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TEMPERATURE REQUIREMENTS OF SALMONIDS

IN RELATION TO THEIR FEEDING, BIOENERGETICS

GROWTH, AND BEHAVIOR

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ABSTRACT

Studies were conducted of the effects of a persistent elevation of temperature above ambient levels on the food consumption and growth of juvenile salmonids held in aquaria and on the survival rates, numbers, biomass, production rates and behavior of salmonids, as well as on biological community composition in model streams. These studies were conducted from 1968 into 1977. This report primarily covers the last phase of this research, 1975-1977, and generally confirms the results of the earlier studies, which are summarized. The salmonids investigated were coho salmon (Oncorhynchus kisutch), chinook salmon (0. tshawytscha), and steelhead trout (Salmo gairdneri). In aquarium studies on the food consumption and growth rates of the salmonids, temperature elevation of 34 C to 78 C above ambient levels of a small natural stream generally increased metabolic rate and maintenance ration levels and reduced growth rates. Only at the highest ration levels were the growth rates of fish held at higher temperatures nearly equal to those of the controls. Persistent temperature elevation of 3-4 C over ambient levels reduced survival, number, biomasses, and production rates of the salmonids in the model streams. Abundance of food organisms and total macroinvertebrate biomass was reduced by temperature elevation in the model streams, with the exception of an aquatic snail, the biomass of which was increased. Macroinvertebrate diversity in the model streams was also reduced by temperature elevation.

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INTRODUCTION

Temperature is one of the most important environmental variables to which plants and animals must adapt. Throughout the world, the temperature range of surface waters ordinarily inhabited by fish is from about 0 C to somewhat over 30 C. Even though many temperate waters fluctuate annually over about this range, the biota of a particular water may be very sensitively adapted throughout this range of temperature. A persistent increase of relatively few degrees over the year. even when annually and seasonally the temperature normally varies over a much greater range, can be expected to alter the metabolism and life history patterns of individuals of different species and so lead to changes in the success of their populations and in the composition of the biological community. This is because such species have come to be adapted through evolution to something like the normal patterns of temperature variation in their natural environments. When human activities persistently alter the temperature patterns of streams, direct and indirect effects on valuable populations can reduce the production and yield of these populations or even eliminate them. And there is no reason to suppose that such effects are restricted to the so-called "cold-water" species.

From July 1968 through June 1977, staff and graduate students of The Oak Creek Laboratory of Biology, Oregon State University, were continuously involved in a U.S. Office of Water Research and Technology project on the effects of persistent temperature increase on juvenile salmonids and stream communities. Studies were conducted on the

bioenergetics and growth of salmonids in aquarian and on the growth, production, and behavior of salmonids and on stream community composition in two rather large model stream channels, one of which was heated over natural ambient temperature levels. This research was supported during three different grant periods: July 1, 1968 through June 30, 1971 (Phase I); July 1, 1971 through June 30, 1974 (Phase II); and July 1, 1974 through June 30, 1977 (Phase III). This report is intended to cover only Phase III of this research. But because of the pertinence of the earlier phases of the research, and because the stream communities were maintained and studied continuously from 1968 into 1977, a few introductory comments concerning results of research during Phase I and Phase II may be worthwhile.

Studies were conducted of the food consumption and growth of juvenile salmonids in aquaria to obtain information on direct effects of temperature that would be of value in the interpretation of the model stream studies. Thus these laboratory studies were conducted at temperatures fluctuating daily according to temperatures in the model streams, and treatment groups of fish were subjected to temperature elevations of from 3 C to 7 C superimposed on the daily patterns of temperature change. Most such experiments were of 10 to 30 days duration, and these were conducted at seasonally appropriate temperatures. One set of experiments was 4 months in duration, and one was 8 months; temperatures during these experiments followed seasonal patterns. At each pattern of temperature exposure, different groups of fish were fed different measured ration levels and their respective growth rates were determined, so as to establish the curvilinear relations between food consumption rate and growth rate, from near maintenance rations to repletion rations.

During Phases I and II of this research, studies were conducted of the food consumption and growth of juvenile coho salmon (Oncorhynchus kisutch), juvenile chinook salmon (0. tshawytscha), and juvenile steelhead trout (Salmo gairdneri) in aquaria (Everson, 1973; Bisson, 1975; Wurtsbaugh, 1973; Wurtsbaugh and Davis, 1976). For all three species, persistent elevations of temperature of 3 C or more above the daily ambient temperatures reduced growth rates at all consumption rates except the very highest ones, the percentage reduction, below control levels, increasing as food consumption rates decreased. This was generally the result of the increased amount of food necessary to just maintain the fish--at zero growth--at the higher temperatures. the metabolic rates of the fish increasing with increasing temperature. At repletion ration levels, little difference in the growth rates of fish at the higher and lower temperatures occurred, not only because the fish tended to eat more at the higher temperatures but also because efficiency of food utilization for growth became nearly equal even at the same high ration levels. But estimates of food consumption rates and growth rates of coho salmon and steelhead trout in nearby natural streams provided strong evidence that food consumption and growth of these species in nature were much nearer the lowest rates than the highest rates of the laboratory fish. And in the 4-month and 8-month experiments with coho salmon in aquaria at daily and seasonally ambient and higher temperatures, fish fed amounts of food near the amounts they could be expected to obtain in nature were 25 and 47 percent smaller at the end of the experiments than control fish when temperatures were maintained 3-4 C and 7-8 C, respectively, above ambient temperatures. In general,

then, increases in stream temperature can usually be expected to reduce growth rates of salmonids at given ration levels when food is limited.

Also during Phases I and II of this research, the effects of temperature elevation -- about 4 C over ambient natural stream temperatures -on the growth, production, and behavior of juvenile coho salmon and juvenile chinook salmon and on food organism abundance and community composition in the model streams were studied (Iverson, 1972; Bisson, 1975; Bisson and Davis, 1976). Coho salmon of the 1970 year class were reared from small fry to smolts--ready to migrate downstream--over a one year period. For this year class, production of the juvenile salmon in the artificially heated stream was only about one-half that occurring in the control stream. Total production of coho salmon of the 1971 year class, which were reared in the streams from the egg stage, was only about onefifth as great in the heated stream as that occurring in the control Biomasses and production rates of aquatic insects were greater stream. in the control stream than in the heated stream. This was especially so for mayfly and stonefly nymphs, which were the most abundant insects in both streams and which appeared to be the major source of food for the juvenile coho salmon. The reduced growth and production rates of the coho salmon in the heated stream probably resulted from direct effects of increased temperature on metabolism and growth of the fish as well as indirect effects resulting from reductions in their food supply.

Persistent temperature increase of about 4 C over ambient natural stream temperatures had much the same effects on juvenile chinook salmon and stream community composition as had been shown when coho salmon

were present in the streams. In 1972, chinook salmon production was about two-fold greater in the control stream than in the heated stream, and in 1973 it was about 30 percent greater. Again, this was apparently in large part owing to direct effects of temperature increase on the metabolism and growth of the chinook salmon and indirect effects of reduced food organism availability on their growth and production.

During Phase III of this research, which extended from July 1, 1974 through June 30, 1975, the growth, production, and behavior of, first, steelhead trout and, then, steelhead trout and coho salmon together were studied. And studies of the effects of temperature elevation on stream community composition were continued. It is to this research that this report is mainly directed. In following sections, we will first describe briefly the model stream channels and conditions within them. Then we will cover the results and interpretation of research conducted during this phase of the investigation, which was primarily the work of Robert Hughes and will be included in his doctoral thesis. Finally, we will attempt to draw some general conclusions from the entire investigation extending from 1968 into 1977.

MODEL STREAM CONDITIONS

A diagrammatic representation of the two model streams used in this investigation is presented in Figure 1. Each stream consisted of two, parallel wooden channels having a slope of about 1.9 percent. One wall of each stream was formed by plexiglas so as to permit observation of fish behavior and stream conditions. Each of the two channels forming one model stream was 10 m long, 1.3 m wide, and 0.8 m deep. Water from the downstream end of one channel was transferred through large irrigation pipe by pump to the upstream end of the other channel, from where it returned through irrigation pipe to the first channel. This recirculation, maintained by a pump for each stream, provided water velocities of approximately 60 cm/second over the riffles, velocities near the pool bottoms approaching zero. An exchange flow of 30 1/min of unfiltered water from a small natural stream was provided each stream.

Each channel of each stream was formed into a shallow riffle and a rather deep pool by cement blocks covered with natural stream bottom materials, this giving each model stream four riffles and four pools having a total bottom surface area of about 22 m². Bottom material composition in the riffles was largely cobbles and gravel with fine sediments in the deeper gravel. Pool substrate was mostly gravel with a considerable accumulation of fine sediments and detritus. Water depths ranged from 1 mm to 20 cm in the riffles and from 70 to 75 cm in the pools.

The streams were shaded by alder trees (<u>Alnus rubra</u>) but were otherwise open to solar radiation, precipitation, the fall of leaf and





Diagram of model streams employed in this study (After Bisson, 1975) Figure 1.

other litter from trees, and the entry of insects and other organisms. Organic debris from terrestrial sources was an important energy resource for the stream organisms, those that depended directly on the litter and those feeding on these. Entry of such litter into the heated stream was about twice as great as entry into the control stream, but less litter persisted in the control stream, apparently owing to higher decomposition rates and greater biomasses of snails in the heated stream. Relatively large biomasses of an aquatic moss (Hygrohypnum bestii) were present in both streams, but these biomasses were greater in the control than in the heated stream. Algae and other microflora also contributed to the energy resource for stream invertebrates. Measurements of gross primary (plant) production and community respiration indicated that more energy was being fixed through photosynthesis in the streams than was utilized by all the stream organisms including plants. Thus gross photosynthesis-community respiration ratios were usually greater than one, and the streams would be classified as being autotrophic rather than heterotrophic. But this in no way should be taken to mean that decomposition of terrestrial litter entering the streams was not a major energy resource for the stream organisms, because it usually is in small shaded streams such as the ones here modeled.

Water temperatures in the control model stream followed the daily, seasonal, and annual patterns of fluctuation of the small stream that was the water source. The other stream received a constant heat energy input from two 6 KW Chromalux immersion heaters. The control stream ranged in mean weekly temperature from about 3 C in

winter to 16 C in summer, the heated stream from about 7 C to 19 C. Thus, as shown in Figure 2, mean temperatures in the heated stream were generally 3 C to 4 C higher than in the control stream.





RESULTS AND INTERPRETATION

Salmonid Numbers, Biomass, and Growth

The eggs and sperm of steelhead trout (Salmo gairdneri) were obtained from the Alsea Hatchery during February, 1975 and 1976. Coho salmon (Oncorhynchus kisutch) eggs and sperm were obtained from the Fall Creek Hatchery in November 1975. Both hatcheries are on the Alsea River in Western Oregon. Gametes were obtained from three fish of each sex. The gametes were immediately brought to the Oak Creek Laboratory, where the eggs were fertilized. In 1975, 500 steelhead embryos were placed in each stream, whereas in late 1975 and early 1976, 500 embryos of each species were placed in each stream. In 1975, steelhead were incubated in gravel-filled boxes placed in the riffles in order to model natural redds. Because of the low number of emergents in 1975, presumably as a result of high sediment levels, the coho and steelhead embryos were incubated in floating gravelfilled boxes in 1976. High mortality of the steelhead emergents necessitated additional stocking with fry from the Alsea hatchery to insure adequate numbers for study. The fish were censused every three weeks by seining each riffle-pool section until no fish were captured in three consecutive attempts.

Survival of steelhead to the time of their emergence as fry was very low in both streams during 1975, probably mainly owing to sedimentation of the streambed gravels. Thus, as shown in Figure 3, numbers of steelhead fry were increased to 120 fish in each stream



by supplemental stocking. Numbers declined rapidly in late spring and early summer and then declined more slowly into winter. Such patterns of decline are typical when salmonid reproductive effort is higher than the carrying capacity of streams. From late summer into winter of 1975, numbers of steelhead were slightly lower in the heated than in the control stream. Emergence as fry was much higher for steelhead in 1976 than it had been in 1975, but because of mortality after emergence, additional steelhead fry were stocked. Emergence of coho salmon was higher than that of the steelhead in 1976 (Fig. 3). After initial heavy mortality, numbers of coho salmon in the control stream remained remarkably constant. But in the heated stream, coho numbers and the numbers of steelhead continued to decline into winter. Survival of steelhead in both the control and heated stream was much lower than that of the coho salmon. And survival of steelhead was much lower during 1976, when coho salmon were present, than during 1975, when coho salmon were not present. Thus, it would appear that survival of both species was depressed by direct or indirect effects of the temperature increase and that survival of steelhead was depressed by the presence of the juvenile coho salmon.

The biomass of salmonids, or any other group of organisms, in a stream at any time represents the sum of some initial biomass and all increments and losses occurring up to that time. It is the amount of material of a given kind existing at a given time and can be expressed as grams of material per unit area. Increases in salmonid biomass in the model stream occurred when additional fish were stocked and as a result of individual growth and consequent population production,

or total tissue elaboration. Losses in biomass occurred as a result of mortality of fish (Fig. 3), weight loss by individuals during periods of starvation, and emigration of some individuals from the streams. Thus biomass and changes in biomass are a result of stream conditions and the responses of the fish to these conditions. During both 1975 and 1976, salmonid biomasses in the heated stream tended to reach maxima several months earlier than in the control stream and then to decline (Fig. 4). Salmonid biomasses in the control stream reached higher levels than they did in the heated stream and remained at higher levels in the control stream even during periods of biomass decline, generally from summer into winter. In the presence of coho salmon during 1976, biomasses of steelhead trout were much lower in both the heated stream and the control stream than they had been during 1975, when no coho salmon were present. Thus, not only increased stream temperatures but apparent competition from coho salmon had very marked effects on the biomasses of steelhead trout in the streams.

The relative growth rate of an organism is a function of the state of the organism and conditions in its environment. The survival of individual organisms and the production or total tissue elaboration by their population are very much dependent on relative growth rate. Mean relative growth rate can be expressed as

$$GR = \frac{W_2 - W_1}{0.5(W_1 + W_2) (t_2 - t_1)}$$

where W_1 and W_2 are mean individual weights, of individuals in a population, at times t_1 and t_2 . Relative growth rates tend to decline with increases in body size. Beyond this, they reflect the



balance between energy and material intake and losses or uses of energy and materials for purposes other than growth. At very low temperatures, food intake may be near zero and fish may lose weight. At high temperatures, growth may be much less than at intermediate temperatures because of higher maintenance metabolic costs and sometimes because of reduced food intake. Food availability is not only a function of the production levels of food organisms but also the biomasses of the fish preying on these organisms. Although growth is clearly a function of this sort of complex of factors, clear separation of the partial effects of these in even a model stream community is not possible. Even so, the mean weight and relative growth rate data presented in Table 1 for steelhead trout and coho salmon in the model stream during 1975 and 1976 can be generally interpreted in terms of stream conditions. Relative growth rates of both species of salmonids tended to be highest in late spring and early summer. This is the period in which, so long as stream conditions are suitable, relative growth rates should be high because of the small size of the fish. And during this period stream temperatures, in both the heated and control streams, were good for growth and food organisms were abundant. But with higher summer temperatures, increased biomasses of fish, and declines in food organism abundance, growth rates tended to decline. With low winter temperature, growth rates were sometimes negative, indicating starvation and weight loss, a not unusual condition in temperate waters. During this period, growth of individual fish in the heated stream was sometimes substantially higher than in the control stream. Relative growth rates of steelhead in the heated stream were generally not very different from those in the control stream during

Mean weights and mean relative growth rates of steelhead trout and coho salmon in model streams during 1975 and 1976.

Table 1

			1975 St	eelhead			1976 Ste	elhead			1976 (Coho	
		Heat	ted Mean	Contr Growth	col Mean	Growth	ed Mean	Cont	rol Mean	Heat	ed	Contr	01 Moon
Date	Code	(mg/g/day)	wt (g)	(mg/g/day)	wt (g)	(mg/g/day)	wt (g)	(mg/g/day)	wt (g)	(mg/g/day)	wt (g)	(mg/g/day)	wt (g)
1/20	1										0.43		
1/20- 2/10	2							,		10.1	0.48		
2/10- 2/25	3									1.8	0.54		0.44
2/25- 3/22	4									7.4	0.60	10.0	0.52
3/22- 4/15	S						0.18		0.18	7.3	0.69	8.1	0.65
4/15-5/8	9		0.62		0.49	18.3	0.19	17.5	0.19	8.2	0.81	13.6	0.82
5/ 8- 5/25	7		0.74		0.55	33.7	0.30	15.3	0.24	7.2	0.95	25.8	1.29
5/25- 6/15	00	-3.5	0.84	10.6	0.69	42.0	0.67	12.9	0.31	21.2	1.32	9.0	1.80
6/15-7/4	6	24.5	1.06	24.5	0.98	28.1	1.35	42.0	0.63	18.6	2.01	11.4	2.24
7/ 4- 7/25	10	11.4	1.48	20.2	1.52	16.7	2.13	22.8	1.20	3.4	2.49	8.9	2.75
7/25- 8/13	11	8.2	1.78	6.0	1.95	0.5	2.52	9.9	1.64	2.1	2.63	4.2	3.12
8/13- 9/ 4	12	-1.9	1.86	5.9	2.18	0.8	2.55	9.8	2.01	0.4	2.69	3.8	3.38
9/ 4- 9/28	13	4.7	1.94	4.7	2.46	0.0	2.56	7.0	2.42	0.0	2.69	2.8	3.63
9/28-10/15	14	4.6	2.13	2.6	2.64	6.0	2.72	0.3	2.60	2.0	2.74	2.5	3.84
0/15-11/ 6	15	3.5	2.28	3.4	2.78	4.7	3.04	-1.4	2.55	-2.9	2.70	-0.9	3.90
1/ 6-11/27	16	6.5	2.52	0.2	2.87	-0.4	3.19	4.0	2.62	2.5	2.68	-0.5	3.82
1/27-12/18	17	0.2	2.66	0.1	2.84	0.6	3.19	-6.5	2.56	-0.5	2.76	-3,3	3.68
2/18- 1/ 9	18	3.5	2.78	4.4	2.97	10.0	3.56	0.4	2.40	1.6	2.79	-0.6	3.53
1/ 9- 1/26	19	17.5	3.04	4.7	3.20	-3.5	3.80	3.6	2.50	5.2	2.98	0.3	3.51

1975, when coho salmon were not present. But during 1976, when coho salmon as well as steelhead were present in the streams, growth rates of both species were lower in the heated stream than in the control stream during the critical summer months. Higher total salmonid biomasses and resultant competition for food, especially for the more limited food in the heated stream, were probably important determinants of low salmonid growth rates in the heated stream during 1976.

Salmonid Production

Production of a population of organisms, such as the steelhead trout or the coho salmon present in the model streams, represents the total elaboration of tissue by that population during some given period of time, whatever may be the fate of that tissue, except that negative production resulting from losses in mean individual weights must be algebraically summed in the total. For a given period of time that is not too long, production can be determined and best understood as the product of mean relative growth rate and mean biomass:

$P = GR \times B$

Production over some longer period of time, such as a year, is determined by summation of the production values for short intervals of time, say about three weeks. In Figure 5, curves representing cumulative production of steelhead trout and coho salmon in the heated and control streams are shown for 1975 and 1976. Positive increments along these curves represent periods when relative growth rates were positive, zero increments periods when growth was zero, and negative



increments periods when growth was negative (Table 1). The magnitude of any increment is dependent not only on growth rate but also on biomass. Total production for each experimental population, over the entire period that population was in a stream, is represented by the ordinal value of the last point on the curve.

During 1975 when coho salmon were not present in the streams, the production of steelhead trout was generally positive throughout the year and a substantial part of the production occurred during the summer and fall months and into the winter. But production was lower in the heated stream than in the control stream, throughout the year. During 1976, when both steelhead trout and coho salmon were present in the streams, production of both species occurred throughout the summer in the control stream, after which little or no production of steelhead trout and negative production of coho salmon occurred. And steelhead production was only about one-third that of the coho salmon (Fig. 5). But in the heated stream, little production occurred after July, this reflecting the critical effects of increased temperature during the summer when intraspecific and interspecific competition for food and space were severe. Increased temperature substantially reduced the production of coho salmon and reduced somewhat the production of steelhead trout during 1976. Presence of the coho salmon apparently was responsible during 1976 for the production of steelhead trout being much lower than it was during 1975.

Salmonid Species Spacial Segregation

Competition between steelhead trout and coho salmon in the model streams is the first factor that comes to mind to account for the much lower levels of steelhead numbers, biomasses, and production rates occurring in 1976 than in 1975 when coho salmon were absent. Competition between species is generally either directly or indirectly for resources such as food and space. This often takes place through aggression of the dominant species directed toward the other species. Such competition generally leads to spacial displacement or other disruption of the subdominant species and resultant decreases in its food consumption, growth, and survival, which tend to decrease its numbers, biomass, and production, such decreases as we have noted for the steelhead trout in the presence of coho salmon.

From May 1976 until mid-December 1976, the behavior of steelhead trout and coho salmon was observed at intervals of 10 days. The vertical and horizontal position, number of feeding attempts, and direction and intensity of aggressive behavior of each fish were recorded. Seven behavioral variables--pool position, riffle position, benthic position, midwater position, number of feeding attempts, aggression directed toward steelhead, and aggression directed toward coho salmon--were examined by multivariate analysis. The multivariate analysis test for variance indicated that each coho population was significantly different from the other and from both populations of steelhead. The behaviors of the control and treatment steelhead were not, however, significantly different, this suggesting that temperature elevation had little direct or indirect effect on the observed steelhead behaviors.

The multivariate analysis test for variance was followed by a canonical analysis of discriminance in order to better determine which behavioral parameters were most responsible for the variance. The canonical analysis of discriminance revealed that 100 percent of the variation among the populations could be accounted for by the first three canonical variables. Canonical variables are vectors along the major axes of dispersion in a multidimensional cluster of points. Consequently, in order to interpret the canonical variables, it is necessary to examine the correlations between the canonical variables and the original behavioral variables. The first, second, and third canonical variables had correlations of 0.89, 0.40, and 0.21 with midwater position, riffle position, and aggression toward steelhead, respectively. A plot of the first two canonical variables (Fig. 6) indicates that there was relatively little difference between the four groups of fish for canonical variable 2. This variable was most closely associated with riffle position and all four centroids (indicated by asterisks) fell between -0.6 and 0.6. However, considerable discrimination between groups was evident for canonical variable 1, or midwater position. There was a greater likelihood of a benthic position of treatment coho compared with control coho as well as of steelhead compared with coho. This is indicated by the spread of the centroids between 3.0 and 1.5 or by the small amount of overlap between the two coho clusters and between the coho and steelhead clusters (Fig. 6). The distance separating the coho centroids is 2.5 times greater than that separating the steelhead centroids. Thus, both multivariate analysis of variance and canonical analysis of discriminance suggest that temperature elevation may result in much



greater disruption of coho behavior than of steelhead behavior.

The relatively greater disruption of coho behavior than of steelhead behavior may be partially responsible for the relatively greater temperature associated differences between coho production, biomass, and numbers than for steelhead production, biomass and numbers. In addition, the tendency for a benthic position by the treatment coho could have resulted in greater competition for space and benthic prey between coho and steelhead in the treatment stream, than in the control stream. This may have increased the interaction between the two treatment species and could be the reason for the greater amount of aggression by coho directed toward the treatment steelhead than toward the control steelhead. A test for canonical correlation between canonical variables 1 and 2 and temperature revealed insignificant relationships. Presumably the lack of correlation was the result of the seasonally variable effects of elevated temperature on prey densities and salmonid feeding intensity.

Although aggression seemed less important than position from the canonical analysis of discriminance, the two behaviors are closely interrelated and therefore difficult to separate by this technique. In both streams, intraspecific and interspecific aggression were especially intense and frequent at the high densities of fry following emergence. Both intraspecific and interspecific predation by larger fish upon smaller individuals were observed. Following attacks by dominant fish, submissive fry were frequently observed to burrow into the gravel. This was initially assumed to be an escape response. However, such individuals often remained buried and eventually died.

During 1975 when coho were not present in the streams, steelhead fed largely from the riffle and pool bottoms, but frequently fed on the drifting invertebrates in the pools as well. When coho were present, steelhead were rarely observed feeding in the pools on drifting invertebrates. In addition, searching behavior by small steelhead was more commonly observed during the year that coho were present than when they were absent. In other words, in the presence of coho, steelhead territories appeared less fixed. This suggests a change from a "sit-and-wait" to a searching foraging strategy, at least on the part of the small steelhead. Thus, the presence of coho was associated with a reduction of the amount of habitat occupied by steelhead, and temperature elevation was associated with increased interaction between coho and steelhead. Both factors may have contributed considerably to the reduced production of treatment steelhead during 1976. And spacial displacement and reduced feeding opportunity were probably involved in lower survival, biomass, and production of steelhead in 1976, when coho were present, than in 1975, when the salmon were absent.

Salmonid Food Organism Availability

The availability of suitable food organisms must be causally related to survival, growth, biomass, and production of fish. Under otherwise similar conditions, higher values of these parameters are, in themselves, strong evidence of greater availability of food. Differences in temperature could, however, obscure such underlying causal relations.

But assessment of actual food availability is rarely possible, even though the abundances of food organisms and sometimes their distribution can be estimated. This is because food organism preferences of the fish, which may be conditioned by availability, are also involved in determining the amounts of food organisms of particular kinds that are eaten. Nevertheless, considerable insight into the relation of food to responses of individual fish and their population can be achieved through examination of abundances and distributions in time and space of potential food organisms, their occurrence in the diets of the fish, and survival, growth, biomass, and production responses.

An electivity index, E = (r - p)/(r + p), was used to rate the prey taxa from -1 to +1 based upon their relative abundance in the ration, r, and their relative abundance in the environment, p. Electivity is a function of numerous characteristics of the predators, such as degree of satiation, predator density, and experience. It is also a function of such prey characteristics as absolute density, relative density, degree of aggregation, cover, behavior, and palatability. Electivity is not an indicator of preference. It was used in this research only as a rough indication of dietary importance. The biomasses of taxa of food organisms usually having positive electivity indices are plotted in Figure 7. Individual differences among the predators were disregarded, although at times some fish consumed specific taxa in considerably different amounts than did other individuals of either species. The two most important prey taxa were similarly distributed in the benthos and drift (Fig. 8), and coho and steelhead fed on nearly the same organisms. Most prey were 3-10 mm long, though occasionally much larger items were taken.





drifting organisms over a 24-hour period. Each point is the mean of two samples taken during a six-week period (After Hughes).

The chief prey items throughout both years could be represented by three taxa (Fig. 7): the baetid mayflies, mostly <u>Baetis tricaudatus</u>; the chironomid midges, chiefly of the subfamily Orthocladiinae; and an ostraced, <u>Herpetocypris chevreuxi</u>. Other taxa only occasionally having positive electivity indices, and therefore not plotted, included: Collembola; the stoneflies, mostly <u>Nemoura</u>; the microcaddisfly, <u>Hydroptila</u>; Simuliidae, or black flies; and a planorbid snail, <u>Gyraulus</u>. The taxon most consistently having a high electivity index was Chironomidae. These insects are frequently considered the most important food source of juvenile salmonids in streams.

In general, prey having consistently high or only occasionally positive densities were slightly greater in abundance throughout both years in the control stream than in the heated stream. The midsummer peaks of prey biomasses coincided with high growth rates of both control and treatment salmonids. The prey biomasses immediately following these peaks were, however, much higher in the control stream than in the heated stream. This higher prey density, together with cooler water temperatures and lower maintenance costs, was probably involved in the higher growth rates of the control salmonids than those of the treatment salmonids during late summer and early autumn. These factors were also probably involved in the extra one to two months of rapid summer growth in the control fish (Table 1). This extended the period of positive production values in the control stream during 1976.

Total invertebrate biomasses in the riffles (Fig. 9) and pools (Fig. 10) of the model streams were higher in the heated stream



ure 9. Biomasses of the snail <u>Oxtrema silicula</u> and of all other macroinvertebrates present in the riffles of the model streams (After Hughes).





than in the control stream. But this was owing to the very high biomasses of the snail <u>Oxytrema silicula</u> (Fig. 9; Fig. 10), which was apparently much favored by the warmer water. All other macroinvertebrates, including those most preyed upon by the salmonids, were generally much more abundant in the riffles of the control stream than in those of the heated stream (Fig. 9). Biomasses of these other invertebrates in the pools of the control and heated streams were not usually very different (Fig. 10).

Diversity of Macroinvertebrates

The Shannon-Weaver information measure of diversity (H') and a redundancy index (R') were estimated for the macro-invertebrate benthic samples. H' was estimated by

$$H'' = \sum_{i=1}^{s} \frac{n_i}{N} \log_e \frac{n_i}{N}$$

where s equals the number of taxa in the sample, n_i is the number of individuals of a taxon, and N is the total number of individuals in the sample. H' is a species composition parameter which is based on the uncertainty with which the taxon of the next individual encountered can be predicted. H" tends to underestimate H', but this bias is small for large sample sizes and the inclusion of rare species results in little change in the value of H". H" incorporates the taxonomic richness and evenness components of diversity, whereas redundancy involves only the evenness component. H" is increased by increased richness or by decreased redundancy. Redundancy, or dominance, was calculated as

$R' = (H''_{max} - H''_{obs})/(H''_{max} - H''_{min})$

where H"_{max} and H"_{min} are the maximum and minimum values of H" given s, and H"_{obs} is the observed value of H". In a sample, R' varies from zero, when all taxa are equally represented, to one when all taxa but one are represented by but one individual.

It is generally believed that disrupted systems exhibit decreased diversity and increased redundancy of organisms present in their communities. Moderate temperature elevation was associated with such changes in the riffles of the model streams. Diversity (H") was almost always greater in the riffles of the control stream than in those of the heated stream (Fig. 11). With the exception of one period in November 1975, there were from two to ten more taxa in the control stream riffles than in the heated stream riffles (Fig. 11). The riffles of the control stream generally showed lower redundance (R') than did those of the treatment stream (Fig. 11). Thus diversity was higher in the riffles of the control stream than in those of the heated stream because the control stream had greater taxonomic richness and lower redundancy than did the heated stream. Although the pools of the control stream tended to have greater taxonomic richness and diversity than did those of the heated stream (Fig. 12), these differences were neither as great nor as consistent as were those of the riffles of the two streams. No increasing divergence in diversity between the two streams was found during 1975 and 1976. Presumably, the differences in macroinvertebrate community composition were the result of conditions prior to February, 1975, the streams having been in operation, one of them heated, and open to colonization for a period of about six years prior to the experiments reported here.









CONCLUSIONS

Although this report has been devoted nearly entirely to model stream studies of steelhead trout and steelhead trout in competition with coho salmon, as well as characteristics of the stream communities during 1975 and 1976, it seems pertinent in statement of conclusions to take into account aquarium and model stream studies involving chinook salmon as well as these species, which were conducted from 1968 into 1977, the entire period of support of this research by the U.S. Office of Water Research and Technology. This will be done in only a very general way, as any more specific treatment of the many experiments conducted would defeat the purpose of this section, which is to provide some broad view of conclusions one might reach on the basis of this work.

1. So far as can be determined by aquarium studies on the food consumption and growth of juvenile coho salmon, chinook salmon, and steelhead trout, increases in temperature of 3-4 C to 7-8 C over the daily, seasonal, and annual ambient temperature of a small natural stream tend to markedly increase the metabolic rates and thus the ration levels necessary to maintain the fish at a level of zero growth. Thus, at all but the highest ration levels, growth rates of the juvenile salmonids were reduced by increasing temperature. When food levels were unrestricted, and the fish at higher temperatures could consume more, growth rates at elevated temperatures were about the same as those of control fish. Studies of growth and estimates of food consumption of salmonids in natural streams indicated that their growth and consumption rates were much nearer to those of fish fed lower ration levels in the aquarium experiments. On the basis of these studies, we must conclude that temperature increases over ambient levels in natural streams would reduce growth of juvenile salmonids, at similar levels of food availability.

2. Survival rates, numbers, biomasses, and production rates of juvenile coho salmon, chinook salmon, and steelhead trout were reduced in model stream experiments when temperatures were persistently elevated 3-4 C above the daily, seasonal, and annual ambient temperatures of a small natural stream, during six experiments of about one-year duration each.

3. Survival rates, numbers, biomasses, and production rates of juvenile steelhead trout were much lower when coho salmon were also present in the model streams than when they were not. Competition between the steelhead trout and coho salmon appeared to be aggravated . by temperature increase, which leads to greater overlap in the stream habitats occupied by the two species.

4. Generally, abundances of fish food organisms and most other macroinvertebrates were reduced in the model stream by temperature elevation of 3-4 C over the ambient temperature of a small natural stream. The major exception to this was an aquatic snail, which occurred in much greater abundance in the heated stream than in the control stream. This snail was not an important food organism for the fish.

5. Diversity of macroinvertebrate organisms was generally reduced in the model stream having a temperature elevation of 3-4 degrees over natural ambient levels.

6. Thus, not only increased maintenance costs and behavioral changes but also changes in stream community composition and the abundance of food organisms, resulting from temperature elevation, appear to have been importantly involved in reduction in survival rates, numbers, growth, biomasses, and production rates of juvenile coho salmon, chinook salmon, and steelhead trout in model stream communities.

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