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Title: ELEVATED TEMPERATURE AND THE PRODUCTION OF
JUVENILE CHINOOK SALMON (ONCORHYNCHUS
TSHA WYTSCHA) IN A MODEL STREAM

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Temperature was elevated approximately 4° C in a model stream relative to an unheated, but otherwise similar control stream. The streams were located outdoors, received identical amounts of exchange water from a nearby creek, and followed natural diurnal and seasonal temperature cycles. Juvenile spring chinook salmon (Oncorhynchus tshawytscha) were introduced into each stream and allowed to remain about 1 year until the following winter. Their production was measured tri-weekly and related to changes in temperature, food availability, and other environmental factors. Ancillary experiments utilizing water from the model streams measured changes in pre-feeding survival and weight and differences in growth efficiencies at various rations. Two year-classes of juvenile salmon were studied.

Chinook production in the unheated control stream exceeded that in the heated stream. In 1972 total production was twofold greater and in 1973 it was about 30 percent higher. Elevated temperature lowered productivity of the heated stream by causing increased mortality of eggs and fry and reduced growth efficiencies of juveniles as food became less abundant. It also resulted in lower biomasses of food organisms, either because the experimental elevation directly affected survival and growth of benthic invertebrates or because increased siltation associated with heavier growths of filamentous algae made riffle substrate less suitable for immature stages of certain insects. Beneficial effects of increased temperature included protection from infection by a trematode parasite (Nanophyetus salmincola) and, possibly, increased tendencies of some invertebrates to enter the drift.

Elevated Temperature and the Production of Juvenile
Chinook Salmon (Oncorhynchus tshawytscha)
in a Model Stream

by

Peter Andre Bisson

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ELEVATED TEMPERATURE AND THE PRODUCTION OF
JUVENILE CHINOOK SALMON (ONCORHYNCHUS
TSHAWYTSCHA) IN A MODEL STREAM

INTRODUCTION

Two model streams, one heated and one unheated, have been employed to examine the effects of elevated temperature on woodland stream life, particularly the factors influencing the production of juvenile salmonid fishes and the productivity of stream ecosystems. Productivity, as used here, means the capacity of a system to produce a species of interest, in this case juvenile spring chinook salmon Oncorhynchus tshawytscha (Walbaum). The model streams were similar in construction, location, and water supply. The obvious environmental factor that could have led to differences in productivity was the elevated temperature. Although heat was introduced in amounts required to maintain a constant differential between the streams, a situation that would probably never arise in nature, the study of such a simplified regime was believed to provide more generality than attempting to simulate a certain type of thermal pollution. Identifying factors governing the productivity of stream systems that were influenced by elevated temperature, rather than modeling the outcome of the addition of a known amount of heat, was the main objective of the research.

Heated discharges, agricultural runoff, and loss of stream cover can all lead to conditions of increased temperature. In some cases, other environmental parameters such as dissolved oxygen are altered by the input of heat, to the point that they can create unfavorable conditions for stream organisms. Each instance of thermal alteration is unique, and whatever changes result depend upon the physical-chemical characteristics of the receiving body of water as well as the ability of its resident plants and animals to tolerate increased temperature and its associated effects. Because of the highly variable nature of thermal increases in naturally flowing waters and because the two artificial streams were very imperfect models of these aquatic communities, the simplest experimental approach possible was used; therefore, caution should be exercised in extrapolating the results. The streams bore little resemblance to large rivers into which heated effluents and dam releases ordinarily drain, and conclusions concerning changes in food availability, for example, may not apply to these ecosystems. Further, their partially closed design, in which water was recirculated, restricted downstream export of materials, an important process in natural streams. In spite of these and other constraints (Warren and Davis, 1971) the model streams shared many physical, chemical, and biological properties with their natural counterparts and provided

useful tools for studying the effects of environmental manipulation on productive capacities.

✓ In a previous study involving the same streams, Iverson (1972) found that the production of juvenile coho salmon (Oncorhynchus kisutch) was significantly reduced in the heated stream compared to the unheated control. He attributed this reduced production mainly to lower biomasses of immature stages of insects in the heated stream, and suggested that elevated temperature was harmful to the cold-adapted fauna that was available for colonization. Laboratory studies of survival, growth, and behavior at different temperatures (e.g., Brett, 1952; Warren, 1971) have identified the direct effects of increased temperature on young salmon, and it was the need to study both direct and indirect effects together that led to the use of large outdoor model streams. By maintaining an unheated control stream for comparative purposes, it was possible to evaluate the importance of different effects, both seasonally and between years.

FACILITIES AND METHODS

Physical Characteristics

The streams were constructed to model as closely as possible small woodland tributaries in which young salmonids commonly reside. Each consisted of two large wooden channels interconnected at the ends by irrigation pipes (Figure 1). Within each stream were 4 riffle-pool regions of equal size; the total surface area available to fish and other organisms was 22 m^2 . Windows were installed along the inner walls to facilitate behavioral observations and an aluminum roof covered the space between the 4 channels.

The slope of each stream was approximately 1.9% so that water pumped into the upstream ends would flow downstream at natural velocities. Using a Type 58 Beauvert Midget Current Meter, velocities were determined to range from about 60 cm/sec in the riffles to near 0 cm/sec at the bottom of the pools. A 2 HP centrifugal pump forced water from the downstream end of one channel to the upstream end of the other. The flow rate, which could be controlled by a gate valve at the pump, was maintained at about 1350 l/min.

Complete freedom of movement for the fish was allowed between the 2 channels. Individuals could pass downstream or upstream through the pipe from one side to the other; they were,

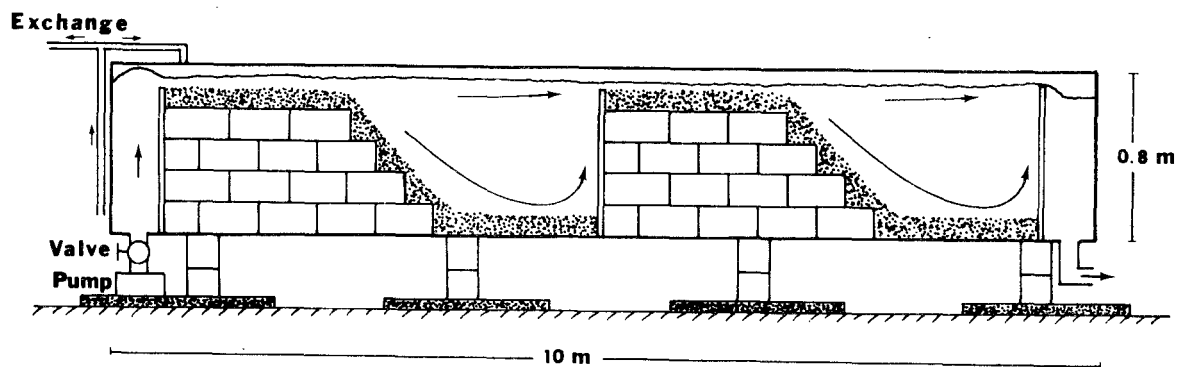
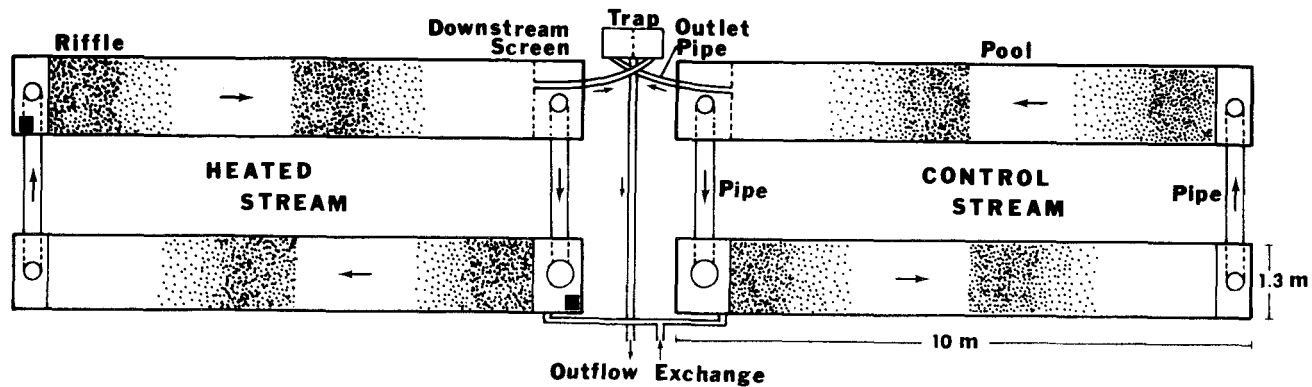


Figure 1. Top. The model streams. Arrows indicate direction of water flow and black squares in the heated stream denote location of heating units. Bottom. Cross section of one of the channels in a model stream.

however, prevented from entering the pump by a screen at the downstream end of the lowermost pool. Those wishing to leave the stream could do so through a 6 cm diameter outlet pipe originating at this screen and terminating in a partitioned trap.

Substrate consisted largely of a layer of rocks approximately 7 cm deep. The riffle areas were supported by concrete blocks that trapped and held some fine sediments, not included in the substrate analysis. Particles of different diameters were fractionated by decanting silts and clays, wet sieving the remainder, and drying each size class at 70° C for 24 hours (Table 1). The silt clay wet fraction was subsampled and filtered under vacuum on a pre-weighed 24 cm disc of Whatman no. 1 filter paper in a large Buchner funnel. Following Cummins' (1962) terminology, cobbles and pebbles comprised the great bulk (>95%) of the substrate, both in the riffles and pools, while larger sand categories were almost absent. No large boulders were present, although a few cobbles projected above the water. A significant difference in the weight of very fine sediments existed between the two streams; this difference will be discussed in connection with their invertebrate faunas.

Table 1. Particle size fractions of the model stream substrates.

	Particle size (mm) fractions as percent of total							MD ϕ
	64-256	16-64	4-16	1-4	.175-1	.088-.175	<.088	
<u>Riffles</u>								
Heated	42.61	54.29	1.41	0.02	0.16	0.09	1.41	-4.3
Control	41.97	56.46	1.39	0.01	0.03	0.01	0.12	-4.4
<u>Pools</u>								
Heated	36.13	59.74	2.06	0.17	0.05	0.70	1.13	-4.2
Control	33.96	61.78	2.12	0.13	0.06	0.78	1.12	-4.2

Water temperature in the unheated control followed natural diurnal and seasonal cycles (Table 2). Two 6 kw stainless steel heaters (Chromalox TL5360) regulated by a variable input timer facilitated temperature elevation in the heated stream. Continuous recordings of the temperature were made by Partlow RFT thermographs which were calibrated periodically with a mercury thermometer and are considered accurate to 0.3° C. The thermograph charts were read at 3 hour intervals and the temperature estimated to 0.1° F. All statistics were transformed from Fahrenheit to Centigrade units. 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. This difference is within the range of temperature elevations caused by heated discharges into running waters (Wilber, 1969; Parker and Krenkel, 1970), and associated with irrigation runoff (Eldridge, 1963) and removal of streamside

Table 2. Monthly temperatures in the model streams ($^{\circ}\text{C}$).

	Heated Stream				Control Stream			
	Mean	Low	High	Std. Dev.	Mean	Low	High	Std. Dev.
Oct. 1971	12.8	5.0	17.2	3.2	10.6	4.7	14.9	2.4
Nov.	13.0	9.8	15.4	1.5	8.8	6.8	10.1	0.9
Dec.	11.6	8.4	14.1	1.5	7.0	3.9	9.6	1.8
Jan. 1972	10.0	5.5	16.1	3.8	6.6	2.2	10.4	1.9
Feb.	10.2	5.5	13.8	1.7	6.1	1.0	10.5	2.0
March	12.2	6.6	16.1	2.5	8.8	5.6	12.5	1.5
April	12.0	8.9	16.0	1.5	8.3	5.6	12.3	1.3
May	15.0	10.6	19.8	1.9	11.2	7.1	15.5	1.7
June	16.8	11.7	21.0	1.6	12.9	9.8	16.2	1.4
July	19.0	14.8	23.3	2.8	15.3	11.3	19.4	1.6
Aug.	19.8	15.5	23.7	1.7	16.5	12.3	20.5	1.7
Sept.	17.3	11.8	22.5	2.4	13.2	8.3	18.3	2.9
Oct.	14.6	9.8	17.2	2.6	11.0	6.7	13.4	1.6
Nov.	13.1	10.2	16.1	1.1	9.4	6.6	12.6	1.2
Dec.	8.9	2.6	15.5	2.9	4.0	0.0	10.0	4.7
Jan. 1973	9.2	4.1	12.8	2.0	5.8	1.0	9.1	1.9
Feb.	11.5	8.8	14.0	1.3	7.6	5.5	10.0	1.2
March	12.0	8.8	14.0	1.0	8.1	5.5	10.1	0.9
April	13.8	10.2	17.2	1.5	9.8	6.1	13.2	1.5
May	16.7	12.2	21.1	2.0	12.8	8.5	17.6	2.1
June	18.1	13.9	23.7	2.8	14.0	10.3	19.3	2.6
July	19.4	14.7	23.8	2.0	15.5	11.1	19.5	1.8
Aug.	19.3	15.6	22.8	1.7	15.5	11.8	18.3	1.6
Sept.	19.3	15.3	23.1	1.4	15.4	11.4	19.0	1.3
Oct.	16.1	13.9	18.2	1.2	12.3	9.5	14.4	1.2
Nov.	12.9	9.8	17.1	1.7	9.1	6.1	13.4	1.6
Dec.	12.5	9.8	15.6	1.1	8.7	6.1	10.6	0.9

vegetation (Brown and Krygier, 1970). It is also within the limits of increase legally allowed by many states (Burd, 1969).

✓ Both streams received approximately equal amounts of unfiltered exchange water from a small spring-fed creek that contained aquatic invertebrates and algae but no fishes. Seasonal changes in various water quality parameters for the creek are given in Table 3. The amount of exchange water varied according to availability, but was usually from 10-20 l/min per stream. During the dry summer of 1973 when flow in the small creek almost ceased, the exchange supply was supplemented by a mixture of well water and unfiltered water pumped from a larger nearby creek. Care was taken not to inhibit the passage of living plants and animals into the model streams in order to permit opportunities for colonization. Outgoing exchange water passed through the overflow pipe and the fish trap before leaving the system.

The model streams were located at the Pacific Cooperative Water Pollution Laboratory (Oak Creek Laboratory) near Corvallis in western Oregon. They have been operating almost continuously since completion of construction in 1969 (Iverson, 1972), this making possible the establishment of a variety of plants and animals. Occasional power failures from a few seconds to several hours caused temporary cessation of flow in the streams, but large-scale changes in community structure resulting from these blackouts were never

Table 3. Dissolved mineral content (mg/l) in the tributary providing exchange water to the model streams. Analyses were made over a period from 1959-1967 and were reported in part by Doudoroff, Leduc, and Schneider (1966).

	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.
Hardness (CaCO ₃)	45-62	40-76	79-92	86-98
Bicarbonate (HCO ₃)	60-84	52-104	107-127	66-133
Conductivity (25° C)	108-148	48-196	128-212	129-214
Dissolved Solids	94-107	84-125	127-154	101-147
pH	7.4-8.0	7.2-7.9	7.2-8.0	7.3-7.8
Silica	24-33	22-35	35-40	35-40
Calcium	11-15	10-19	18-24	12-25
Magnesium	4.3-8.6	3.7-6.8	7.8-8.4	5.4-8.6
Sodium	5.2-6.5	4.4-7.3	7.8-9.2	6.3-9.2
Potassium	0.4-0.6	0.3-0.6	0.5-0.9	0.2-0.8
Sulfate	0.8-2.2	0.2-1.6	0.6-2.2	0.2-2.4
Chloride	4.0-4.8	4.0-5.0	4.5-5.2	5.0-7.0
Fluoride	0.1	0.1	0.1	0.1
Nitrate	0.1-0.5	0.0-0.4	0.1-0.3	0.0-0.9
Iron	0.20-0.47	0.11-0.53	0.21-0.37	0.14-0.21
Phosphate	0.05-0.13	0.04-0.10	0.11-0.13	0.01-0.24

detected. On two occasions, however, the streams were shut down for significant periods. In October 1971, the main pumps were replaced. The 2-day changeover took place prior to initiation of bottom sampling so that its impact on the invertebrate community could not be assessed. In early December 1972, unusually cold weather caused ice to form between the glass observation windows and concrete blocks supporting the riffles in the unheated stream. Expansion of this ice cracked the glass and a considerable amount of water was lost. Replacing broken windows required that all but a small amount of water be drained and part of the riffle sections be removed. As a result, the entire riffle substrate in the unheated stream was exposed for several days while new windows were being installed and many plants and animals were lost despite efforts to keep the riffles wet. One window was also replaced in the heated stream at this time, necessitating exposure of one riffle. Spraying the rocks to maintain moisture within the substrate resulted in fine sediments and detritus being washed into the pools.

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 that fell into the streams. Some material was blown in from shrubs

and grasses, but because the streams were raised from the ground, this amount was small. Surrounding vegetation provided only partial shading during summer, in contrast to the dense canopy that forms over many woodland streams in western Oregon and reduces direct solar radiation to low levels (McIntire and Phinney, 1965).

Periphytic algae comprised 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. Cladophora became so abundant during summer months that some had to be removed from the streams in order that the salmon could be collected. Filamentous algae of this type occur infrequently in western Oregon because of low incident light levels and the scouring effects of winter freshets (McIntire, 1973) - two attributes the model streams did not simulate. Following heavy mortality associated with repairs in the control stream during December 1972, Cladophora was slow to become reestablished and it was not until June 1973 that it again became dominant. Another filamentous green alga, Stigeoclonium subsecundum, was observed on the riffles from April to July but was reduced or absent during other months.

Various diatoms also made up a significant proportion of the stream 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. Less common diatom species observed in seasonally variable numbers included Fragilaria vaucheriae, Achnantes lanceolata, Rhoicosphenia curvata, Cocconeis placentula, Navicula tripunctata, Navicula cryptocephala, Navicula salinarum, Gyrosigma sp., Gomphonema parvulum, Gomphonema intricatum, Cymbella sinuata, Cymbella prostrata, Epithemia turgida, Nitzschia linearis, Nitzschia dissipata, and Surirella apiculata.

Blue-green algae were generally found in late spring and summer. Calothrix and Nostoc were both more abundant in the heated stream and appeared there earlier in the year. A red alga, Batrachospermum moniliforme, was first observed in spring 1972 and then in increased numbers in subsequent years. The only higher plant was an unidentified dense moss attaching to large cobbles in the riffles.

Diatoms and desmids, in addition to plant materials from terrestrial sources, were common in the drift. Closterium lunula was

abundant in spring and early summer and was an important food source for filter feeding invertebrates. Filamentous algae, particularly Melosira and Cladophora, were frequently dislodged from riffles through the grazing activities of snails and other herbivores and floated downstream to become entangled in different areas of the substrate or to accumulate on the outlet screen. This screen was scrubbed daily and any plants or detritus discarded from the streams.

Analytical Methods

Fish

Races of chinook salmon are identified by the period of adult migration to spawning grounds. In Oregon, the spring race enters fresh water throughout spring and early summer, with peak spawning taking place in late summer and fall. Juveniles hatch and emerge from the gravel in fall, and many are believed to remain in fresh water until their second spring (Rich, 1920, 1925; Rich and Holmes, 1929). While recent investigations have identified significant variations in the time of seaward migration of young spring chinook (French and Wahle, 1959; Mattson, 1962, 1963) and it has also been found that some juvenile fall chinook may remain in natal streams for a year (Reimers and Loeffel, 1967; Reimers, 1971), spring chinook were used in the experiments because of their general tendency to remain longer in fresh water.

Fertilized eggs were obtained from Marion Forks Salmon Hatchery egg taking station (Oregon Fish Commission) on the North Santiam River, a Willamette River tributary. Eggs for the 1972 experiment taken October 3, 1971 were the spawn of a single male and female; those for the 1973 experiment taken October 1, 1972 were selected at random from the spawn of 3 females and 4 males. Following fertilization the eggs were transported immediately to holding facilities where they were incubated at a constant 12° C. Separate groups of eggs were placed in baskets in the heated and control streams on the day they were fertilized in September 1973 for studies of early survival, developmental rates, and growth.

In 1971 eggs were not introduced to the streams until they had reached the "eyed" stage. Thereafter they were hatched in the floating baskets and released just prior to yolk absorption. 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 2 streams was identical. A 10 week recolonization period following repairs delayed introduction in 1973 until mid-March, when identical numbers were released simultaneously.

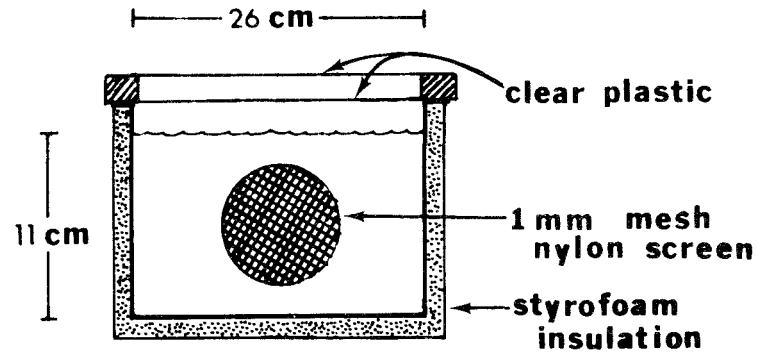
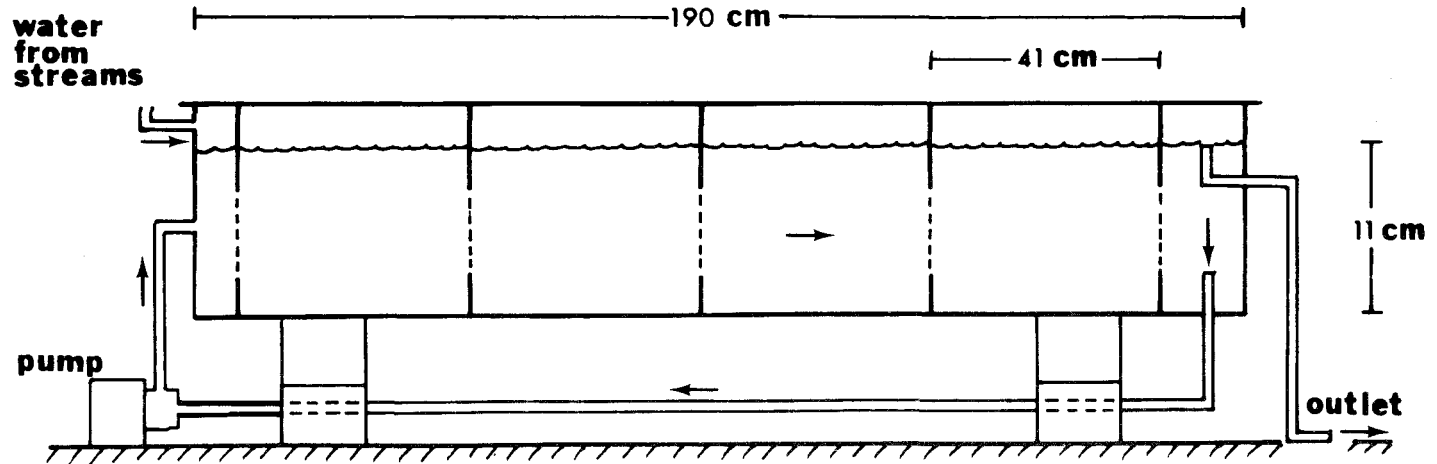
Once they were large enough to handle --about 0.4 g wet weight --fish were removed from the streams for weighing and measuring every three weeks until an experiment was terminated. Each

rifle-pool section was screened and then seined until all individuals had been caught. Following anesthesia in tricaine methanesulfonate (MS 222) fork length measurements to the nearest mm were made and blotted wet weights determined to the nearest 0.01 g on an electronic balance.

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 ml of water were gently injected into the stomach, forcing the contents out through the mouth into a collecting beaker. Seaburg (1957) has discussed the merits of a sampler designed to flush material from the stomach with water. Food samples were sorted within 48 hours under a dissecting microscope. The combined whole food organisms and identifiable fragments of each taxon were weighed to the nearest 0.1 mg; unidentified fragments, algae and detritus, and exuviae were not included in the analyses. Each taxon was assigned a percentage of the diet based on its fraction of the total wet weight of the sample.

Ancillary experiments were conducted to estimate the effect of elevated temperature on food conversion efficiency. Fish of the same parentage and size as those in the model streams were placed into partitioned troughs (Figure 2) having translucent covers where they were fed rations of live Tubifex ranging from near maintenance

GROWTH EXPERIMENT TROUGH



CROSS SECTION SHOWING PARTITION

Figure 2. Troughs used for studies of growth and early development.

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. Growth experiments were carried out once each season during 1973. Fewer individuals were used in summer and fall experiments because they were larger and the effects of crowding became severe.

Early development was compared in a separate study carried out during fall 1973. Fertilized eggs were incubated in 50x50x15 cm covered wire baskets that had been coated with non-toxic paint and floated in the lowermost pools of the two streams. Baskets were checked daily for dead eggs, which were counted and removed, and newly hatched alevins, which were segregated according to hatching date and placed into the partitioned troughs that had been used for the growth experiments. As soon as the fry could swim actively for 5 minutes without settling to the bottom, they were counted as having reached the "swim-up" stage, while the "button-up" stage was attained when no yolk material was visible on the ventral surface. Samples of fry were removed at each life stage from hatching to button-up for caloric determinations, and any dead fry in the troughs counted and removed immediately.

Production, growth rates, and mean biomasses of salmon in the streams were calculated according to the procedures used by Warren et al. (1964). 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 fishes' weight (grams) divided by the cube of its fork length (cm). Figure 9 (p. 630) of Warren et al., describing this relationship for cutthroat trout, was used for graphical estimates of calories per gram of wet weight for juvenile chinook salmon.

The measurement of evenness in biomasses of invertebrates employed an index proposed by McIntosh (1967) and discussed by Pielou (1969). Evenness expressed the equitability of species biomasses as fractions of the total weight of invertebrates in the benthos; where it was not possible to recognize separate species (Appendix I), values for entire taxa were used. The formula was $(N - (\sum n_i^2)^{1/2}) / (N - N/s^{1/2})$ where N was the total biomass of a sample, n_i was the biomass of the i^{th} species (or taxon), and s was the number of species in the sample.

Invertebrates

Plants and animals occurring in the benthos were sampled tri-weekly. Wire baskets (Figure 3) painted with non-toxic paint and having wood bottoms were filled with substrate and placed against supporting blocks under the riffles. The 2 cm mesh wire sides were small enough to retain most of the particles but sufficiently large that movement of invertebrates into and out of the baskets was

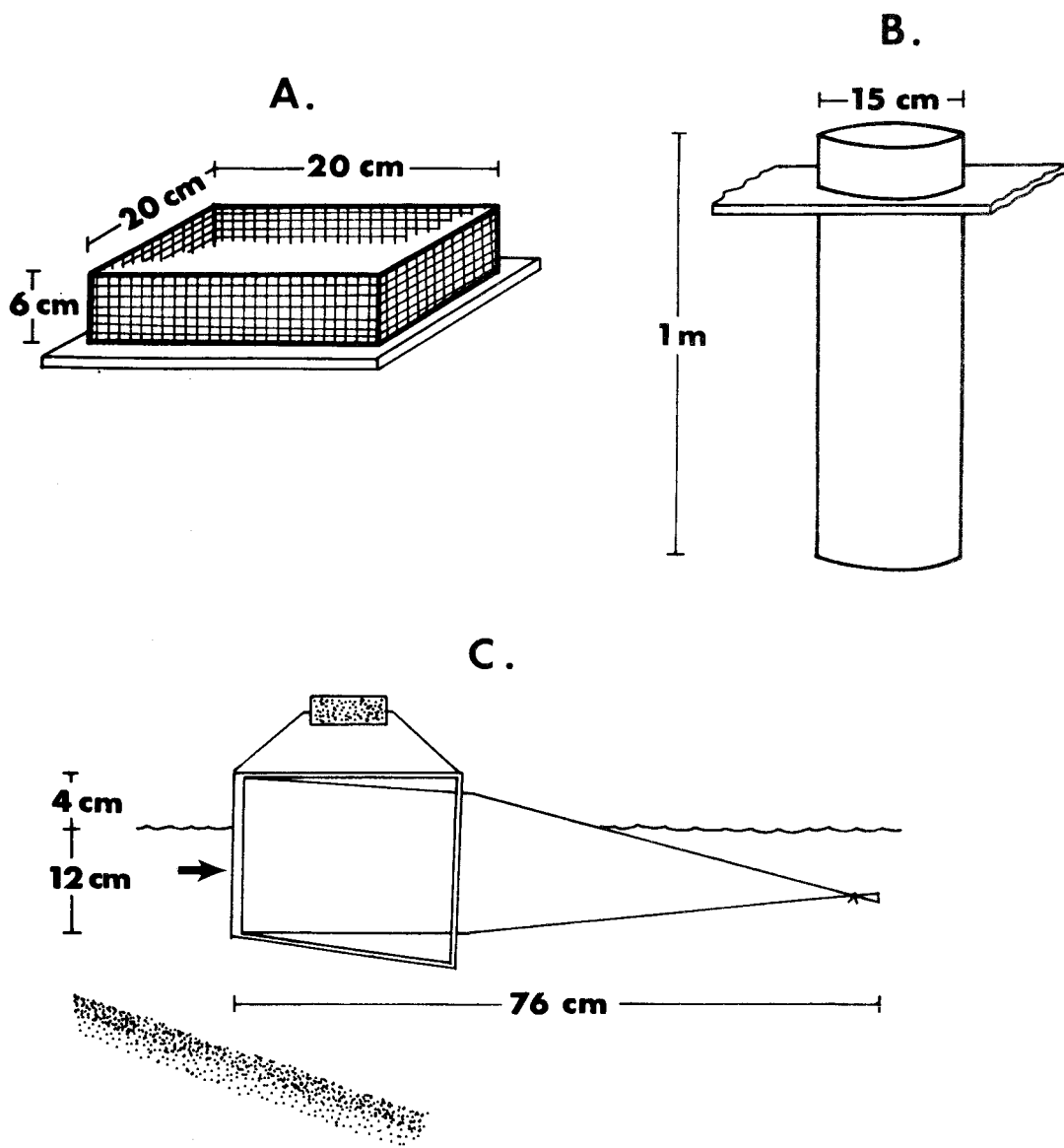


Figure 3. Materials used for sampling invertebrates. A. Wire basket for riffle benthos. B. Aluminum pipe for pool benthos. C. Drift net shown suspended from wooden crossmember.

probably not inhibited. 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 4 baskets (0.16 m^2 total) were then collected in a 200μ mesh Nitex bag and preserved initially in 10% formalin. Cleaned material was returned to the riffles and the baskets refilled with unsampled substrate and placed in an area next to the original location. Baskets were emptied in regular rotation so that 3 months elapsed between sampling times for each basket. Wire baskets for sampling stream benthos were first used by Wene and Wickliff (1940) and subsequently in other studies, (e.g., Sheldon, 1972; Iverson, 1972). Their limitations have been discussed by Cummins (1962) and Hynes (1970).

Pools were sampled by pushing an aluminum pipe (0.018 m^2 cross sectional area) into the bottom and scrubbing the enclosed substrate thoroughly for 15 minutes with a long-handled fiber brush while siphoning dislodged plants, animals, and detritus into a 200μ mesh bag. One sample was taken from each of two pools in the streams and the collected material combined and preserved in 10% formalin. Each pool was sampled once every six weeks; the location of samples within pools was haphazard.

Drifting organisms were also collected tri-weekly by means of rectangular drift nets (Anderson, 1967) that were suspended at the downstream end of the riffles where surface turbulence ceased. Two nets were fished in each stream (one per channel) for a 24 hour period. Samples were removed and preserved at approximately sunrise and sunset so that diurnal differences in drift rates could be detected. The nets were constructed of 333 μ mesh nylon and were held in place by metal frames. The upper part of the openings extended 4 cm above the water line so that surface floating organisms could also be trapped. 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 mouth (300 cm²). 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. Mundie (1971) noted that drift nets having mesh sizes larger than 200 μ would fail to retain the larvae of certain Chironomidae, and the biomasses of these and other very small organisms were probably underestimated in the collections. Further, juvenile salmon could feed on drifting invertebrates before they entered the nets, although very few individuals stationed themselves over the riffles.

All samples were allowed to remain in formalin for 1-2 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 by eye to remove invertebrates larger than 4 mm, and then subsampled (10% by volume) and preserved in ethanol for examination under a dissecting microscope. All organisms were measured to the nearest millimeter, assuming that no length change took place in the preservative, using a metric grid placed on the stage of the microscope. The number of individuals of 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^o C for 4 days and then ashed at 600^o 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 on 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 value obtained from 5 samples combusted in a Parr 13031 oxygen bomb calorimeter.

Because weight loss takes place in 10% formalin and 70% ethanol and because different species lose weight at different rates (Howmiller,

1972; Stanford, 1973) invertebrate biomasses were not computed from preserved wet weights. Live specimens were collected from a nearby stream, grouped according to size and species, and their blotted wet weights recorded individually to the nearest 0.1 mg. After drying 4 days at 70° C they were again weighed and their dry weights converted to calories by values obtained from Cummins and Wuycheck (1971) or determined directly by combustion in a Parr 1411 semimicro calorimeter. 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: 6.25 for the riffles, 27.78 for the pools. 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 biomass for each taxon. All data (sample number, size class, number of individuals, taxon code) were recorded on standard punch cards for computer processing.

Food habits of invertebrates were determined by examining gut contents of specimens taken from the streams, or when insufficient

numbers of individuals were available, from appropriate literature sources (Jones, 1950; Usinger, 1956; Teal, 1957; Chapman and Demory, 1963; Hynes, 1970; Cummins, 1973). Temporary wet mounts of thoracic gut contents were examined at 100X and the percentages of animal and plant-detritus remains were estimated. No attempt was made to separate plants from detritus in the ingested food. Length of specimens was noted, because the relative percentages of plant and animal components in the food changed with increased size for many species. Early instars of carnivorous forms apparently consumed mostly detritus; Sialis californica larvae, for example, did not begin to feed heavily on prey (chiefly worms) until they had attained a length of at least 5 mm. Others such as the caddisfly, Psychomyia lumina, began eating other animals at 5-7 mm, but still retained a substantial fraction of plants and detritus in its diet. Percentages of the 2 food categories were assigned to all size classes present in each species. Multiplying the biomass of each size class by these percentages gave carnivore and herbivore-detritus-feeder biomasses, i.e., each species contributed a certain fraction of its total standing crop to carnivore and herbivore functional groups within the community. Many organisms subsisted exclusively on plant and detrital materials and their associated microflora; no species was solely carnivorous throughout its life history.

RESULTS AND INTERPRETATION

Temporal Changes in Production

Table 4 summarizes survival, growth, and production statistics of the experimental spring chinook populations. Total production in the heated stream was less than half that of the control in 1972. The following year, after repairs, control stream production was only about 30 percent higher than 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 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 around April and May (Figure 4), this being related to the exceptionally high growth rates that took place in mid-spring. Negative production occurred during fall months, when many fish had stopped growing and some were losing weight. Low growth rates observed following release in 1972, just after yolk absorption, were average figures and may have been misleading. Some individuals grew very rapidly during their first few weeks of residence; others

Table 4. Mean production statistics of experimental chinook salmon populations. H = heated stream, C = control stream.

Time Interval	Indiv. Size (kcal)		Population Size (no.)		Mortality Rate (%/day)		Biomass (kcal/m ²)		Growth Rate (cal/kcal/day)		Production (kcal/m ²)		Production Rate (kcal/m ² /day)	
	H	C	H	C	H	C	H	C	H	C	H	C	H	C
1972														
12/20-1/24	.31		302		1.607		4.12		1.85		.27		.008	
1/25-2/14	.49		169		.461		3.09		21.48		1.39		.063	
2/15-3/7	.84	.48	140	358	1.218	.618	4.20	7.24	26.50	3.08	2.23	1.14	.112	.022
3/8-3/27	1.18	.92	112	271	.743	.808	5.14	8.62	16.00	33.03	1.73	5.42	.087	.319
3/28-4/15	1.41	1.32	91	233	1.226	.733	5.38	11.91	9.31	19.21	.95	4.26	.050	.224
4/16-5/6	2.18	2.01	65	184	1.627	1.388	5.32	14.04	23.80	47.42	2.27	5.89	.108	.280
5/6-5/27	2.77	2.79	47	145	.915	.497	5.29	15.82	11.35	15.48	1.26	5.14	.060	.245
5/28-6/16	3.61	3.36	40	125	.476	.839	5.80	17.61	13.17	9.27	1.53	3.27	.077	.164
6/17-7/7	4.36	3.75	34	105	.877	.751	6.25	16.97	8.96	5.22	1.18	1.86	.056	.089
7/8-7/28	4.53	4.32	31	92	.005	.347	6.26	16.97	1.82	6.73	.24	2.40	.011	.114
7/29-8/22	4.82	4.35	26	85	1.240	.345	5.26	16.65	2.48	.28	.34	.12	.013	.005
8/23-9/8	5.68	4.74	19	67	.840	2.033	4.65	13.84	9.64	5.05	.76	1.19	.045	.070
9/9-10/3	5.79	5.01	17	52	.222	.150	4.56	11.52	.77	2.22	.09	.64	.004	.026
10/4-10/19	5.61	5.76	16	48	.735	.612	4.15	11.87	- 1.44	9.29	-.13	1.65	-.008	.103
10/20-11/7	6.15	5.73	14	46	.350	.004	3.88	12.01	4.83	-.27	.36	-.06	.019	-.003
11/8-11/30	6.45	5.50	14	45	.000	.002	4.01	11.49	2.07	-1.78	.19	-.47	.009	-.022
Totals											14.66	32.45		
Means							4.84	13.33					.045	.117

Table 4. Continued.

Time Interval	Indiv. Size (kcal)		Population Size (no.)		Mortality Rate (%/day)		Biomass (kcal/m ²)		Growth Rate (cal/kcal/day)		Production (kcal/m ²)		Production Rate (kcal/m ² /day)	
	H	C	H	C	H	C	H	C	H	C	H	C	H	C
1973														
3/16-4/7	.98	1.02	187	185	.568	.659	7.14	7.48	14.49	12.70	2.38	2.19	.103	.095
4/8-4/26	1.57	1.48	154	168	1.233	.154	8.93	9.55	24.36	19.37	4.13	3.51	.217	.185
4/27-5/18	3.33	2.75	109	150	1.741	.889	12.14	14.42	32.65	27.30	8.72	8.66	.396	.394
5/19-6/7	4.69	3.63	65	106	2.415	2.261	11.85	15.37	17.85	14.52	4.02	4.24	.211	.223
6/8-6/27	6.92	4.98	41	63	1.087	1.753	10.82	12.33	19.31	15.68	4.16	3.87	.208	.193
6/28-7/19	7.31	5.99	34	45	.417	.900	11.00	11.22	2.49	8.37	.60	2.07	.027	.094
7/20-8/9	6.87	6.96	32	41	.303	.010	10.31	12.07	-2.96	7.13	-.64	1.81	-.030	.086
8/10-8/30	7.00	7.10	30	40	.154	.116	9.46	12.78	.89	.95	.18	.25	.008	.012
8/31-9/19	6.76	7.89	29	37	.167	.750	9.07	12.61	-1.66	5.02	-.32	1.33	-.015	.063
9/20-10/10	6.48	8.23	29	33	.000	.280	8.73	12.09	-2.01	2.01	-.37	.51	-.018	.024
10/11-10/31	6.35	9.00	26	29	.862	.781	7.58	11.36	-.97	4.26	-.15	1.02	-.007	.048
11/1-11/21	6.65	8.71	22	25	.595	.529	6.50	10.06	2.18	-1.56	.30	-.33	.014	-.016
11/22-12/12	6.07	8.66	19	23	.907	.198	5.49	9.08	-4.34	-.27	-.50	-.05	-.024	-.002
Totals											22.51	29.08		
Means							9.16	11.57					.084	.108

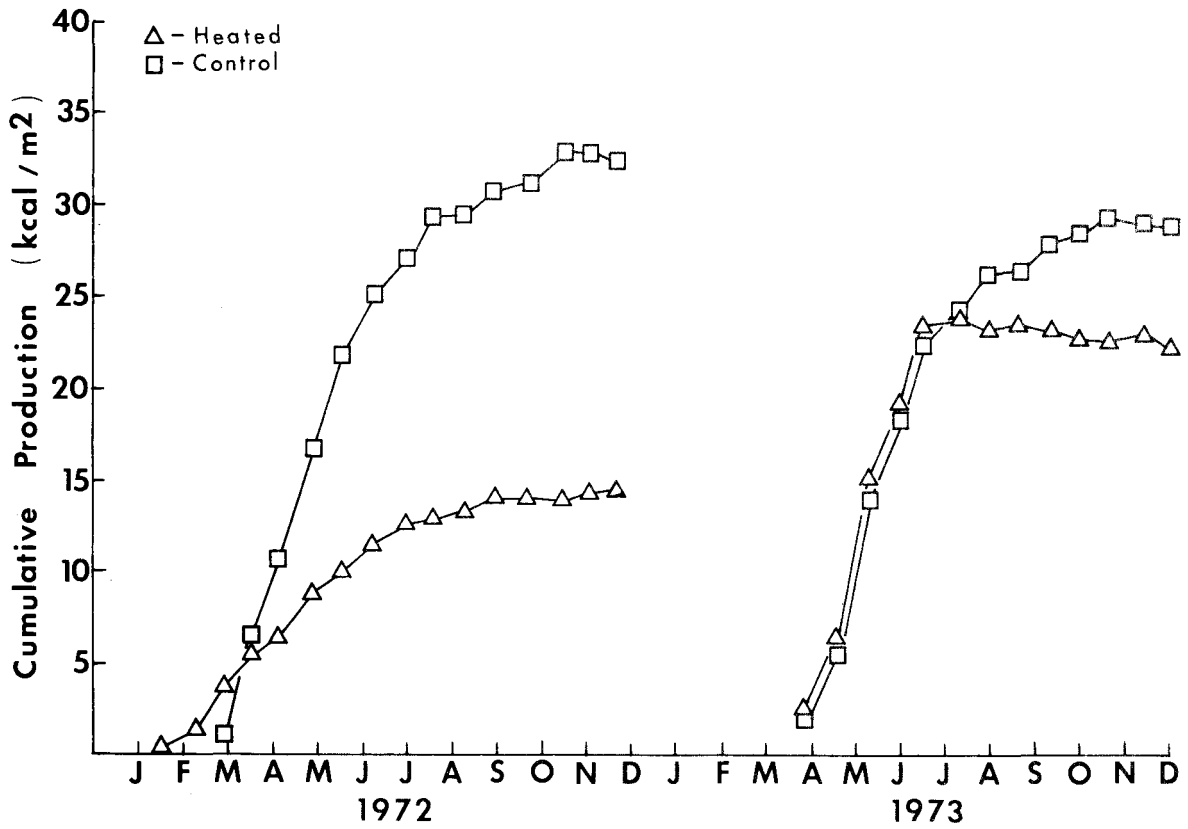


Figure 4. Cumulative production of juvenile spring chinook salmon in the model streams during 1972 and 1973.

apparently did not make the transition to feeding in the model streams and died from problems associated with starvation.

Table 4 shows that considerable variation in production occurred within each stream not only among seasons but also between years. In seeking an explanation of temporal changes in production it becomes necessary to examine in detail factors that influence key elements of the production process: a population's biomass and the growth rates of its members. Because growth and biomass were generally reduced in the heated stream, its rate of production was lower than in the control. Elevated temperature acted both directly and indirectly on the juvenile chinook, and an understanding of temporal changes in production requires that these different avenues of influence be considered.

Direct Effects of Temperature

Early Development

Developmental rates, mortality, and weight changes were studied from fertilization to yolk absorption, prior to active feeding by young fry. Because eggs were incubated in the model streams and fry were reared in troughs receiving water directly from the streams, experimental temperature regimes were similar to those summarized in Table 2 from October to December 1973. The results are given in

Table 5. As expected, eggs and fry developed much more rapidly in the heated stream, with active feeding commencing almost a month earlier than in the control. Biomasses (expressed in caloric units and including yolk material) declined from hatching yet wet weights increased as the fish took on water. Mean biomasses per individual at each developmental stage did not differ greatly between the streams, although control fish were about 5 percent larger at the bottom-up stage. Mortality (given as a fraction of the initial number of eggs) was considerably greater in the heated stream, with heaviest losses occurring in the period between hatching and initial swimming. The total mortality of 38.5 percent was higher than generally occurs in nature. Briggs (1953) gave an average mortality of 14.0 percent over the same developmental interval for fall chinook in a California stream, a figure very similar to 13.3 percent observed in the control, while Vronskiy (1972) found instances of less than 10 percent mortality.

Increased mortality of chinook eggs and fry associated with elevated temperature has been studied by Donaldson (1955), Combs and Burrows (1957), Olsen and Nakatani (1968) and Eddy (1972), with the general conclusion that, at near air-saturation oxygen levels, temperatures in 12-15^o C range result in significantly reduced survival. Table 2 shows that mean monthly temperatures in the heated stream for October through December 1973 were at or above

Table 5. Developmental rates, mortality, and individual biomasses of juvenile chinook salmon maintained in water from the model streams. Mean values are followed by ranges (in parentheses).

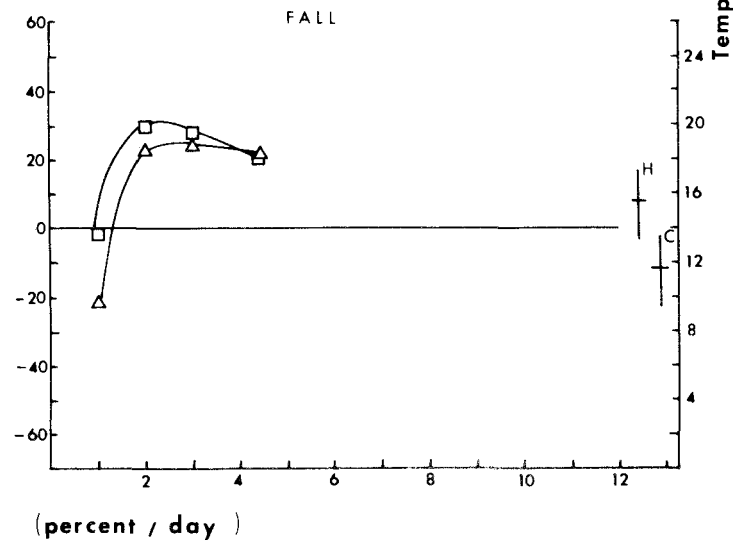
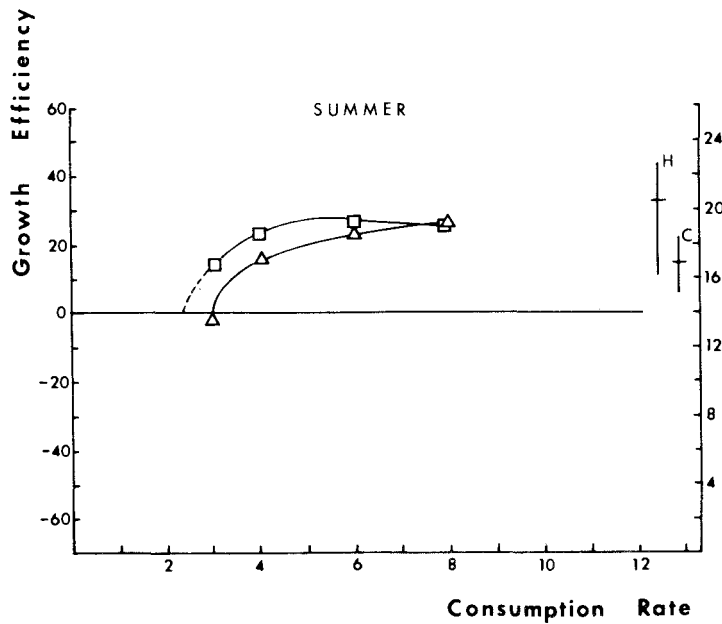
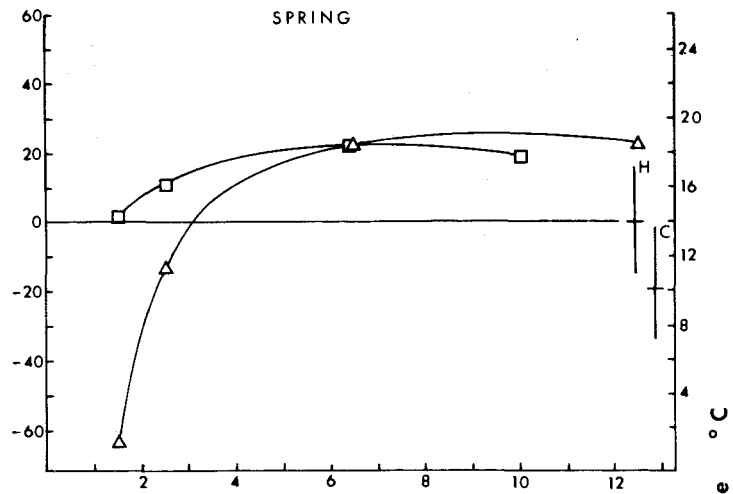
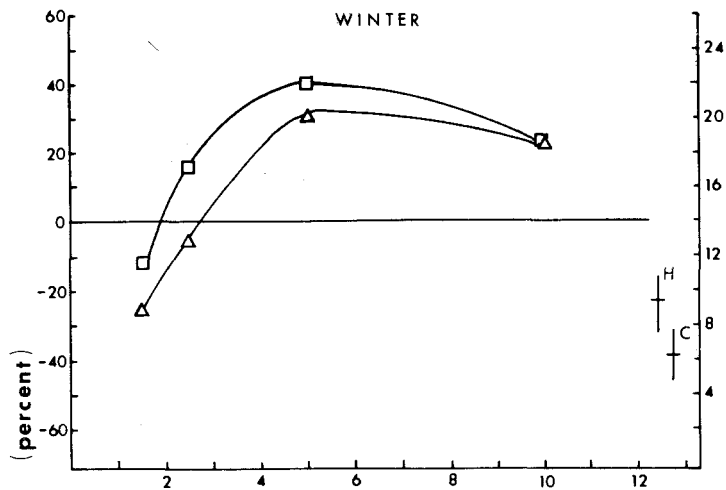
		Heated Stream	Control Stream
Developmental Rates (days)	Hatching	37 (29 - 40)	52 (44 - 56)
	Initial Swimming	56 (52 - 59)	77 (74 - 79)
	Button-up (approx.)	73	99
Mortality (%)	Pre-hatching	13.0	7.1
	Hatching	7.3	2.8
	Hatching to Initial Swimming	17.9	3.3
	Initial Swimming to Button-up	.3	.1
	Total	38.5	13.3
Biomass (cal/individ.)	Hatching	502 (404 - 583)	511 (455 - 593)
	Initial Swimming	428 (354 - 482)	415 (303 - 449)
	Button-up	330 (249 - 366)	345 (285 - 413)

these levels. Although some experimental mortality was probably induced through handling or from lack of support in the troughs where considerable effort was expended by sack fry in attaining an upright position (the "righting response" of Bams, 1969), the threefold difference in mortality indicates that 4° C elevation during incubation and yolk absorption caused a significantly lower survival rate. Had fish been released into the model streams in proportion to their pre-feeding survival, instead of being introduced in equal numbers, differences in production would have been even greater than those observed.

Growth Efficiencies

In ancillary experiments, the efficiency with which ingested food was converted to new tissue varied over the range of experimental rations, between temperature regimes, and also between seasons (Figure 5). Differences between fish held in heated and unheated water were greatest at low rations and least at high ones. At low levels, control individuals were much more efficient; at high levels, there was no appreciable difference except during spring when the elevated temperature facilitated increased consumption and slightly higher efficiencies. The highest rations were close to the maximum amount of food that the young salmon would eat in a day, and the graphs for summer and fall show that maximum consumption declined

Figure 5. Seasonal changes in growth efficiencies of juvenile chinook, calculated according to the formula $E = (G/C) \times 100$, where G was the average relative growth rate (percent body weight/day) and C was the consumption rate (percent body weight/day). All experiments lasted 10 days and were preceded by a 10 day acclimation to temperature regime and ration size. Triangles represent the heated stream; squares represent the control. Each point is the mean value derived from a number of fish held together and receiving similar rations. Sample sizes were as follows: winter - 20 indiv./level, spring - 20 indiv./level, summer - 12 indiv./level, fall - 10 indiv. per level. Mean biomasses at the start of each experiment were: winter - .59 kcal, spring - 1.26 kcal, summer - 7.05 kcal, fall - 8.37 kcal.



as individuals size increased. A similarly converging relationship with increased ration between growth efficiencies at different temperatures was established for coho salmon by Averett (1969) and for steelhead trout (Salmo gairdneri) by Wurtsbaugh (1973). It illustrates that when food is relatively scarce, increased metabolic requirements associated with elevated temperature act to reduce growth rates.

These experiments showed that, at high consumption rates, growth rates were not appreciably lowered by thermal increases and were sometimes higher when greater appetite gave rise to increased consumption. However, it is doubtful that in nature food is generally so abundant as to permit fish to compensate for high temperatures, so that reductions in growth resulting from elevated temperature would probably occur.

Indirect Effects of Temperature

Disease

Intermediate stages of a parasitic trematode, Nanophyetus salmincola, were present in the streams beginning in late spring and continuing through summer and fall. Infective cercaria emerged from the snail Oxytrema silicula to encyst in the skin and tissues of juvenile chinook as metacercaria. Figure 6 compares the incidence of heavy infection between the two populations and also shows the difference in mean weights between heavily and lightly infected

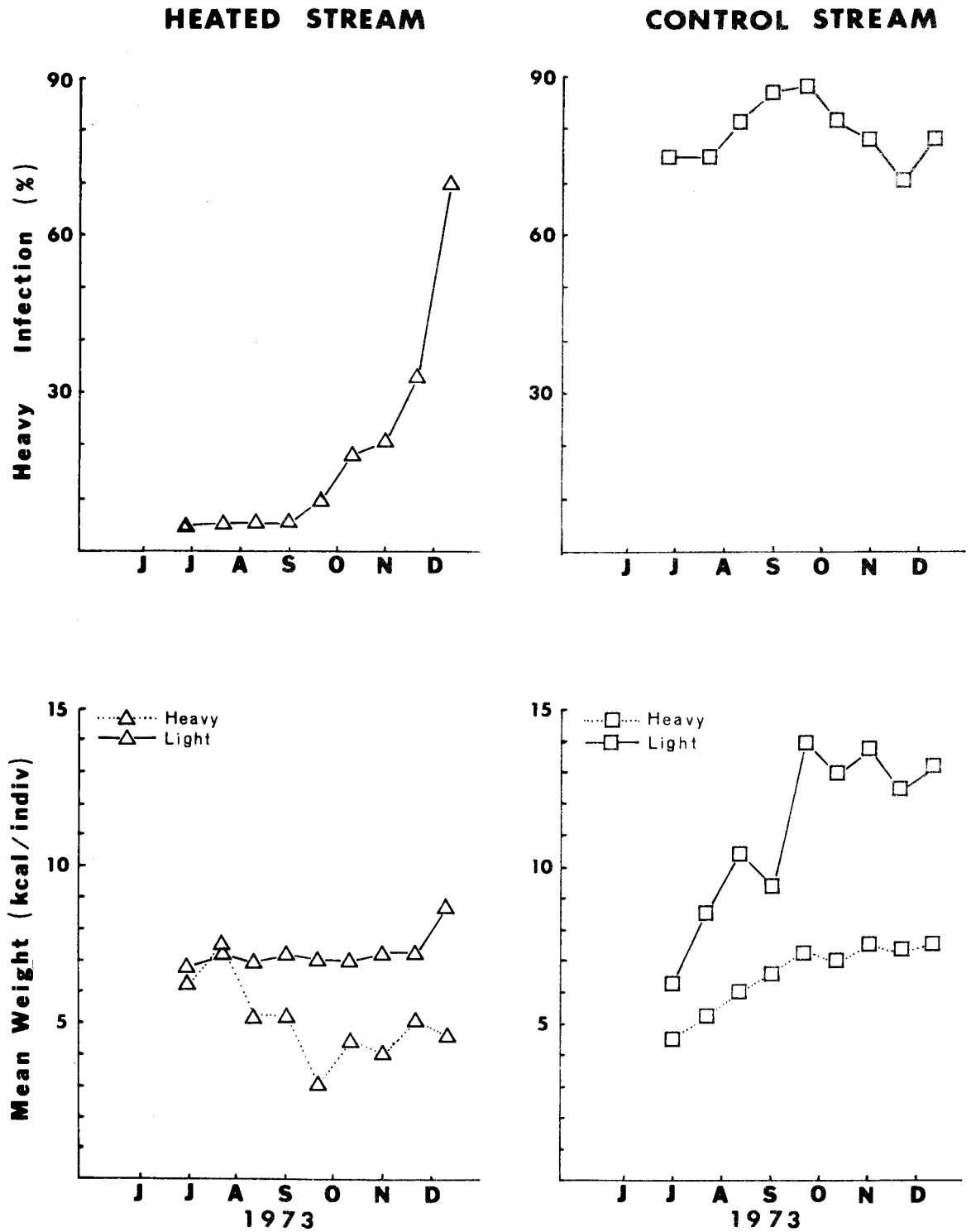


Figure 6. Infection rates and weight differences of juvenile chinook infected by metacercaria of Nanophyetus salmincola.

individuals. The distinction between heavy vs. light infections was made visually and was somewhat arbitrary; conspicuous bumps at the base of the caudal peduncle, darkening of fins, and papules on the body surface were considered symptoms of heavy infection.

While the disease was obviously present in 1972, it was not until after its appearance in 1973 that attempts were made to quantify its effects.

Infection rates in the heated stream remained low through summer and early fall and began to increase with the onset of winter until termination of the experiment. Heavy infections were present in most of the control fish soon after cercaria had begun emerging from the snails. In addition, a greater difference existed between the mean weights of heavily and lightly infected individuals in the control stream. Apparently the impact of this disease was much more severe in the control than in the heated stream. R. E. Milleman (personal communication) has suggested two reasons why this might have been so: (1) elevated temperature, if it was high enough, may have been directly lethal to cercaria, and (2) it may have considerably reduced the amount of time cercaria had to search for a host.

Sharply increased infection rates during late fall in the heated stream pointed to a greater incidence of heavy infection as temperature dropped below about 19^o C. A third possible explanation for differences in disease severity between the two streams was that

cercaria were much more abundant in the control than in the heated stream, but there was no evidence to support this. The biomass of Oxytrema, the first intermediate host, was usually greater in the heated stream. Further, periodic sampling of snails throughout summer and fall failed to detect a single individual containing Nanophyetus sporocysts and rediae in either stream, this indicating that cercaria were entering in approximately equal numbers with exchange water, rather than emerging within the streams themselves.

Position in the social hierarchy within a pool appeared to be connected with the degree of infection. Large, dominant fish occupied positions in swift water at the base of the riffles where they had first opportunity to intercept drifting food organisms. These dominant individuals rarely showed signs of heavy infection, whereas socially subordinate ones in slack water at the back of the pools were strongly affected. This was particularly true of those remaining next to the bottom, where cercaria were presumably numerous.

Differences in mean weights between heavily and lightly infected fish show that the parasite had a depressant effect upon growth rate, an effect that caused an unequal reduction in production for the two streams. Although it was impossible to attribute mortality directly to infection, it must certainly have contributed to deaths occurring in late summer and fall, particularly in the control. As a result, the magnitude of difference in summer and fall production between

the heated and control streams was narrowed; had the parasite been absent, control production would have been proportionately higher than in the heated stream, where overall effects of parasitism were comparatively minor. Disease protection associated with elevated temperature is apparently a rare occurrence in nature. For bacterial infections, at least, increasing temperatures often precede outbreaks in Pacific salmon (Ordal and Pacha, 1963; Colgrove and Wood, 1966), and a serious protozoan pathogen Ceratomyxa shasta is not found where water temperature is low all year long (Sanders, Fryer, and Gould, 1970).

Food Availability

An accurate measure of food availability requires, (1), that preferred food items be identified, (2) that it be determined when they are available for consumption, and (3) that their relative abundance be 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 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.

Table 6 relates the percentage composition of various invertebrate taxa from stomach samples with the percentages of those taxa in the day drift during different periods. Oligochaetes were almost completely excluded from the diet of large fish even though they comprised an important fraction of the drift. Mollusca (exclusively Gyraulus sp.) and Trichoptera were larger food items and were consumed more readily by larger fish. Ostracods (Herpetocypris chevreuxi) were taken throughout the year in proportion to their 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 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 7) were not well correlated with measurements of the biomass of those organisms in the riffle benthos (Figure 8). Moreover, seasonal patterns in drift differed greatly between 1972 and 1973, with

Table 6. Percentage of different taxa (by weight) in the food of juvenile spring 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	
	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		Misc.	
	H	C	H	C	H	C	H	C	H	C
1972										
Winter	25 (9)	52 (52)	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)

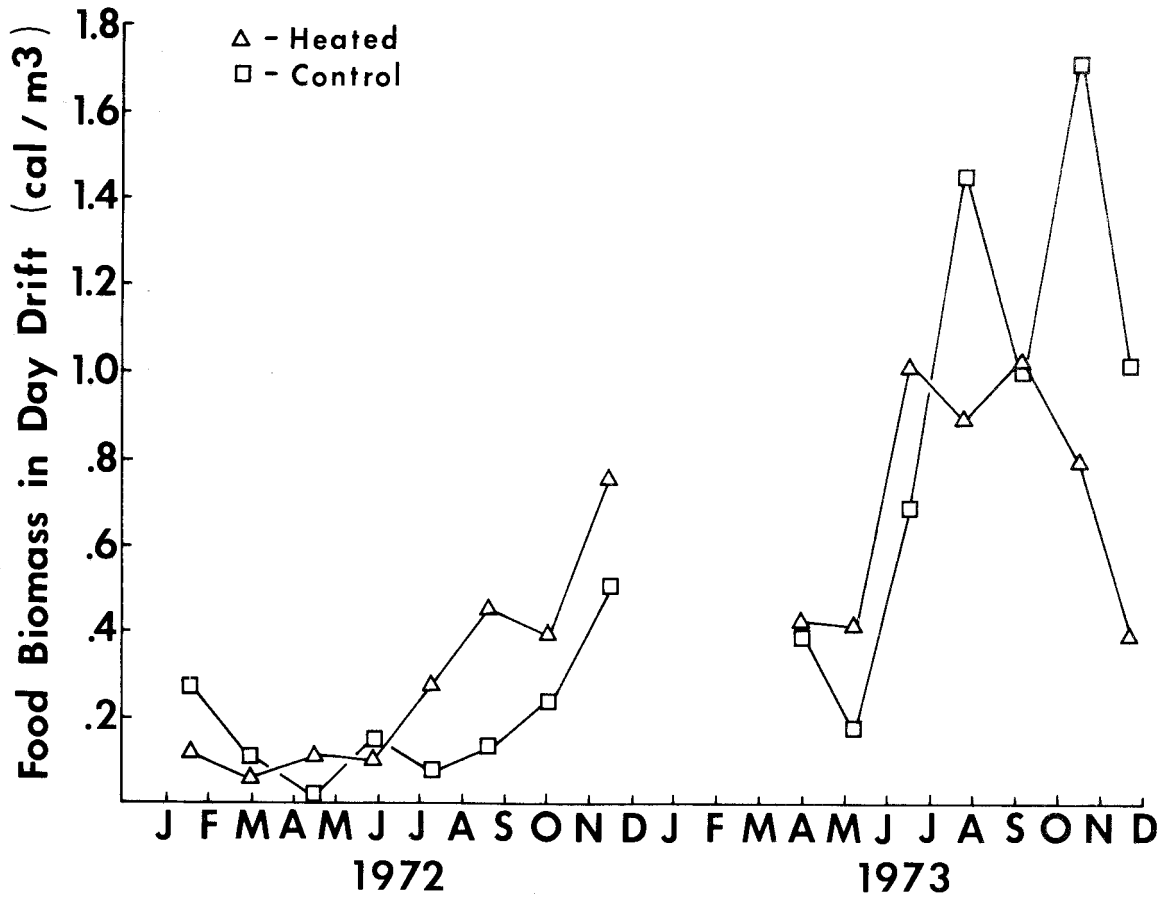


Figure 7. Seasonal changes in the biomass of food organisms present in the day drift. Each point is the mean of 2 samples taken during a 6-week period.

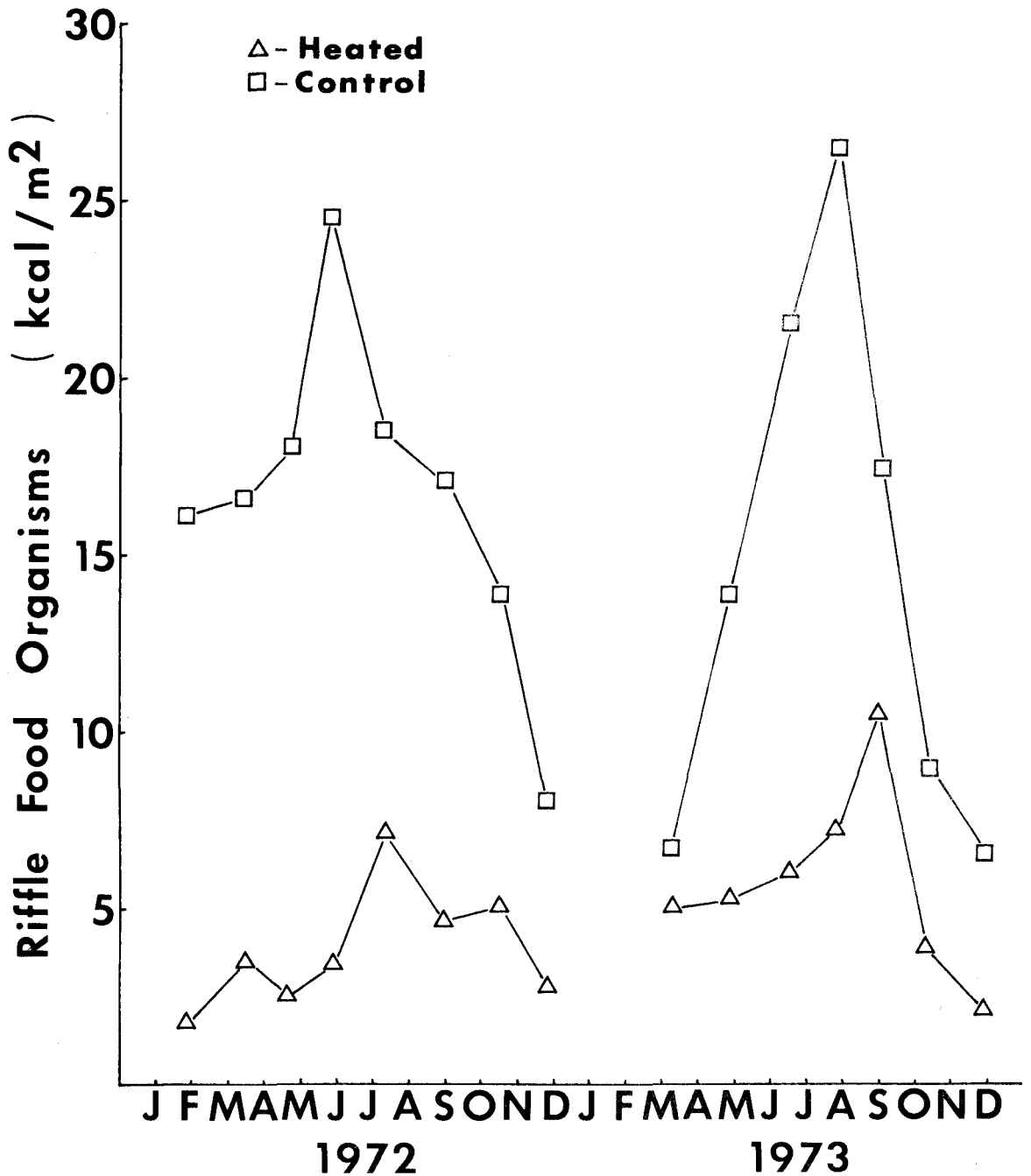


Figure 8. Seasonal changes in the biomass of food organisms present in the riffle benthos. Each point is the mean of 2 samples taken during a 6-week period.

both streams exhibiting higher drift biomasses during the second year. Although benthic biomasses were markedly greater in the control stream, 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.

Table 7 compares the mean annual biomass, mean day drift, and drift ratio (the ratio of drift to biomass) of major aquatic food groups. In 1972, drift ratios of every group except Mollusca and Trichoptera were higher in the heated stream. The next year nearly all drift ratios increased, and many were higher in the control stream, where the total invertebrate biomass was usually much greater. Of taxa showing increased drift ratios in the heated stream, Ephemeroptera and Plecoptera were apparently most strongly influenced by elevated temperature. In 1972 Chironomidae also exhibited a greater tendency to drift in the heated stream. These three groups were important components of both the day drift and the diet of juvenile salmon and were largely responsible for the greater availability of food in the heated stream during certain periods. It is possible that higher relative consumption of these forms by fish in the control stream caused them to be underrepresented in the samples, but the difference in magnitude of their drift ratios strongly suggests that temperature was indeed an important factor. Increased drift associated with increasing temperature was described for certain

Table 7. Drift ratios of major aquatic taxa (excluding winged adults), calculated according to the formula $\frac{\text{mean day drift (cal/m}^3\text{)}}{\text{mean annual biomass (kcal/m}^2\text{)}} \times 100$.

Taxon	1972						1973					
	Heated			Control			Heated			Control		
	Mean Annual Biomass	Mean Day Drift	Drift Ratio	Mean Annual Biomass	Mean Day Drift	Drift Ratio	Mean Annual Biomass	Mean Day Drift	Drift Ratio	Mean Annual Biomass	Mean Day Drift	Drift Ratio
Oligochaeta	7527	.118	.00156	9509	.008	.00092	4275	.045	.00104	4229	.117	.00277
(Gyraulid only)												
Mollusca	746	.048	.00637	119	.011	.00945	913	.116	.01267	109	.038	.03456
Ostracoda	747	.055	.00733	188	.009	.00465	259	.048	.01840	206	.050	.02411
Ephemeroptera	314	.027	.00844	8077	.027	.00033	438	.053	.01210	4494	.207	.00460
Plecoptera	395	.013	.00323	6214	.053	.00085	176	.013	.00739	3801	.038	.00101
Trichoptera	674	.002	.00022	2381	.018	.00077	821	.014	.00175	2490	.088	.00352
Chironomidae	1113	.129	.01155	1617	.053	.00329	2664	.365	.01371	2011	.548	.02727

invertebrates by Müller (1963), Waters (1968) and Pearson and Franklin (1968), although in other studies (Bishop and Hynes, 1969; Wojtalik and Waters, 1970; Müller, 1970; Reisen and Prins, 1972) significant positive associations between drift and temperature were not detected. It is also important to note that within a major taxon, considerable intraspecific variation existed with respect to drift ratios.

The association between day and night non-catastrophic drift and invertebrate standing crop was believed by Waters (1961, 1972) to be a mechanism of population regulation in instances where individuals in excess of the carrying capacity of an area of substrate were displaced downstream. Dimond (1967) and Pearson and Franklin (1968) found evidence to support this claim; other studies (e. g., Elliott, 1967; Elliott and Minshall, 1968) have shown increased drift rates to be correlated mainly with life history phenomena. In a study designed to evaluate density-dependent drift as a population regulating mechanism, Hildebrand (1974) concluded that most of the Pigeon River invertebrate fauna drifted in density independent patterns while only three taxa (<4 percent of the fauna) showed an exponential fit of the regression of drift on density, his criterion for density dependence. Bishop and Hynes (1969) suggested that streams in forested areas not subject to flooding and dominated by multivoltine species would be likely to have their carrying capacities exceeded,

with density dependent drift removing excess production. In the model streams, where flow was held constant, this was apparently not the case for daytime drift. In 1972, highest drift biomasses occurred when benthic biomasses were low (the biomasses and numbers of organisms in both the drift and benthos were closely correlated) while in late spring and summer the reverse was true. A closer correspondence existed between benthic and drift biomasses in 1973, but there was still no benthic density above which drift was markedly increased nor below which it sharply declined. Day drift was therefore believed not to act as a major factor in the regulation of invertebrate populations inhabiting riffle areas of the model streams.

No sure explanation was found for increased drift in 1973 relative to 1972. Flow rates may have been inadvertently set higher following the winter repairs, but the magnitude of change, if any, was small. A second possibility was that greater consumption by fish reduced drift catches in 1972, but this also was unlikely. Fish biomasses, and presumably consumption rates, were lower that year in the heated stream; in the control stream biomasses were higher but growth slightly lower suggesting that total consumption differed little between the 2 years. 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 known,

although severity of infection by Nanophyetus was not compared over the 2 years and may have been more serious in 1973.

Primary Production and Siltation

Seasonal variation in plant and detritus biomasses for both riffles and pools is illustrated in Figure 9. Except for a brief period following the winter repairs, when many dead animals increased detritus in the control, plants and detritus were always more abundant in the heated stream. Riffle differences were due primarily to higher densities of filamentous algae while pool differences were due to a greater accumulation of organic detritus and its associated heterotrophic microorganisms. These differences could have resulted from (1) increased primary production in the heated stream, and (2) for the riffles, greater consumption of plants and detritus by herbivores in the control stream (Figure 10). Higher levels of primary production associated with elevated temperature in laboratory streams were measured by Kevern and Ball (1965) and Phinney and McIntire (1965). The dominant algal species, Cladophora glomerata, has been found by many authors (e.g., Whitton, 1971; Adams and Stone, 1973) to grow better at higher temperatures. The ability of consumers to significantly affect periphyton standing crop has been documented by Warren (1971), Kehde and Wilhm (1972), and Elwood

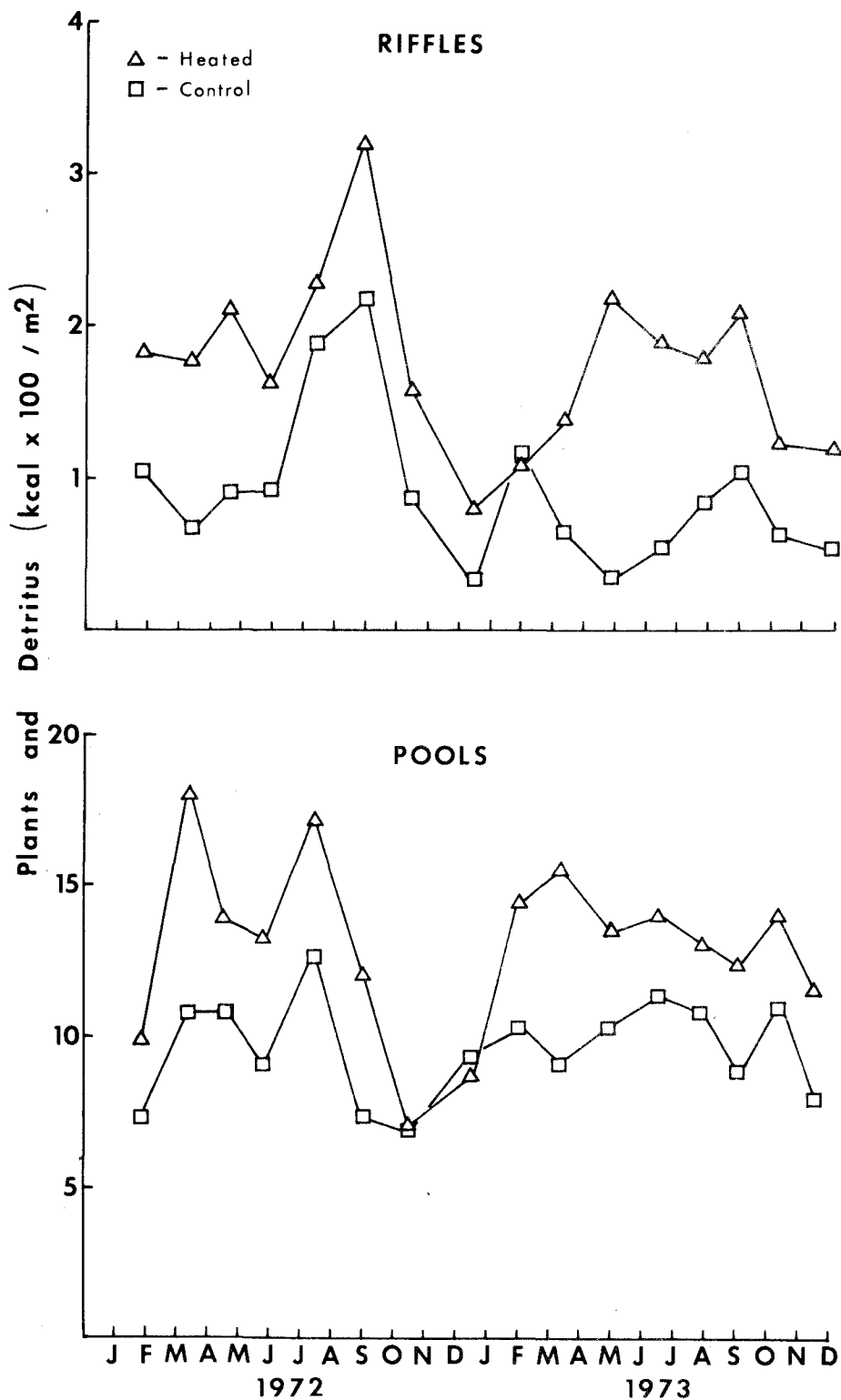


Figure 9. Biomasses of plants and detritus in riffles and pools of the model streams. Each point is the mean of 2 samples taken during a 6-week period.

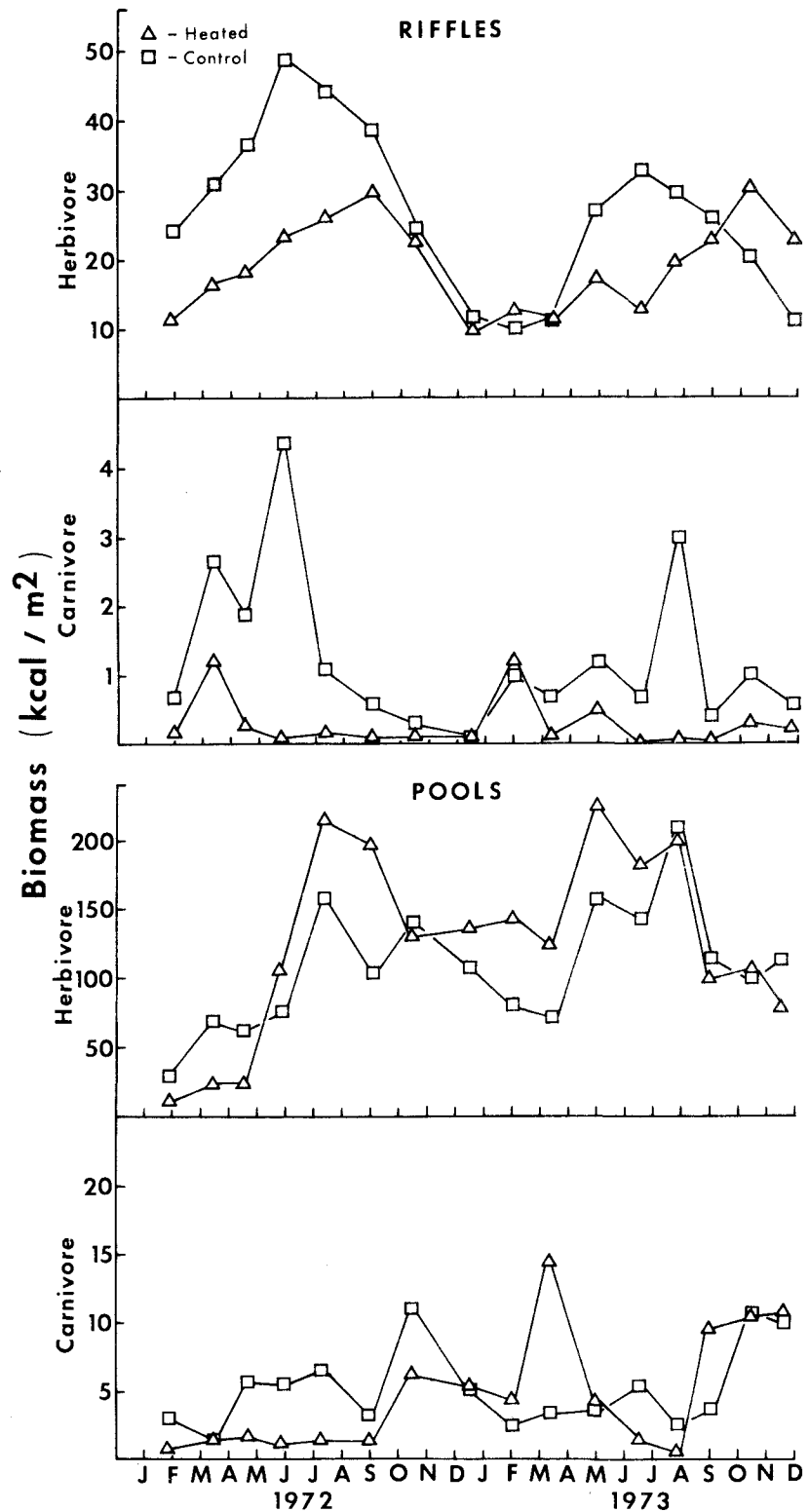


Figure 10. Biomasses of herbivorous and carnivorous invertebrates inhabiting riffles and pools of the model streams. Each point is the mean of 2 samples taken during a 6-week period.

and Nelson (1972), and explored in a computer simulation by McIntire (1973).

Heavy growth of filamentous algae on the riffles apparently accelerated siltation rates in the heated stream (Table 8) by acting as filters to trap and consolidate fine sediments introduced with exchange water. Even during winter when Cladophora ceased growing, epiphytic diatoms encrusting dead algal filaments continued to trap silt and clay. Hynes (1960) described how interstices can become clogged by siltation, altering the habitat of many invertebrates, with the result usually being a reduction in bottom fauna standing crop (Cordone and Kelly, 1961; Chutter, 1969). Greatly reduced mean annual biomasses of Ephemeroptera, Plecoptera, and Trichoptera in the heated stream (Table 7, Appendix 1) compared to the control suggest that these groups may well have been influenced by the amount of fine sediments in the substrate. Thus, while elevated temperature promoted primary production, concurrent siltation associated with higher levels of plants and detritus acted to reduce the suitability of riffle habitat for species belonging to several groups of insects. These insects, it happened, were often preferred food items of juvenile chinook. In the pools, where filamentous algae did not grow, fine sediment levels in the substrates of the stream were virtually identical.

Table 8. 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.

	Particle Size (mm)		
	.175-1	.088-.175	<.088
<u>Riffles</u>			
Control (17 mo.)	41	19	169
Heated (17 mo.)	147	37	943
Heated (31 mo.)	167	91	1443
<u>Pools</u>			
Control	94	1219	1746
Heated	86	1064	1728

Community Structure and Ecosystem Productivity

The productivity of a community depends to a large extent upon its structure. Competitors, for example, can limit the amount of food available to a species of interest. Predators can influence production by regulating the biomass of prey, but do not limit the productivity of a system unless they affect nutrient levels or determine the outcome of interactions among prey. There were no predators on young salmon in the model streams. Their elevated construction effectively prevented entry by snakes, raccoons, and herons. A belted kingfisher (Megace ryle alycon) was occasionally observed in the vicinity of the streams, but was never seen entering them. Predatory fishes, salamanders, crayfish, and other large aquatic carnivores were absent.

Juvenile chinook in both streams rarely consumed carnivorous invertebrates, which were usually large insects that did not enter the drift. Instead, their diet consisted mainly of herbivorous forms. Davis and Warren (1965) and Brocksen, Davis, and Warren (1968) found that perlid stonefly naiads (Acroneuria pacifica and A. californica), when abundant, could be important competitors of fish for food organisms in laboratory streams. Seasonal changes in the biomass of herbivores and detritus feeders ("herbivores") and carnivores are shown in Figure 10. Riffle herbivores were usually present in greater amounts in the control stream despite lower resource levels (Figure 9). Riffle carnivores were likewise more abundant in the control stream, although carnivore biomasses in both streams were small fractions (<10 percent) of herbivore biomasses. Consistent differences did not extend to the pools, which often had standing crops several times greater than those of the riffles.

Because the young salmon fed almost exclusively upon organisms originating from riffle areas, and because carnivore biomasses in the riffles were relatively low, interspecific competition for food between fish and insects was believed to be much less intense than intraspecific competition among members of the fish populations.

What competition existed among carnivores was probably greater in the control than in the heated stream.

Fewer macroinvertebrate species were present in the heated stream, both on a total annual basis (Table 9) and on a seasonal basis (Figure 11). Most of those species that were unique to one stream or the other were very rare and contributed little to fish production. Major biomass differences arose because many species had greater population densities in the control while only a few fared better in the heated stream. Several species 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 species in the control (Figure 12). The two most abundant invertebrates were Oxytrema silicula in the riffles and Limnodrilus sp. in the pools (Appendix I). Oxytrema may have been more successful in the heated stream because of higher plant biomasses. Limnodrilus was probably more abundant there because more detritus was present and because it may have preferred warmer temperatures (Aston, 1973). Neither of these two species were consumed in significant quantities by young chinook; thus, increased dominance in the heated stream did not give rise to greater food availability.

Species composition of drifting invertebrates may also have influenced productive capacities of the streams. Growth rates of juvenile chinook dropped dramatically in summer and fall, resulting in low or negative production. While the effects of disease, increased metabolic demands associated with higher temperatures, and lower

Table 9. Number and relative abundance of macroinvertebrate species or taxa in the model streams. "Unique species" means species that were present in one stream but absent from the other over the same interval. H = heated stream, C = control stream.

	Riffles				Pools			
	1972		1973		1972		1973	
	H	C	H	C	H	C	H	C
Total number of species	56	68	56	68	44	51	42	49
Unique species	5	17	7	19	1	8	4	11
Species exhibiting higher biomass than in other stream	10	41	15	34	15	28	14	24

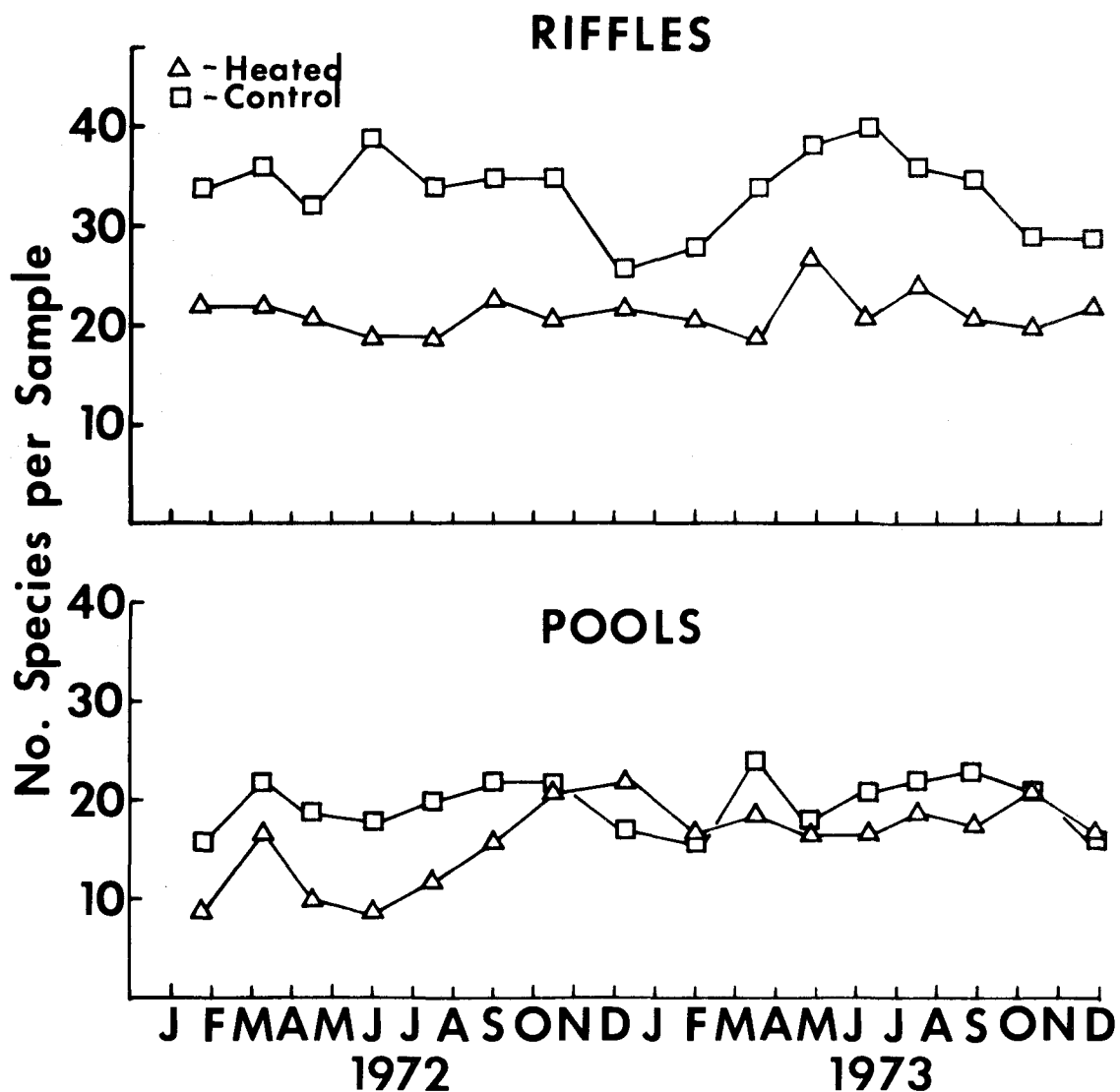


Figure 11. Seasonal changes in the average number of invertebrate species present in bottom samples. Each point is the mean of 2 samples taken during a 6-week period.

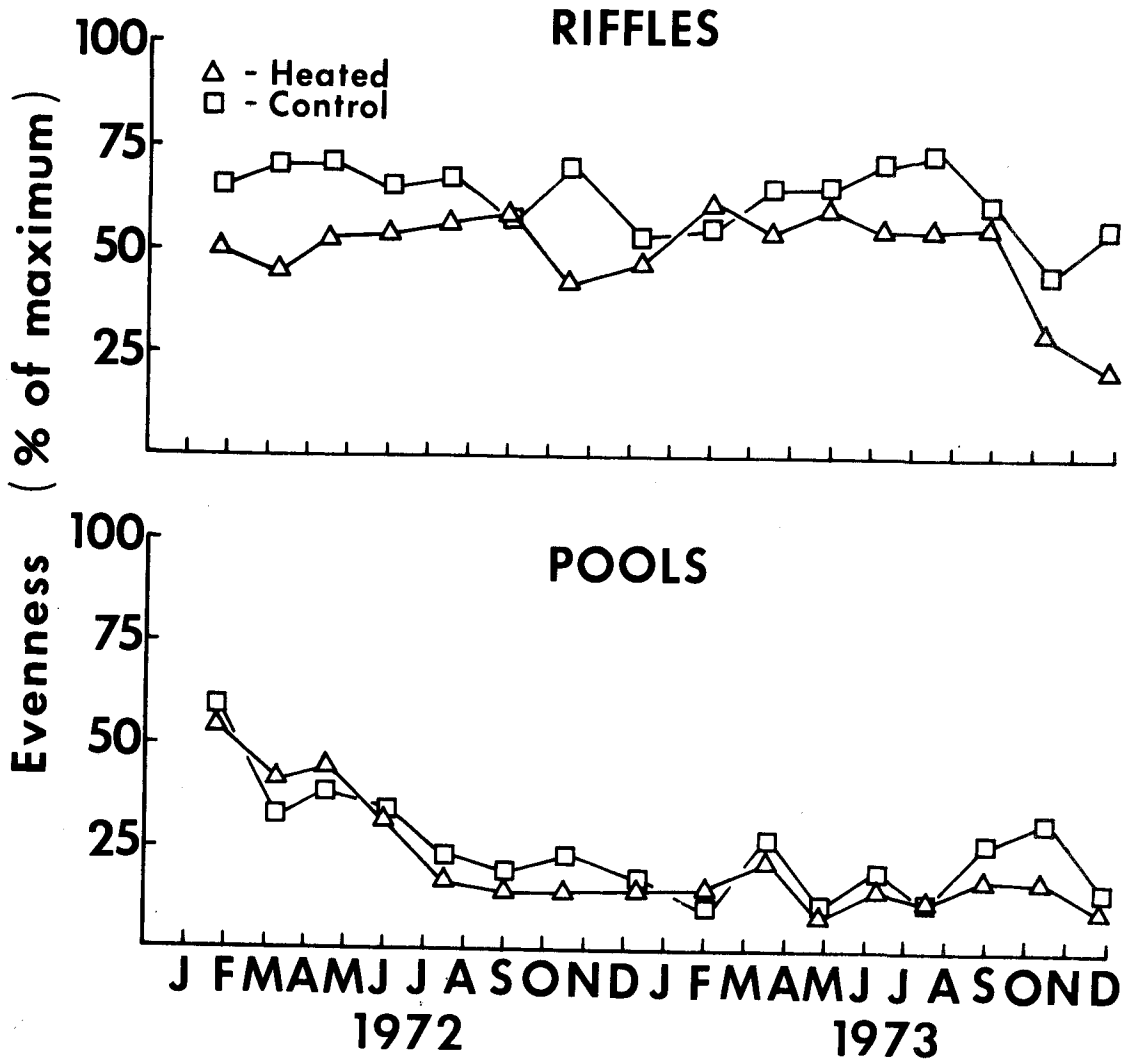


Figure 12. Evenness of the distribution of biomass among benthic invertebrates, expressed as a percent of maximum that would occur if all species were equally represented. Dominance of the fauna was inversely related to unevenness; low values of evenness indicate increased dominance by the most common species. Each point is the mean of two samples taken during a 6-week period.

growth capacities of larger fish (Brown, 1957; Paloheimo and Dickie, 1966; Warren and Davis, 1967) were probably all significant factors, there was evidence that the day drift was not being exploited as efficiently as it was during winter and spring. A high percentage of summer and fall drift was composed of very small invertebrates such as oligochaetes (Nais communis) and chironomids (Table 6). During those seasons tiny organisms were not preferred food items of the young salmon, which were larger and less numerous. High growth rates exhibited by fish during winter and spring when drift rates were comparatively low suggests that smaller, more abundant fish were better able to utilize the entire range of sizes of invertebrate species that left the substrate. It was impossible to determine whether the phenomenon of size preference affected populations in the two streams identically, but based on overall composition (Appendix I, Table 7) small species seemed to be relatively more abundant in the heated stream, where summer and fall growth was most sharply curtailed.

Total chinook production in each stream was roughly equal to production of juvenile coho salmon reported by Iverson (1972). Production of young salmon in the heated stream, even though lower than that of the control, was still higher than generally occurs in running water ecosystems (Chapman, 1967; LeCren, 1969). Productive capacities of the model streams exceeded most natural streams

because competitors were largely absent, and also possibly because residence in the streams was enforced.

DISCUSSION

The relationship between production and biomass of a species of interest as an indication of the productivity of an ecosystem has been discussed in detail by Brocksen, Davis, and Warren (1970) and Warren (1971). In Figure 13, these two parameters were plotted and each point was numbered sequentially according to its particular sample time. Although there were probably no sampling intervals through which productivities of the streams remained constant, there were periods where it appeared to vary little. Curves were drawn to indicate the approximate productivity of the streams during these periods, making it possible both to illustrate differences between the streams and to identify times of transition within the streams from one level of productivity to another. Nearly all points were located on the descending limbs of the curves, indicating that reduced production rates resulted from biomass increases.

In 1972, the control stream was clearly more productive than the heated stream during all seasons. Productivities were highest in the control and heated streams (curves A and C respectively) from March through June, this period being characterized by increasing biomasses and declining production rates. July and August marked a transition to lower productive capacities that lasted from September through December (curves B and D). Productivity was similar for

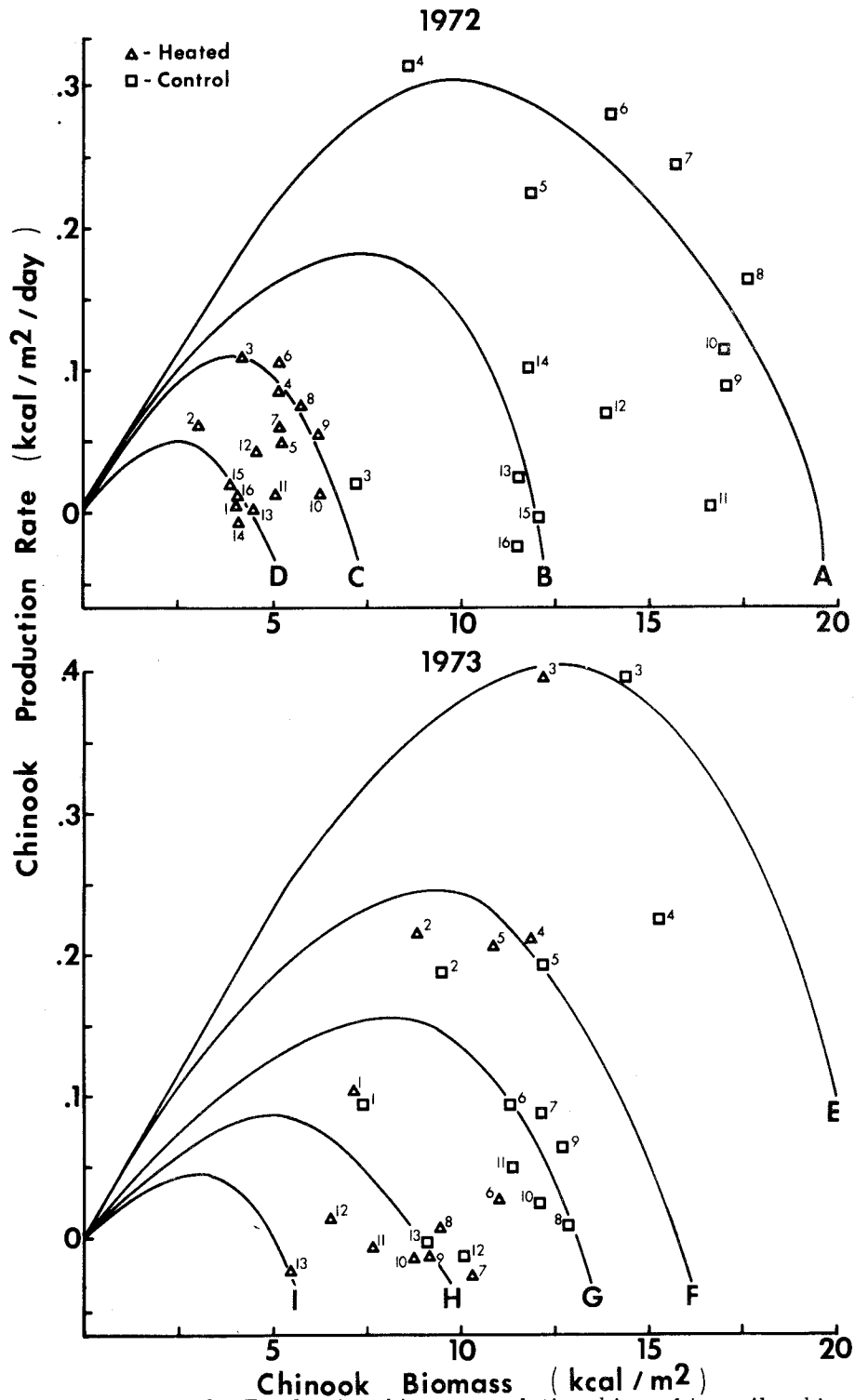


Figure 13. Production-biomass relationships of juvenile chinook in the model streams. Each point is numbered sequentially beginning with the first sampling date (Table 4). The first point for 1972 control fish is labelled "3" so that other numbers denote sample times in common with the heated stream.

both streams during spring 1973, reaching a brief but very high level (curve F) in late May and June. The production rate in May was so high that more than a third of the total annual production in the heated stream took place during one 3-week period. Curves G and H approximate productive capacities that existed from July through September when the control stream appeared to be more productive. By late fall the control stream had dropped to the level represented by curve H and the heated stream to the level represented by curve I.

Production of salmon in the streams was high in spring because the small fish were apparently able to efficiently exploit available food, parasitism by Nanophyetus had not yet become an important factor, and because temperature was in a range that was favorable to growth. Summer was generally a period of declining production because high temperatures exacted a proportionately greater metabolic demand, and, for the control stream, because parasitism had attacked the majority of the population. Low production in fall months was associated with high levels of infection and apparent inability to fully exploit small food organisms that were abundant in the drift.

Seasonal averages of producer and consumer biomasses for major food groups from fish to plants were plotted against each other in order to further elucidate productivity differences between the

streams. Figure 14 shows that (1) consumer-resource relations followed a rather cyclical pattern with high points in spring and summer and low points in fall and winter, (2) at least for 1972, greater densities of invertebrates were supported in the control stream at a given level of plant-detritus biomass, and (3) likewise, higher chinook biomasses were maintained in the control stream at a given level of invertebrate density. Plant-detritus biomasses were higher in the heated stream due to increased primary production and generally lower herbivore biomasses. Overall, invertebrate biomasses were lower in the heated stream because of increased siltation 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, but very early developmental stages and life history patterns may well have been affected (Macan, 1961a, 1961b; Hynes, 1970). Salmon biomasses were lower in the heated stream because growth efficiencies were reduced, and, for most periods, because less food was available (Figure 6). While invertebrate biomasses were occasionally at similar levels in the two streams, dominance of the heated stream benthos by species that juvenile chinook did not eat acted to reduce potentially available food. ✓ The only apparent explanation for the large increase in

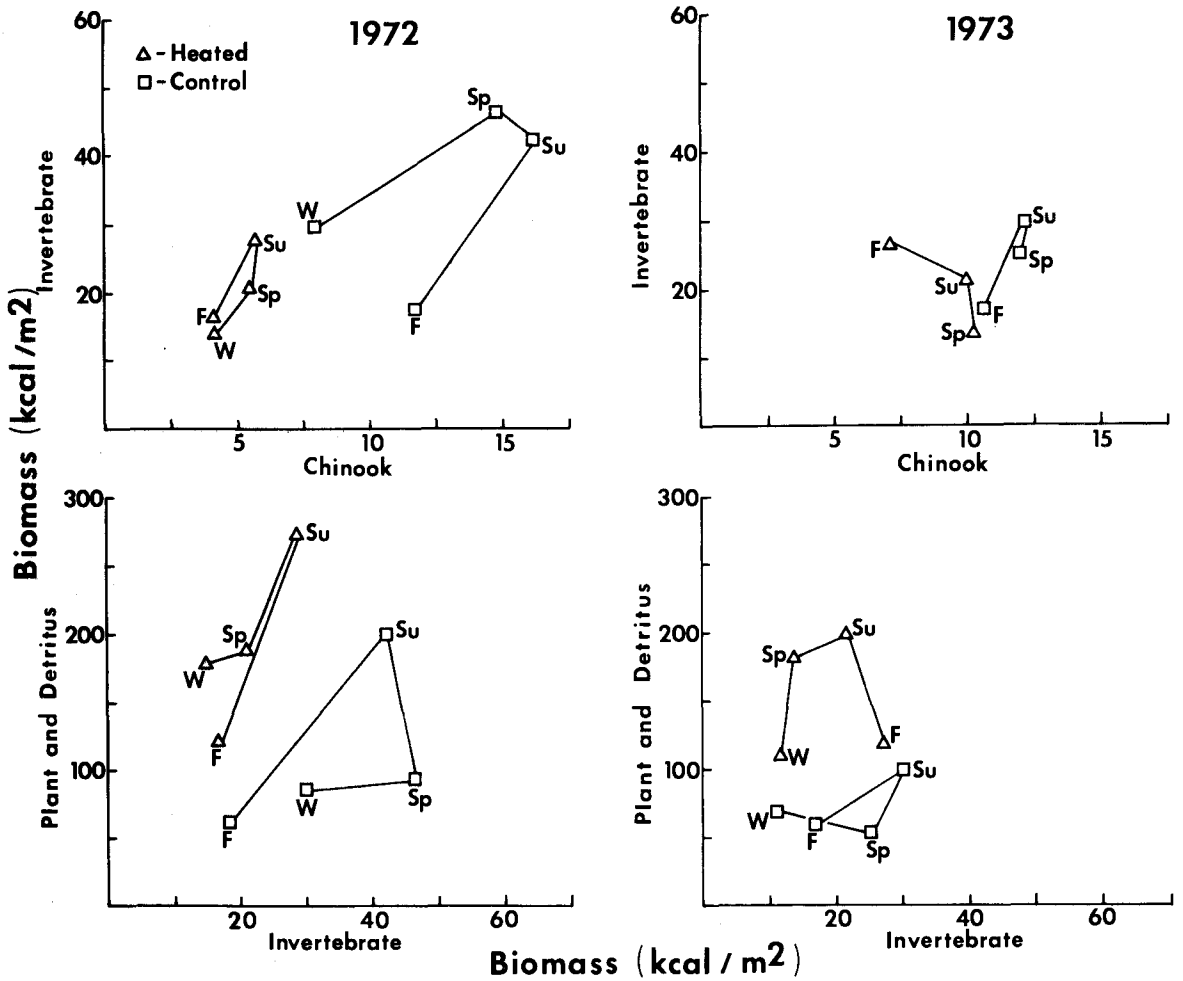


Figure 14. Seasonal changes in producer-consumer biomass relationships in model stream riffles. Triangles represent the heated stream; squares represent the control. W = winter, Sp = spring, Su = summer, F = fall.

production in the heated stream during 1973 was that drift rates were much higher in that year. Invertebrate biomasses during the same period were about the same as the previous year and plant biomasses were generally lower.

Constant 4° C elevation above natural diurnally fluctuating temperatures acted in various ways both to promote and to reduce the production of juvenile chinook salmon in a model stream, and it is now possible to summarize these beneficial and harmful effects. Fish benefited in two ways. First, the temperature increase afforded considerable protection from infection by intermediate stages of a trematode parasite, which heavily infected the majority of individuals in the control stream and acted to reduce their growth rate and probably contributed to summer and fall mortality. Second, although the evidence is equivocal, elevated temperature may have stimulated certain invertebrates to enter the drift in greater proportion to their benthic biomasses and thus become more available as food. Fish were harmed in at least three ways. First, their pre-feeding mortality rate was several times greater than that of eggs and fry held in unheated water. Second, growth efficiencies were lowered at all but the highest food levels (which may never have been reached in the model streams). And, third, food availability was generally reduced despite higher drift ratios of some taxa, either because elevated temperature acted directly upon invertebrates through

survival and growth of different life cycle stages or indirectly through increased siltation accompanying heavier growths of filamentous algae.

The results of these experiments show that temperature elevations of a few degrees can cause profound changes, not only to the structure of benthic communities in streams, but also to the production of commercially valuable anadromous salmonids. In addition to being directly harmful, thermal increases can lead to the proliferation of species that compete with the fish themselves or with their food organisms, or that alter the environment in such a way as to reduce its productivity. Consideration of a wide spectrum of direct and indirect effects will provide the best possible approach in evaluating the impact of elevated temperature on natural flowing water ecosystems.

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APPENDIX

Appendix I. Mean annual biomasses (cal/m²) of invertebrates inhabiting riffles and pools of the model streams during 1972 - 1973. Parentheses denote very tentative identifications. H = heated stream, C = control stream.

Taxon	Riffles				Pools			
	1972		1973		1972		1973	
	H	C	H	C	H	C	H	C
CNIDARIA								
<u>Hydra sp.</u>	1	2	0	1	1	22	2	8
PLATYHELMINTHES								
<u>Polycelis sp.</u>	1	1162	0	53	7	16	0	0
NEMATODA								
<u>Gen. sp.</u>	0	0	1	2	1	4	1	1
ANNELIDA								
<u>Chaetogaster sp.</u>	0	1	0	4	8	3	1	1
<u>Nais communis</u>	4839	8008	1580	2645	7899	7505	1058	1476
<u>Limnodrilus sp.</u>	2688	1500	2695	1580	87374	74536	126585	101646
MOLLUSCA								
Gastropoda								
<u>Gyraulus sp.</u>	746	119	913	109	1409	339	3694	1739
<u>Physa sp.</u>	0	0	0	1	0	0	0	1
<u>Ferrissia sp.</u>	0	2	0	5	0	0	0	0
<u>Oxytrema silicula</u>	8411	6470	7522	5011	1329	871	4722	2583
Pelecypoda								
<u>Pisidium sp.</u>	5	0	6	1	40	17	54	31
ANTHROPODA								
Cladocera								
<u>Pleuroxus aduncus</u>	8	4	10	12	57	33	102	39
Ostracoda								
<u>Herpetocypris chevreuxi</u>	747	188	259	206	4477	2893	2677	4012

Appendix I. Continued

Taxon	Riffles				Pools			
	1972		1973		1972		1973	
	H	C	H	C	H	C	H	C
Copepoda								
<u>Eucyclops agilis</u>	8	4	4	2	77	11	46	21
<u>Canthocamptus oregonensis</u>	1	3	1	7	2	1	6	21
Insecta								
Collembola								
<u>Smythuridae Gen. sp.</u>	1	0	1	0	0	0	0	0
<u>Onychiuridae Gen. sp.</u>	0	0	2	0	0	0	0	0
<u>Isotomidae Gen. sp.</u>	1	3	1	0	0	0	0	0
Ephemeroptera								
<u>Cinygma integrum</u>	59	2015	20	1041	0	90	0	1
<u>Cinygmula reticulata</u>	0	48	0	7	0	0	0	90
<u>Epeorus nitidus</u>	5	2666	4	591	0	155	0	0
<u>Epeorus longimanus</u>	12	42	9	8	0	0	0	0
<u>Ameletus spp.</u>	29	371	7	124	118	277	0	351
<u>Paraleptophlebia temporalis</u>	3	449	1	91	70	345	12	171
<u>Paraleptophlebia debilis</u>	0	64	1	106	195	492	0	824
<u>Ephemerella sp.</u>	16	39	0	22	0	0	0	0
<u>Callibaetis sp.</u>	40	0	1	0	291	334	480	2
<u>Baetis (tricaudatus)</u>	149	1634	396	2378	22	7	7	75
<u>Baetis (parvus)</u>	1	749	0	126	0	40	0	62
Odonata								
<u>Cordulegaster dorsalis</u>	87	0	0	0	0	0	0	0
<u>Octogomphus specularis</u>	0	300	0	74	426	1019	0	0
<u>Aeshna (interrupta)</u>	0	0	0	0	0	0	7	0
Plecoptera								
<u>Peltoperla brevis</u>	0	8	0	0	0	0	0	0
<u>Nemoura spp.</u>	164	4010	65	3265	64	668	1	182
<u>Leuctra (augusta)</u>	0	1	0	0	0	16	0	0
<u>Capnia sp.</u>	0	47	0	19	78	163	0	9

Appendix I. Continued

Taxon	Riffles				Pools			
	1972		1973		1972		1973	
	H	C	H	C	H	C	H	C
<u>Brachyptera pacifica</u>	82	955	92	19	0	38	0	0
<u>Pteronarcella regularis</u>	91	638	18	255	142	0	0	0
<u>Isoperla mormona</u>	50	346	0	67	8	26	1	0
<u>Isoperla sp. 2</u>	1	22	0	12	0	0	9	15
<u>Isoperla sp. 3</u>	0	62	0	38	0	0	0	0
<u>Kathroperla perdita</u>	0	2	1	20	0	2	0	0
<u>Alloperla sp.</u>	8	20	1	11	1	1	3	60
<u>Acroneuria pacifica</u>	0	103	0	95	0	0	0	0
Megaloptera								
<u>Sialis californica</u>	0	0	122	131	776	311	4759	1658
Trichoptera								
<u>Rhyacophila spp.</u>	43	52	22	32	0	0	0	69
<u>Rhyacophila pupae</u>	0	0	9	0	0	0	0	0
<u>Wormaldia anilla</u>	14	17	2	56	0	0	0	0
<u>Wormaldia pupae</u>	0	0	0	1	0	0	0	0
<u>Psychomyia lumina</u>	173	1055	343	1312	880	7222	4357	5684
<u>Psychomyia pupae</u>	10	551	41	543	1	236	55	806
<u>Parapsyche sp.</u>	0	39	33	0	0	0	0	0
<u>(Agraylea) sp.</u>	60	103	162	82	124	57	182	199
<u>(Agraylea) pupae</u>	28	13	44	59	9	16	79	18
<u>Limnephilidae Gen. sp. 1</u>	248	490	147	96	121	786	144	0
<u>Limnephilidae sp. 1 pupae</u>	85	43	0	44	0	0	0	0
<u>Limnephilidae Gen. sp. 2</u>	0	0	8	103	0	0	0	0
<u>Limnephilidae sp. 2 pupae</u>	0	0	0	94	0	0	0	0
<u>Lepidostoma sp.</u>	13	13	6	35	3	185	44	18
<u>Lepidostoma pupae</u>	0	5	0	34	0	0	0	0
<u>(Micrasema) sp.</u>	0	0	4	0	0	0	0	0
Coleoptera								
<u>Hydroporus axillaris adults</u>	0	0	1	0	0	0	0	0

Appendix I. Continued.

Taxon	Riffles				Pools			
	1972		1973		1972		1973	
	H	C	H	C	H	C	H	C
<u>Paracymus</u> sp. larvae	1	0	0	0	0	0	0	0
<u>Lara</u> sp. larvae	28	2	2	3	6	13	0	0
<u>(Heterlimnius)</u> sp. larvae	4	25	162	7	64	4	41	6
<u>(Heterlimnius)</u> adults	3	2	6	1	0	0	0	0
<u>(Cleptelmis)</u> sp. larvae	0	0	5	0	0	0	6	0
<u>(Cleptelmis)</u> adults	0	0	0	1	0	0	0	0
Diptera								
<u>Dicranota</u> sp.	54	51	5	71	9	9	0	59
<u>Liriope</u> sp.	2	31	9	4	90	155	177	59
<u>(Bibiocephala)</u> sp.	2	4	0	1	0	0	0	0
<u>Dixa</u> sp.	0	1	0	0	0	0	0	0
Simuliidae Gen. spp.	18	89	28	149	0	0	0	0
Simuliidae pupae	1	10	11	45	0	0	0	0
<u>Pentaneura</u> sp.	0	16	0	14	11	602	92	260
<u>Tanypus</u> sp.	14	59	0	48	1207	1778	1030	1608
<u>Diamesa</u> sp.	0	24	54	341	0	0	22	24
<u>Prodiamesa</u> sp.	3	14	19	6	322	369	216	566
<u>Corynoneura</u> sp.	1	6	1	11	0	2	0	2
Orthoclaadiinae Gen. sp. 1	170	479	21	62	32	115	8	2
Gen. sp. 2	580	760	1591	496	43	148	122	263
Gen. sp. 3	59	35	13	19	68	176	145	148
Gen. sp. 4	1	20	17	101	0	18	10	80
Gen. sp. 5	0	1	0	0	0	0	0	0
Gen. sp. 6	1	1	0	0	0	0	0	7
Gen. sp. 7	0	0	419	615	0	0	57	75
<u>Tanytarsus</u> sp.	269	130	461	102	135	168	134	313
<u>(Chironomus)</u> sp.	12	40	6	20	558	549	1303	1189
<u>Polypedilum</u> sp.	4	30	63	176	24	206	59	135

Appendix I. Continued

Taxon	Riffles				Pools			
	1972		1973		1972		1973	
	H	C	H	C	H	C	H	C
Chironomidae pupae	334	326	490	413	179	274	347	244
(<i>Bezzia</i>) sp.	1	1	7	2	1	14	31	15
Dolichopodidae <u>Gen. sp.</u>	0	3	0	0	0	0	0	0
(<i>Hemerodromia</i>) sp.	1	2	0	1	1	1	0	0
(<i>Hemerodromia</i>) pupae	0	0	0	1	0	0	0	0
Arachnida								
Hydracarina <u>Gen. sp.</u>	1	1	1	1	0	0	1	1