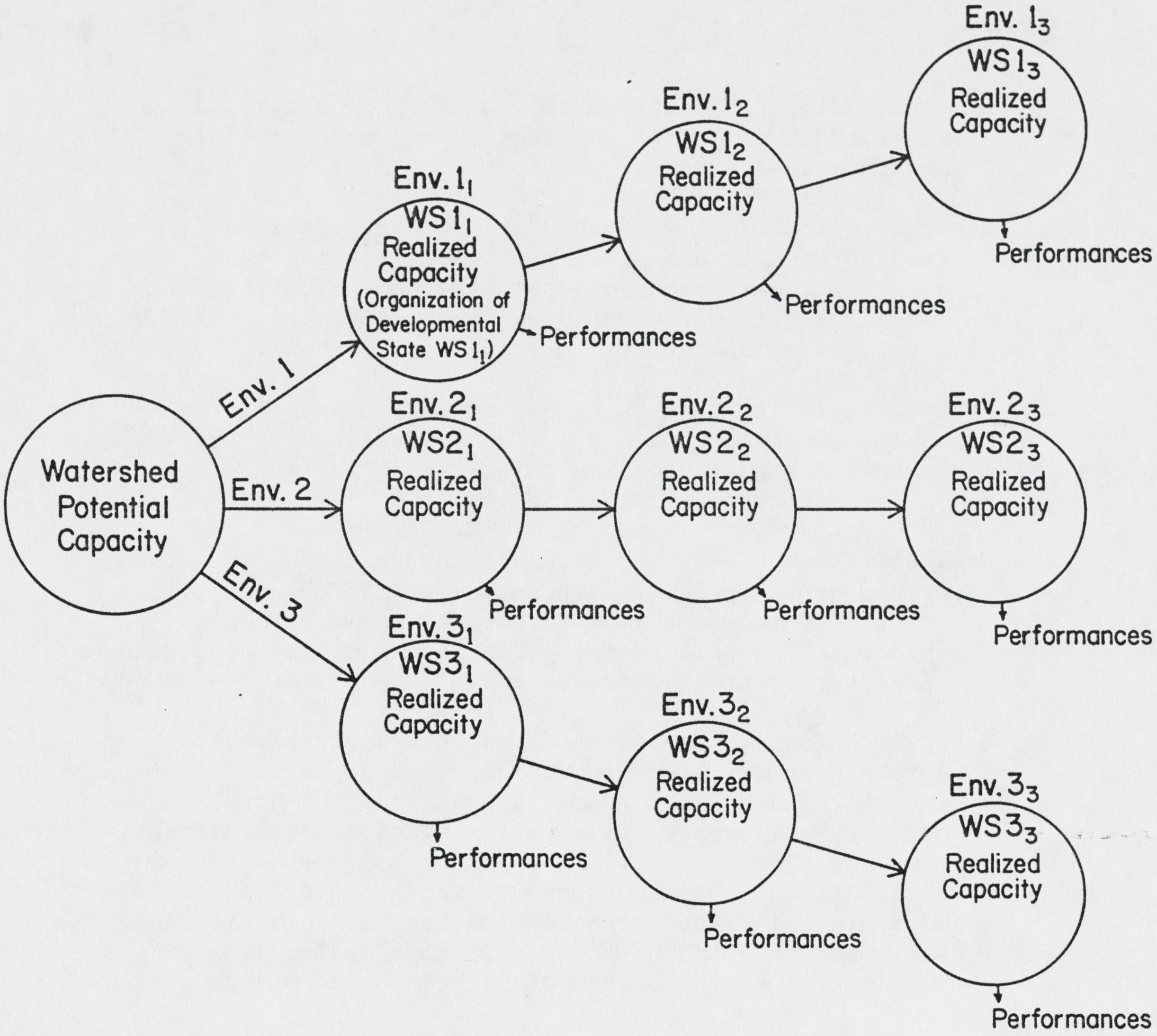

Figure 1. Development, from its potential capacity, of the realized capacities and performances of a watershed system (WS) in concordance with its incorporating environmental system (Env.). From some abstract potential capacity, a watershed system of a given class is shown to develop through states (e.g. $WS1_1$, $WS1_2$, $WS1_3$) as its environment develops through states (e.g. Env 1_1, Env. 1_2, Env.1_3). At each state, the watershed has a state-specific realized capacity and organization as well as performances determined by its capacity and the state of its environment system.

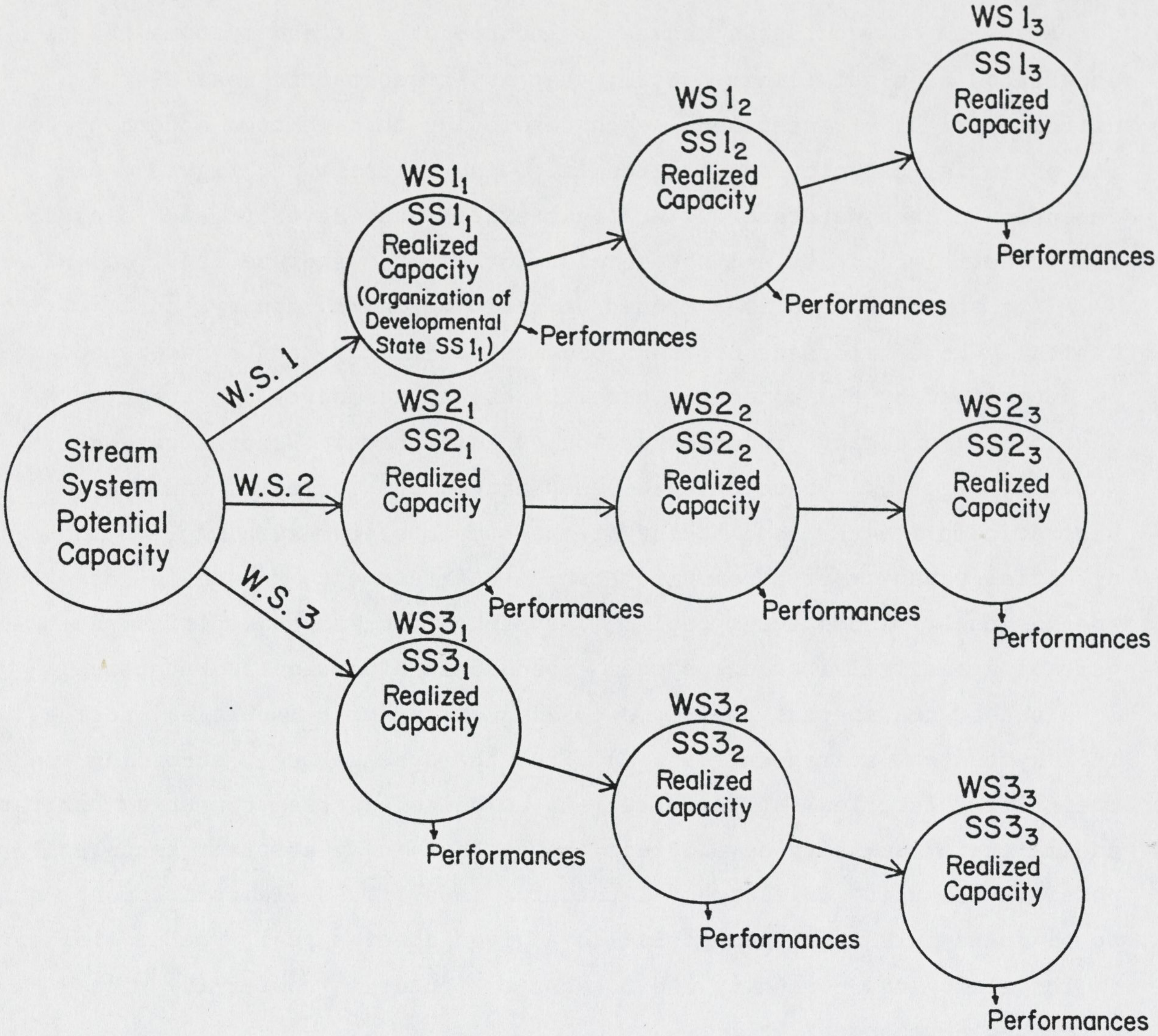

Figure 2. Development, from its potential capacity, of the realized capacities, organization, and performances of a stream system (SS) in concordance with its incorporating watershed system (WS). A stream system of a given class will develop through a series of states, e.g. $SS1_1$, $SS1_2$, $SS1_3$ as its watershed environment develops through states, e.g. $WS1_1$, $WS1_2$, $WS1_3$. And in each state the stream system will have a state-specific realized capacity, organization, and performances according to its potential capacity and watershed state.

A system of watersheds and their incorporated stream systems can be understood as a polyclimax system, that is, a geographic mosaic of different kinds of watersheds, each developing through time according to its potential capacity and environment (Generalization 2, Fig. 3). And embedded in each watershed is a stream system that develops according to its potential capacity and the development of its watershed environment.

The stream system is composed of a biological community and its habitat. The development of the biological community can be understood to be determined by the potential capacity of the community and the development or change in organization of its habitat (Generalization 6, Table 1, Fig. 4). Co-occuring development of the community and its habitat comprise the development of the stream system as a whole. The potential capacity of a community can be understood to reside in the species pool. The species pool is a system of stream communities, each a part of a particular stream system embedded in a particular watershed. In a sense, the species pool, viewed as a system of communities, resides in a system of watersheds (Fig. 3). From the species pool, according to their life histories, stream organisms colonize a stream community habitat and maintain community development there. Thus in an abstract sense, all possible community developmental patterns in all possible environments are to be found in the species pool. In a given species pool, the development of the biological community and its habitat occur in conformity with watershed development.

Stream systems can be understood as hierarchically organized systems incorporating, on successively lower levels, interacting and interpenetrating segment systems, reach systems, pool/riffle systems, and microhabitat systems (Frissell, MS). Each level in the hierarchy is composed of a habitat subsystem and its conformant biological community subsystem. Further, each level forms the environment of the next lower level. Thus, a reach system as a whole forms the environment of each of its incorporated pools and riffles.

Stream subsystems at each level can be understood to have potential capacities, realized capacities, and performances and thus develop and persist through time. The potential capacities of subsystems on different levels are defined on different scales of space and time (Generalization 5).

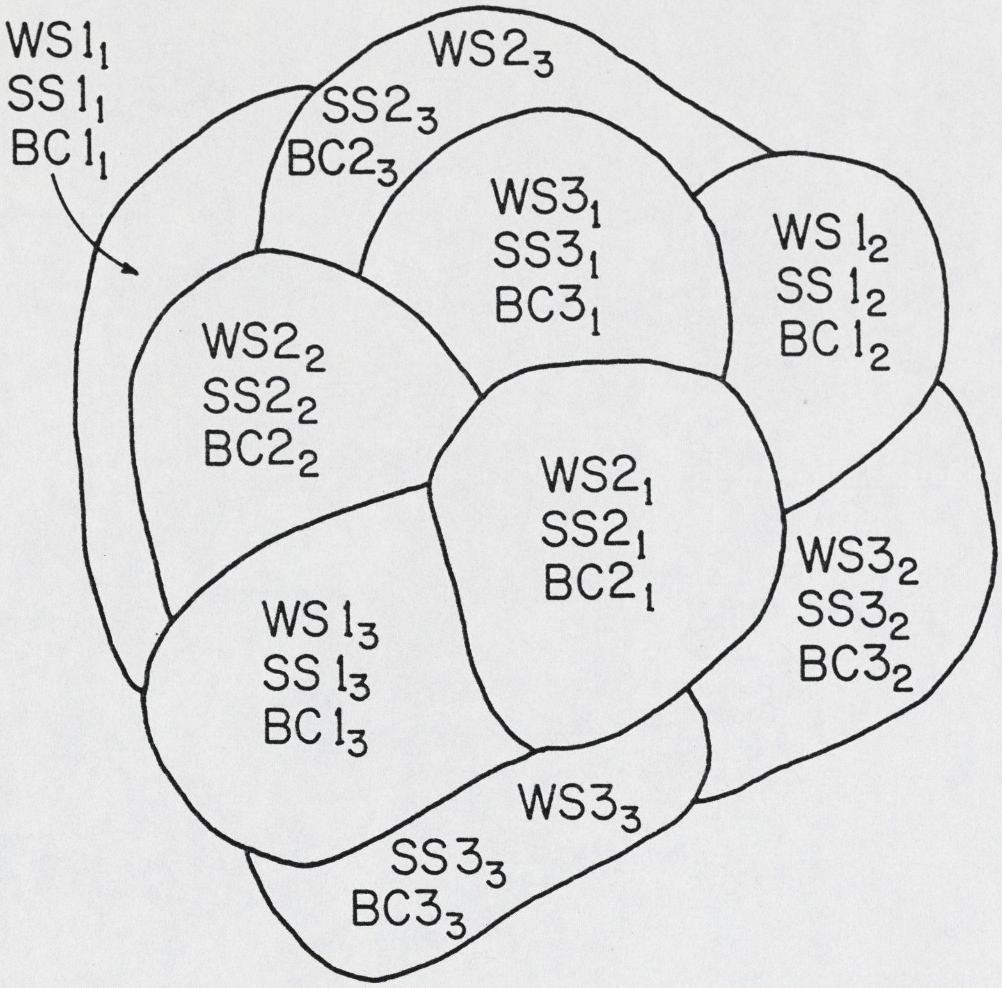

Figure 3. Polyclimax view of the organization of a system of watersheds, consisting of watersheds (WS), stream systems (SS), and stream communities (BC) of kind or class i in developmental state j. Different classes of systems have different potential capacities. At any time the system is composed of different classes of watersheds, stream systems, and communities in different developmental states. Through time watersheds of a class and their incorporated stream systems and communities develop or change states, according to their respective potential capacities and developmental environments. (Figs. 1, 2, and 4).

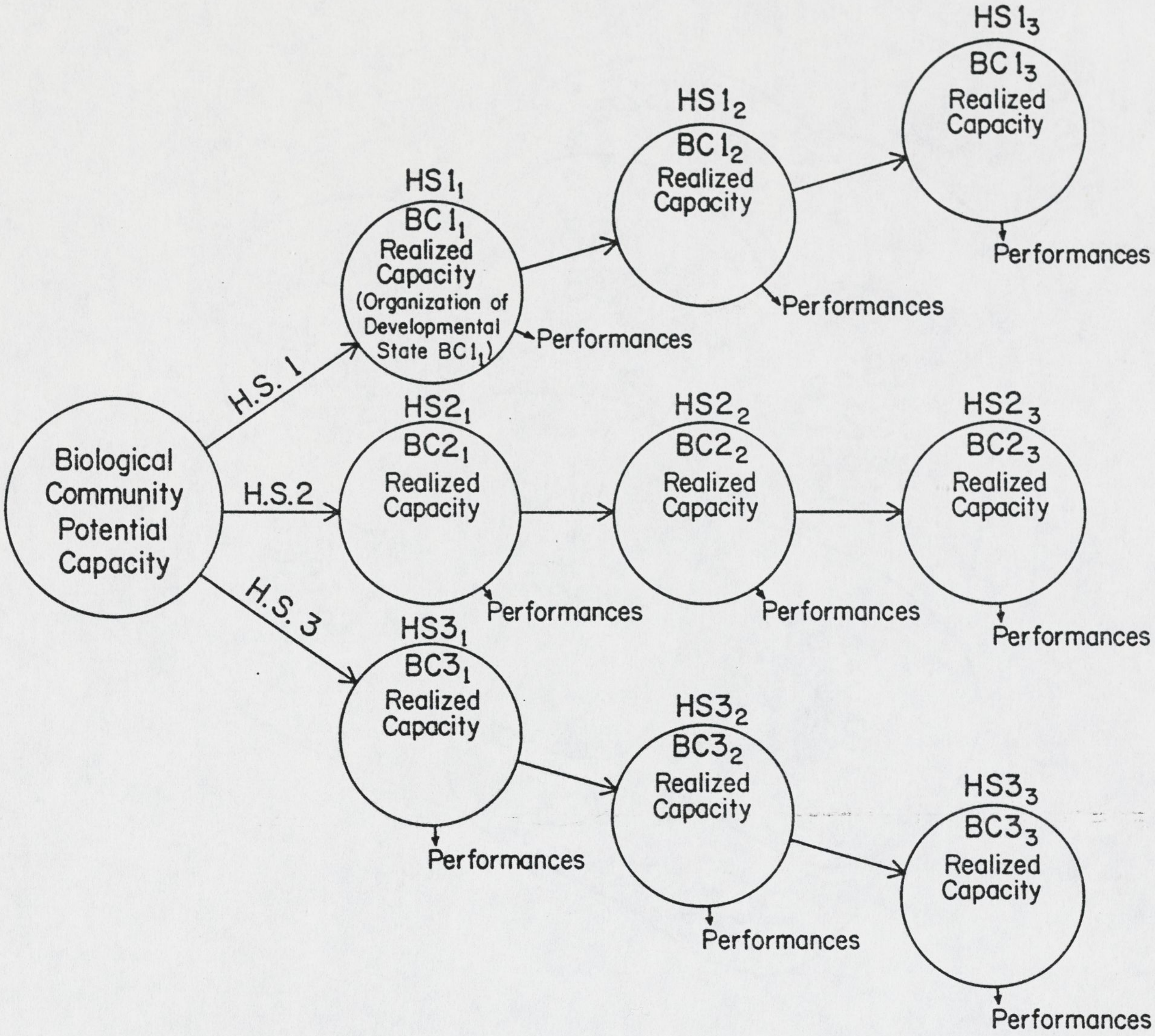

Figure 4. Development, from its potential capacity, of the realized capacity, organization, and performances of a biological community (BC) in concordance with its habitat system (HS). The community and its habitat together form the stream system (SS). A biological community of a given class developing on a habitat system of a class will develop through a series of states, eg. $BC1_1$, $BC1_2$, $BC1_3$ as its habitat system (environment) develops through states, eg. $HS1_1$, $HS1_2$, $HS1_3$. In each state the biological community will have a state-specific realized capacity, organization, and performances according to its potential capacity, which resides in the species pool, and habitat system state.

Processes of low frequency and high magnitude determine the capacity of stream, segment, and reach subsystems, while relatively high-frequency, low-magnitude events determine pool/riffle and microhabitat capacity (Table 2). Table 3 shows the spatial boundaries that constrain the development of each kind of subsystem. Both the boundaries and conformant processes determine the potential capacity of each kind of system. A subsystem will persist so long as its potential capacity and the potential capacity of its environment remain unchanged (Generalization 5). Processes bringing about a change in potential capacity of each kind of subsystem are given in Table 2.

In structuring a stream theory, we have attempted to keep biological subsystems coupled to their habitats, the boundaries of biological subsystems at each level being determined by the boundaries and processes defining the habitat subsystem at that level. Development of a habitat system at any level is change in its organization, which entails the development or change in organization of its incorporated habitat subsystems. Habitat developmental processes at each level are suggested in Table 2. The development of a biological system entails development or change in organization of its incorporated subsystems, and this occurs in conformity with the development of the habitat. Since stream subsystems are defined spatially as well as temporally, a system at any level can be conceptualized as a polyclimax mosaic of its incorporated subsystems.

Such a hierarchical view of stream systems permits development of systematic understanding of their organization. Another important aspect of the organization of stream systems is the interpenetration of subsystems, rendering their boundaries somewhat indiscrete. In this sense streams are continuum-like.

The capacities and performances of stream systems are strongly influenced by events in their watershed environments. Thus, in developing this theory, we have attempted to keep the stream system and its subsystems coupled to the watershed. We are convinced that stream systems can best be understood as developing systems, their organization and development being concordant with organization and development of the watershed environment. We believe this is a fundamental theoretical premise, one that accords very well with total experience of watersheds

Table 2. Stream Habitat Hierarchy in Time -- Processes After Frissell (MS).

SYSTEM LEVEL	LINEAR SPATIAL SCALE[1]	EVOLUTIONARY (Generative or Perturbational PROCESSES (Δ POTENTIAL CAPACITY)	DEVELOPMENTAL PROCESSES (NO Δ POTENTIAL CAPACITY)	TIME SCALE[1] OF POTENTIAL PERSISTENCE AS IDENTIFIABLE SYSTEM (NO Δ POTENTIAL CAPACITY)
Stream System	10^3 m	Tectonic uplift, dropping; Catastrophic volcanism; Sea level changes; Stream piracy	Davisian baselevelling; Denudation; Drainage network development	10^7-10^6 yrs
Segment System	10^2 m	Glaciation; Earthquakes; Local volcanism; Very large landslides	Trib. junction, bedrock nickpoint migration; Channel bedrock weathering	10^4-10^3 yrs
Reach System	10^1 m	Debris torrents; Landslides; Log input or washout; Channelization, culverts, debris manipulation by man; Channel shifts, cutoffs	Aggradation/degradation associated with large sediment-storing structures; Bank erosion; minor changes in jammed debris	10^2-10^1 yrs
Pool/riffle system	10^0 m	Input or washout of wood, boulders, etc.; Small bank failures; Flood scour or sediment pulse obliteration; Human activities	Small-scale lateral or elevational changes in bed forms; minor bedload resorting	10^1-10^0 yrs
Microhabitat System	10^{-1} m	Annual sediment transport, deposition, resorting; Plant cropping by grazers or scour, etc.	Accumulation of fines; Microbial breakdown of organics; Plant growth; Seasonal H_2O depth, velocity changes	10^0 - 10^{-1} yrs

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[1] Scaled to second order mountain stream

Table 3. Stream Habitat Hierarchy in Space -- Landform "Boundaries[1] After Frissell (MS)

SYSTEM LEVEL	CAPACITY TIME SCALE[2]	VERTICAL BOUNDARIES (Profile view)	LONGITUDINAL BOUNDARIES (Plan or Profile)	LATERAL BOUNDARIES (Plan or X-section)	LINEAR SPATIAL SCALE
Stream System	$10^7 - 10^6$ yrs	Total initial basin relief; Sea level	Drainage divide and sea coast, or chosen trib. junction, etc.	Drainage divides; Bedrock faulting and jointing controlling valley, ridge development	10^3 m
Segment System	$10^4 - 10^3$ yrs	Bedrock elevation; Trib. junction or falls elevation	Trib. junctions; Major falls; Bedrock joints	Valley side slopes; Bedrock outcrops controlling lateral migration	10^2 m
Reach System	$10^2 - 10^1$ yrs	Bedrock or resistant alluvium elevation, topography; Relief of major sediment dams	Sediment storing structures capable of withstanding ≤ 50-yr flood logs, boulders, etc.); Slope breaks	Local side slopes; Erosion-resistant channel banks	10^1 m
Pool/riffle System	$10^1 - 10^0$ yrs	Depth of bedload subject to scour in ≤ 10-yr flood	Water surface and bed profile slope breaks; Location of formative structures	Channel banks; Bed topography	10^0 m
Microhabitat System	$10^0 - 10^{-1}$ yrs	Sediment particle size, arrangement; Organic debris accumulations; Vegetation; Wood			$10^{-1} - 10^{-2}$m

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[1] If geographical boundaries are "broken" by perturbance, capacity of system may change

[2] Scaled to the second order mountain stream

and streams. And, in the way we have structured this theoretical perspective, even the lowest level stream subsystem has context within the watershed as a whole, and its capacities and performances can be related to watershed events.

A watershed can be conceived of as a natural-cultural system, as shown with the generalized model in Figure 5. Such a model will be useful in discussing our approach to watershed and stream classification and the significance of classification. A watershed is embedded in a geographically-organized system of watersheds which forms it environment. Such a system of watersheds can be understood as a system of natural-cultural systems.

A natural-cultural system has its own capacities and performances, including structure, organization, development, and persistence. It can be taken to be composed of interpenetrating climatic (Cl), cultural (C), substrate (S), water (W), and biotic (B) subsystems, each of these subsystems having its own level-specific capacities and performances. The natural-cultural system gets its capacity through incorporation of the capacities of its subsystems.

The natural-cultural system as a whole forms the environment of any of its subsystems. This is simply to say that the environment of the biotic subsystem is composed of the interrelated climatic, substrate, water, and cultural subsystems. Any performance of this subsystem at a particular time is determined by its capacity (organization) and the state of its environment, that is, the state of the natural-cultural system. In an important sense, then, the biotic or any other subsystem cannot be understood apart from the natural-cultural system as a whole.

A stream system is embedded in a watershed, which forms its environment (Fig. 6). The stream system entails part of the watershed biota (pB), part of the watershed water (pW), and part of the watershed substrate (pS). The stream community is symbolized by pB, while the community habitat is composed of pS and pW.

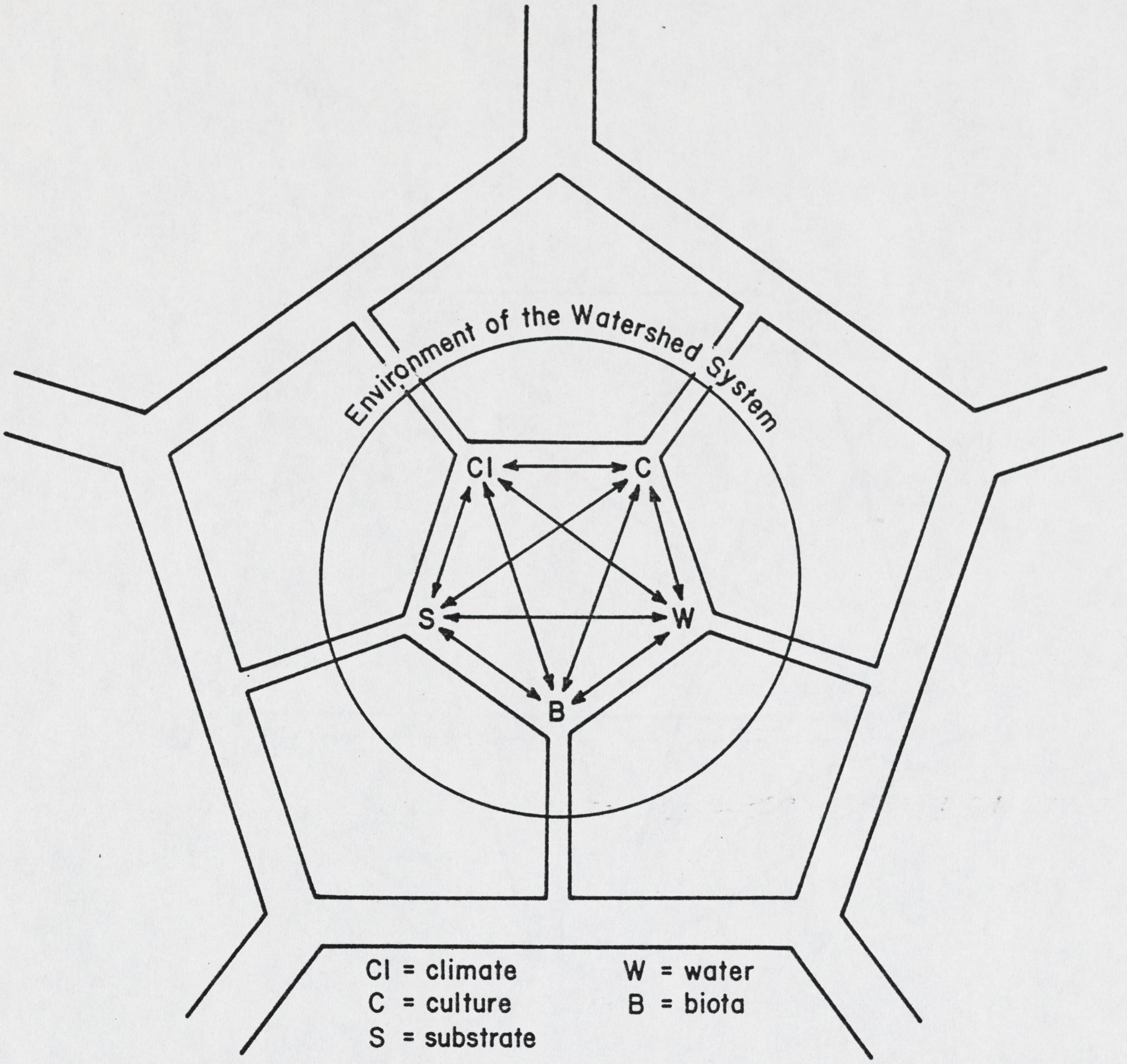


Figure 5. System of watershed systems. Natural-cultural system entailing compositional hierarchy of culture (C), climate (Cl), biota (B), water (W), and substrate (S). Geographic hierarchy or system of natural-cultural systems forms environment of natural-cultural system of interest. After Gregor (1982).

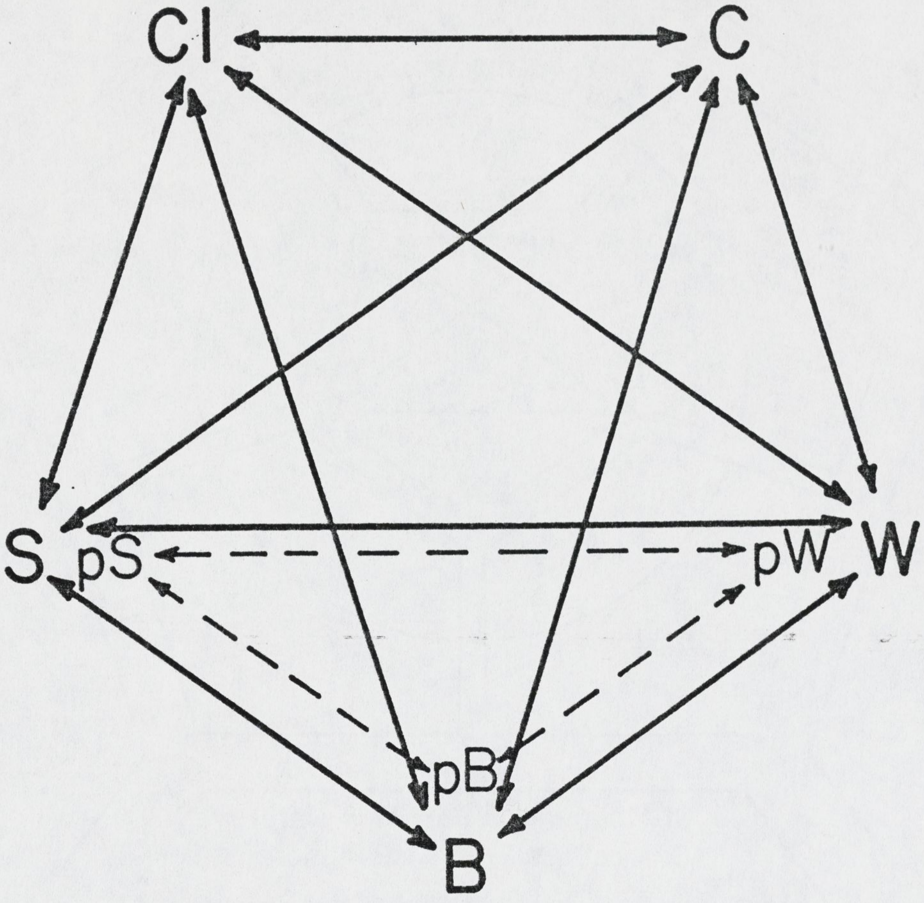


Figure 6. Stream system embedded in its watershed environment. Stream system entails part of the watershed biota (pB), part of the watershed substrate (pS), and part of the watershed water (pW). After Wevers (MS).

C. Multisteady-State Models of Toxicant Community Effects

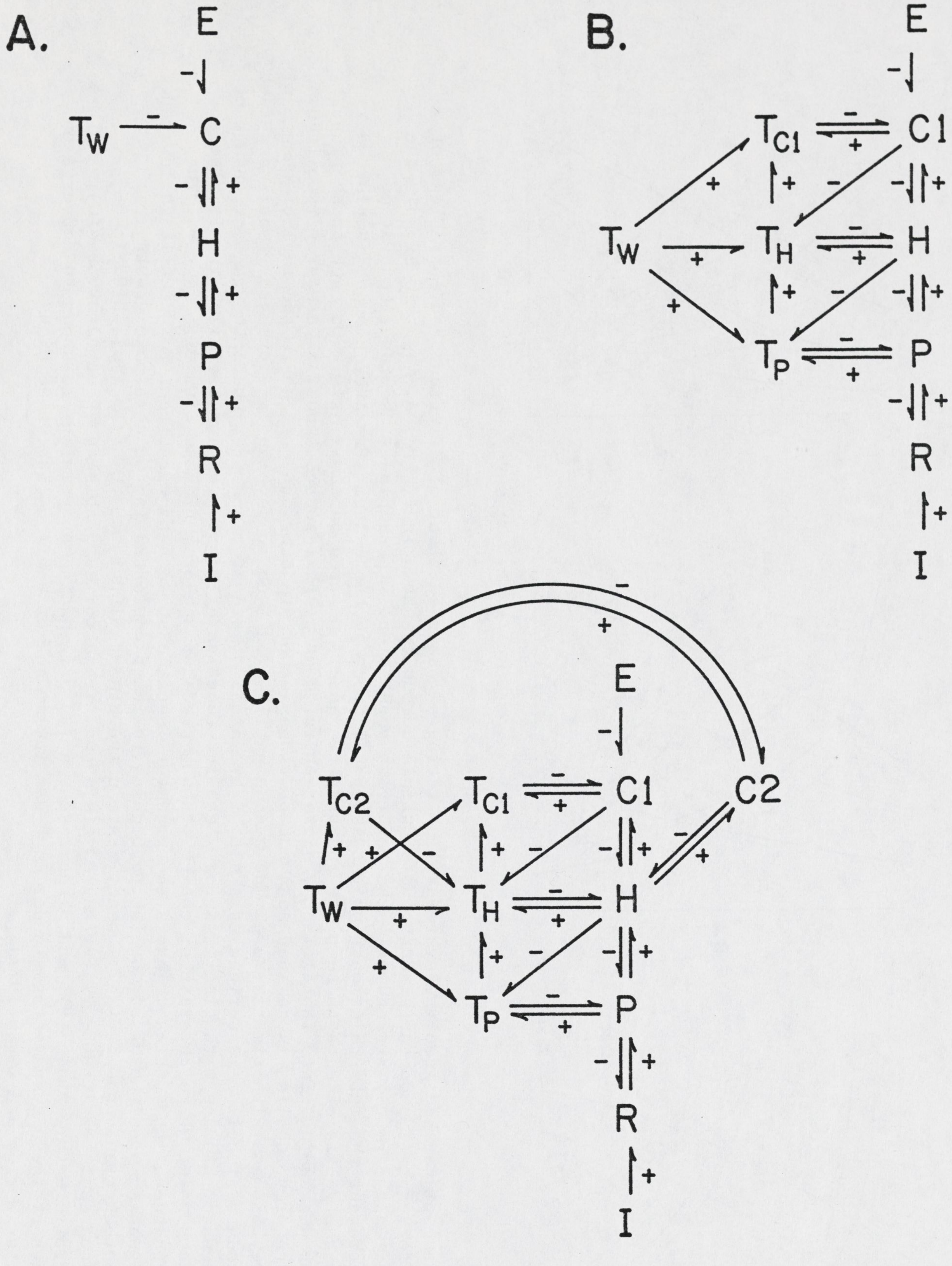
According to our theoretical perspective, the effects of a toxicant on a community can be understood to be dependent upon the capacity of a toxicant, the capacity of the community, and the capacity of the environment of the community. Community capacity at a particular time is determined by the organization of the community. The environment of an aquatic community can be understood as the climatic (Cl), substrate (S), water (W), and cultural (C) subsystems of a natural-cultural system.

Mathematical models can be used to symbolize, partially articulate, and provide a perspective on the effects of toxicants on communities, but they do so in a more restricted and particular way than does theory. Here we will use models to illustrate the joint influence of community organization and environment on toxicant effects.

The interrelationships between populations composing simple communities can be usefully illustrated with systems of isoclines on phase planes. Isoclines and phase planes symbolizing a community that has been exposed to a toxicant (Figure 7A) are shown in Figure 8. The intersecting isoclines define systems of steady-state relationships between the populations composing the system. The position and form of the isoclines is determined by systems of graphs or equations representing the rates of change in biomass of the populations composing the system (Booty 1976, Liss 1977, Thompson 1981). A complete set of isoclines on all phase planes provides at least a partial view of the structure and organization of a system in relation to environmental conditions.

Under different states of the environment of a community, the community will come to have different steady-state structures and organizations and so can be understood to be a multisteady-state system. The formal basis for understanding systems as multisteady-state systems was derived by Thompson et al. (MS). In the example shown here (Fig. 8), for each set of environmental conditions I and E, there exists a single steady-state point on each phase plane, each of these points being a two-dimensional projection of a single, multidimensional system steady-state point in phase space. The set of these two-dimensional points defines the steady-state structure of the system for a given set of environmental conditions. For example, the steady-state structure of the system at High I,

Figure 7. A. A food chain composed of a carnivore population (C), a herbivore population (H), a plant population (P), and plant resources (R). Level of exploitation of the carnivore (E), energy and material input rate (I), and toxicant (T_W) form the environment of the system. Arrow indicates interactions between populations composing the system and between these populations and the environment. B. The same food chain as in A but with quantities of toxicant in the carnivore (T_{C1}), herbivore (T_H), and plant (T_P) added as components of the system. Arrows indicate interrelationships influencing toxicant concentration in each component. C. Addition of a competitor C_2, changing the organization of the system. Quantity of toxicant in C2 (T_{C2}) is also shown.


A.
E
C
H
P
R
I
T_W
B.
E
C1
H
P
R
I
T_W
T_C1
T_H
T_P
C.
E
C1
C2
H
P
R
I
T_W
T_C1
T_C2
T_H
T_P
+
–

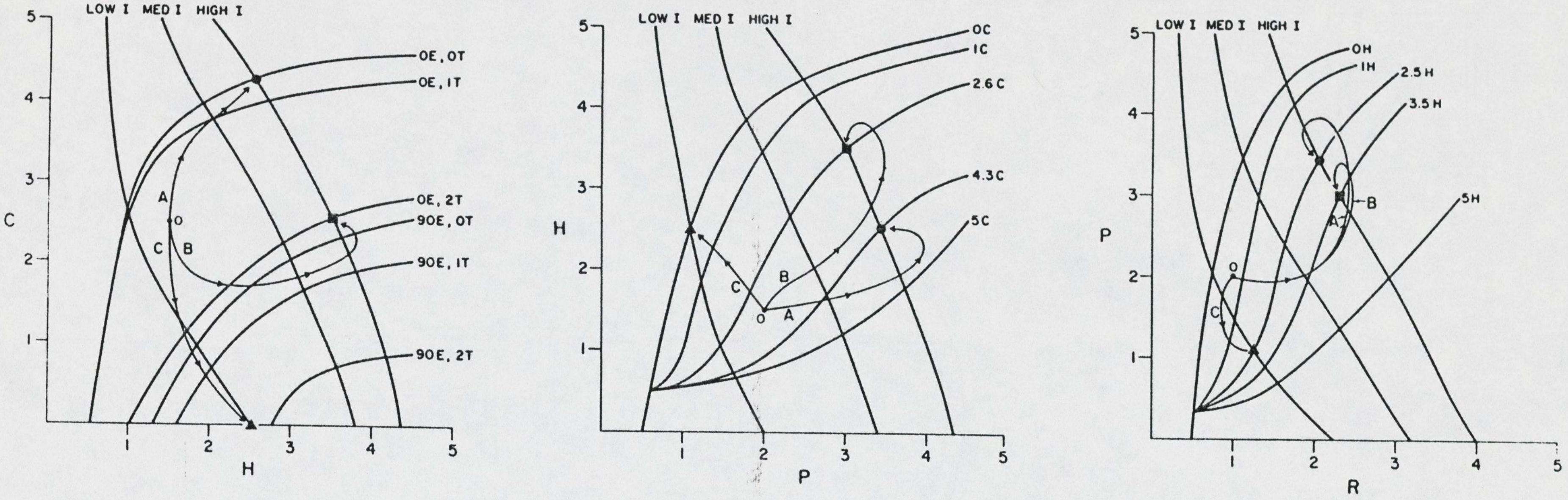


Figure 8. Phase planes and isocline systems illustrating a possible effect of different concentrations of a toxicant (T_W) on the structure of a simple community shown in Figure 7A. In this example the toxicant directly affects only the carnivore population. Phase planes and isocline systems represent the interrelationships between populations in the system. Predator biomass is plotted on the y-axis of each phase plane and prey biomass is plotted on the x-axis. On each phase plane, the descending lines identified by different rates of plant resource input, I, are prey isoclines. Each prey isocline is defined as a set of biomasses of predator and prey where the rate of change of prey biomass with time is zero. The ascending lines on each phase plane are predator isoclines. Each predator isocline is defined as a set of biomasses of predator and prey where the rate of change of predator biomass with time is zero. Each intersection of a predator and prey isocline is a steady-state point where the rate of change of both predator and prey biomass with time is zero. The presence of the toxicant lowers the predator isocline at each E, the extent to which it is lowered depending upon the effect of the particular toxicant concentration on carnivore growth, reproduction, and survival. Steady-state structure at HIGH I, 0E, 0T (circles); HIGH I, 0E, 2T (squares); LOW I, 90E, 2T (triangles) is shown. Trajectories of biomasses of carnivore (C), herbivore (H), plant (P), and plant resource (R) originating at point 0 are shown to converge on each of these steady-states under each particular set of environmental conditions.
After Warren and Liss (1977).

0E,0T is given by the solid circle on each phase plane. Changing the state of the system's environment (for example, from High I, 0E,0T to High I, 90E,0T or Med I,0E,0T) brings about a change in the steady-state structure of the system. A system may have an infinite number of possible steady-state structures depending upon the states of its environment.

On each phase plane, trajectories represent the changes through time in densities of the populations composing the system. If environmental conditions are fixed, trajectories will converge upon the steady-state points locating the steady-state structure of the system under those conditions (Fig. 8). In natural systems, environmental conditions are rarely constant for long enough periods of time to permit systems to reach steady-states. Thus, trajectories can be understood to be in continuous pursuit of a steady-state point whose location in phase space is constantly being shifted as a result of changes in environmental conditions. For an n-dimensional system, the trajectory on each phase plane is a two-dimensional projection of an n-dimensional trajectory in phase space.

Introduction of toxic substances can alter the structure and organization of systems, which is symbolized on phase planes by a shift in the location of the steady-state points (Fig. 8). Thus, at High I,0E, introduction of a toxicant at concentration 2T shifts the steady-state structure of the system from the circle to the square. The response of communities to toxic substances is affected by their organization and conditions in their environments such as I and E (Warren and Liss, 1977). For example, in Figure 8, the carnivore population is able to persist at LOW I when it is heavily exploited (90E) if a toxic substance (T) is not present (the predator isocline identified by 90E, 0T intersects the prey isocline identified by LOW I). But, under these same environmental conditions at a toxicant concentration of 2T, the carnivore population is driven to extinction (the prey isocline identified by LOW I does not intersect the predator isocline identified by 90E, 2T; C trajectory). Under different sets of environmental conditions the carnivore is able to persist, although at reduced biomass, at a toxicant concentration of 2T. Persistence at 2T is possible at LOW I when the carnivore is unexploited (0E), or at MED I and HIGH I when C is heavily exploited (90E).

Changes in the organization of the community will also affect its response to a toxicant. For example, the addition of C2, a competitor of carnivore C1 for the herbivore prey, brings about a change in the steady-state structure of the system at each level of I and E (Lee 1983) and so will influence the magnitude of effect of the toxicant. In particular, in this simple system, introduction of C2 reduces the steady-state density maintained by C1 at each I and E and so alters its ability to persist when exposed to toxicant (Liss et al. 1983).

D. Multisteady-state Models of Toxicant Behavior

The behavior or dynamics of toxicants in communities, like toxicant effects, can be understood to be dependent upon the organization of communities and conditions in their environment. And, like toxicant effects, behavior can be understood as a multisteady-state phenomenon.

In terrestrial systems the primary method of toxicant uptake by an organism is by consumption of contaminated food items. In aquatic systems the mode of uptake is not as clearly defined. There has been much discussion as to the relative contributions from food and water to the amount of toxicant taken up by an organism (Reinert 1972; Spigarelli et al. 1983). Hamelink at al. (1971) rejected the hypothesis of food chain transfer as the controlling process of biological accumulation in aquatic systems. Since this time, toxicologists have generally rejected the idea that ecological mechanisms play any major role in influencing the process of bioaccumulation.

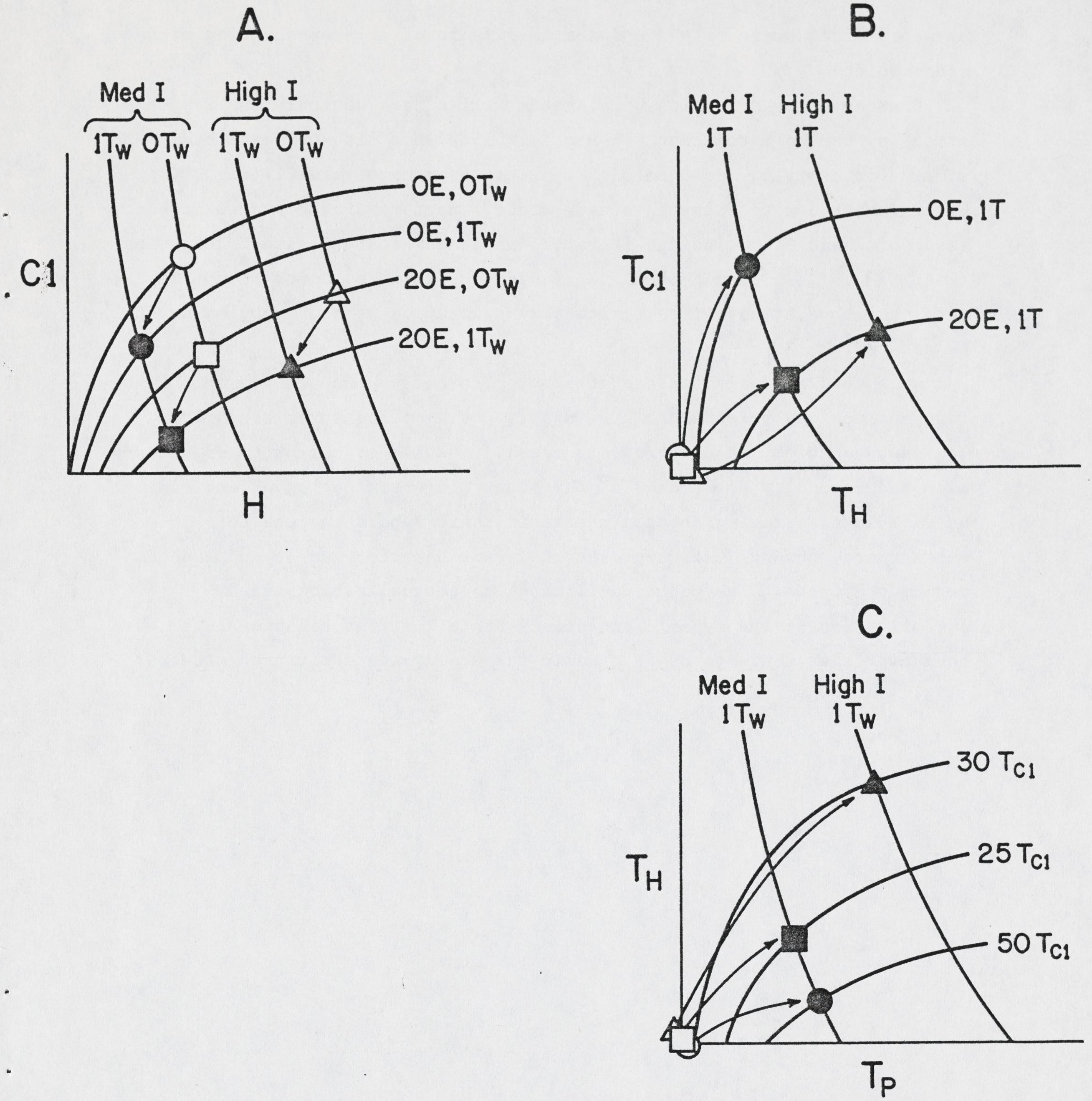
Recent toxicological research concerning bioaccumulation has been dominated by studies of uptake and elimination to determine bioconcentration factors for a variety of compounds in various organisms. Most laboratory efforts have been aimed at correlating bioconcentration factor with physiochemical properties of the compound, most commonly octanol-water partition coefficients (Kanazawa 1980) Such studies may shed some light on accumulation potential of compounds but, beyond this, their application to communities and ecosystems is uncertain. Implicit in attempts to apply this information to communities is the assumption that physico-chemical properties of the toxicant determine concentration in components of a community, independent of community organization and environment.

In our view, the behavior a toxicant, including concentration in the components of a community, is determined by the potential and realized capacities of the compound (perhaps indicated by its physico-chemical properties), the organization of the biological community, and the organization of the environment of the community including physical and chemical conditions.

Our modeling work is very preliminary at this time, but it does indicate that toxicant dynamics can be understood from a multisteady-state perspective. The system in Figure 7B can be used to illustrate the multisteady-state nature of toxicant behavior. The hypothetical toxicant is taken up through both the food and water. Preliminary work indicates that the phase planes and isocline systems symbolizing toxicant behavior and effect in this system may be something like those sketched in Figure 9. In Figure 9A, the effects of toxicant concentration 1 T_w on system structure for three different sets of environmental conditions, High I, 20E, Med I, 0E, and Med I, 20E, are shown. These effects consist of shifts in structure from steady-states indicated by the open symbols ($0T_w$) to steady-states indicated by the closed symbols ($1T_w$). The steady-state concentrations of toxicant in the carnivore (T_c), the herbivore (T_h), and the plant (T_p) under each set of environmental conditions are shown in Figures 9B and 9C. Under different sets of environmental conditions, there exist different steady-state toxicant concentrations in each population. If this is so for many compounds, bioaccumulation ratios determined in the laboratory under a single set of conditions may not have much relevance to bioaccumulation in communities and ecosystems.

If environmental conditions are fixed, trajectories of toxicant concentration, like trajectories of population density, will converge upon the steady-state points locating the steady-state concentrations in the populations under that set of conditions. If environmental conditions are continually changing, trajectories of concentration will be in continuous pursuit of an ever-shifting steady-state point. This suggests that one or a few measurements of toxicant concentrations in the components of natural ecosystems may not have much significance, for these measurements would be merely a few points on a trajectory that may be moving throughout

Figure 9. Phase planes showing possible toxicant effects and behavior in the systems shown in Figure 7B. Our modeling work is very preliminary at this time but indicates that toxicant behavior can be understood as a multisteady-state phenomenon, perhaps something like we show here. The position and form of the isoclines symbolizing toxicant behavior can be determined from graphs or equations incorporating rates of toxicant uptake and elimination by each population. Uptake rates for each population can be taken to be dependent upon concentration or availability in the water and in the food. Rate of trophic uptake by a predator can be understood to be a function of the concentration of toxicant in the prey and the rate of prey consumption, which is a function of the densities of both the predator and the prey. Predator and prey densities in turn, are determined by the levels of environmental factors I,E,and T_W. Thus different levels of these environmental factors lead to different steady-state concentrations of toxicant in the populations composing the community. A. C1-H phase plane illustrating effects on system structure of introduction of a toxicant at concentration $1T_W$. Open symbols indicate steady-state structure prior to toxicant introduction under each of three sets of environmental conditions. Solid symbols indicate structure after toxicant introduction. B. Phase plane relating steady-state quantity of toxicant in carnivore C1 (T_{C1}) to quantity in herbivore H(T_H) under each set of environmental conditions. C. Phase plane relating steady-state quantity of toxicant in H(T_H) o quantity in P(T_P) under each set of environmental conditions. Trajectories representing dynamic behavior after toxicant introduction at Med I, 0E, Med I, 20E, and High I, 20E are shown.


A.
Med I
High I
1T_W
0T_W
1T_W
0T_W
0E, 0T_W
0E, 1T_W
20E, 0T_W
20E, 1T_W
C1
H
B.
Med I
1T
High I
1T
0E, 1T
20E, 1T
T_C1
T_H
C.
Med I
1T_W
High I
1T_W
30 T_C1
25 T_C1
50 T_C1
T_H
T_P

a rather wide domain of phase space in pursuit of an ever-shifting steady-state point.

Changes in organization of a system will affect not only the response of the system to a toxicant (Liss et al. 1983) but also toxicant behavior. For example, addition of a competitor of carnivore C1 (Fig. 9C) brings about a change in the steady-state structure of the system at each level of I and E, including alteration in steady-state C1 and H densities (Lee 1983). As a result of these changes in densities, trophic uptake rates and thus steady-state toxicant concentration of each population will be altered.

With this approach, we are attempting to unify perspectives in toxicology and ecology to obtain better understanding of toxicant behavior. Toxicant behavior, in our view, is closely coupled to community organization and community environment. Any change in organization or environment is capable of bringing about a change in toxic substance behavior. Furthermore, through this approach, toxicant behavior can be coupled to toxicant effects. The model facilitates conceptualization and symbolization of the dynamic and steady-state toxicant behavior in a community that corresponds to dynamic and steady-state toxicant effects.

V. CLASSIFICATION SYSTEMS FOR STREAM ECOSYSTEMS

A. Introduction and Significance

There is a great diversity of kinds of stream systems and stream communities developing in different kinds of watersheds, these different kinds of systems having quite different capacities to respond to perturbations by man. How can such a problem of diversity be approached both theoretically and empirically to gain some understanding of the possible impacts of man's activities on these different kinds of systems and to manage the systems to reduce environmental problems? Any adequate approach to problems of this sort in natural resource science and management would seem to have to entail a means of classification that would order systems into groups according to their capacities to perform. For the past six or so years our laboratory has been developing and demonstrating a contextualistic systems classification of watershed and stream systems that may be adequate for natural resource science and management.

The classification system is a hierarchical one capable of dealing with classes of watersheds and systems of watersheds from large to small geographical scales as well as with classes of riffles and pools in particular stream systems. This has a number of advantages. First, it enables us to deal with problems on any level or scale, according to the nature of the problems and the objectives of the work. Second, the context of systems is continuously maintained with this classification. Fundamentally we would classify a system by its capacity and the capacity of its environment, a system at any level in a geographic hierarchy forming the environment of a system at the next lower level. We would conceptualize a system at any level as a natural-cultural system (Fig. 5) and so take into account in its classification climate, substrate, water, biota, and culture. Our environmental problems are fundamentally problems of natural-cultural systems as wholes. But in approaching environmental problems we have tended to take mechanistic views and have uncoupled the elements of natural-cultural systems. It is as though we believe that we can abstract the biological community and understand and manage it independent of the rest of the system. In disciplines like fisheries and pest management, we have gone even farther. We have abstracted from the community a single or a few populations and, for the purposes of modeling, have reduced these complexly organized, developing, evolving systems to a few variables that we somehow believe are empirically determinable and perhaps even controllable. Classification that theoretically and empirically begins to take into account all the elements of natural-cultural systems is a way of keeping these elements in context and preventing us from forgetting about things that might be important in our theoretical and empirical work and in management.

The system of classification we are developing articulates with our theoretical perspective of watershed and stream systems (Table 1). In accordance with our view of stream system organization (Tables 2 and 3), classification would extend from watersheds, to stream systems, down to riffles, pools, and microhabitats, with classification of a system at each level being based upon its capacity and the capacity or class of its environment, the next higher level (Frissell MS). In our view, habitat subsystems such as riffles, pools, and microhabitats become the primary basis for determining the organization of stream communities (Wevers MS). Thus this system of classification articulates quite closely with stream community theory, making the classification meaningful from a biological perspective. Furthermore, as entailed in our theoretical perspective, this system of classification keeps stream habitat subsystems and their conformant biological subsystems in the context of and so coupled to the stream system and its watershed environment. In the process of classification of watersheds and streams, much understanding of their capacities and performances is gained.

B. Watershed and Stream System Classification

The form of any classification system is jointly determined by the objectives of the classification, that is, what it is going to be used for, the theoretical perspective or framework upon which the classification is based, and the nature of the objects or systems being classified (Warren 1979). The framework that is the basis for the classification system was partially explicated in the previous section.

eg - changing flows

The framework implies that systems should not be classified on the basis of their performances, which are continually changing as their organizations and environments change (Figs. 1, 2, and 3). If systems were classified in this way, then every time the performances of a system changed, the system would change class. Thus a system would be changing class continually.

Systems must be classified by something much more general and invariant than their performances. According to our framework, systems theoretically should be classified by their potential capacities and the capacities of their environments. Thus systems would be grouped according to similarities in their capacities and the capacities of their environments. By so classifying, all possible realized capacities and performances of the system would be theoretically entailed or taken into account.

A watershed system consists of substrate (S), climate (Cl), water (W), biota (B), and culture (C), as we have shown in Figure 5. Embedded in and interpenetrating this watershed system is a stream system (Fig. 6). The watershed system is, then, the environment of the stream system. A watershed system can be understood to be in the context of a system of watershed systems, each of the incorporated watersheds and thus the system of watersheds having substrate, climatic, water, biotic, and cultural capacities (Fig. 5). A system of watershed systems becomes the environmental system of any watershed of interest. There is, then, a geographic hierarchy of watershed systems, the larger systems geographically incorporating the smaller. There is also a compositional hierarchy, in which any watershed or system of watersheds entails substrate, climate, water, biota, and culture and their subsystems.

Our theoretical approach to watershed and stream system classification will be combined with extant classificaton systems utilizing geographic hierarchies, such as the ecoregion classification of Bailey (1976, 1978; Warren and Liss 1983). Then, as shown in Table 4, we will have sectional watershed systems, district watershed systems, landtype association watershed systems, and so on. We can understand the environment of a particular watershed system to be the system of watersheds, or the next higher organizational level that incorporates the particular watershed.

Table 4. Geographic hierarchical systems, environments, capacities, and performances.

Geographic[1] Hierarchical System	Environment of system	Capacities of system	Performances of system
Sectional watershed system	Provincial watershed system	Substrate climate water biological cultural	States or structures changes in states yields
District watershed system	Sectional watershed system	Substrate climatic water biological cultural	States or structures changes in states yields
Landtype association watershed system	District watershed system	Substrate climatic water biological cultural	States or structures changes in states yields
Landtype watershed system	Landtype association watershed system	Substrate climatic water biological cultural	States or structures changes in states yields
Site watershed system	Landtype watershed system	Substrate climatic water biological cultural	States or structures changes in states yields

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[1] Domain, division, province, and any other higher, intermediate and lower levels in a geographic hierarchy would have analogous environmental relations, capacities, and performances.

Thus the environment of a landtype association watershed system is a district watershed system . We would classify a watershed at any level in the hierarchy according to its capacity, here taking into account its substrate, climatic, water, biological, and cultural capacities, and the capacity of its environment, the next higher level. And, we would classify stream systems according to their capacity and the capacity or class of their watershed environments.

Although our classification is capacity-based, capacity is a theoretical concept: it can be neither directly nor fully observed. We need empirical approaches to classification. Capacity classification is a perspective that leads us to select as a basis for classification empirical vairables that are the most invariant, most general, and most determining of system performances. These sets of variables serve as proxies for capacity. At some levels of the hierarchy we may not employ, say, cultural or biological variables, but variables for classification would be selected in such a way that cultural and biological performances would be taken into account. - eg. life history patterns ?

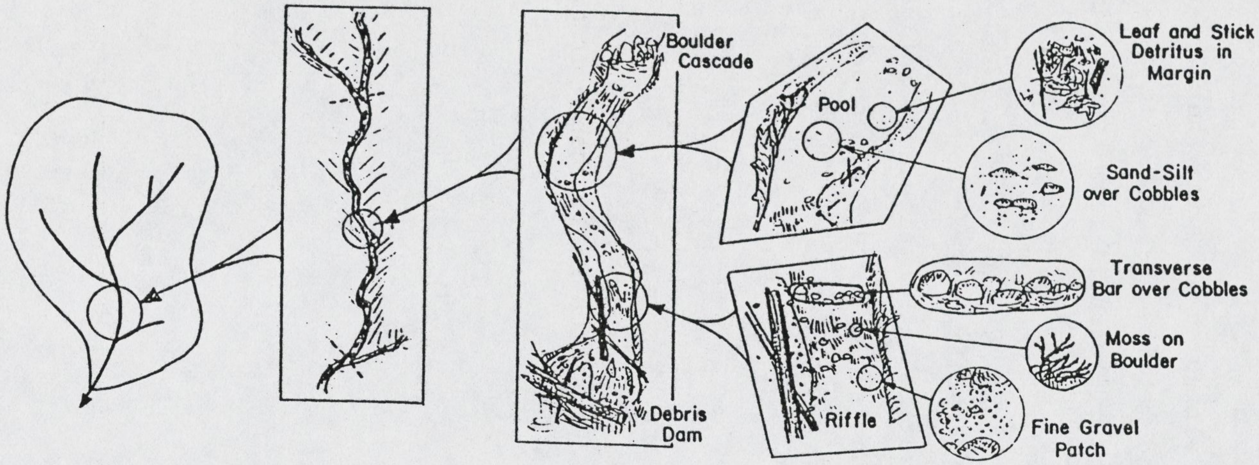
Stream systems, then, should be classified by some proxies for their capacities and by the class of their watershed environment. Proxies for stream system capacity in moderately sized watersheds might be taken to be network structure, including longitudinal profile, drainage area, and drainage density. Factors such as topography, geology, and soils may be taken into account in classification of the watershed according to its substrate capacity. The species pool in the system of watersheds will determine biological community development in the stream system, even though biota may not be explicit in stream classification. Similarly, culture is taken into account indirectly through classification of watersheds and systems of watersheds.

C. Stream Habitat System Classification

We can never duplicate the organization of a stream or class of streams in the laboratory. At best, we can attempt to model some significant features of a stream type. Stream habitat classification is a means of measuring, understanding, and summarizing the organization and development of a stream or stream type of interest, and this provides a tool for abstracting ecosystem characteristics that we can model.

The hierarchical classification scheme we have developed relates stream habitat organization to watershed organization on a range of scales. The classification decomposes stream systems into stream segments, segments into reaches, reaches into pools, riffles, rapids, etc. and pool/riffle systems into microhabitats. These hierarchical levels are defined with respect to the potential capacities of the systems to persist and develop in time and space, from 10^6 or more years and km^2 for stream systems, to less than a year and cm^2 for microhabitats. We suggest a small set of general variables, or capacity proxies, for each level, which relate to geomorphic processes that can be viewed as most significant, most determinant, in that space-frame. Fig. 10 summarizes these variables and illustrates how habitat systems might look in a second- or third-order mountain stream.

Since the class of any habitat system is determined by the class of the higher level system in which it is embedded, the classification system preserves the causal-deterministic relationship between stream habitats, stream communities, and the watersheds that encompass them. By further classifying habitats based on geomorphic features associated with their genesis, we account for their origin in predominantly terrestrial or riparian processes (e.g. landslides, tree fall, vegetation encroachment) impinging on the stream channel and interacting with processes more basin-wide in nature (e.g. hydrologic capacity, sediment regime, organic debris transport). Also, we account for the capacity of the reach, pool, or other habitat system to persist only so long as a particular causal geomorphic structure or process persists at a location. In this way, for example, we can define a gradient of pool classes, from those associated with highly persistent bedrock outcrops or boulders to those associated



STREAM SYSTEM	SEGMENT SYSTEM	REACH SYSTEM	"POOL/RIFFLE" SYSTEM	MICROHABITAT SYSTEM
10^3m	10^2m	10^1m	10^0m	10^{-1}m
Capacity Proxies	Capacity Proxies	Capacity Proxies	Capacity Proxies	Capacity Proxies
Watershed capacity	Stream system capacity	Segment system capacity	Reach system capacity	"Pool/riffle" system capacity
Network structure	Bedrock type & basic slope	Basic slope	Formative structure or process	Substrate type
Long profile	Valley side slopes	Bedrock relief	Bed topography	Local water depth and velocity
	Position in drainage network	Formative structure or process	Water surface slope	
	Potential climax riparian vegetation	Sediments immovable in 50-yr flood	Basic substrate size	
		Local side slopes or floodplain extent	Bank configuration	
		Riparian vegetation		

Figure 10. Organization and capacities of stream systems, segment systems, reach systems, pool and riffle systems and microhabitat systems.

with unstable gravel bars or small woody debris. Habitat systems of a class, given similar environments, should have similar potential developmental trajectories, similar organization at a given stage of development, and thus similar biological communities. Stream systems in a class, given watersheds in similar states, should have similar kinds of segment, reach, pool/riffle, and microhabitat subsystems.

Here we have specified capacity variables only in general terms, because the particular parameters and metrics used to apply this scheme might vary in different regions, with different stream types. In a rugged terrain of the Oregon Coast Range, for example, we might identify stream segment subsystems, which are larger than reach systems, to account for patterns in stream habitat owing to very large earthflows or debris torrents. Such events might be of sufficient magnitude to influence stream channels over many tens of hundreds of meters and thousands of years.

VI. STUDIES OF NATURAL STREAMS FOR CLASSIFICATION, MODEL DESIGN, AND EVALUATION

A. Introduction and Significance

The purpose of our field work is to begin to demonstrate our watershed, stream system, and stream habitat classification and to serve, together with our theoretical perspective, as a basis for design and evaluation of the laboratory stream studies. To demonstrate the classification, we are applying it in classification of watersheds, stream systems, and stream habitats in the Coast Range of Oregon. In our theoretical perspective, streams of a class are viewed as developing systems, their development being concordant with the development of their watershed environment (Generalization 3, Table 1; Figs. 1, 2, and 3). Thus we are studying and classifying habitats in streams that are not only of different classes, but also, for some classes, streams that are in different developmental states due to differences in their watersheds.

Through community studies in these streams, we intend to begin to demonstrate the utility of our stream theory. In particular, we hope to show that, through our system of stream habitat classification (Fig. 10), watershed and stream classification can be coupled to stream community organization and development. Thus the organization and classification of stream habitats can be shown to serve as a basis for the organization and classification of stream communities and their subsystems.

Toxic substances will behave differently and have different effects in different classes of watersheds and streams. Thus watershed and stream classification can serve as a rational basis for design of laboratory streams to evaluate toxicant effects. Our laboratory streams are designed to model two classes of stream systems that have been studied in the field, each class being modeled in two different developmental states. With this approach, some evaluation of laboratory stream studies can be achieved, for we will be able to compare laboratory stream system organization and development to the organization and development of natural stream systems of similar class and state.

B. Classification Field Studies

Field research in MacDonald State Forest, near Corvallis in the Oregon Coast Range, is intended both to help in the conceptual and methodological development of a stream habitat classification system and to demonstrate an application of the system.

After preliminary classification of watersheds and their stream systems throughout the study area by means of available topographic, geologic, soils, and climatological maps, we selected two second-order streams for intensive field investigation. At these sites we are developing criteria for identifying and classifying stream habitat systems from reach to microhabitat scales (Fig. 10). And we are examining how different habitat classes relate to their surrounding stream and watershed systems. A second objective is to document the dynamics of different habitats through the year, so that we may better understand how habitat classes differ in development and persistence.

The watershed/stream systems chosen for intensive study appear very similar in climate, geology, topography, and soils, and thus can be considered in the same class (Table 5). They differ in land use and vegetation states -- one basin is roaded, selectively cut, and clearcut in its headwaters, while the other is predominantly undisturbed old-growth forest (Fig. 11). We classified reaches throughout the second-order segments of the streams, and inventoried their pool/riffle systems. In fall 1983, two reaches in each stream were surveyed and mapped in great detail, to gain understanding of their organization at pool/riffle and microhabitat scales. These sites will be remapped in summer of 1984 to record changes that occured during winter storms. Analysis of these data is helping us to formalize and demonstrate the habitat classification scheme. Moreover, it is furthering our understanding of how differences in habitat organization, development, and persistence relate to differences in watershed states.

Preliminary analysis of field data confirms that reach systems of similar geomorphic origin have predictable morphology and similar kinds of pools and riffles, and that different kinds of pools and riffles have different kinds of microhabitats. Slight differences between the two

Table 5. Some Classification Variables for the MacDonald Forest Watershed/Stream Systems

	Strahler order	Slope of lowermost segment	Drainage area	Basin relief ratio	Total channel length	Network structure	Valley sideslopes	Soils	Bedrock lithology	Potential climax vegetation	Average annual precipitation	Biogeo-climatic environment
Soap Creek Tributary Q	2	12%	.36 ha	.26	1.50 km	dendritic	moderate, locally steep	95% Dixon-ville series	Siletz volcanics	Grand fir/ bigleaf maple	140 cm/y	Border of coast range and Willamette Valley provinces
E. Fork E. Fork Oak Creek	2	14%	.34 ha	.26	1.30 km	dendritic	moderate, locally steep	85% Dixon-ville series	Siletz volcanics	Grand fir/ bigleaf maple	140 cm/y	Border of Coast Range and Willamette Valley provinces

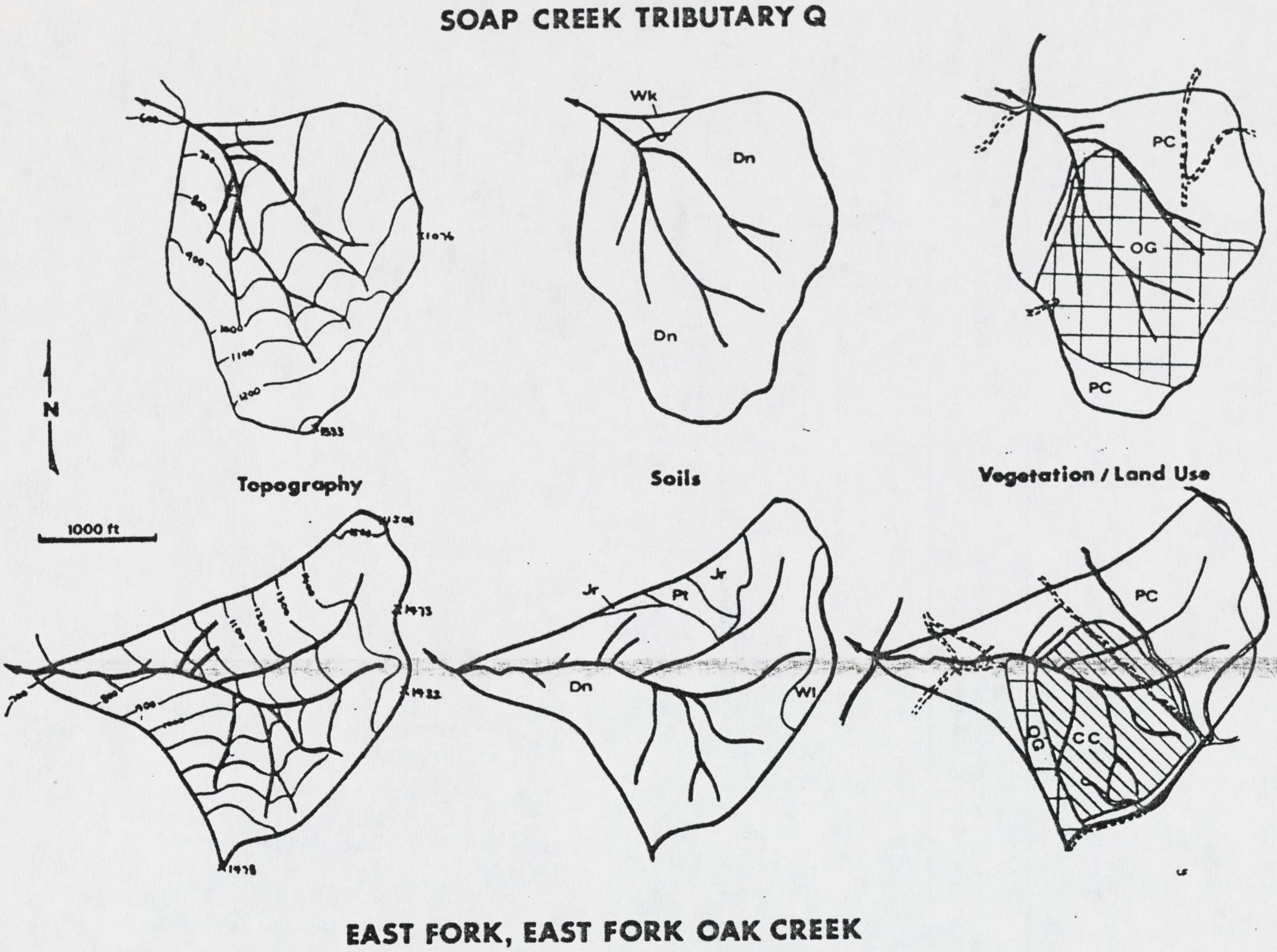


Figure 11. Topography, soils and vegetation/land use states of the study watersheds.

Soils: Dn = Dixonville silty clay loam, 35"; Jr = Jory silty clay loam, 60"; Pt = Price-Ritner silty clay loam, 50"; WK = Witham silty clay, 60"; Wl = Witzel cobbly loam, 15".

Vegetation/Land Use: OG = Old growth Douglas fir, bigleaf maple; PC = selective cut, *ca*. 1940; CC = clear cut, 1970. Solid double lines are maintained roads; dashed double lines are abandoned roads.

streams in the kinds and spatial arrays of reaches reflect both man's influence and paleolandslide history in the watersheds (Table 6). Pool/riffle-level organization appears similar between streams when these habitats are classified by form or morphology alone, but when associated geomorphic features are considered, they differ significantly (Fig. 12). The logged stream has many pools and riffles associated with unstable small wood and gravel bars and few associated with stable, large woody debris. This reflects changes in forest vegetation owing to logging. Large conifer wood is abundant in the old-growth stream, but alders and abundant maples tend to supply only smaller, fast-decaying debris to the logged stream (Fig. 13). Microhabitats vary between the streams, even within analogous pool/riffle systems in analogous reaches (Table 7). This is probably owing to basin-wide hydrologic or sediment source differences, related either to land-use history or fundamental differences in geomorphology and soils.

In Table 8, reach organization of the East Fork, East Fork of Oak Creek is compared to that of another Oak Creek tributary, Tributary 6. The vegetational states of the watersheds of these streams are similar, but the streams are of different classes and have fundamentally different capacities.

With increased understanding of stream/watershed relationships, we might improve the area-wide watershed classification system by mapping geomorphic/soils/vegetation units at smaller scales than available soils maps allow. Landscape units can be identified that incorporate the paleolandslide history of these watersheds, which field experience suggests is a significant determinant of stream habitat organization. (See Table 4, Figure 4). Further field research will involve habitat surveys of several streams to better describe relationships between stream habitat organization and the capacities and states of watersheds across the study area.

Stream community studies were conducted in the Oak Creek and Soap Creek tributaries on MacDonald Forest. Developmental states of the two streams are designated as "clear cut" and "old growth." Community studies were also conducted in a Willamette Valley floor stream that is of a different class than the MacDonald Forest streams. Two stream segments

Table 6. Summary of reach-level organization of two watershed/stream systems of similar capacity, but different vegetation/land use states. Increased large-wood-related reaches in East Fork East Fork Oak Creek are due mostly to old logging road crossings. Increased steep colluvium-erosional reaches and small alluvial terraces are associated with mass movement which pre-dates logging. Increased channel width in the logged stream may be due to higher peak flows or greater bank erodibility.

	Soap Creek Tributary Q	E. Fork E.Fork Oak Creek
.mean reach length	14.3 m	11.4 m
. mean reach slope (excluding terminal falls, cascades)	9.4%	8.4%
.% of elevation drop in falls, cascades	3.6%	2.0%
.Reach-forming features		
Bedrock	33%	22%
Colluvium-constructional	33%	22%
Large woody debris	22%	33%
Root blockage	11%	6%
Colluvium-erosional	0%	11%
Small woody debris	0%	6%
.% Constructional reaches	71%	36%
.% Erosional reaches	29%	64%
.Bank composition	Colluvium	Colluvium, alluvial terraces
.Mean channel width	1.85 m	2.16 m
.Riparian vegetation	Douglas-fir, grand fir, yew, bigleaf maple, rare alders; sparse understory	Red alder, bigleaf maple, some grand fir, young Douglas-fir; dense brushy understory

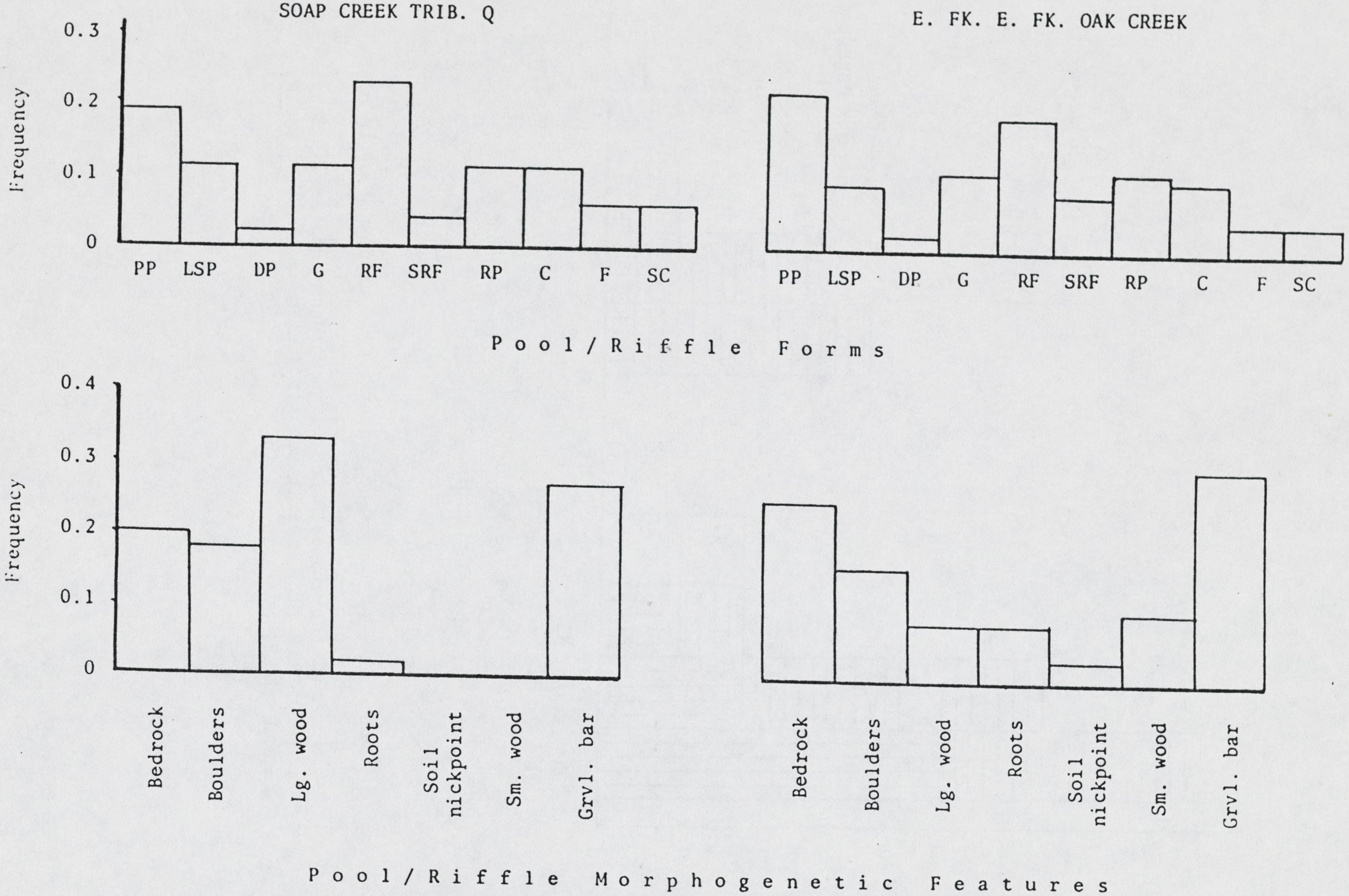


Figure 12. Frequency distributions of pool/riffle systems in the study streams classified in two ways. Morphometric feature distributions are significantly different between streams ($X^2 > 29.36$, $d^f = 6$, $\alpha = 0.99$). Pool/riffle forms are plunge pools (PP), lateral scour pools (LSP), dammed pools (DP), glides (G), riffles (RF), steep riffles (SRF), rapids (RP), cascades (C), falls (F), and side channels (SC).

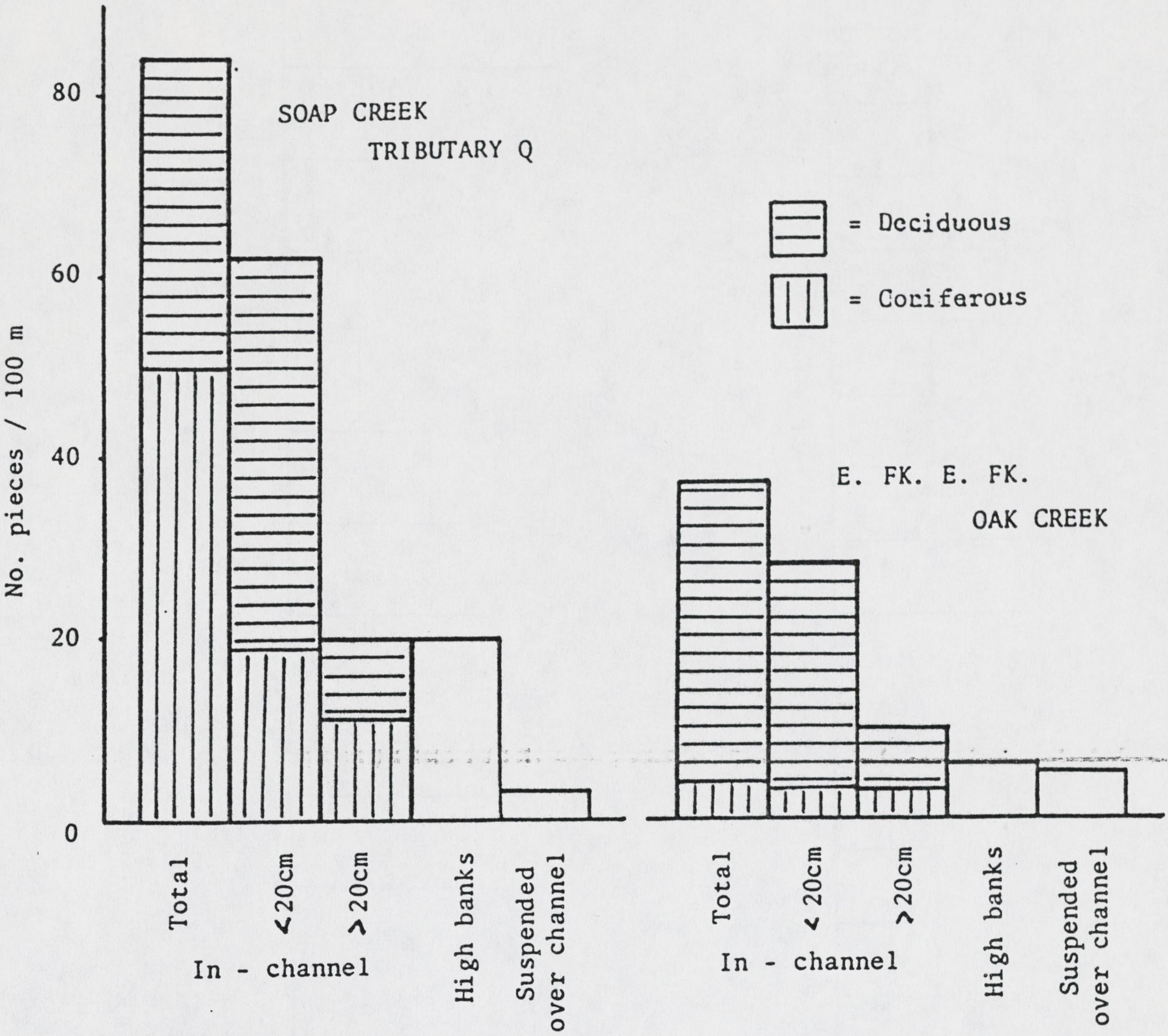


Figure 13. Abundances of large woody debris (>10 cm diameter) in old-growth (Soap Cr. Trib. Q) and logged (E.Fk, E.Fk. Oak Cr.) streams. In-channel wood is grouped as coniferous (Douglas-fir, grand fir, Pacific yew) or deciduous (bigleaf maple, red alder, etc.) in origin.

Table 7. Preliminary summary of microhabitat differences between two watershed/stream systems of similar capacity, but different vegetation/land-use states. Coarser particle sizes, poorer sorting, increased angularity, presence of freshly excavated bedrock saprolite, and less moss cover suggest the logged stream has greater recruitment and transport of bedload sediments and greater disturbance of microhabitats during winter. In summer, sloughing from streambanks perturbs some marginal areas. Fall microhabitat dynamics differ between streams due to different quantity, quality, and timing of leaf litter inputs.

	Soap Creek Tributary Q	E. Fork E. Fork Oak Creek
. Bedrock particle size distribution in riffles, bars	somewhat finer (d_{84} 10-20mm)	somewhat coarser, (d_{84} 15-30mm)
. Estimated particle sorting	moderate-poor	poor-very poor
. Particle roundness	mostly subangular, semi-rounded	many angular-very angular
. Soft, saprolitic particles	uncommon, small well-rounded	locally common, large, angular
. Moss in channel	common on bedrock, boulders, cobbles, wood	common on bedrock but rare on cobbles, etc.
. Cobble transverse ribs	at pool tails only	large, found at pool tails and commonly within riffles
. Wood substrates	widespread, common, stable, largely coniferous	uncommon, small, unstable, mostly deciduous
. Dominant mode of winter perturbation of coarse substrates	scour, burial by fine gravel, sand	scour, downstream transport
. Overhanging banks	abundant, stabilized by roots	less common, shallow, unravelling

Table 8. Comparison of reach-level organization of E. Fork E. Fork Oak Creek and Oak Creek Tributary 6, a watershed of similar size and vegetation state, but whose valley is filled deeply with ancient colluvial/alluvial debris. A watershed classification scheme should account for these differences; capacities of these stream systems are clearly different.

	E. Fork E. Fork Oak Creek	Oak Creek Tributary 6
.Drainage pattern	dendritic	subparallel, anastomosing, seepy side channels
.Channel incision	moderate	alternate deeply and very shallowly incised reaches
.Mean reach length	14.3 m	37.5 m
.Mean reach slope (excluding terminal falls, cascades)	9.4%	3.8%
.% elevation drop in falls, cascades	2.0%	6.6%
.Reach-forming features	wide range	roots, headcut scarps associated with shifting channels
.% constructional reaches	36%	20%
.% erosional reaches	64%	80%

broadly representing two different developmental states of this class of stream were studied. One segment flows through an agricultural field and is designated "valley field." It had been channelized, is open to sunlight, and has extensive emergent vegetation. The other segment flows through an ash forest and is designated "valley forest." It has a much lower incidence of solar radiation and contains much more woody debris in the channel.

The general purpose for sampling streams in the field was to determine if biological stream community organization reflected the same differences in stream class and state as the streams' physical habitat. A more specific purpose would be to determine if consistent and significant comparisons and contrasts can be developed within streams and between streams. Within stream comparisons entail determination of how stream communities are organized in relation to the habitat organization of the stream and how this organization relates to the stream's watershed environment. Between stream comparisons could be utilized to explore whether differences in community and habitat organization reflect differences in stream class and state.

Prior to the actual sampling process, each stream was surveyed to identify representative habitat reaches (Fig. 10) to be sampled. For each stream we attempted to identify two major habitats: depositional and erosional (although neither valley stream segment an erosional reach). Each habitat reach was subdivided into four potential subhabitats: riffle, pool, cascade, and run (Fig. 10). Subhabitats were then reduced to their respective microhabitats. Microhabitat identification was based on the following criteria: a) depth (substrate surface to water surface), b) current velocity, and c) substrate types (mineral and/or organic). Microhabitats sampled per reach ranged from 0 to 21 (See table 9). Examples of microhabitats sampled include backwaters, side channels, exposed-wetted cobble bars, transverse cobble bars, main channels with differing substrate composition, etc.

Each of these habitat subsystems has developing on it a biological subsystem, the organization of the habitat thus determining community organization. With the sampling procedure, we will be able to determine the organization of the habitat and species composition and trophic

Table 9. Reaches, reach habitat subsystems, and number of microhabitats sampled in each reach habitat subsystem in field stream community studies.

Stream	Reach Habitat	Reach Habitat Subsystems	Number of microhabitats sampled
Clear cut	Depositional	riffle	5
		pool	5
		run	3
		cascade	0
		TOTAL	13
	Erosional	riffle	5
		pool	8
		run	4
		cascade	0
		TOTAL	17
Old Growth	Depositional	riffle	12
		pool	5
		run	2
		cascade	2
		TOTAL	21
	Erosional	riffle	12
		pool	4
		run	0
		cascade	1
		TOTAL	17
Valley Forest	Depositional	riffle	0
		pool	4
		run	3
		cascade	0
		TOTAL	7
	Erosional	-	0
Valley Field	Depositional	riffle	0
		pool	0
		run	4
		cascade	0
		TOTAL	4
	Erosional	-	0

organization of the biological subsystem developing on each habitat subsystem in each developmental state of each stream class.

After the microhabitats in each subhabitat of a stream were identified, sampling was begun. Tools and supplies in the sampling process include: a) PVC benthic samplers (4",6",8"), b) sieves (300μ, 125μ), c) vacuum cleaner (wet-dry, shoptype), d) gas-powered electric generator, e) water pump, f) formalin, g) plastic, one gallon sample bags (Ziplock®), h) water bottles, i) five gallon buckets, and j) meter stick and tape, stop watch, metric ruler, and rock brushes. For each microhabitat sampled, and beginning downstream, the substrate composition was recorded, the mean depth was measured, and the mean current velocity (float time per given distance) was determined. An appropriately-sized benthic sampler was placed in the stream over the area of the microhabitat to be sampled. The substrate and water within the sampling tube were removed and placed in the five gallon buckets, manually and mechanically (vacuum). Substrate removal was carried out to a maximum substrate depth of 10 cm whenever possible. The mean depth was reassessed prior to removal of the sampling tube. The sample was then processed by pouring the water through the 300μ - 125μ sieves in tandem, washing the substrate within the buckets, and pouring the washings into the sieves. The substrate remaining in the buckets and the substrate captured in the sieves were then removed to the plastic sample bags. The samples were then preserved with formalin. During the entire sampling procedure, a free-hand sketch was made of each habitat reach being sampled. An attempt was made to draw sketches to approximate scale, by making use of meter tape measurements placed at various points along the length and width of the reach sampling site.

VII. MODEL STREAM ECOSYSTEMS

A. Introduction and Significance

The goal of our model stream work is to advance understanding of the effects of toxic substances on stream systems. According to our theoretical perspective, the organization and development of a stream community is determined by the organization of the species pool of potential colonists and the organization and development of the community habitat (Generalizaton 6, Table 1; Fig. 4), habitat development occurring in concordance with watershed development. Moreover, stream communities of different classes can be understood to respond differently to toxic substances, the responses or effects consisting of alterations in community organization and development. We have designed our laboratory stream work around these principles.

One set of stream studies was intended to demonstrate that, in a given species pool, different kinds of communities will develop on different kinds of habitats and that these different kinds of communities will respond differently to toxicants. In another set of studies, laboratory streams were designed to model two different classes of natural streams, each class in two different developmental states. Part of the evaluation of these streams will consist of comparison of their community and habitat organization to the organization of natural streams of similar class and state that we have been studying in the field.

B. Model Stream Design and Construction

The model stream facility presently consists of two large outdoor streams used to provide a known species pool by supplying exchange water and organisms to 12 small streams located in a greehouse building and 8 streams in a controlled light building. Additionally, eight other streams have been located at our fish rearing site near our high-volume well water source.

1. Large Outdoor Streams

Each of these two streams consist of two wooden channels 10 x 1.3 x 0.8 m elevated above the ground and having inner walls of plexiglass.

Water from a nearby springfed stream supplies about 40 l/min exchange flow to each stream. The channels slope at about 1.7 percent and are connected at each end by large irrigation pipes. A 2 hp pump maintains water recirculation between the two channels. Riffle areas are formed by concrete blocks overlain with natural stream substrate. Such habitat structures as shallow riffles, deep riffles, pools, and woody debris are present.

Previous studies (Wevers 1983) provided a detailed description and explanation of the organization and development of these stream communities, including species present and their abundances throughout the year. These streams serve as the species pool from which our laboratory stream ecosystems are continuously colonized. The large streams are colonized continuously from a small stream and through the air from nearby streams.

To each outdoor stream is fitted a standpipe through which water and colonizing organisms are delivered by gravity flow to the laboratory stream buildings. In each standpipe a vertical slot runs from the water surface to the stream bottom. In this way organisms drifting throughout the entire water column are collected and delivered to the laboratory streams.

Care was taken to ensure that all streams have equal probabilities of receiving colonizing organisms from the species pool. In each laboratory stream building, a continuously rotating head or carousel delivers equal quantities of water to the intakes of individual delivery pipes leading to each of the laboratory streams. Water from an additional intake is passed through a fine mesh drift net to monitor kinds and densities of organisms incoming from the species pool.

2. The 12 Stream Channels

These 12 streams are each composed of an epoxy-painted wooden trough 3.3m x 66cm x 25cm divided into two channels by an open-ended median partition. Electrically driven paddlewheels provide a current velocity over constructed stream habitats. Exchange flow is about 3 l/min per stream.

Three fundamentally different substrate types representing different classes of habitats were established in these streams. The habitats are slate-bedrock, gravel-rubble, and silt-sand (Fig.14). Each of these substrates is present alone in three laboratory streams, a total of nine streams being so used. Each of the reminaing three streams has a combination of the three habitat types. A continuous flow diluter provides constant low-level introduction of toxicants to the streams. Water flow from the two large model streams is equally distributed to the 12 streams by a water outlet rotating over a carousel flow-splitter box.

3. Eight Stream Enclosures

These stream enclosures were developed to model important physical and biological aspects of selected natural streams of two different classes, each of these in different states resulting from differences in their watershed environment. The MacDonald Forest streams are representative of one class of streams and the Willamette Valley floor streams representative of another. Stream developmental states are named according to the states of their watersheds. Thus streams of the MacDonald Forest class are designated "clearcut" and "old growth" and streams of the valley floor class "valley forest" and "valley field".

A first design requirement was that the size of the enclosures be sufficient to model such stream morphological characteristics as gradient and bed form, including gravel bars, riffles, debris dams, and stream banks in approximately full scale of the first- and second-order streams being studied in the field. The enclosures were constructed largely of 1 1/4" marine plywood with 2"x4" frame supports. Each enclosure is 3.66 m long by 2.44 m wide by 0.46m deep with an open-ended median partition forming connecting channels (Fig.15). A stainless steel paddlewheel 61cm in diameter and 33 cm wide lifts water from the lowest to the highest portion of the substrates, gravity flow providing most of the resulting current.

Each paddlewheel is driven by a valve-controlled hydraulic motor continuously variable between about 30 to 2 rpm. All eight motors are supplied by one 2 hp hydraulic pump. This system provides high torque over a wide rpm range, good speed control, and reliability.

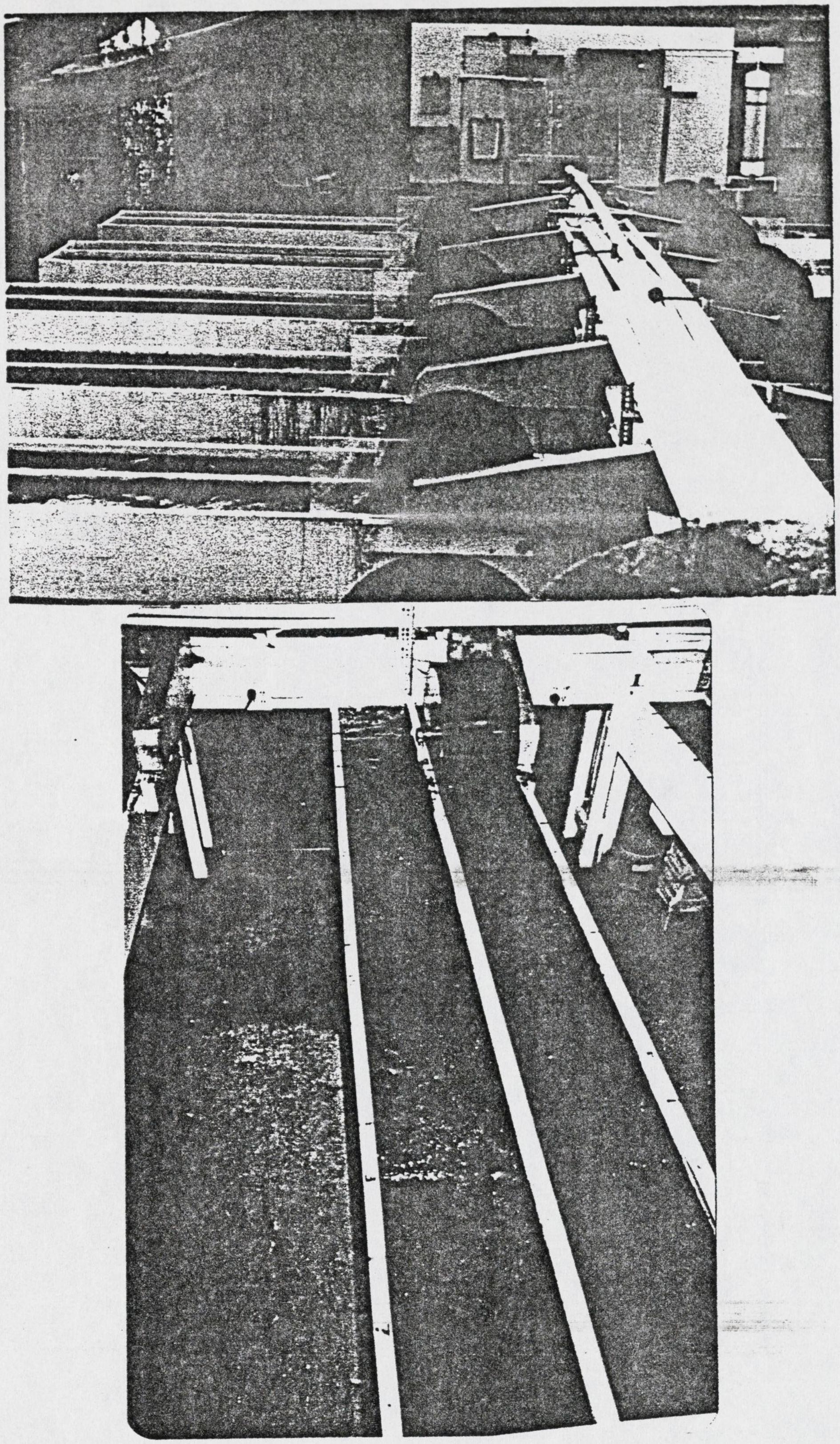


Figure 14. The 12 stream channels showing the toxicant delivery system against the back wall (upper picture) and one of the three stream habitats (lower picture).

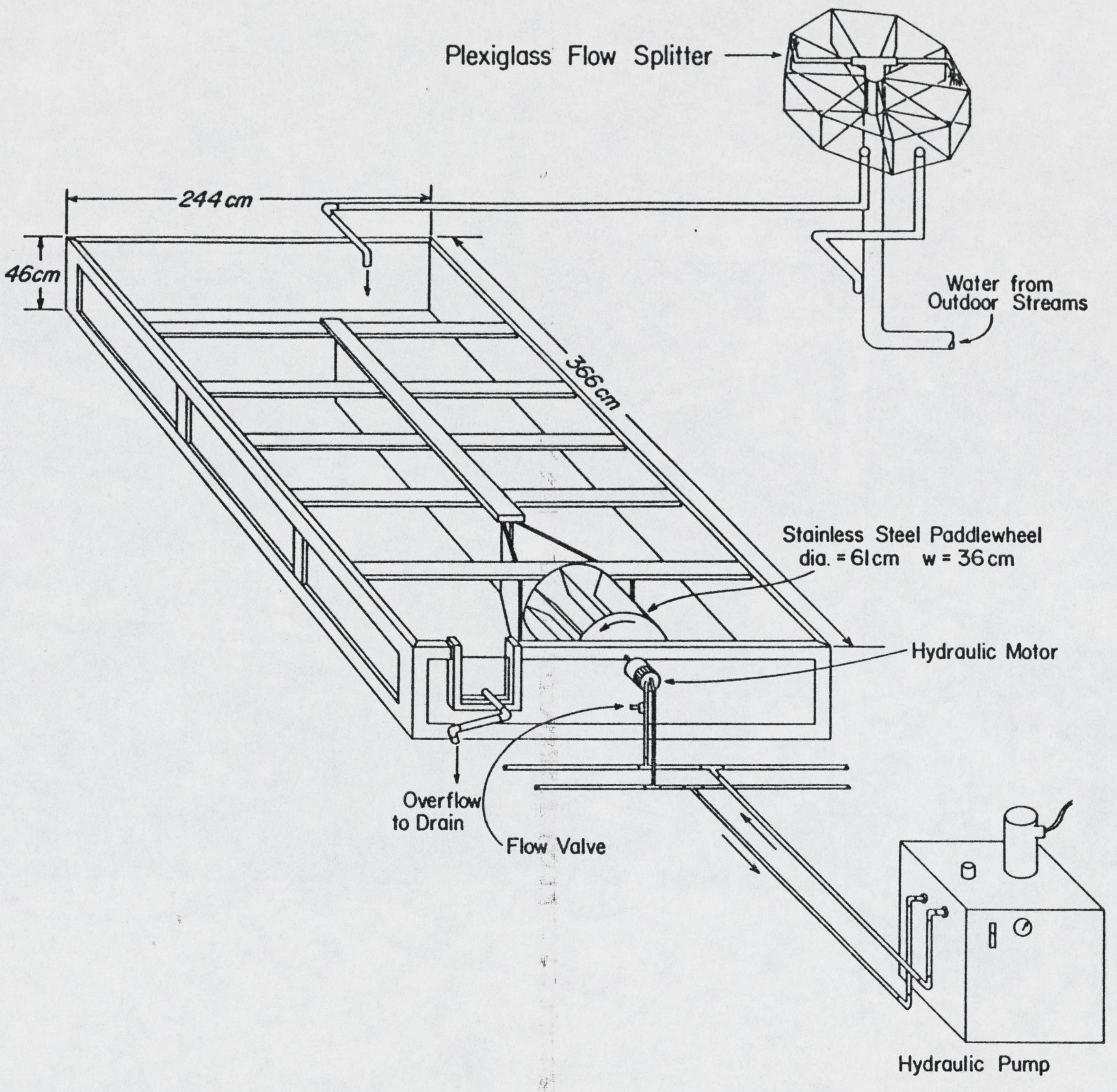


Figure 15. One of the laboratory stream enclosures showing the hydraulic system which rotates the paddlewheels and the flow splitter which divides incoming water equally between the eight streams.

Most of the stream flow recirculates, although 4 l/min exchange flow is provided to each stream from the two large outdoor streams. This water and entrained organisms are partitioned to each stream by a carousel splitter box 1.2 m in diameter over which a delivery head roatates. The carousel is divided into nine partitions, each of eight partitions being used to deliver water and organisms to a different stream and one partition being used for sampling incoming organisms.

These eight streams are in a small building with light provided by timer-controlled, metal halide fixtures. Light quality from this fixture type most closely mimics natural light wave-length composition. This system has the potential to expose the streams to light levels from low shade to nearly full sunlight. Light levels now used are stylized representations of the seasonal levels recorded at the four field study sites.

4. Instrumentation

Light measurement is by Li-Cor quantum radiometers. Both instantaneous and integrated readings are available for field sites and for individual model streams. The Li-Cor solar monitor utilizes type and memory storage of integrated quantum values with interface capability to our computer (HP 9816). Temperature data is automatically recorded for each stream by an HP 3421A data aquisition controller. This unit hourly stores thermister readings on a mass storage tape drive compatible with our laboratory computer, which interfaces via a modem with the Cyber computer on the OSU campus.

5. Habitat Construction

Our intent in structuring the habitats of the laboratory streams was to idealize and model in the laboratory the major classes of reaches, pools and riffles, and micro-habitats found in each developmental state of each stream class. In doing so, we were concerned with gradient, profile, fundamental substrate characteristics, hydrological regime including current velocity, temperature, and energy and material source and pattern of input (Table 10).

The gradient and stream bed morphology of all streams was formed from the heavy local clay. Bedrock pieces of local basalt were fitted as

Table 10. Factors considered in the design of the modeled streams.

Modeled Stream	Stream Substrate	Stream Gradient	Bank Stability	Riparian Vegetation	Solar Penetration
Old Growth	Well rounded and well sorted with much woody debris	Moderate	stable and gently sloping	old-growth Douglas fir with fern understory	Very low
Clear cut	Angular and poorly sorted with much exposed bedrock	Moderate	Unstable with highly eroded vertical banks	second growth Douglas fir, alder and vine maple	Low
Valley Forest	Silt with rooted aquatic plants much woody debris	Low	Stable and gently sloping	Ash forest	High
Valley Field	Silt and "islands" of slumping vegetation	Low	Unstable with vertical slumping banks	Farmland	Very high

needed, followed by logs or other embedded structures. Gravel was mixed to model particle size distribution of samples taken at the field sites. Soils were added to the valley floor streams to represent fine sediment deposition. Plants collected near the field sites were then added to complete the construction (Fig 16).

Characteristics that determine stream class, such as gradient, were first modeled. Then characteristics specific to watershed and stream state were added. For instance, the old growth mountain stream was a relatively stable environment, with much woody debris forming dams trapping finer particles. Substrate particle size was comparatively small in correspondence with the more stable stream discharge. Ferns and other plants grew close to the water or overhung the stream. Bedrock common in this class was present but largely gravel covered, although rocky outcroppings or woody debris formed scouring plungepools. Thus for this stream such features were incorporated into the habitat construction. The functional relationships between structures were maintained: for instance, finer gravels were placed in deposition areas, and exposed bedrock was placed in plunging flows. Spatial relationships between structures were abbreviated, however, and the model was not considered to replicate the study site but to model its common features. Similar considerations were used to select habitat structures for the clearcut stream and the two states of the valley floor stream (Figs. 17, 18).

As well as taking great care in modeling the quality and quantity of substrate, light, and riparian vegetation found at the natural streams, we have also attempted to model the quality and relative quantity of litter entering the natural streams. Litter-fall traps are placed at the natural stream sites to collect litter. This is subsequently dried, sorted, weighed, and then introduced into the appropriate model stream.

Eight additional streams have been placed in a fenced, outdoor area adjacent to our fish-rearing site. This site was chosen because of a very large supply of high quality well water.

6. Design, Conduct, and Results of 12 Stream Study

Figure 19 shows theoretically how we anticipated communities in bed-bedrock, gravel, silt, and combination substrate habitats would develop

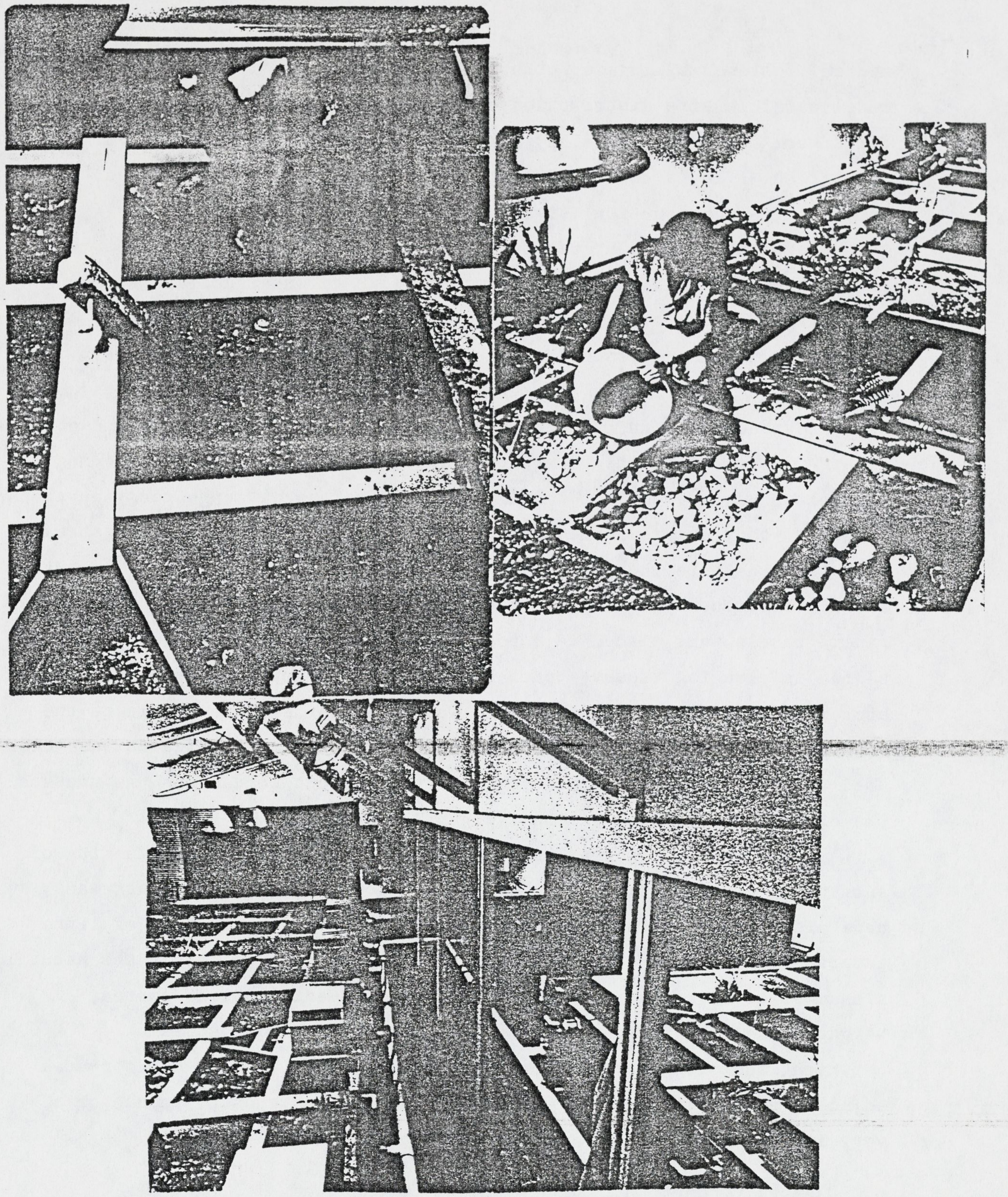


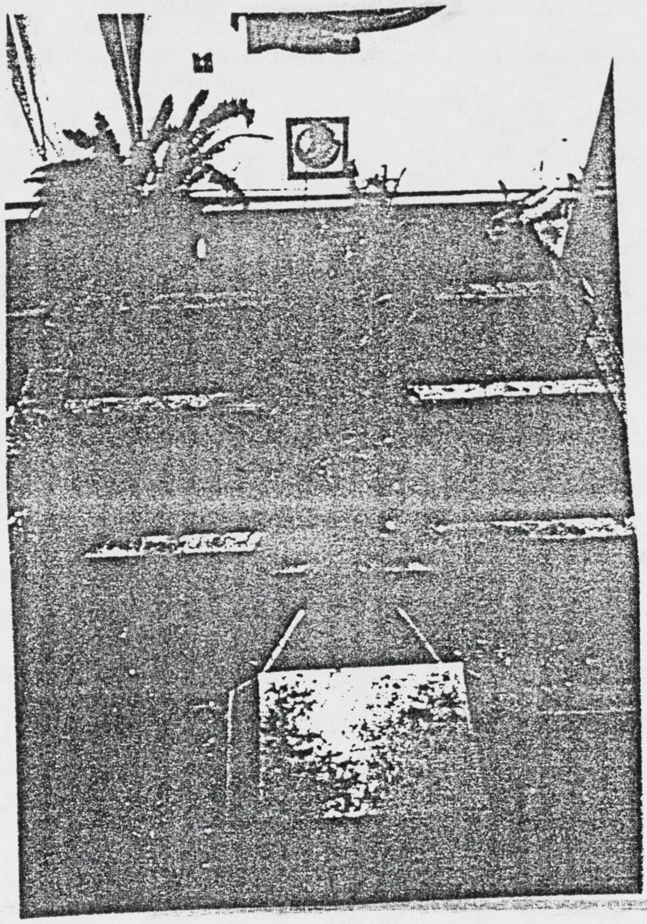
Figure 16. Upper photos depict steps in habitat construction beginning with bed formation from clay followed by addition of substrate materials and plants. Lower photo shows the arrangement of the stream enclosures, lights and shading material.

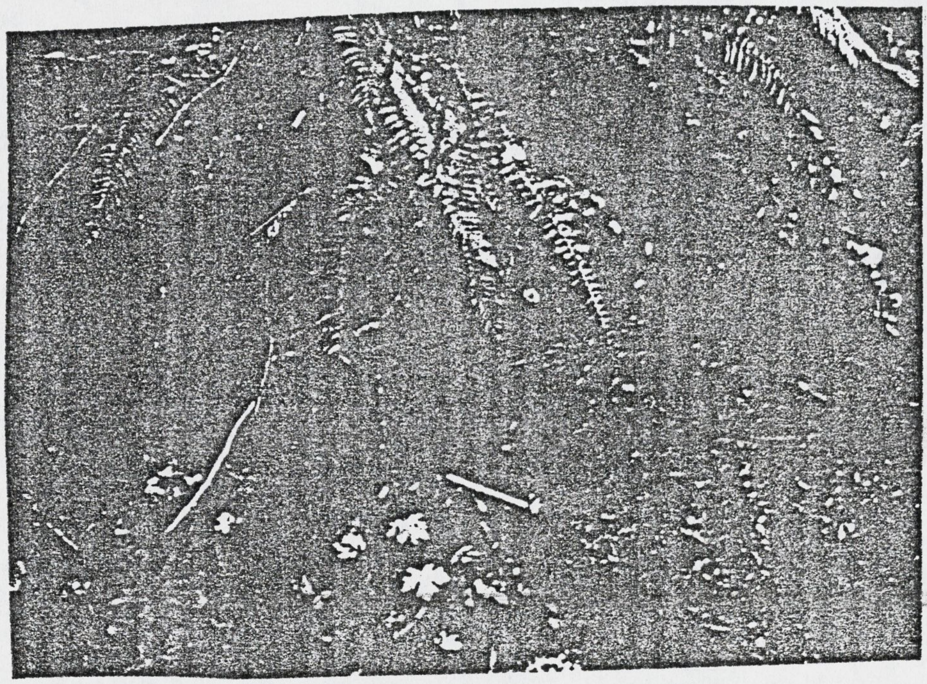
given a common species pool. We expected communities in model stream channels having the same substrate type, bedrock for example, to develop very similar communities. We also expected stream channels of different substrate or habitat types to develop communities that were comparatively dissimilar. Moreover, we anticipated that if during its development a model stream community was perturbed by introduction of a toxicant, its continued development would be along a trajectory different from another model stream community of the same habitat type but not perturbed by a toxicant.

Since the initiation of this experiment in March 1980, benthic, drift, and emergence samples have been taken regularly to assess community development in the model stream channels. Results show that the communities are quite complex and have as many as 65 macroinvertebrate taxa. Figure 20 shows the number of individuals in macroinvertebrate trophic subsystems and species number within each trophic subsystem for model stream channels of different habitat types. Community structure between streams of the same habitat type is quite similar. Yet communities in streams of different substrate or habitat types are dissimilar in number of individuals in each trophic subsystem as well as different in species number and composition.

Fenvalerate, a synthetic pyrethroid insecticide, was introduced at a concentration of 0.07 ppb into one set of model stream channels (one bedrock, one gravel, one silt, and one combination stream) from 30 August through 7 December 1982. Dieldrin, an organic insecticide, was introduced at a concentration of 0.05 ppb into another set of streams from 22 February through 2 September 1983. The third set of model steams has been kept as controls.

Invertebrate samples have been processed and the data are presently being analyzed. In general, community response to the toxicants has resulted in decreased insect populations (except for Tipulidae), and slight increases in the abundancees of some algae, snails, and crustaceans. Macroinvertebrate and algae sampling continues in these model stream channels, so that we can observe further community change, including recovery from toxicant exposure.





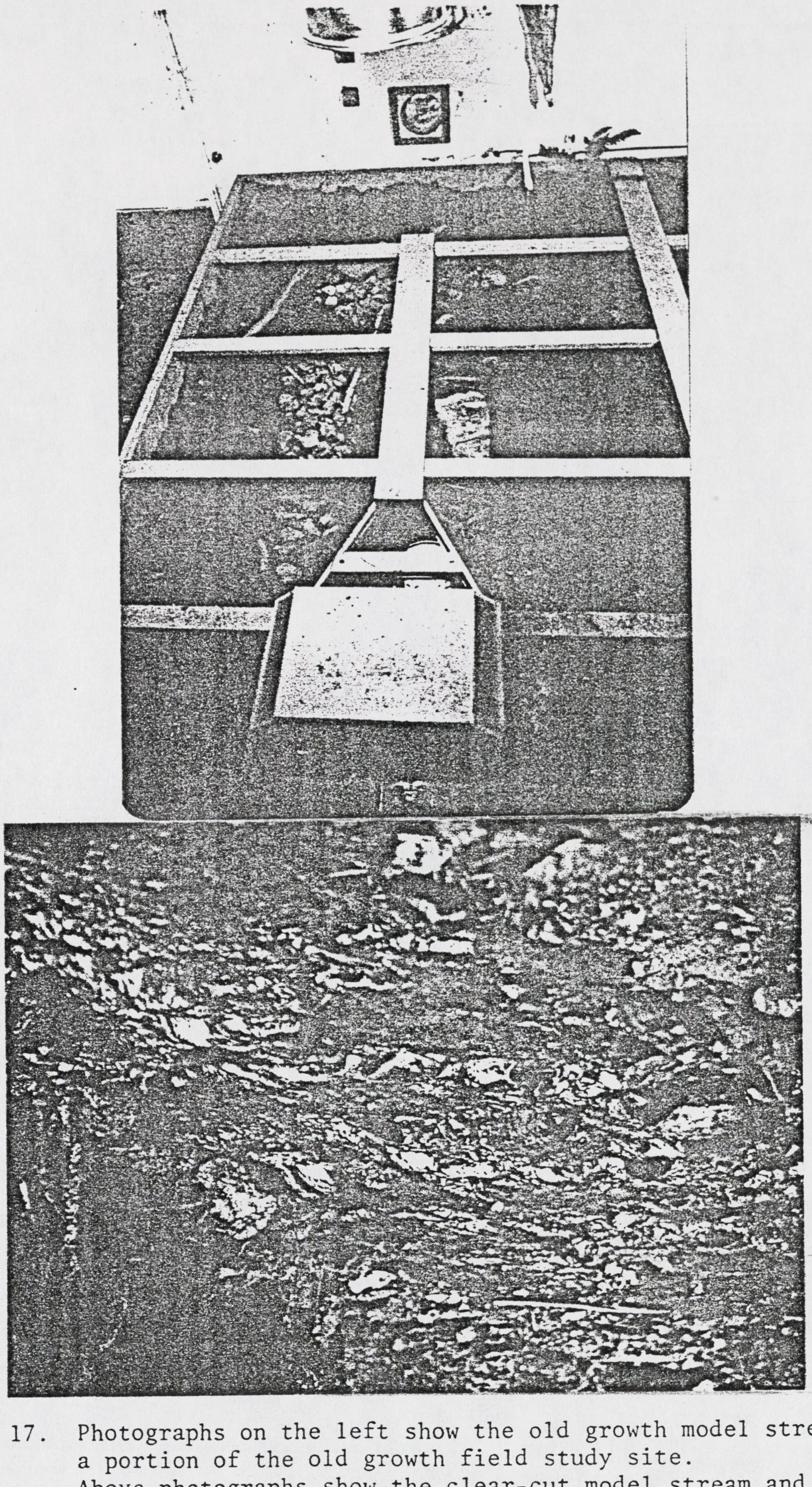
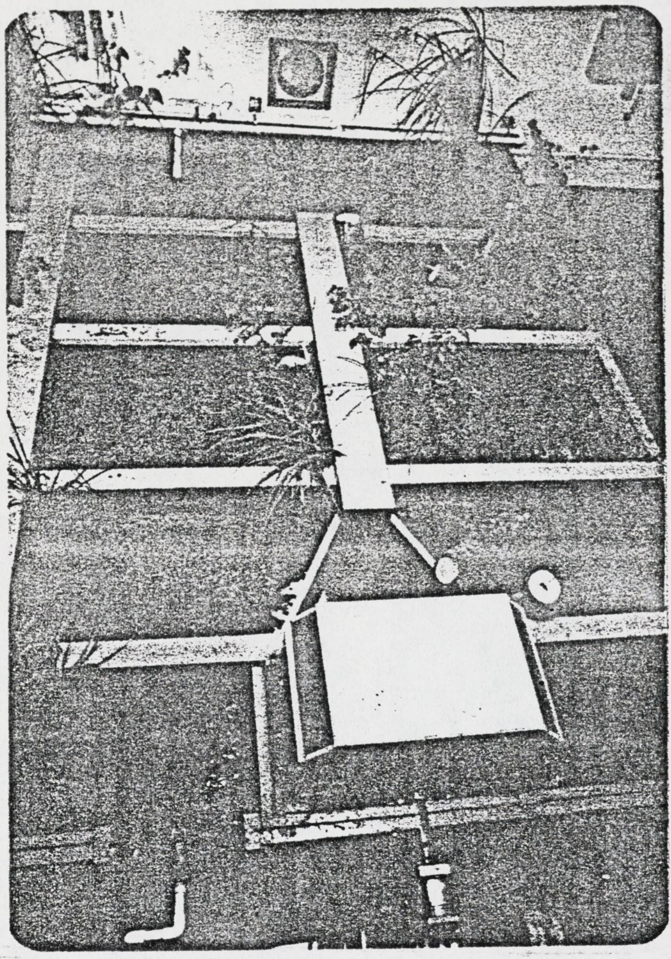


Figure 17. Photographs on the left show the old growth model stream and a portion of the old growth field study site.
Above photographs show the clear-cut model stream and the corresponding field site.



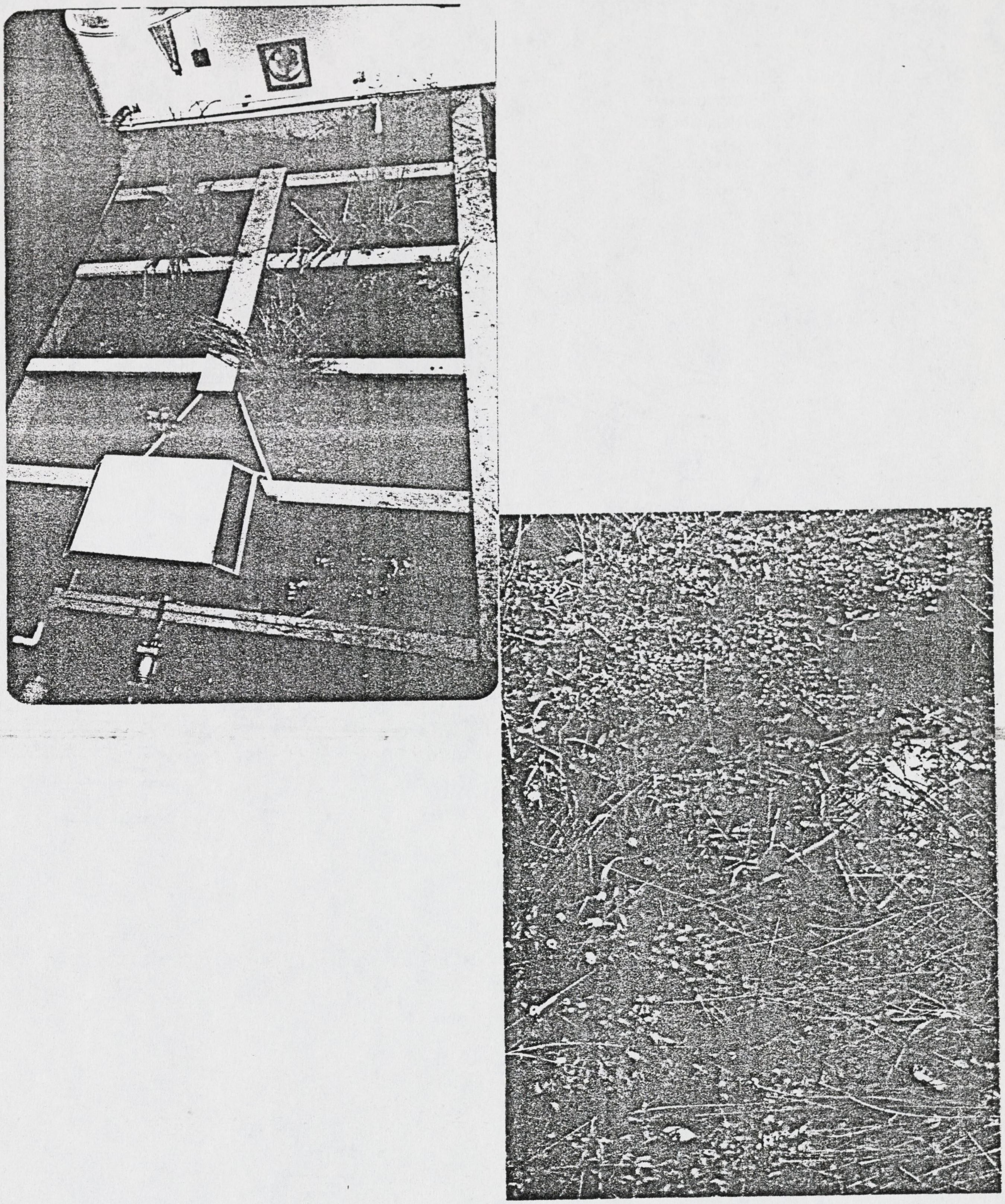


Figure 18. Photographs on the left show the forested valley model stream and a portion of the field site. Those above show the model of the channelized valley stream and corresponding field study site.

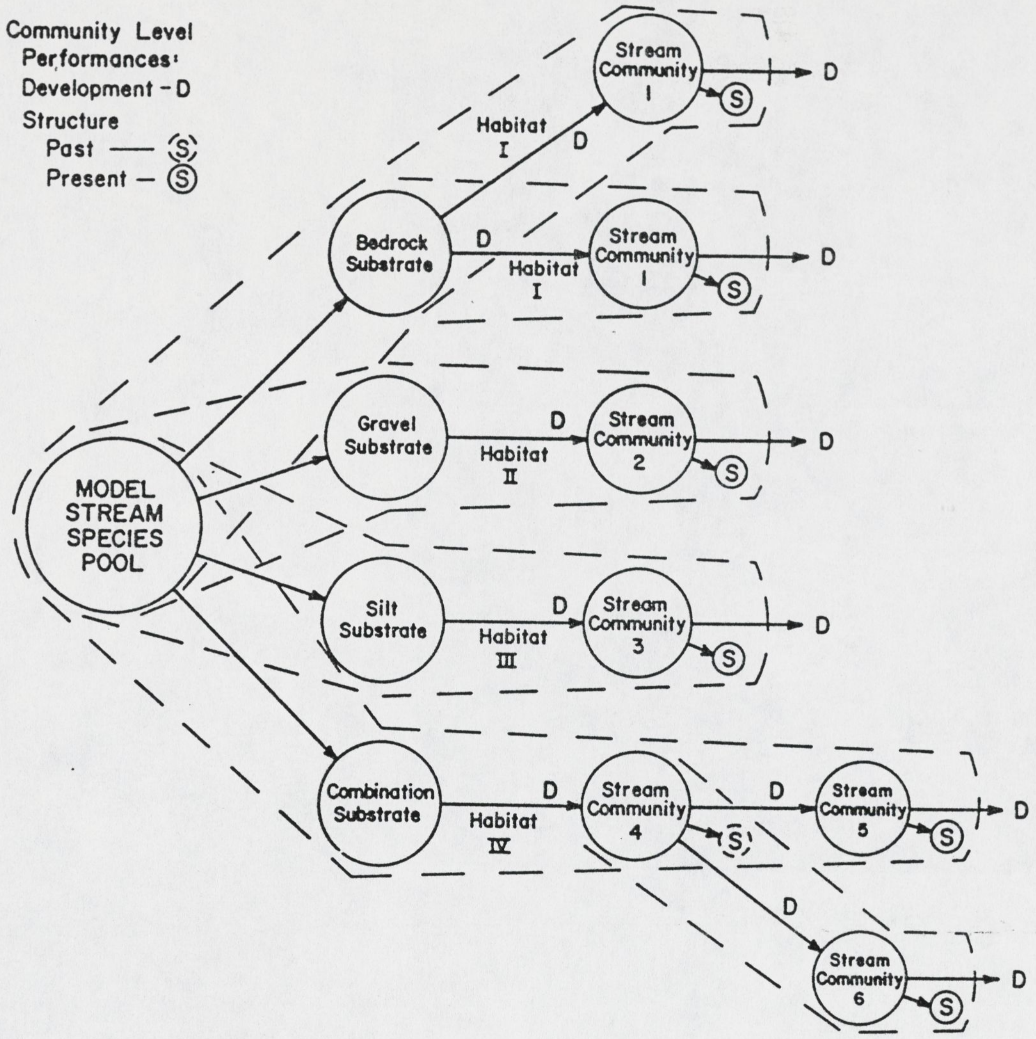


Figure 19. Polyclimax view of stream community development for the 12 model stream channels.

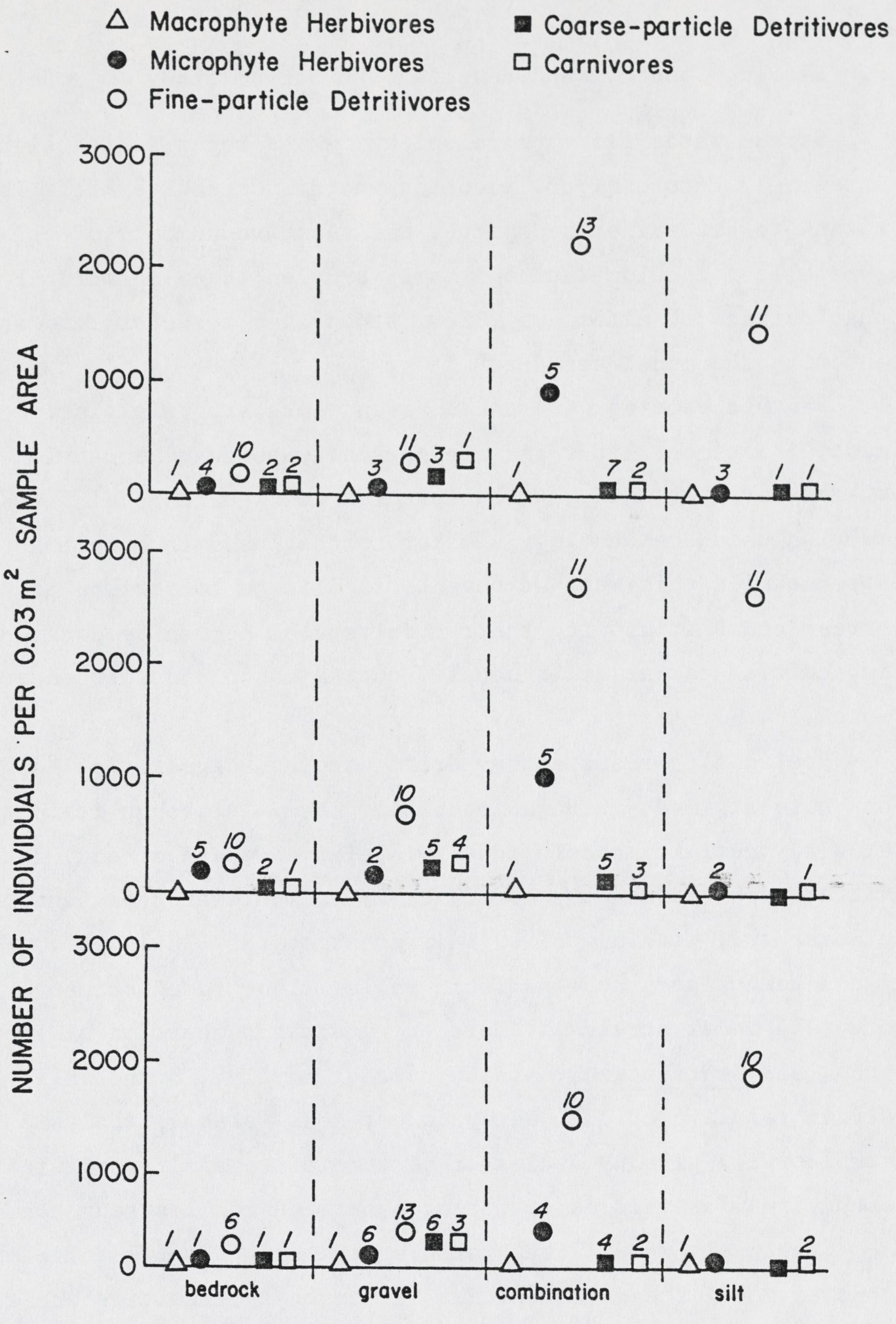


Figure 20. Community organizaton in model streams of different habitat type. Number of individuals in each trophic subsystem are shown for each model stream habitat type. Numbers above each data point show the number of taxa within the trophic subystem. Data are from the benthic samples taken in August 1982.

7. Design, Conduct, and Results of 8 Stream Study

Stream water flow and colonization was begun in the eight indoor model streams 17 October 1983. Incoming macroinvertebrate drift is sampled once a week to determine the species and relative numbers of organisms available for colonization. Early samples taken in October 1983 showed that ostracods, mites, mayflies, stoneflies, caddisflies, and midges were entering the model streams.

Benthic samples were taken seven weeks after initiation of the experiment, 5 December 1983, and are currently being taken at 13-week intervals, or once every season. Microhabitats within each model stream habitat are sampled using methodology similar to that used in sampling the natural streams. In this way, we hope to facilitate comparison of the natural stream communities with their model stream community counterparts. We are in addition taking drift samples once a month and emergence samples once a month.

Preliminary results from drift samples suggest that the model streams now have at least 28 taxa inhabiting them. Although it is too early to draw any definite conclusions, we beleive we can already detect subtle differences between the model stream communities representing different classes and, within a class, different states (Table 11). We are finding far more copepods and snails in valley floor model streams than in coastal mountain model streams. There are greater numbers of oligochaetes, copepods, and Centroptilum, a slow-current mayfly, in the valley field model stream relative to the valley forest model steam. Analysis of benthic samples will give us a clearer picture of community organization within each stream as well as differences between model stream communities.

Eventually we will be examining the effects of a toxicant on these complex model steam communities, after the communities are allowed to develop for approximately one year. We are tentatively planning to begin in the fall of 1984 toxicant introduction into one set of model streams (one old growth, one clear cut, one valley forest, and one valley field model stream). The remaining set of model streams will serve as controls.

Table 11. Taxa found in the eight indoor model stream enclosures.
Data taken from January, February and March 1984 drift samples.

key: o few individuals present
+ individuals common
* individuals abundant

	Class: Coastal Mountain	Class: Valley Bottom	
Taxa	(state: old growth)	(state: valley forest)	(state: valley field)
Hydra		+	
Planariidae		o	o
Nematoda	o		
Oligochaeta	+	+	*
Eucopepoda			
Harpacticoida		o	
Cyclopoida	o	+	*
Cladocera	+	+	*
Ostracoda	+		
Collembola	+	+	+
Ephemeroptera			
Ameletus		o	
Baetis	+	+	+
Centroptilum		+	*
Cinygma		o	
Paraleptophlebia		o	
Plecoptera			
Nemouridae	+	+	+
Taeniopterygidae			+
Diptera			
Chironomidae	+	+	+
Mollusca			
Physa		+	+
Gyraulus		+	

8. Possible Uses of Additional 8 Stream Study

The eight outdoor model steam enclosures located at the OSU Smith Farm facilities are currently under construction. As with the model stream enclosures at the Oak Creek Laboratory, we intend to use these enclosures to model streams of different classes and/or states. A small amount of Willamette River water will supply aquatic organisms for the model streams and so provide a species pool different from that found at the Oak Creek facilities. Most of the exchange water will be from a high-volume well. This water has lower total dissolved solids than our Oak Creek Laboratory supply. This would make these streams more suitable for acid rain studies, should such studies be undertaken. We can more easily regulate water pH and could use these model stream enclosures to study metal toxicity under varying pH conditions.

VIII. TOXICANT BEHAVIOR AND EFFECTS IN SIMPLE AQUATIC ECOSYSTEMS

Introduction and Significance

The effects of toxic substances on ecosystems are related to and in part determined by their behavior in these systems. Understanding toxic substance behavior entails understanding toxicant transport, transformation, and distribution within the ecosystem, including how concentrations within the components of the ecosystem change through time and the determinants of these changes. Our theoretical work supports the view that the behavior and effects of a toxicant are determined by the capacity of the toxicant and the organization of the biological community and its environment. Changes in the organization of the community and changes in its environment alter the behavior and the kinds and magnitudes of effects of a toxicant having a given capacity.

Analysis of toxicant behavior in systems that are as open, complex, and dynamic as our model streams is very difficult. We have established persistent laboratory ecosystems that are simpler in organization than the laboratory streams and are more amenable to the analytical chemistry necessary for evaluating toxicant behavior. The goal of the research conducted with these systems is to advance understanding of toxicant behavior and effects in ecosystems. More specifically, we intend to explain the dynamic and steady-state behavior and effects of a toxicant as influenced by community organization and community environment. The greatest significance of this work is that it will begin to demonstrate the utility of our theory and models for understanding toxicant behavior and effects. More particularly, we hope to be able to demonstrate that both community organization and community environment influence toxicant behavior and effects and that behavior, as well as effects, can be understood as a multisteady-state phenomenon. Further, with phase plane representations of the empirical information and model interpretations of these, we hope to show the dynamic and steady-state concordance of the toxicant behavior and effects.

B. Design, Conduct, and Results

Laboratory ecosystems including only guppy populations, only snail populations, or guppy and snail populations together were established (Lee 1984). Each system resides in a 40-liter glass aquarium that has been adapted for flow-through usage. Each aquarium receives 200 ml min^{-1} of well water at 21°C ± 0.5°C and is exposed to a 14/10 hour light-dark cycle. Fourteen of the systems receive a low rate of energy and material input in the form of an alfalfa ration (60% alfalfa and 40% Oregon Test Diet), and the other fourteen systems receive a high rate of energy and material input. These treatments are identified as LOW I and HIGH I, respectively. Both guppies and snails consume the alfalfa ration as their major source of food and thus are competitors.

Twelve of the systems, six at LOW I and six at HIGH I, have only guppy and algae populations. The populations in two systems in each subgroup of six are exploited at 0 percent, 25 percent, or 40 percent of the population biomass present at the time of sampling (0E, 25E, and 40E). Twelve systems are composed of guppy, snail, and algae populations with six systems at LOW I and six at HIGH I. Again, guppy populations in two systems in each subgroup are exploited at 0E, 25E, and 40E. The remaining four systems, two at LOW I and two at HIGH I, are maintained with only snail and algal populations.

Each system is sampled every 28 days. The length, weight, and numbers of all individuals in the guppy and snail populatons are recorded. At the time of sampling, guppy populations are exploited according to a systematic exploitation schedule that provides for the removal of a proportion of the population corresponding to the designated exploitation rates (Liss 1974).

In February 1984, after all systems had established near steady-states (NSS), continuous introduction of one ppb of the organochlorine insecticide dieldrin was begun. NSS structure for the systems under each set of environmental conditions (I and E) was assumed when the trajectories of biomasses of the interacting populations in the system fluctuated in a very restricted region of phase space relative to previous fluctuations (Figs. 21, 22). The insecticide dilution and delivery system is similar to the continuous flow dilution apparatus described by Chadwick et al. (1972).

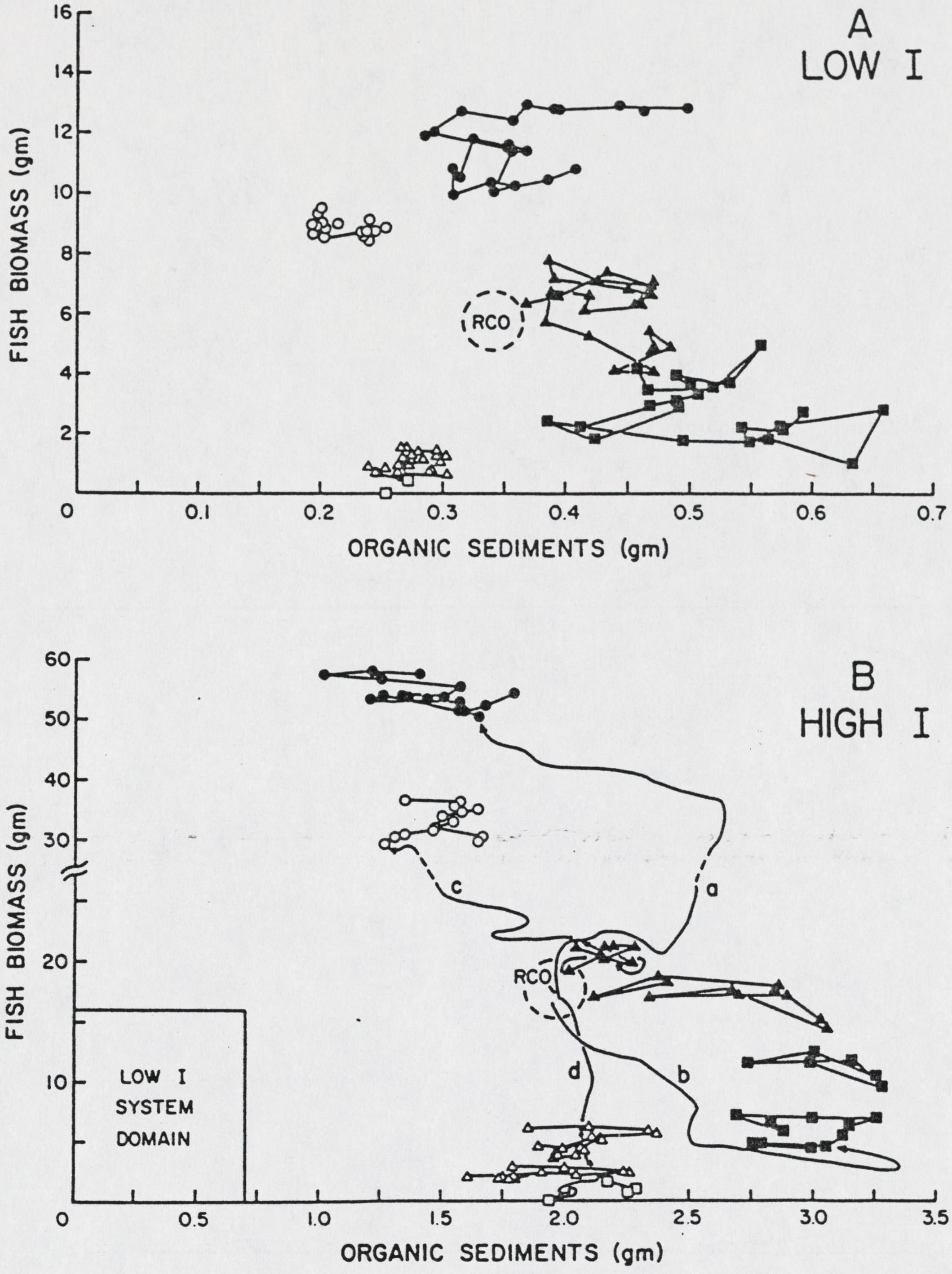


Figure 21. Phase planes representing NSS guppy and organic sediment biomasses at LOW I (A) and HIGH I (B) when the snail competitor is absent (G-A systems, solid symbols) and when snails are present (G-S-A systems, open symbols). NSS behavior of systems at 0E (circles), 25E (triangles), and 40E (squares) is shown. Actual trajectories of G-A systems at HIGH I, 0E (A) and HIGH I, 40E (B), and G-S-A systems at HIGH I, 0E (C) and HIGH I, 40E (D) are shown. RCO is the region of common origin of all trajectories, that is, the biomasses at which populations were first introduced into the systems. After Lee (1984).

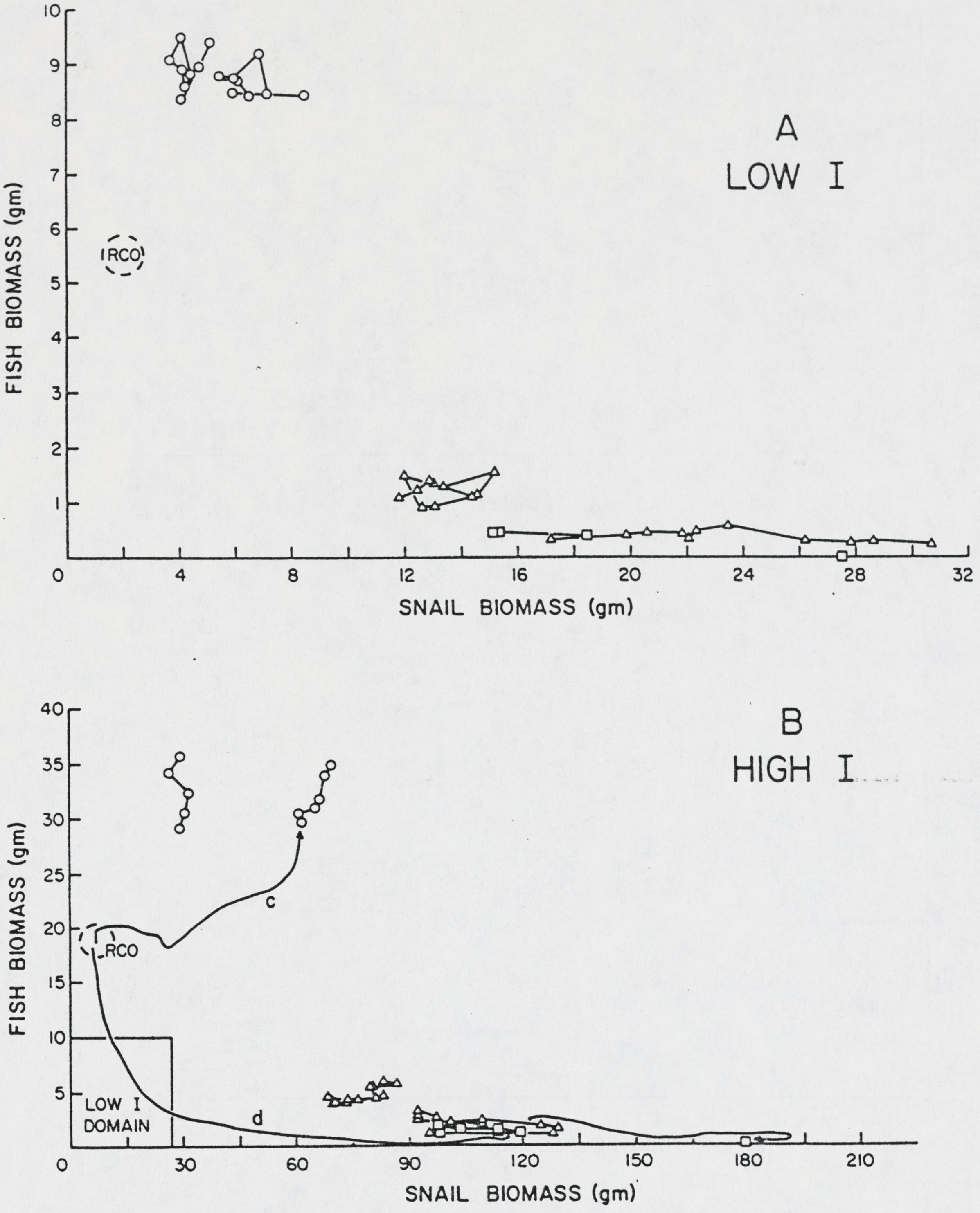


Figure 22. Phase plane representing NSS guppy and snail biomasses at LOW I (A), and HIGH I (B). NSS behavior for systems at OE (cirlces), 25E (triangles), and 40E (squares) is shown. Actual trajectories of G-S-A systems at HIGH I, OE (C) and HIGH I, 40E (D) are shown. RCO is the region of common origin of all trajectories that is, the biomasses at which populations were first introduced into the systems. After Lee (1984).

Guppies removed from each system through exploitation are frozen for gas chromatographic analysis of dieldrin residues in tissues. At each sample period, samples of snails as well as organic sediments, which consist primarily of uneaten alfalfa, are also analyzed for dieldrin residue. The objective is to define, under each set of environmental conditions, NSS dieldrin concentrations in each component of the system and the trajectory of concentration as it approaches NSS (Figure 9B and C).

NSS structures of the systems prior to dieldrin introduction are shown in Figures 21 and 22. The alfalfa ration, food resource of both guppies and snails, is introduced daily and becomes part of the organic sediment. Thus organic sediment biomass may be an index of food biomass and this should be related to the biomasses of guppies and snails. At both LOW I and HIGH I, when the snail competitor is not present in the system, guppy biomass is inversely related to sediment biomass (Fig. 21), with increased E resulting in a reduction in guppy biomass and an increase in sediment biomass. The relationship between guppy and sediment biomass was shifted to the right on the phase plane when I was increased from LOW I to HIGH I (Fig. 21B). At each E, both guppies and sediments maintained higher biomasses at HIGH I than at LOW I.

At both HIGH I and LOW I, the presence of a snail competitor shifted the relationship between guppies and organic sediments to the left on the phase planes. At each level of I and E, both guppies and sediments maintained lower biomasses when snails were present than when they were absent. Presumably the presence of the snail competitor made less food available for guppies, which was reflected in reduction in sediment biomass. Consequently guppies were not able to maintain the NSS densities they maintained when snails were not present.

At each I, in systems where snails were present, the phase plane relationship between guppy and snail biomasses was an inverse one, with a decrease in guppy biomass brought about by increased E being accompanied by an increase in the biomass of the snail competitor (Fig. 22). Increased I shifted the inverse relationship between these populations to the right on the phase plane, increasing the biomasses of both guppies and snails at each E.

Determination of toxicant effects will consist, in part, of how NSS structure is altered for systems having different organizations under each set of environmental conditions (Fig. 9A). Dynamic and steady-state toxicant concentration in the components of the system will be displayed and interpreted with a parallel set of phase planes (Fig. 9B, C).

IX. TOXICANT TRANSPORT, EFFECTS, AND FATES IN INDIVIDUAL ORGANISMS

A. Introduction and Significance

Understanding the effects of toxicants on individual organisms may help interpret toxicant behavior in populations, simple ecosystems, and in the field. We have chosen accumulation of dieldrin by rainbow trout for this purpose. Accumulation of dieldrin has been of interest because of its persistence in both abiotic and biotic components of the environment. Bioconcentration factors (ppm in organism/ppm in water) (BCF) for fish and other aquatic organisms have been calculated for comparisons between species and chemicals. The term bioaccumulation is used to describe accumulation from both food and water by individual organisms. There is no corresponding accumulation factor for exposure via diet, but percent accumulation (accumulation efficiency) may be calculated if the total amount of chemical administered is known.

The experiments detailed below illustrate the difficulty in incorporating laboratory data into mechanistic accumulation models for toxicants in ecosystems. More or better numbers for accumulation efficiences or BCF's are not solutions to the problems inherent in modeling toxicant behavior such as accumulation. Fluctuating environmental conditions and ecological responses to toxicant introduction will produce more variations in conditions of exposure than could possibly be reproduced under laboratory conditions, and there is no assurance that empirical results in themselves will lead to better understanding or prediction of toxicant behavior. Understanding the contribution of such factors as nutritional state, exposure concentration and duration, and as many other factors as feasible will lead to increased appreciation of the parameters that must be considered in assessing the effects of toxicants entering an aquatic system.

B. Design, Conduct, and Results of Studies

Studies were conducted with juvenile rainbow trout in flowing well water at 10-13°C. Acute tests determined LC50 and LD50 values for fish exposed to dieldrin in water and diet. Subchronic testing was then done at two concentrations of dieldrin in water, two dietary concentrations, two ration levels, and controls, for a total of 18 test conditions. Fifteen fish were exposed to each combination of conditions. Fish were removed for dieldrin analysis after 2, 4, and 8 weeks of exposure, and at 16 weeks all remaining fish were removed for analysis of lipid content and dieldrin concentration.

Acute tests resulted in a 96 hr LC50 of 0.62 μg dieldrin/l, a 12 day LC50 of 0.26 μg dieldrin/l, and an 18 day LD50 of 2.7 μg dieldrin/g fish/day. Whole body residues were also measured for fish exposed to acute doses. Accumulation was proportional to both exposure duration and dieldrin concentration. The mean body burden of fish exposed to the highest water concentration (3.1 μg/l) was 2.8 μg dieldrin/g fish. Mean body burden in the highest dietary exposure (39 μg dieldrin/g fish/day) was 5.2 μg dieldrin/g fish.

Subchronic testing provided information on the time course of dieldrin accumulation in fish maintained at different ration levels (Fig. 23). At early time points (2 and 4 weeks) fish held on a maintenance ration accumulated nearly the same or more dieldrin than growing animals exposed to equivalent amounts of the toxicant in 3 exposure regimens. By the 8th and 16th weeks of exposures this trend was reversed. Growing fish accumulated much more dieldrin than those on the maintenance ration, where weight loss was apparent in most individuals. Measurement of whole body lipid at the end of the test indicated 3.5 - fold more lipid in control fish held on the growth ration than maintenance ration fish. Since dieldrin is a highly lipophilic compound, differences in body composition partially explained our results. The large decline in whole body dieldrin concentration in maintenance ration fish probably reflected loss in body fat with time. Chlorinated hydrocarbons are well known to be mobilized under starvation conditions. Correction for lipid content minimized accumulation differences between exposure routes and ration levels. At 16 weeks, for example, values for exposure to water or diet at both ration levels range from 18 to 22 ng dieldrin/mg lipid. A difference was observed beween maintenance and growth ration fish receiving a combination

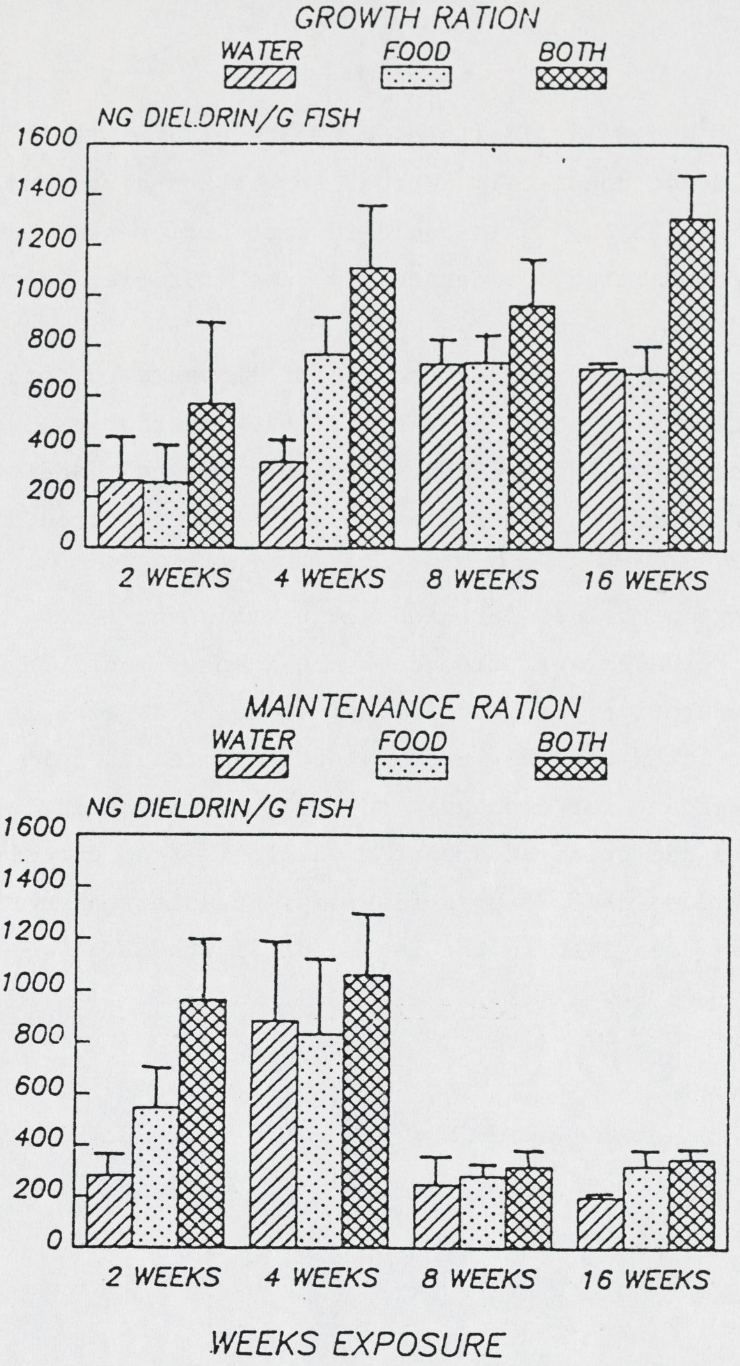


Figure 23. Whole fish residues during 16 weeks exposure to dieldrin via water and/or diet at two rations. Juvenile rainbow trout were exposed to dieldrin in water, ration, or water and ration and sampled at the indicated times for residue analysis. The growth ratio was 4 percent and the maintenance ration 2 percent of body weight/day. An equivalent dose of dieldrin (0.087 μg/g fish day) was given in either case. Maintenance ration fish accumulated 3.3 percent of dieldrin given in food and growing fish accumulated 7.2 percent. Data for orally exposed fish were not substantially altered by correction for lipid content. The dieldrin concentration in exposure water was 0.08 μg/L. BCF's calculated for the maintenance and growth ration fish exposed only to dieldrin in water resulted in 16 week BCFs of 2,500 and 8,800.

of exposures, 30 and 44 ng/mg lipid, respectively. In this case total body lipid could not completely account for ration-dependent differences in dieldrin accumulation. This could reflect differences in lipid distribution, composition, or metabolism rate (turnover) between nutritional states.

The contribution of different routes of exposure to total accumulation was also differently affected by ration. Growing fish exposed both in ration and water accumulated dieldrin in an apparently additive manner. In contrast, accumulation by fish fed a maintenance ration did not appear additive.

A broad range of values for bioconcentration and accumulation efficiency can be calculated from data obtained by modifying exposure concentration, duration, and nutritional state. For example, accumulation efficiency calculated for the 18 day acute test resulted in values of 10 percent to 34 percent for exposures to 5.1 to 39 μg dieldrin/g fish. The fish accumulated the greatest amount of dieldrin from exposure to 12 μg/g/fish at a daily dose of 0.75 ug/g fish/day. Examples taken from the subchronic study are given in the legend of Figure 23.

X. PRELIMINARY EVALUATION OF APPROACHES AND RESULTS

Although we are less than two years into the first three years of this research, we find it certainly desirable and perhaps necessary to render our own preliminary overall evaluation of the approaches we have taken and the results we have achieved or surely will have achieved in another year. First, there is even now a general need for such evaluation. And second, it can help us to determine needed emphasis in continuing our work. Although much work remains to be done, we do have distinct impressions of the relative importance of the different aspects of our work, as might be expected.

We find the articulation of general theory to be essential in providing the perspective, insights, direction, and order necessary for us to do original work of general importance to watershed and stream science and management. We take theory to be a set of statements providing a relatively abstract and universal perspective on some domain of total experience. As such, it provides a partial way of symbolizing and articulating that experience. In so doing, theory gives form to experience and suggests the possibilities of further experience. Mathematical models require ancillary assumptions and provide a narrower view within the perspective of a theory. The apparent gain in particularity is generally associated with a loss of universality.

Certainly theory, and models, mean different things to different people, and we do not intend to press our understanding on others. But theory as a perspective or point of view is essential to classification, modeling, empirical studies, and their interpretation and application. Thus, for our purposes, we must be clear about what we are to mean by theory.

Now not so much attention is given to theory, in the above sense, as is given to modeling and empirical studies in resource science and management. We believe this to be most unfortunate, for any classification, model, hypothesis, or empirical study implies some higher level theory or perspective on experience. When this is not made explicit, fundamental assumptions and restrictions on domain are not recognized and the results of research are erroneously employed. Beyond this, the heuristic power and ordering of experience and relations provided by theory are not effectively exploited. And empirical studies then appear as isolated events unrelated and unrelatable to our other experience and our needs. Not everyone need develop theory. But theory certainly should be more generally employed.

There has not been, up until now, a unified watershed and stream system theory. Watershed studies and stream studies have gone their separate ways, failing to unify geological, climatic, hydrological, biotic, and cultural aspects of these systems. This has prevented classification and study of watershed and stream systems in ways adequate for resource science and management. Over the years we have devoted much time and effort to the development of a (supratheoretical) conceptual framework. This can be thought of as an organismic general systems theory. As such it has provided us with the "blueprint" for a unified theory of watershed and stream systems and for an ecological theory of toxic substances.

We have now largely completed work on the unified watershed and stream system theory. And we believe that, with minor future development, this theory will meet needs for watershed and stream science and management. We are now working on an ecological theory of toxic substances. Because we understand the behavior and effects of toxic substances to be jointly determined by the capacities of biological communities as well as the capacities of the substances, development of an adequate ecological theory of toxic substances had to await development of an adequate unified theory of watershed and stream systems. With the latter now in hand, we intend to have the theory of toxic substances completed within a year.

For some time we have had multisteady-state isocline models of simple communities. These models allow us to understand the dynamic as well as the steady-state behavior of populations in simple communities in terms of environmental conditions such as energy levels, nutrient levels, and exploitation. We have also developed and demonstrated isocline models of the effects of toxic substances in simple communities. And as a part of our EPRI research program, we are now completing parallel models of the behavior of toxic substances in simple biological communities. We believe that the relationships between models, model results, and experience are very indirect and most problematical. Nevertheless our models continue to provide us with schemes for experiments and the interpretation of experimental results from simple microcosm and laboratory stream research. And these models do warn us that there is very little interest and probably no reliable applicaton of transfer and other coefficients estimated under any single set of conditions.

Watershed and stream science is not interested in particular events but in relations among classes of events. And although watershed and stream management does have a concern for particular events, management rules must be written and administered for classes of events. All this is so whether or not formal classification systems have been developed or adopted.

But a very general concern now exists for the protection of streams and lakes over large regions, not simply from the highly publicized acid precipitation phenomena but also from poor forestry, agricultural, and other land use practice. And the protection of streams and lakes involves the protection or better management of their watersheds and even airsheds. Moreover, in one region after another, we are now considering thousands and even hundreds of thousands of miles of streams and hundreds of lakes.

We can, with direct empirical studies, investigate and make recommendations, on a case by case basis, for but an infinitisimal part of these lakes, streams, and land areas. And yet, if there is to be any management adequate at all, scientific knowledge must be developed and applied. The possibilities of adequate systems classification of watersheds, streams, and lakes are not generally appreciated. A classification based on organismic general systems theory and upon well-articulated watershed and stream system theory can not only order experience and make its generalization possible, it can also make prediction more reliable than can existing models. Unfortunately, we do not find most efforts at watershed and stream classification even nearly adequate to fulfill these functions.

We are convinced the systems classification of watershed and streams we have developed will prove to be much more adequate to needs in watershed science and management than models and other classification systems that have been developed. It is generally believed that numerical models should provide explanation, prediction, hypothesis generation, and logical unification. There is, we think, neither theoretical reason nor empirical evidence for believing such models to be adequate for fulfilling these functions in watershed and stream science and management. But we do believe that a classification system based on the capacities of watershed and stream systems and their environments, when coupled with sufficient empirical qualitative as well as quantitative experience, can provide significant explanation, predication, hypthesis generation, and logical unification.

We were well along in development of such a systems capacity classification of watersheds and streams when we began the here reported research for the Electric Power Research Institute. This has allowed us to progress rapidly in both field and laboratory stream studies. Moreover, it allowed us to move rapidly, as a part of the EPRI research program, to extend the classification system from watershed and stream systems of moderate scale down to small watersheds and streams and even to classification of stream segments, reaches, riffles and pools, and microhabitats. This then has allowed us to couple the classificaton system to the organization and development of stream biological communities. And we have begun empirical studies, both in the field and in laboratory streams, to make clear this coupling of stream class, organization, and development to the organization and development of stream communities. This provides, we believe, an adequate basis for stream science and management, including dealing with problems of toxic substances. In the 30 years our laboratory has worked in this area, this classification system may be the most fundamental contributon we have made. We believe a major part of our continuing EPRI research should be in demonstrating applications of this classificaton system.

An important part of this demonstration should include continuing studies with the laboratory streams we have developed as the major thrust of the initial phase of our EPRI program. These laboratory streams have been developed so that different sets of them model different classes and states of development of natural watershed and stream systems we have been studying. This is allowing us to make clear certain principles upon which our watershed and stream classification system and its application are based.

First it is important for us to demonstrate convincingly that the organization and development of a stream community depends upon the organization and development of its physical habitat and upon its species pool. For then we can classify watershed and stream systems primarily on the basis of their physical properties and have some assurance that their biological properties are indirectly accounted for. The presumed necessity for detailed biological studies at an indefinite number of sites has been and continues to be a stumbling block to the work necessary to protect stream communities. The difficulty of doing adequate biological studies makes this so. Certainly biological studies will continue to be necessary, both in the field and in the laboratory, but the theoretical perspective and classification system we believe should be further demonstrated make clear the most effective design and use of further biological studies.

Second we can, through laboratory stream studies, demonstrate how the effects of toxic substances in stream communities and populations must take into account the organization and development of stream communities as well as the organization and development of stream habitats and watersheds. The effects of toxic substances are in large part determined by watershed and stream system organization and developmental state. Moreover, any toxicant-initiated change in these will be superimposed upon already existent organizational development and dynamics. Our experience with laboratory stream research and the outstanding laboratory stream facilities EPRI financial resources have allowed us to develop together make it possible for us to demonstrate the effects of toxic substances on stream community organization and development.

And because our laboratory stream and other research has proceeded in the context of theory and classification, we are able to relate changes in laboratory stream systems to probable changes in natural stream systems affected by toxic substances. It is our belief that others will then be as convinced as we now are that watershed and stream classification of the sort we are suggesting provides a sound basis for progress in dealing with the large scale problem the electric power industry, other elements of society, and our society as a whole, must face.

Our laboratory has over the years accomplished a great deal of work on the transport, fates, and effects of toxic substances in microcosms smaller than our laboratory streams. And much work has been completed on the behavior and effects of toxic substances in individual organisms. Some of this work has most recently been conducted with financial support from the Electric Power Research Institute. This work has played an important role in the development of our thinking concerning toxic substances in the environment and scientific and management possibilities for dealing more adequately with associated problems.

Our inescapable impression is of the overwhelming complexity and difficulty of these problems. We do not believe that the endless conduct of bioassays, microcosm studies, local field studies, and numerical modeling will make much if any difference in the resolution of these problems, unless they become a part of more adequate theoretical perspectives and classification systems. Our laboratory will probably continue to do some such studies. But we do believe that for the electric power industry and for watershed science and management in general, the most important work we can do with financial support from the Electric Power Research Institute is to demonstrate through field and laboratory stream research the application of watershed and stream systems classification.

XI. NEEDED EMPHASIS IN CONTINUING RESEARCH

Research supported by the Electric Power Research Institute at our laboratory has been guided for the past two years by four objectives. These have entailed development and demonstration of a watershed and stream system classification, theory and multisteady-state models for such systems, laboratory stream ecosystems, and field and ancillary studies necessary to evaluate these. The emphasis during this period has clearly been on the development and demonstration of laboratory stream ecosystems, the other studies providing the context of understanding making the laboratory stream research more effective and meaningful.

But having substantially accomplished the objectives of this initial phase of research, we must now consider whether some shift of emphasis would increase the value of our work for the electric power industry and the scientific and resource management community in general. Such a shift in emphasis in any continuing research would require some reallocation of our resources among our four initial objectives.

It seems clear to us that there is a critical need nationally and locally for the power industry to deal with watershed, lake, and stream phenomena on a large scale and yet in ways convincing on the local and site levels. It is our belief that our watershed and stream system classification can do just this and that it would be of immense value if we could demonstrate this in a moderately large-scale field study. There are certain principles of habitat organization, species pools, community organization, and toxicant effects entailed in the theoretical perspective (Table 1) upon which our classification system is based. And it is our belief that our laboratory stream ecosystem studies should receive continued emphasis so as to demonstrate convincingly these principles.

We must continue to utilize our watershed and stream system theory and, to a lesser extent, our multisteady-state models, for these provide the perspective on which all our other work is based. And in so employing the theory and models, their continued evaluation and development is assured. But these have such a high level of maturity, that we do not foresee having to expend on their development much of our resources.

We believe that as a part of our EPRI program we have done sufficient work on transport, fates, and effects of toxic substances in simple laboratory microcosms and in individual organisms. There will continue to be the need for such studies. And as a part of other programs in our laboratory, we will probably be conducting some of these. But in future work on the EPRI program, we believe financial resources would better be reallocated to field demonstration of watershed and stream classification and laboratory stream ecosystem demonstration of the theoretical principles underlying this classification and its application to watershed and stream system management.

Over the past six or so years, under contracts from the Environmental Protection Agency and the U.S. Forest Service, our laboratory has developed a hierarchical systems classification for watersheds and streams (Warren 1979, Warren and Liss 1983). With support from EPRI, we have developed methods of similarly classifying segments, reaches, pools and riffles, and microhabitats of stream systems (Tables 2 and 3, Fig. 10). It seems to us that there is a pressing need for demonstration of our watershed and stream classification system over a moderately large area. Because of problems with low-head hydroelectric power development, forest management, and fisheries management, the Oregon Department of Fish and Wildlife has expressed interest in our undertaking such a demonstration over a very large area of Southwestern Oregon. And we know that the Environmental Protection Agency, the Bonneville Power Adminstration, the U.S. Forest Service, and the U.S. Geological Survey have similar interests. Interest and possible collaboration would enhance the value of any such demonstration.

Laboratory stream ecosystems may be employed in studies directed toward understanding basic stream ecology, fish production, thermal, oxygen, and other environmental changes, including the effects of particular toxiants, combinations of toxicants, and complex industrial wastes. Over 25 years our laboratory has conducted laboratory stream studies of all of these problems, and as the need arises we may do so in the future. But it seems to us now to be most important to conduct laboratory stream ecosystem studies mainly to demonstrate those principles upon which our watershed and stream system classification depends, especially as it relates to the protection of aquatic life.

In summary, then, we believe laboratory stream studies with toxic substances should be continued, for there is much to be gained from this kind of work in relation to demonstration of theoretical principles underlying systems classification and principles dealing with toxic substance effects on stream systems, some of which would be nearly impossible to demonstrate convincingly in the field. In future work, more emphasis should be placed on moderately large scale field demonstrations of our classificaton system. We believe this is of critical importance to the electric power industry; their problems are diverse but fundamentally they all involve watersheds and streams. Approaches to any of these problems demand adequate ways of understanding watersheds and stream systems on all levels and scales. We believe we are developing these adequate ways. Funding from EPRI has already made possible significant advancements in this area, as we hope this report has reflected.

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