PRODUCTION OF JUVENILE CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN A HEATED MODEL STREAM[1]

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ABSTRACT

Temperature was elevated approximately 4°C in a model stream, compared with an unheated but otherwise similar control stream. The streams were located outdoors and received identical amounts of exchange water from a nearby creek. Diel and seasonal temperature fluctuations were similar to those of area streams. Juvenile spring chinook salmon, *Oncorhynchus tshawytscha*, were introduced into each stream either as eyed eggs or fry and allowed to remain for approximately 1 yr. Two consecutive year classes of juvenile salmon were studied. Their production was measured triweekly and related to changes in temperature, food availability, and other environmental factors. Ancillary experiments utilizing water from the model streams permitted measurement of differences in growth rate of salmon fed various rations.

Salmon production in the control stream exceeded that in the heated stream. In 1972, total production in the control stream was twofold greater and, in 1973, it was approximately 30% greater than in the heated stream. Elevated temperature resulted in reduced growth rates of the fish especially as food became less abundant and at times also resulted in lower biomasses of food organisms, either because the temperature increase directly affected survival and growth of benthic invertebrates or because increased sedimentation associated with heavier growth of filamentous algae made riffle substrate less suitable for certain species. Beneficial effects of increased temperature appeared to include protection from infestation by a trematode parasite (*Nanophyetus salmincola*) and, possibly, increased tendencies of some invertebrates to enter the drift.

Studies of the effects of elevated temperature on stream dwelling organisms have been largely confined to short-term laboratory experiments or to field surveys associated with man-caused thermal increases. We have employed two large model streams, one heated and one unheated, to examine the effects of constantly elevated temperature on production of juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), under conditions similar to natural streams, but where temperature could be controlled. Identifying the factors governing productivity of the streams that were influenced by increased temperature and measuring the impact of the addition of a known amount of heat on chinook salmon production were the two main objectives of the research.

Temperature change can affect salmonid fishes in two general ways. First are the direct effects, e.g., accelerated developmental rates, altered food conversion efficiencies, and, under certain conditions, lethality. These kinds of effects have received considerable attention in laboratory experiments. Less well understood are the indirect effects, one of the most important being resultant changes in the abundance of food organisms. In a previous study involving the same streams, Iverson (1972) found that the production of juvenile coho salmon, *O. kisutch*, was significantly reduced in the heated stream compared with the unheated control, and he attributed this reduction mainly to lower biomasses of immature stages of insects in the heated stream. Evaluating the importance of indirect consequences of temperature elevation on juvenile chinook thus became one of our major concerns, for water quality guidelines relating to the temperature requirements of salmon and trout are based primarily upon knowledge of direct effects and to a much lesser extent upon possible indirect or secondary effects.

MATERIALS AND METHODS

Physical Characteristics of the Streams

The model streams were located at the Oak Creek Laboratory of Biology near Corvallis in

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western Oregon. They consisted of two large wooden channels interconnected at the ends by pipes (Figure 1). Within each stream were four riffle-pool sections of equal size; the total surface area available to fish and other organisms was 22 m^2. Minor differences in substrate composition, water velocity and depth, and shading from terrestrial vegetation existed among the riffle-pool sections. These variations were sufficient to prevent the sections from being treated as replicates; therefore, samples from each of the four sections were composited.

The slope of each stream was approximately 1.9% so that water pumped into the upstream ends flowed downstream at velocities typical of natural streams (approximately 60 cm/s in the riffles to near 0 cm/s at the bottom of the pools). A 2-horsepower centrifugal pump forced water from the downstream end of one channel to the upstream end of the other. A gate valve controlled the flow rate, which was maintained at approximately 1.35 m^3/min.

Complete freedom of movement for the fish was allowed between the two channels. Individuals could pass downstream or upstream through the pipe from one side to the other; they were, however, prevented from entering the pump by a screen at the downstream end of the lowermost pool. Movement of the fish from the streams took place through a 6-cm diameter outlet pipe that originated at the screen and terminated in a partitioned trap. Fish that entered the trap were returned to the uppermost riffle both to avoid fortuitous losses and to provide the fish with an adequate opportunity to establish residence.

Substrate consisted of a layer of rocks approximately 7 cm deep. Following Cummins' (1962) terminology, cobbles and pebbles composed more than 95% of the substrate, both in the riffles and pools, while larger sand was almost absent. No large boulders were present, although a few cobbles projected above the water. A difference in the amount of very fine sediments existed between the two streams; this difference will be discussed in connection with their invertebrate faunas.

Temperature Regulation

Water temperature in the unheated control followed natural diel and seasonal cycles (Figure 2). Two 6-kw stainless steel heaters regulated by a variable input timer facilitated temperature elevation in the heated stream. Continuous recordings of the temperature were made by Partlow RFT thermographs.[4] Differences between monthly means ranged from 3.3°C (August 1972) to 4.9°C (December 1972): the average temperature difference between the streams was 3.9°C.

Both streams received 10-20 liters/min of unfiltered water from a small spring-fed creek that contained aquatic invertebrates and algae, but no fishes. During periods of low stream flow, the water supply was supplemented by a mixture of well water and unfiltered water pumped from a large nearby creek. The model streams have been operating continuously at approximately the same temperature differential since completion of construction in 1969 (Iverson 1972). However, in December 1972 unusually cold weather caused

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

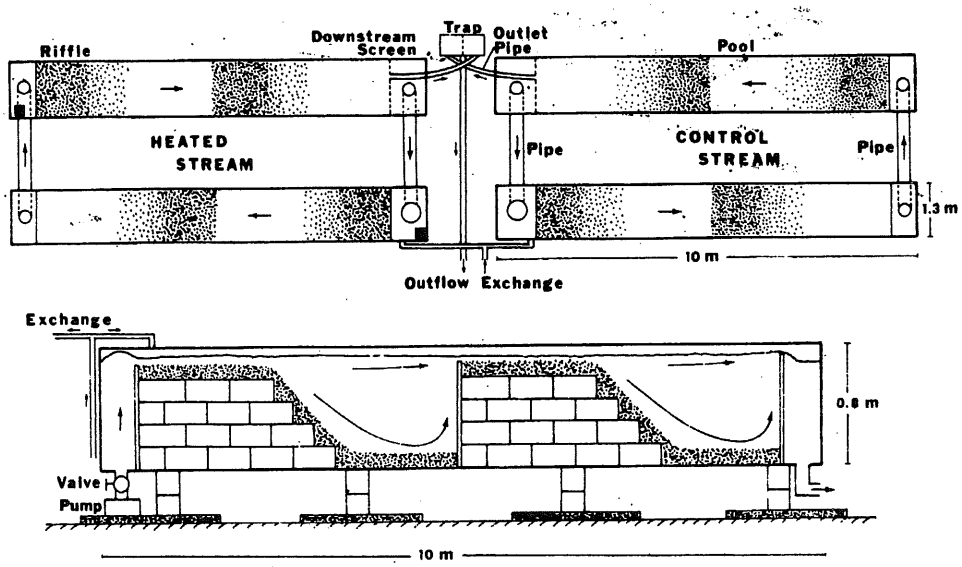

FIGURE 1.—Top. Plan view of model streams. Arrows indicate direction of water flow and black squares in the heated stream denote location of heating units. Bottom. Cross section of one of the channels in a model stream.

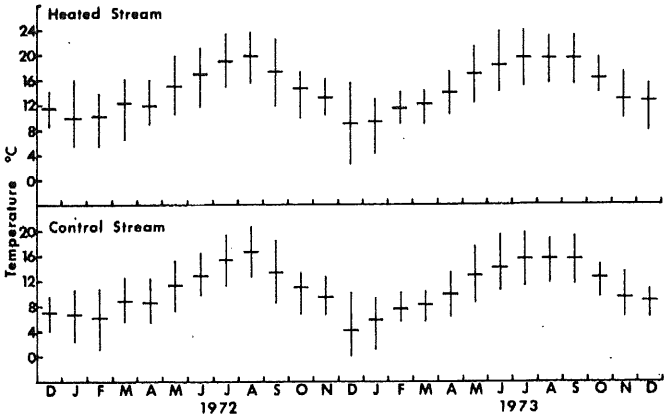

FIGURE 2.–Temperature conditions in the model streams. Horizontal and vertical lines represent monthly means and ranges, respectively.

glass observation windows in the control stream to break; as a result, the entire riffle substrate was exposed for several days while new windows were being installed and some losses of periphyton and invertebrates occurred. One window was also replaced in the heated stream at this time, necessitating exposure of one riffle.

Associated Flora

Vegetation surrounding the streams included red alder, *Alnus rubra*, and apple, *Malus* sp. These trees contributed leaves, catkins, and flowers as well as a variety of terrestrial invertebrates.

Periphytic algae composed the bulk of living plant material within the streams. The same plant species were found in both heated and control streams, although differences in biomass and temporal succession occurred. The dominant species from late spring to fall was *Cladophora glomerata*, a filamentous green alga that attached to large particles in the riffles and often trailed into pool areas. Various diatoms also made up a significant proportion of the flora. Two species exhibited especially heavy seasonal blooms. In early spring, filaments of a colonial diatom, *Melosira varians*, covered both riffles and pools; this species was noticeably more common in the control than in the heated stream. In summer and fall *Synedra ulna* became the dominant diatom, occurring both in the water mass and among living and dead algae on the bottom. Blue-green algae were generally found in late spring and summer. *Calothrix* and *Nostoc* were more abundant and appeared earlier in the heated stream than in the control. An unidentified dense moss colonized some of the large cobbles in the riffles. Diatoms and desmids, in addition to plant materials from terrestrial sources, were common in the drift. The desmid *Closterium lunula* was abundant in spring and early summer and was found to be an important food resource for filter-feeding invertebrates.

Benthos and Drift

Benthic plants and animals were sampled triweekly. Wire mesh baskets 20 × 20 × 6 cm painted with nontoxic paint and having wood bottoms were filled with substrate and placed against supporting blocks in the riffles. The mesh size (2 cm) was small enough to retain most of the particles and large enough to allow movement of invertebrates into and out of the baskets. Each riffle in the streams contained four baskets placed about 1 m apart from upstream to downstream end. One basket was selected from a different location in each riffle, the contents emptied into a bucket, and all large particles cleaned with a plastic scrub brush. The combined samples from four baskets (0.16 m^2 total) were then collected in a 200-μm mesh bag. One sample was taken from a pool in each channel, and collected material was combined and preserved in 10% Formalin.

Drifting organisms were collected triweekly by means of 333-μm mesh drift nets (Anderson 1967) that were suspended at the downstream end of the riffles. Two nets were fished in each stream (one per channel) for a 24-h period. Samples were removed and preserved at approximately sunrise and sunset so that diel differences in drift rates could be measured. Current velocity was measured at each sampling position and the amount of water passing through the nets during an interval was determined by multiplying this velocity by the cross sectional area of the water (330 cm^2) at the mouth of the net. During periods when considerable masses of leaves or algae were present in the drift, usually late summer and fall, some clogging took place and the volume of water entering the nets was overestimated.

All samples were allowed to remain in Formalin for 1 or 2 days, after which they were washed briefly with water. Drift samples were transferred directly to 70% ethanol prior to enumeration, while bottom samples were first sorted to remove invertebrates larger than 4 mm, and then subsampled (10% by volume) and preserved in ethanol. All organisms were measured to the nearest millimeter by means of a metric grid placed on the stage of the microscope. We assumed that no

length changes occurred during preservation. The number of individuals for each species in each size interval was recorded for every sample.

The remaining 90% of a bottom sample—that not sorted under magnification—was dried at 70°C for 4 days and then ashed at 600°C. Ten percent of its organic weight was arbitrarily assumed to have been lost during preservation. Subtracting the estimated biomass of small (<4 mm) invertebrates within this subsample from the total loss of ignition yielded the ash-free dry weight of filamentous algae, some diatoms, detritus, and organisms too small to be seen during the sorting process. Conversion to energy units (kcal) was accomplished by multiplying the plant-detritus biomass by 4.05, the mean of five samples combusted in an oxygen bomb calorimeter.

Computations of invertebrate biomasses were based on live specimens collected from a nearby stream, grouped according to size and species, and weighed after drying 4 days at 70°C. Their average dry weights were converted to calories by values obtained from Cummins and Wuycheck (1971) or determined directly by calorimetry. When no representatives of a certain size were available, a value for that interval was estimated by interpolation. Very similar forms were assumed to have identical values. For bottom samples, the biomass (kcal/m^2) of each size class of each taxon was taken as the product of the number of individuals in that class, the estimated caloric value for individuals of that size, and the appropriate area conversion factor. The product of the number of individuals and the caloric value was divided by the total amount of water passing through the nets to give biomass estimates per unit volume (cal/m^3) for the drift samples. Summing the values of all size intervals gave the total caloric content for each taxon.

Fish

Fertilized chinook salmon eggs were obtained from the Marion Forks Salmon Hatchery of the Oregon Department of Fish and Wildlife. Eggs for the 1972 experiment, taken 3 October 1971, were from a single pair mating. Eggs used in the 1973 experiment, taken 1 October 1972, were obtained by crossing three females with four males. This was done in order to increase genetic heterogeneity among fish in the 1973 experiment. Following fertilization, the eggs were transported immediately to holding facilities where they were incubated at 12°C.

In 1971, eggs were introduced into the streams when they reached the eyed stage. They were hatched in floating baskets and the fry were released shortly before yolk absorption was completed. Owing to accelerated development in warmer water, fish in the heated stream were released sooner than those in the control, although the initial number of individuals placed in the two streams was identical (425). A 10-wk recolonization period following repairs delayed introduction of salmon until mid-March 1973, when 200 fry were released simultaneously into each stream.

When the fish had reached approximately 0.4 g wet weight, they were all removed from the streams for measurement of individual length and weight every 3 wk until an experiment was terminated. From 5 to 20 fish were randomly drawn from the populations for stomach analyses. A blunted 22-gauge needle on a 5-ml syringe was inserted through the esophagus of an anesthetized fish into the anterior limb of the stomach. Several milliliters of water were gently injected into the stomach, forcing the contents out through the mouth into a collecting beaker. The combined whole food organisms and identified fragments of each taxon were weighed to the nearest 0.1 mg, and each taxon was assigned a percentage of the diet based on its fraction of the total wet weight of the sample.

Direct effects of the model stream temperature regimes on chinook salmon growth rates at different levels of food availability were studied in concurrent experiments. Fish of the same parentage and size as those in the model streams were placed in insulated streamside troughs, where they were fed live *Tubifex* at rations ranging from near maintenance to near repletion. The troughs received water directly from the model streams, and temperature differences between the troughs and streams were never greater than 0.3°C. Ten-day growth experiments were carried out once each season during 1973. Each experiment was preceded by a 10-day period of acclimation to temperature and ration size. Numbers of individuals tested at each ration level ranged from 10 to 20 depending upon fish size.

Average relative growth rates (Warren 1971) of the salmon were calculated as:

$$ARG = \frac{\bar{W}_2 - \bar{W}_1}{0.5\,(\bar{W}_1 + \bar{W}_2)\cdot t}$$

where ARG represented growth, $\bar{W}_1$ and $\bar{W}_2$

represented the mean weights of the fish at the beginning and end of the sampling interval, and t was the sampling interval in days. Growth was assumed to be linear over the relatively short 3-wk period. Relative growth rates, which were essentially the same as instantaneous growth rates, were considered more appropriate for comparison with relative food consumption rates.

Average biomass ($\bar{B}$) was calculated as:

$$\bar{B} = \frac{B_1 + B_2}{2}$$

where B_1 and B_2 represented the total weights of the fish at the beginning and end of the sampling interval.

Production during each sampling interval was calculated as the product of average relative growth rate (ARG) and average biomass ($\bar{B}$).

The conversion of wet weights to calories was accomplished by relating caloric content of tissue to condition factors of the fish, where condition factor was taken as 100 times a fish's weight (g) divided by the cube of its fork length (cm). Figure 9 of Warren et al. (1964:630), describing this relationship for cutthroat trout, *Salmo clarki*, was used for graphical estimates of calories per gram of wet weight for juvenile chinook salmon.

RESULTS

Temporal Changes in Production

Total production of chinook salmon in the heated stream was less than half that of the control in 1972 (Table 1). During the following year, production in the control stream was approximately 30% higher than in the heated stream. Mortality was greatest immediately after release into the streams, with populations attaining fairly stable levels by late summer. Population biomasses rose during winter and spring, were highest during late spring, and gradually declined through summer and fall. The mean annual biomass in the

TABLE 1.–Mean production statistics of experimental chinook salmon populations. H = heated stream, C = control stream.

Time interval	Individual size (kcal)		Population size (no.)		Mortality rate (%/day)		Biomass (kcal/m²)		Growth rate (cal·kcal/day)		Production (kcal/m²)	
	H	C	H	C	H	C	H	C	H	C	H	C
1972:												
20 Dec. -24 Jan.	0.31		302		1.61		4.12		1.85		0.27	
25 Jan. -14 Feb.	0.49		169		0.46		3.09		21.48		1.39	
15 Feb. - 7 Mar.	0.84	0.48	140	358	1.22	0.62	4.20	7.24	26.50	3.08	2.23	1.14
8 Mar. -27 Mar.	1.18	0.92	112	271	0.74	0.81	5.14	8.62	16.00	33.03	1.73	5.42
28 Mar. -15 Apr.	1.41	1.32	91	233	1.23	0.73	5.38	11.91	9.31	19.21	0.95	4.26
16 Apr. - 6 May	2.18	2.01	65	184	1.63	1.39	5.32	14.04	23.80	47.42	2.27	5.89
7 May -27 May	2.77	2.79	47	145	0.92	0.50	5.29	15.82	11.35	15.48	1.26	5.14
28 May -16 June	3.61	3.36	40	125	0.48	0.84	5.80	17.61	13.17	9.27	1.53	3.27
17 June - 7 July	4.36	3.75	34	105	0.88	0.75	6.25	16.97	8.96	5.22	1.18	1.86
8 July -28 July	4.53	4.32	31	92	0.01	0.35	6.26	16.97	1.82	6.73	0.24	2.40
29 July -22 Aug.	4.82	4.35	26	85	1.24	0.34	5.26	16.65	2.48	0.28	0.34	0.12
23 Aug. - 8 Sept.	5.68	4.74	19	67	0.84	2.03	4.65	13.84	9.64	5.05	0.76	1.19
9 Sept.- 3 Oct.	5.79	5.01	17	52	0.22	0.15	4.56	11.52	0.77	2.22	0.09	0.64
4 Oct. -19 Oct.	5.61	5.76	16	48	0.74	0.61	4.15	11.87	−1.44	9.29	−0.13	1.65
20 Oct. - 7 Nov.	6.15	5.73	14	46	0.35	0.01	3.88	12.01	4.83	−0.27	0.36	−0.06
8 Nov. -30 Nov.	6.45	5.50	14	45	0.00	0.01	4.01	11.49	2.07	−1.78	0.19	−0.47
Total											14.66	32.45
Mean							4.84	13.33				
1973:												
16 Mar. - 7 Apr.	0.98	1.02	187	185	0.57	0.66	7.14	7.48	14.49	12.70	2.38	2.19
8 Apr. -26 Apr.	1.57	1.48	154	168	1.23	0.15	8.93	9.55	24.36	19.37	4.13	3.51
27 Apr. -18 May	3.33	2.75	109	150	1.74	0.89	12.14	14.42	32.65	27.30	8.72	8.66
19 May - 7 June	4.69	3.63	65	106	2.42	2.26	11.85	15.37	17.85	14.52	4.02	4.24
8 June -27 June	6.92	4.98	41	63	1.09	1.75	10.82	12.33	19.31	15.68	4.16	3.87
28 June -19 July	7.31	5.99	34	45	0.42	0.90	11.00	11.22	2.49	8.37	0.60	2.07
20 July - 9 Aug.	6.87	6.96	32	41	0.30	0.01	10.31	12.07	−2.96	7.13	−0.64	1.81
10 Aug. -30 Aug.	7.00	7.10	30	40	0.15	0.12	9.46	12.78	0.89	0.95	0.18	0.25
31 Aug. -19 Sept.	6.76	7.89	29	37	0.17	0.75	9.07	12.61	−1.66	5.02	−0.32	1.33
20 Sept.-10 Oct.	6.48	8.23	29	33	0.00	0.28	8.73	12.09	−2.01	2.01	−0.37	0.51
11 Oct. -31 Oct.	6.35	9.00	26	29	0.86	0.78	7.58	11.36	−0.97	4.26	−0.15	1.02
1 Nov. -21 Nov.	6.65	8.71	22	25	0.59	0.53	6.50	10.06	2.18	−1.56	0.30	−0.33
22 Nov. -12 Dec.	6.07	8.66	19	23	0.91	0.20	5.49	9.08	−4.34	−0.27	−0.50	−0.05
Total											22.51	29.08
Mean							9.16	11.57				

heated stream was about twice as high in 1973 as in 1972, while average biomasses were slightly reduced following repairs in the control stream. Peak production in both streams occurred from April to June (Table 1, Figure 3), this being related to the high growth rates that took place during spring. Differences in production between the streams, however, were related primarily to higher population biomasses maintained in the control stream than in the heated stream, rather than to differences in growth rate.

Production of salmon in the heated stream during the spring, 1973, was higher than in the spring 1972 (Figure 3). The fish were stocked as fry in 1973, whereas in 1972 they were introduced as eyed eggs. The low average growth rate and survival (Table 1) of fish reared in the heated stream from the egg stage suggest that production was influenced by conditions during early development. Some individuals grew very rapidly during their first few weeks of residence; others apparently did not make the transition to feeding in the heated stream and died from the effects of starvation. Negative production occurred during fall months, when many fish had stopped growing and some were losing weight.

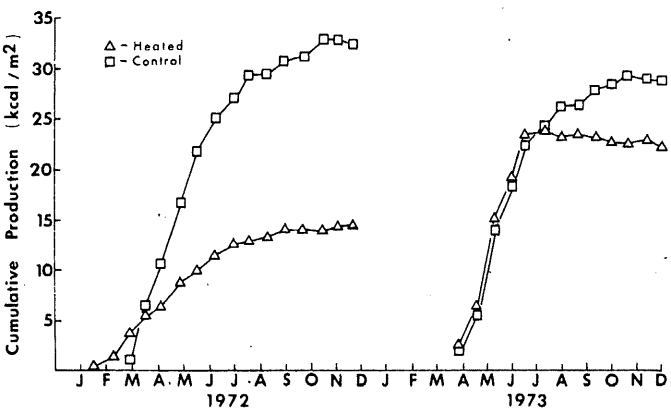

FIGURE 3.—Cumulative production of juvenile chinook salmon during 1972 and 1973.

Direct Temperature Effects on Growth

Relationships between average relative growth rate and food consumption rate of juvenile chinook salmon held in water from the model stream (Figure 4) showed that differences between fish held in heated and unheated water were greatest at low rations and least at high rations. At low rations, control individuals were most efficient; at high levels, there was no appreciable difference except during spring when the elevated temperature facilitated increased food consumption and growth efficiency. The highest rations were close to the maximum amount of food that the young salmon would eat at one feeding in a day, and the graphs for summer and fall indicate that maximum consumption declined as individuals' size increased.

The relationships observed in the experiments between temperature, ration level, and fish size were consistent with the results of laboratory studies of sockeye salmon, *O. nerka* (Brett et al. 1969; Brett and Shelbourn 1975); coho salmon (Averett 1969); and steelhead trout, *Salmo gairdneri*, (Wurtsbaugh 1973). At low levels of food availability, increased metabolic requirements associated with elevated temperature resulted in reduced growth rates; at high levels of food availability, growth rates were not appreciably altered by thermal increases. If responses of juvenile chinook to the range of ration levels in the aquarium growth experiments approximated growth of fish in the model streams at differing consumption rates (Carline and Hall 1973), the growth rate data of Table 1 suggest that during most of the year the fish were feeding well below their maximum possible consumption. Only during certain periods in late winter and spring did growth rates approximate the maximum rates shown in Figure 4. From this we concluded that,

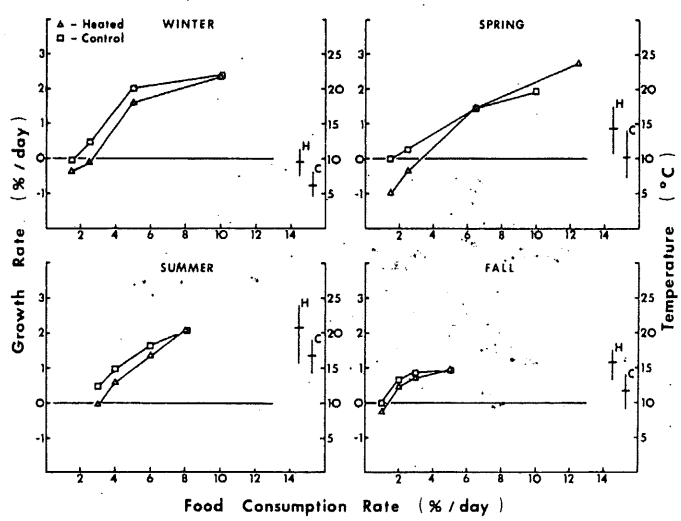

FIGURE 4.—Seasonal changes in the growth rates of juvenile chinook salmon. Experiments continued for 10 days and were preceded by 10 days of acclimation to temperature and ration size. Plotted values of growth rate at each feeding level were based upon the following numbers of fish: winter - 20; spring - 20; summer - 12; and fall - 10. Mean caloric contents (kcal) of the fish at the beginning of each experiment were: winter - 0.59; spring - 1.26; and summer - 7.05; and fall - 8.37.

during most of the year, the experimentally elevated temperature contributed directly to the reduced growth and production of the fish.

Disease

An unexpected indirect effect of elevated temperature was apparent protection from infestation by an intermediate stage of the trematode *Nanophyetus salmincola*, which was present in the streams from late spring through fall. Infective cercaria emerged from the snail *Oxytrema silicula* to encyst in the skin and tissues of juvenile chinook as metacercaria. The distinction between heavy vs. light infestation was made visually and was somewhat arbitrary (Figure 5): conspicuous bumps at the base of the caudal peduncle, darkening of fins, and papules on the body surface were considered symptoms of heavy infestation. While the parasite was obviously present in 1972, it was not until after its appearance in 1973 that attempts were made to quantify its effects.

Infestation rates in the heated stream remained low through summer and early fall and increased until termination of the experiment. Heavy infestations were present in most of the control fish

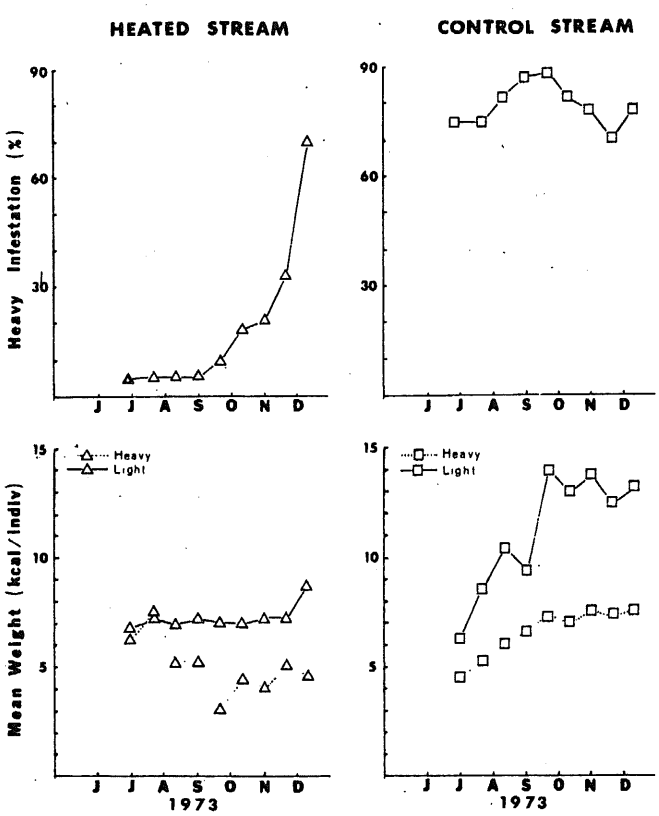

FIGURE 5.—Infestation rates and weight differences of juvenile chinook salmon infested by metacercaria of *Nanophyetus salmincola*.

soon after cercaria had begun emerging from the snails. In addition, a greater difference existed between the mean weights of heavily and lightly infested individuals in the control stream than in the heated stream. The impact of this parasite thus appeared to be more severe in the control than in the heated stream.

Food Availability

An understanding of changes in food availability required: 1) that preferred food items be identified, 2) that it be determined when they were available for consumption, and 3) that their relative abundance was estimated under comparable circumstances. In this study, the second requirement was met through observation; food organisms became available only when they entered the drift and then mainly during daylight. Unlike many other salmonids, juvenile spring chinook salmon placed in the model streams were never seen feeding on invertebrates in the benthos. The extent of feeding during darkness was not determined, but was believed to be small. Identical sampling procedures were assumed to fulfill the third requirement, although differential consumption of food before it entered the drift nets could have caused some error.

Oligochaetes were almost completely excluded from the diet of large fish even though they composed an important fraction of the drift (Table 2). Mollusca (exclusively *Gyraulus* sp.) and Trichoptera were comparatively large food items and were consumed more readily by large fish than by small fish. Ostracod *Herpetocypris chevreuxi* was taken throughout the year in proportion to its relative abundance, while Ephemeroptera and Chironomidae—generally small organisms that were usually numerous in the drift—were preferred by smaller fish although these groups were always major components of the diet. In general, differences in food habits between populations in the streams were related to differences in the relative abundance of various food groups. One exception was the greater consumption of terrestrial forms (primarily aphids and spiders) by fish in the heated stream, despite approximately equal input of these invertebrates into both streams.

Measurements of food organisms drifting during daylight hours (Figure 6) were not well correlated with measurements of the biomass of those organisms in the riffle benthos (Figure 7).

TABLE 2.—Average percentages of different taxa (by weight) in the food of juvenile chinook salmon compared with percentages of those organisms in the day drift (in parentheses). H = heated stream, C = control stream.

	Oligochaeta		Mollusca		Ostracoda		Collembola		Ephemeroptera	
Season	H	C	H	C	H	C	H	C	H	C
1972:										
Winter	0(45)	<1(24)	1(4)	0(5)	5(4)	0(0)	1(<1)	0(4)	2(4)	30(2)
Spring	0(43)	0(37)	0(13)	0(4)	18(7)	4(2)	<1(<1)	<1(<1)	11(3)	45(24)
Summer	1(34)	<1(56)	0(5)	0(2)	32(28)	3(3)	<1(1)	0(<1)	10(<1)	10(8)
Fall	<1(7)	0(13)	2(18)	0(4)	7(4)	4(5)	7(1)	4(1)	12(15)	4(6)
1973:										
Spring	13(14)	15(43)	0(6)	<1(<1)	4(7)	1(<1)	<1(<1)	0(<1)	22(11)	25(6)
Summer	6(3)	1(8)	11(7)	1(2)	12(8)	4(11)	<1(<1)	<1(<1)	10(8)	30(18)
Fall	<1(6)	<1(1)	54(33)	4(5)	4(4)	<1(1)	6(2)	4(2)	4(3)	18(19)

	Plecoptera		Trichoptera		Chironomidae		Terrestrials		Miscellaneous	
Season	H	C	H	C	H	C	H	C	H	C
1972:										
Winter	25(9)	52(42)	0(0)	0(0)	51(26)	16(3)	14(10)	2(14)	<1(<1)	<1(<1)
Spring	12(7)	6(3)	3(<1)	5(21)	27(24)	36(6)	27(2)	7(2)	2(<1)	1(<1)
Summer	1(1)	4(<1)	<1(<1)	9(1)	49(65)	67(36)	2(2)	5(8)	2(5)	2(1)
Fall	2(1)	33(13)	21(1)	25(4)	33(39)	27(33)	14(10)	1(18)	<1(4)	1(1)
1973:										
Spring	<1(<1)	1(<1)	9(<1)	3(<1)	44(30)	49(32)	5(23)	2(16)	2(8)	3(1)
Summer	<1(3)	11(2)	11(1)	12(6)	38(65)	26(36)	8(2)	11(16)	2(3)	4(2)
Fall	<1(1)	9(5)	1(4)	33(10)	11(35)	25(55)	20(6)	7(2)	1(6)	1(1)

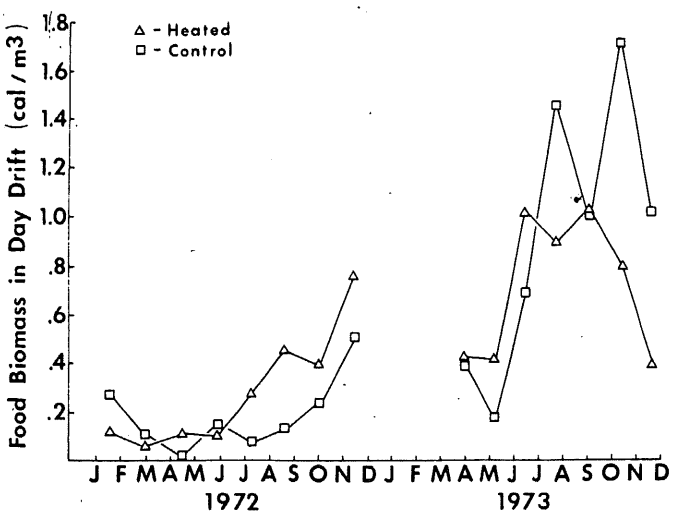

FIGURE 6.—Seasonal changes in the biomass of food organisms present in the day drift. Each point is the mean of two triweekly samples.

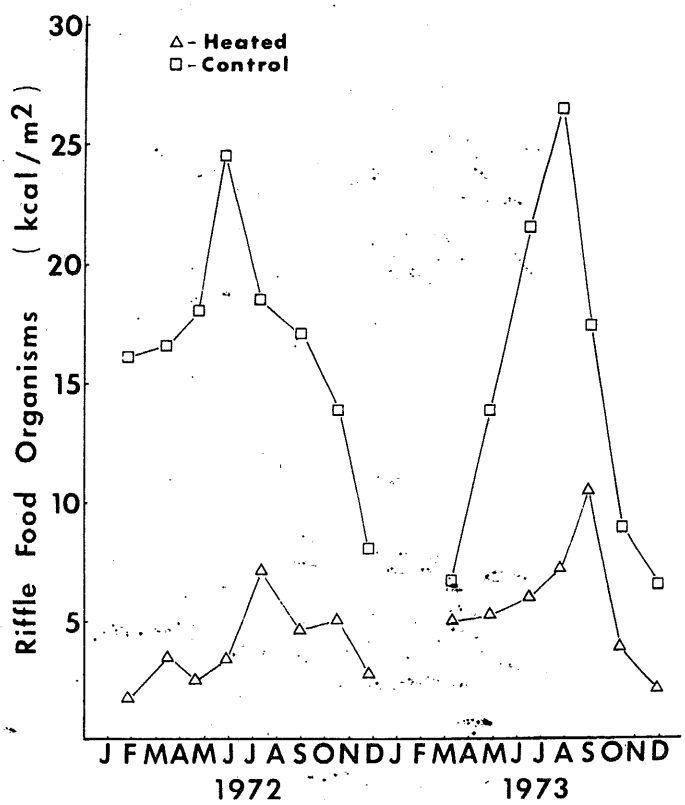

FIGURE 7.—Seasonal changes in the biomass of food organisms present in the riffle benthos. Each point is the mean of two triweekly samples.

Moreover, seasonal patterns in drift differed greatly between 1972 and 1973, with both streams exhibiting higher drift biomasses during the second year than during the first. Although benthic biomasses were significantly greater in the control than in the heated stream, ($P<0.001$, paired t-test), these differences were often not translated into drift; in fact, during the latter part of 1972 and spring 1973, more food was available in the heated stream. No explanation was found for increased drift in 1973 relative to 1972, but it appeared that increased food availability in 1973 resulted in more growth, higher biomasses, and increased production of fish in the heated stream. Why production in the control stream population did not reflect the greater abundance of food is not

TABLE 3.—Annual average biomasses (cal/m²), drift rates (cal/m³), and drift ratios of selected aquatic taxa, excluding winged adults. Drift ratios were calculated according to the formula (day drift/riffle biomass) × 10^5. Asterisks denote values for the heated stream that were significantly different ($P<0.05$, single classification analysis of variance) from the control.

	1972						1973					
	Heated			Control			Heated			Control		
Taxon	Riffle biomass	Day drift	Drift ratio	Riffle biomass	Day drift	Drift ratio	Riffle biomass	Day drift	Drift ratio	Riffle biomass	Day drift	Drift ratio
Oligochaeta	8,532	0.117	1.74	10,698	0.106	1.43	4,112	0.036	1.26	4,034	0.043	1.56
Mollusca[1]	778	0.031	2.71	127	0.008	6.98	906	0.104	13.18	132	0.029	29.08
Ostracoda	703	0.055	23.63	177	0.010	8.87	273	0.036	29.23	218	0.030	28.40
Ephemeroptera	308	0.024	12.14*	7,812	0.011	0.23	430	0.031	8.46	4,150	0.102	3.12
Plecoptera	378	0.009	7.95*	5,966	0.033	0.59	173	0.002	20.37*	3,717	0.035	1.32
Trichoptera	516	0.001	0.22	1,643	0.018	0.36	570	0.010	5.86	1,569	0.039	2.48
Chironomidae	1,202	0.021	3.26*	1.661	0.011	0.95	2,549	0.052	2.20	1,979	0.045	3.67

[1]*Gyraulus* sp.

known, although severity of infestation by *Nanophyetus* was not compared over the 2 yr and may have been more serious in 1973.

In 1972, drift ratios (the ratio of drift to biomass) of several invertebrate taxa were higher in the heated stream than in the control (Table 3). The next year some of the drift ratios increased, and although many were higher in the control stream, the differences were not statistically significant. Of taxa showing increased drift ratios in the heated stream, Ephemeroptera and Plecoptera were most consistently influenced by elevated temperature. In 1972, Chironomidae also exhibited a significantly greater tendency to drift in the heated stream than in the control. These three groups were important components of both the day drift and the diet of juvenile salmon and often contributed to the greater availability of food in the heated stream than in the control during certain periods.

Fewer macroinvertebrate taxa were present in the heated stream than in the control. Paired *t*-tests indicated that number of taxa were significantly different in both riffles (treatment mean = 21, control mean = 34; $P<0.001$) and pools (treatment mean = 16, control mean = 19, $P<0.01$). Most of those taxa that were unique to one stream or the other were very rare and contributed little to fish production. Major biomass differences arose because many taxa had greater population densities in the control while only a few fared better in the heated stream. The several taxa that did exhibit higher biomass in the heated stream were very abundant and tended to dominate the bottom fauna to a greater extent than did common taxa in the control. The two most abundant invertebrates in the heated stream were *Oxytrema silicula* in the riffles and *Limnodrilus* sp. in the pools. Neither of these two species was consumed in significant quantities by the young salmon; thus, increased dominance in the heated stream did not give rise to greater food availability.

Periphyton Biomass and Sedimentation

Plants and detritus were significantly more abundant in the heated stream ($P<0.001$, paired *t*-test) than in the control (Figure 8). The greater amounts of plants and detritus in the heated

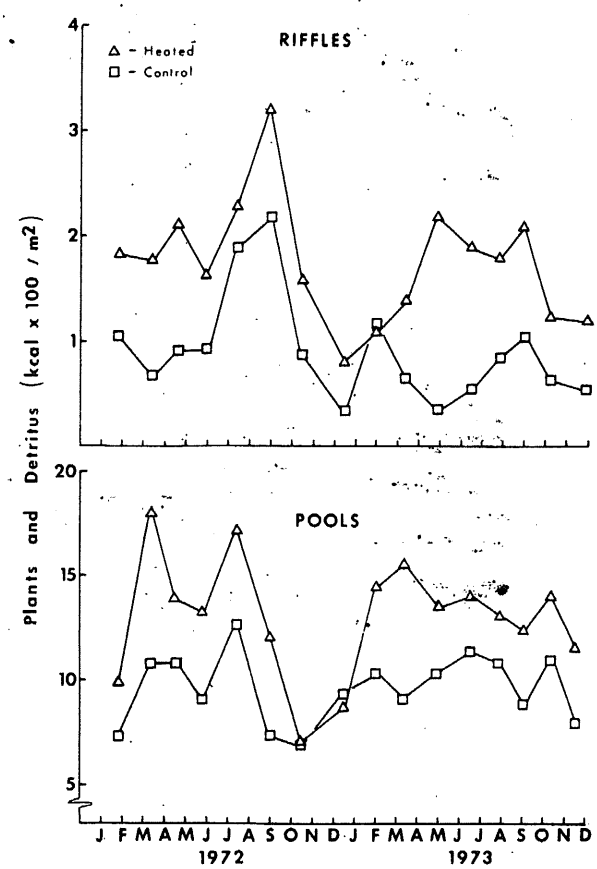

FIGURE 8.—Biomasses of plants and detritus in riffles and pools of the model streams. Each point is the mean of two triweekly samples.

stream than in the control were due to the high densities of filamentous algae in the riffles and the considerable accumulation of organic detritus in the pools. Increased primary production associated with elevated temperature in laboratory streams has been measured by Kevern and Ball (1965) and Phinney and McIntire (1965). The dominant algal species in our model streams, *Cladophora glomerata*, grows rapidly at high temperatures (Whitton 1971; Adams and Stone 1973).

Heavy growths of algae on the riffles apparently accelerated sedimentation rates in the heated stream (Table 4) by acting as filters to trap and consolidate fine particles introduced with exchange water. In the pools, where filamentous algae did not grow, fine sediment levels in both streams were similar. By indirectly enhancing sediment accumulation, elevated temperature probably had an important effect on the numbers of food organisms available to salmon in the heated stream. Hynes (1960) described how siltation alters the habitat of many invertebrates, with the result usually being a reduction in benthic biomass (Cordone and Kelly 1961). Greatly reduced mean annual biomasses of Ephemeroptera, Plecoptera, and Trichoptera in the heated stream (Table 3) compared with the control suggest that these groups were influenced by the amount of fine sediments in the substrate, and these insects were often preferred food items of the fish (Table 2).

TABLE 4.—Levels of fine sediments, expressed as grams dry weight per square meter, in the model streams during May 1974. The figures in parentheses refer to the amount of time that had elapsed since a major disturbance to the riffles.

Item	Particle size (mm)		
	0.175-1	0.088-0.175	0.088
Riffles:			
Control (17 mo)	41	19	169
Heated (17 mo)	147	37	943
Heated (31 mo)	167	91	1,443
Pools:			
Control	94	1,219	1,746
Heated	86	1,064	1,728

DISCUSSION

Our study was designed to examine the effects of elevated temperature on the production of juvenile chinook salmon. The constantly elevated temperature was not meant to simulate a particular type of thermal increase, but was within the range of temperature elevations caused by heated discharges into running waters (Wilber 1969, Parker and Krenkel 1970), irrigation runoff (Eldridge 1963), and removal of streamside vegetation (Brown and Krygier 1970). It was also within the limits of temperature increase legally allowed by some regulations (Burd 1969).

Both direct and indirect temperature effects influenced chinook salmon production, but the magnitude of these effects varied seasonally. Production was high in spring because temperature was in a range that was favorable to growth, parasitism had not yet become an important factor, and the small fish were able to efficiently exploit available food. Summer was generally a period of declining production because high temperatures resulted in an increase in maintenance requirements and, for the control stream, because parasites had attacked the majority of the population. Low production during late summer and fall was associated with high levels of infestation and the ineffectiveness of large fish in exploiting small organisms that were abundant in the drift.

The lack of correlation that existed between growth rates (Table 1) and food availability (Figure 6) may have been related to the species composition of drifting invertebrates. A high percentage of summer and fall drift was composed of very small forms such as oligochaetes (*Nais communis*) and chironomids (Table 2). During those seasons, tiny organisms were not preferred food items of the young salmon, which were larger and less numerous than during the spring. High growth rates exhibited by fish during winter and spring when drift rates were comparatively low suggest that smaller, more abundant fish were able to utilize the entire range of sizes of invertebrate species that left the substrate. It was impossible to determine whether food size preference affected fish in the two streams identically, but based on overall invertebrate composition (Table 3), taxa containing species of large size (Ephemeroptera, Plecoptera, Trichoptera) were more abundant in the control than in the heated stream. This was reflected in higher growth rates of salmon in the control than in the heated stream during summer and fall. Clearly, more intensive examination of the relationship between prey size and prey selection by salmonids is needed.

Low benthic invertebrate biomasses in the heated stream were associated with increased sedimentation rates and reduced numbers of taxa. Iverson (1972) suggested that the poor success of certain invertebrates in the heated stream was

due to their being cold-adapted species. No large scale mortality of larvae or pupae was detected in the heated stream, even during summer months. However, very early developmental stages and life history patterns may have been altered (Macan 1961a, b; Hynes 1970).

The tendency of certain invertebrates in the heated stream to enter the drift in greater proportion to their benthic biomasses (Table 3) was probably related both to elevated temperature and to fine sediment levels. Increased drift associated with increasing temperature was described for certain invertebrates by Müller (1963), Waters (1968), and Pearson and Franklin (1968). In other studies, significant positive correlations between drift and temperature have not been detected (Bishop and Hynes 1969; Wojtalik and Waters 1970; Müller 1970; Reisen and Prins 1972). Experimental additions of sediments to a stream were found by Rosenberg and Weins (1975) to significantly increase the drift of some invertebrate taxa and to have inconsistent effects on others.

Although the influence of elevated temperature on the production of juvenile chinook salmon was complex, we were able to identify both beneficial and harmful effects. The fish benefited in several ways. First, the temperature increase may have stimulated higher consumption rates when suitable food was very abundant, although this condition was rarely achieved. Second, higher temperatures afforded protection from infestation by a trematode parasite, which heavily infested the majority of individuals in the control stream. Third, certain invertebrates may have been stimulated to enter the drift and thus became more available as food. Fish were harmed in at least two ways. First, growth efficiencies were lowered at all but the highest consumption levels. Second, despite high drift ratios of some taxa, food availability was generally reduced because preferred food organisms were much less abundant in the substrate of the heated stream than in the control. The net result was that salmon production in the heated stream was about 50% less in 1972 and 25% less in 1973 compared with the unheated stream.

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