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Title: EFFECTS OF ELEVATED TEMPERATURE ON JUVENILE COHO SALMON AND BENTHIC INVERTEBRATES IN MODEL STREAM COMMUNITIES

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Juvenile coho salmon (Oncorhynchus kisutch (Walbaum)) and aquatic invertebrates were subjected to experimentally increased, but naturally fluctuating, temperatures in a model stream channel. Coho of the 1969, 1970, and 1971 year classes were reared in the heated model stream and in an unheated control stream, both located at the Oak Creek laboratory west of Corvallis, Oregon. The average increment of experimental over control temperature was 4.3 C over the entire experimental period of 22 months. Temperatures in the control stream were generally favorable for growth of coho if food organisms were scarce, while temperatures in the heated stream were favorable for growth if food organisms were abundant.

Coho of the 1969 year class were reared for one winter as yearlings, and total production of this group was approximately the same in the two streams. Coho of the 1970 year class were reared from

small fry to smolts over a one-year period. In this group, total production in the control stream was approximately twice as great as in the heated stream. While population size was nearly the same in the two streams, coho in the control stream grew much more rapidly than in the heated stream. Total production of coho of the 1971 year class, which were reared from the egg stage, was approximately five times as great in the control as in the heated stream when the experiment was terminated in August 1971. The difference in production resulted from larger population size and higher growth rate in the control stream.

Production of aquatic stages of insects was approximately twice as great in the control as in the heated stream over the period May 1970-May 1971. This difference between streams was especially marked in mayfly and stonefly nymphs, which were the most abundant insects in both streams, and which appeared to be the major sources of food for coho.

The reduced growth rates of coho in the heated as compared to the control stream probably resulted from effects of temperature on the invertebrate food supply as well as from direct effects of temperature on the coho in raising their standard metabolic rates so that energy available for growth was reduced. Winter growth rates of coho in the heated stream were generally higher than in the control, probably as a result of an increase in appetite with increased temperature. Winter growth rates of the 1969 year class were high, probably because young coho fry were available as food. Winter growth rates of coho of the 1970 year class, which had a more natural food supply, were low in both streams.

The insect fauna of the Oak Creek area is probably adapted to cool water temperatures, and this adaptation presumably contributed to the reduced insect production in the heated model stream. If heat-tolerant species of insects were present in or able to migrate into a stream receiving a heated effluent, the simplication of the invertebrate fauna caused by the thermal pollution might increase the amount of food available to the top carnivore. Such heat-tolerant forms apparently were not present in the model streams or, if present, were not able to contribute significantly to total production.

Effects of Elevated Temperature on Juvenile Coho Salmon and Benthic Invertebrates in Model Stream Communities

by

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INTRODUCTION

Discharges of heated effluents into natural bodies of water in this country consist largely of cooling water from power plants, either nuclear- or fossil-fueled. Increasingly, waste heat from such plants is being dissipated to the atmosphere by means of cooling towers or cooling ponds. Such towers add significantly to the construction cost of power generating plants and under some atmospheric conditions may cause local fogging or icing (Krenkel and Parker, 1968). Thus economic and other pressures exist which promote the discharge of waste heat directly to natural waters.

The undesirable effects of heated discharges, or "thermal pollution" are primarily biological and aesthetic. The capacity of a stream to oxidize a given load of organic sewage while desirable levels of dissolved oxygen are maintained can be significantly reduced by heating (Krenkel and Parker, 1968). Since the animal life of streams is poikilothermic and lives in a medium which readily conducts heat to or from the body, these animals are particularly susceptible to physiological effects of temperature change. In streams the problem may be compounded by turbulent mixing of the water mass so that no strata having unchanging or slowly changing temperature are established as in lakes. Furthermore the volume of water in a stream receiving a heated discharge is quite small as compared to a large lake or marine bay and so is vulnerable to rapid temperature change. In fact, many heated discharges from power plants or other industrial sources fluctuate considerably with time, subjecting the biota of the receiving water to fluctuating temperature with little opportunity for the organisms to acclimate.

Previous studies of the effects of temperature on aquatic organisms have consisted largely of experimental laboratory studies and observational field studies. For juvenile salmonid fishes an extensive literature exists on the physiological role of temperature. The studies of juvenile sockeye salmon, Oncorhynchus nerka (Walbaum), by Brett and his coworkers have been especially thorough. This group has investigated temperature tolerance, preferred temperature, and effects of temperature on metabolic rates, swimming performance, rate of digestion, appetite, and growth rate at various rations. Their results were summarized by Brett (1971). All their experiments were conducted at constant temperatures. Averett (1969) estimated the energy expenditures of juvenile coho salmon, Oncorhynchus kisutch (Walbaum), kept at several constant temperatures and fed several ration levels.

Studies of temperature effects on aquatic invertebrates have been largely observational. Nebeker and Lemke (1968) reported on techniques for estimating the temperature tolerance of aquatic insects. Hynes (1970a) and Hynes (1970b) reviewed European and American literature on field studies of temperature effects and correlation of species distribution to temperature.

Few studies of temperature effects have extended experimental techniques to the field or simulated field situations. Alabaster and Downing (1966) studied behavioral responses of fish to the introduction of heated water into long stream channels. Wojtalik and Waters (1970) examined effects of a measured discharge of warm water on the invertebrate drift of a stream. My study was of this third type, in that it was a controlled study of the effects of an experimentally increased temperature on aquatic animals which was conducted in large model streams in which the stream community and its intrarelationships could develop in an approximately natural way, with temperatures fluctuating both diurnally and seasonally. In the model streams I attempted to simulate a habitat in which juvenile coho salmon are typically found. Coho habitat in streams and rivers has been described by Chapman (1965), Hartman (1965), and Lister and Genoe (1970). The life history of the coho salmon was summarized by Clemens and Wilby (1961). Coho often inhabit forest streams with a stony substrate which is essential for sheltering the eggs and young fry. They tend to be found in pools or behind logs and other obstructions rather than in the swift water of riffles. Coho spend at least one year in fresh water and are thus subjected to both low summer flows and winter freshets. They are visual feeders, capturing drifting invertebrates of both aquatic and terrestrial origin. A simulated coho stream should have the following features: location in the shade of trees; a riffle-pool topography to provide eddies of quiet water; a gravel substrate; opportunity for continuous colonization by aquatic insects; and seasonal variation in flow, the winter rate being much greater than that of summer.

I conducted a continuous experiment from the fall of 1969 to the summer of 1971, with juvenile coho salmon of three year classes. My objectives were to estimate long-term effects of increased temperature on juvenile coho and aquatic invertebrates in the model streams. Of particular interest were survival, production, equilibrium biomasses attained, behavior, and community composition.

METHODS

Experimental Facilities

Each model stream consisted of two wooden tanks, each 10 m long, 1.3 m wide, and 0.8 m deep. The area occupied by fish was approximately 22 m^2 in each stream. These tanks were connected by large irrigation pipes at each end (Figure 1). Tanks were constructed of one-inch exterior plywood with viewing windows of plate glass or plexiglass along one side. Inside wooden surfaces and caulking were covered with grey-tinted hatchery paint. Bioassay indicated that paint and caulking used were not toxic to juvenile coho. A 2.0 hp irrigation pump provided flow of about 1200 $l \cdot min^{-1}$ in each stream. Each tank was set at a slope of about 1.7 percent which permitted gravity flow of water to the pump and created water velocities typical of streams. A riffle-pool topography was simulated using concrete blocks (Figure 2). A layer of coarse (2-10 cm diameter) river gravel about 10-20 cm thick was used as stream substrate, the riffle substrate being generally coarser than that of the pools. With time the pool substrate came to contain considerable fine sediment. Exchange water was introduced (20 $l \cdot m^{-1}$ per model stream) from a spring-fed stream nearby. This small stream contained no resident fishes.

During most of the experiment, no barriers to movement of fish were present except for a screen (Figure 1) which prevented the

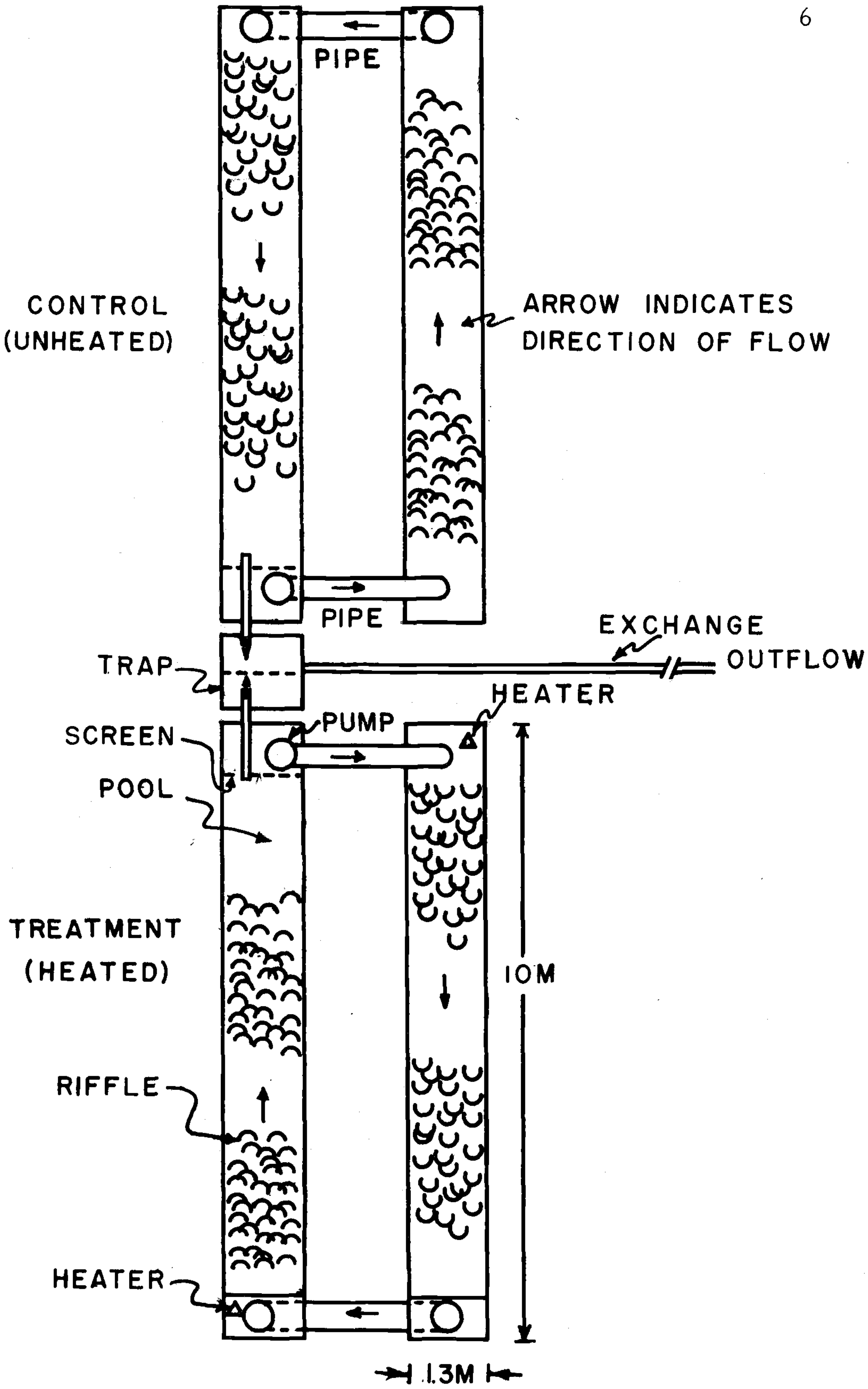


Figure 1. Model streams (diagrammatic top view).

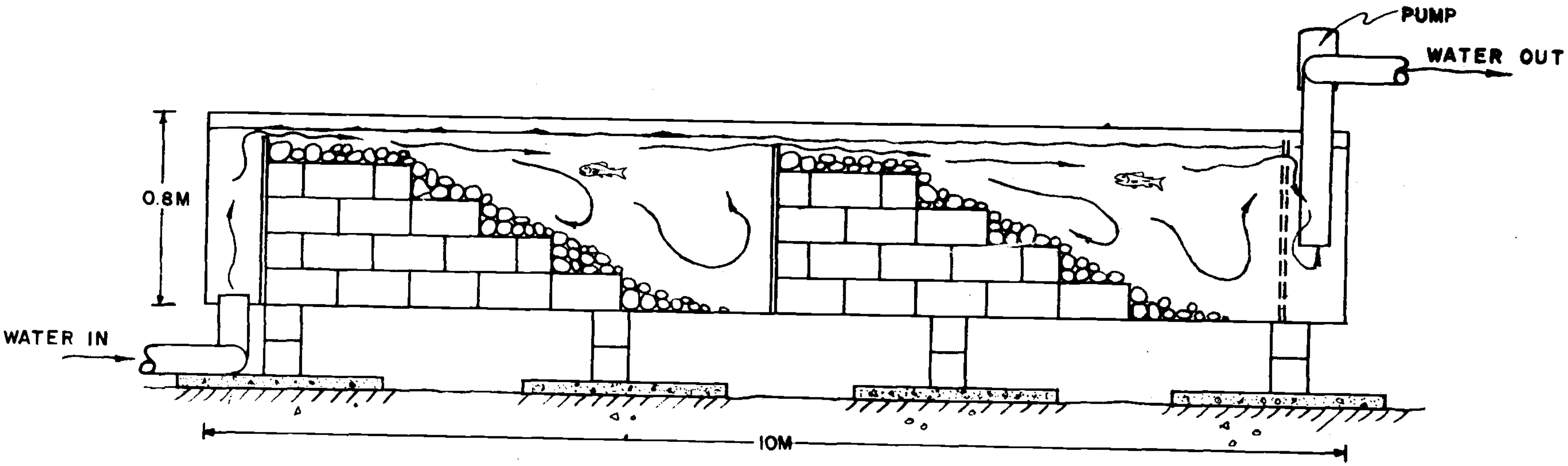


Figure 2. Wooden tank comprising one-half of a model stream (Diagrammatic side view).

fish from entering the pump. Movement through the large irrigation pipe connecting the wooden tanks was frequently observed. Screens could be inserted at various points along the stream for separating groups of fish, young fry and yearlings for example. Until October 1970 fish were not able to leave the streams but in that month a trap was constructed which fish could reach by entering the outlet pipe (6 cm diameter).

Plant cover consisted of large alder (Alnus sp.) and apple (Malus sp.) trees growing beside the model streams. These provided partial shading and a considerable fall of leaves, blossoms, catkins, and insects into the streams.

Seasonal variation in flow was the one major feature of coho streams for which no simulation was attempted. Simulation of a winter freshet would have required a ten- or twenty-fold increase in flow. This could not have been achieved with the available pumps and would have certainly damaged the tanks.

Temperatures in the heated stream were maintained 3.5-5 C above those of the control. This elevation is within the range of increase observed in streams receiving cooling water from power plants (Alabaster, 1969).

Two industrial heaters (Chromalox Model TL5360) were immersed in the treatment stream (Figure 1). Each 6 kw heater was composed of three resistance coils which were suspended in areas of maximum turbulence at the upstream end of each of the two wooden tanks. Flow rate and turbulence in the streams apparently were sufficient to maintain uniform temperature throughout the streams, since no variations in temperature between different points in the water mass were ever detected.

Temperatures in each stream were recorded continuously with a spring-driven thermograph (Partlow Model RFT). Each recorder had one temperature probe, placed about 0.5 m below the water surface in a pool. Recorders were periodically checked for accuracy by comparing readings with those of mercury thermometers. Recorders could be adjusted with a precision of about 0.1-0.2 C.

Information taken from the temperature records included daily maxima and minima, daily means, and number of hours per day spent within each Centigrade degree interval (10-11 C, 11-12 C...), hereafter referred to as the temperature distribution. Maxima and minima were determined by eye. Daily means and daily temperature distribution were determined mechanically using a digitizer (Calma Model 303) which recorded time-temperature coordinates along the stylus trace (Figure 3). Coordinates were taken every 0.01 inch and this information was recorded on magnetic tape for computer use. Some idea of the precision of this technique may be given by noting that the Fahrenheit degree lines on the chart (Figure 3) are about 0.04 inches apart and the hour lines range from 0.10

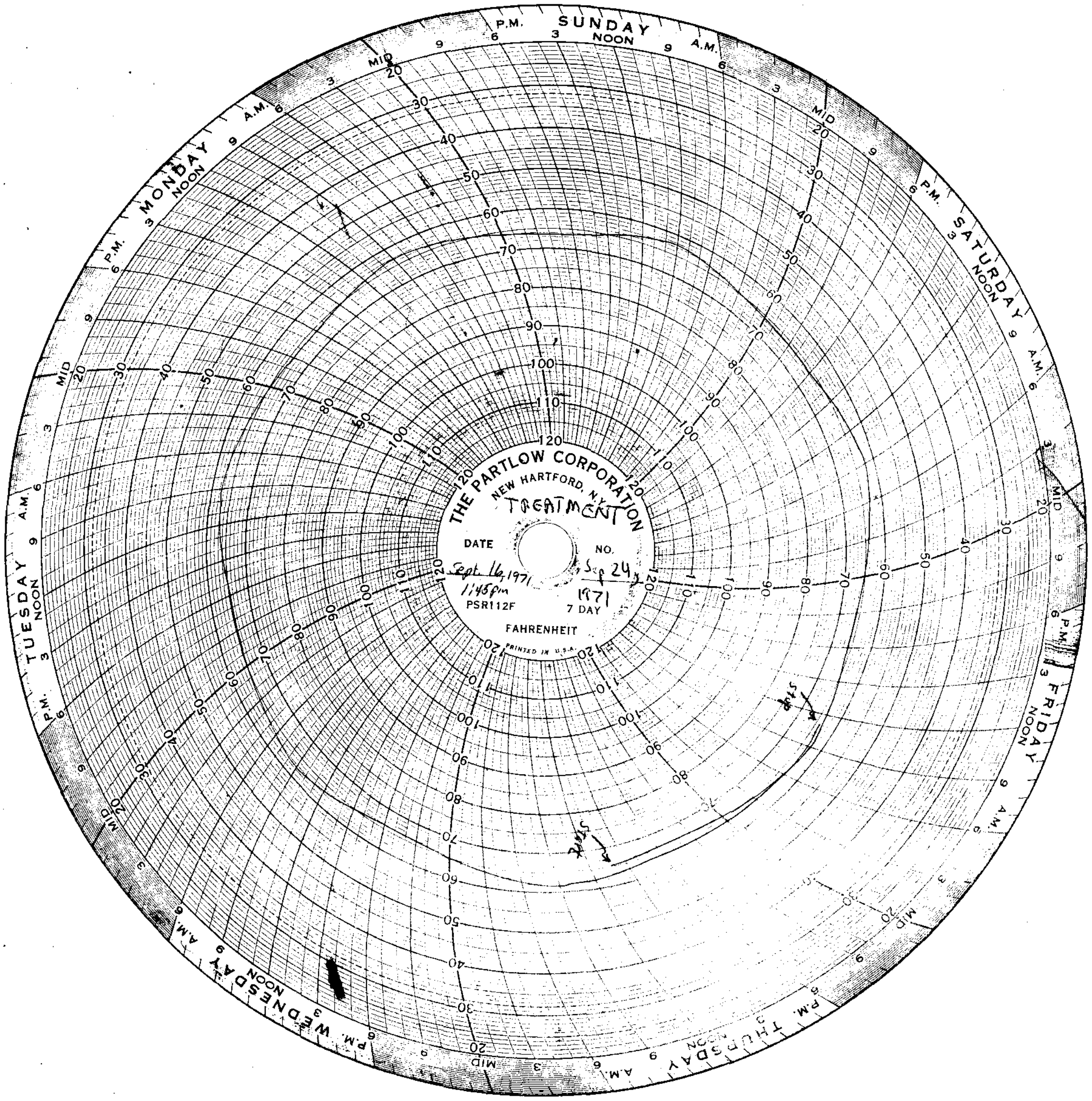


Figure 3. Temperature record from the heated model stream. Units are degrees Fahrenheit.

inches (at 75 F) to 0.16 inches (at 35 F) apart. Some error was introduced because the machine processing required that an operator follow the temperature trace by hand with a recording instrument, but this should have been random.

Experimental Animals

Juvenile coho salmon of three year classes were placed in the model streams (Table 1). Coho of the 1969 and 1970 year classes were obtained from Tobe Creek, a small stream in the Alsea watershed in western Oregon. Coho of the 1971 year class were taken as eggs from one adult female captured at the Fall Creek salmon hatchery located in the Alsea watershed about 25 miles west of Tobe Creek. Eggs and the milt from four males were transported to the Oak Creek laboratory where eggs were fertilized, mixed, and placed in an incubator. When eggs reached the eyed stage in January 1971 they were placed in floating baskets in the model streams. Hatching took place in the baskets. Alevins were retained in the baskets until the process of epidermal growth over the yolk sac ("buttoning up") was complete and were then released into the streams.

Eggs were also taken at the Fall Creek hatchery in the fall of 1969 and reared in baskets in the model streams. Egg losses were heavy because we attempted to rear young, fragile eggs in the baskets. Fry losses were also high because of high winter temperatures in the

Table 1. Sources, numbers, and weights of the three year classes of juvenile coho salmon stocked in the model streams.

Year class	Stocking date	Source	Stocked as	Stream	Number stocked	Weight stocked (g)
1969	Nov-Dec 69	Tobe Cr.	large fry	Control	57	104
				Treatment	51	90
1970	Apr 70	Tobe Cr.	small fry	Control	150	92
				Treatment	150	90
1971	Jan 71	Fall Cr. hatchery	eyed eggs	Control	800	320
				Treatment	800	320

heated stream, predation by yearling coho, and crushing of weak-swimming fry against screens. As a result it was decided not to use this group of fry and the survivors were removed from the streams, to be replaced by fry from Tobe Creek.

Fish longer than about 55 mm were individually marked using the cold-branding technique (Edmundson and Everest, 1967). Growth of individual fish could thus be followed and numbers present could be accurately determined. If a fish escaped capture on one sampling date but was captured on the next, the estimate of numbers on the previous date was adjusted. The fish's weight on the previous date could be estimated by interpolation and added to obtain a corrected weight of the population on that date. In order to express population weight values in biomass terms ($g \cdot m^{-2}$) the total weight of salmon was divided by the number of square meters of stream area. At intervals of about two weeks fish were seined from the streams and anesthetized with tricaine methanesulfonate for measurement of fork lengths and blotted weights. Fish were weighed within an hour of their removal from the stream, so their weights included weights of food in the stomachs. It was believed that this error was compensated for by reduced mortality or other effects of prolonged holding. After the fish were weighed, they were returned to the streams. Most appeared to resume feeding within an hour or so.

Production of juvenile coho was estimated by summing values of growth of marked individuals. The term production is used here in the sense of Ricker and Foerster (1948) to mean the total quantity of tissue elaborated in a given period of time, regardless of whether that quantity survives to the end of the time period. Production of juvenile coho during a given sampling interval was thus equal to the total growth of all individuals including those which did not survive to the end of the period, and was expressed in grams per square meter of stream area ($g \cdot m^{-2}$). If a fish disappeared during a sampling interval, its growth was estimated by assuming that it had survived until the middle of the time interval and had grown at the mean rate of growth of the entire population in that time interval. The growth rate used in my calculations was the average relative growth rate, expressed in milligrams per gram per day, and equivalent to $\frac{\Delta W}{\overline{W} \cdot t}$

where ΔW = growth during the sampling interval

$\overline{W}$ = average biomass (weight per unit area) during the sampling interval

t = length of the sampling interval, in days

Production of young coho fry too small to mark individually was estimated by multiplying the change in mean weight per fish over the sampling interval by the estimated population size at the end of the interval. Growth of young fry that died during the sampling interval was assumed to be zero, as there was evidence that the great majority of such mortalities resulted from starvation.

Fish of the 1969 and 1970 year classes were removed in late winter and early spring, at the time when coho normally leave the stream as smolts. To introduce an element of volition, yearling coho in each model stream were placed in the upstream tank in late winter. If a yearling moved through the pipe and into the downstream tank, this was taken as evidence of a desire to migrate downstream, and the fish was removed from the experiment. Movement of yearlings back into the upstream tank was possible in winter 1970 but was presumably prevented in winter 1971 by a wire funnel placed in the connecting pipe. Fish in very poor condition were removed from the streams whenever found and were discarded.

Two procedures were used to obtain stomach contents of fish. One was to place additional fish that were obtained from Tobe Creek into screened-off sections of the model streams so that they could feed without competition from experimental fish. These fish were removed after several days and killed for stomach analysis. A second method was to extract food from the stomachs of living experimental fish with ear forceps (Wales, 1962). This was possible only for fish over about 65 mm fork length.

In order to provide a comparison of experimental growth and size distribution with that of a natural population, juvenile coho in

Tobe Creek were sampled periodically in 1969, 1970, and 1971. A variety of sites and habitats were seined in order to obtain a representative size distribution of coho. Fish were brought back to the Oak Creek laboratory for weighing and measuring, then returned to Tobe Creek.

Studies of Invertebrates

The model streams were initially stocked in the fall of 1969 with aquatic insects from Oak Creek. Colonization continued throughout the experiment through egg deposition and import of young stages as described earlier.

Riffle organisms were sampled by placing wooden-bottomed baskets with low wire sides on the riffles, filling them with gravel so that they formed a part of the substrate, leaving them in place for about a month, and then lifting them out for removal of invertebrates. When the baskets were lifted out a screened box was fitted over them to prevent escape of insects. Surface area of each basket was 0.058 m^2. A monthly riffle bottom sample consisted of three of these baskets per stream, each from a different riffle. Since water velocity decreased and depth increased from the head to the foot of each riffle, baskets were positioned in the lower, middle, and upper portions of riffles in each stream to provide a composite sample representing the entire riffle habitat.

Pool organisms were sampled by pushing a six-inch aluminum irrigation pipe (cross-sectional area 0.018 m^2) into the substrate, stirring up the enclosed gravel, and siphoning out the insects and debris into a net with a garden hose.

From October 1969 until June 1970, drifting organisms were sampled with a Nitex net having a mesh size of 300 microns and dimensions: 56 mm long, 46 mm wide at the mouth, and 31 mm high at the mouth. To alleviate clogging, a larger Nitex net (107 x 56 x 31 mm) with mesh of 300 microns was used from June 1970 until the end of the experiment. The surface area of the larger net was approximately four times larger than that of the smaller. Drift nets were fished at the foot of the riffle for about 24 hours per sample. Usually one sample per month was taken in each stream. Drift nets were also used periodically to filter the incoming exchange water to determine the types of organisms being imported.

Large insects were removed while alive from the total benthic sample and were later preserved in 70 percent ethanol. Subsamples of 10-25 percent were also preserved, and these were later examined under magnification for small organisms.

Relationships between body length (minus cerci and antennae) and preserved wet weight were established for various insect species, genera, or larger groups. Insects captured in samples were measured to the nearest millimeter of length and the length-weight relationship applied to obtain a biomass estimate.

Production of insects was estimated by the method of Hynes and Coleman (1968) as modified by Hamilton (1969). In this procedure annual production of a taxon or combination of taxa is estimated by summing the losses of individuals from an "average" cohort as that cohort grows from one length class to the next, as indicated by

$$\hat{P} = i \sum_{j=1}^{i} \left[(\bar{n}_j - \bar{n}_{j+1}) \frac{(\bar{w}_j - \bar{w}_{j+1})}{2} \right]$$

where

$\hat{P}$ = estimated annual production of the taxon of interest

i = the number of length classes through which the animals grow and also the number of "average" cohorts per year

$\bar{n}_j$ = the average number of animals per sample which fall into the $\underline{j}$th length class

$\bar{w}_j$ = the average weight per individual in the $\underline{j}$th length class

Hamilton (1969) listed several assumptions made in using this estimating procedure. The most important assumption, in terms of the effect on the estimated production value, is that all species within the taxon of interest be univoltine. If this assumption is erroneous and they are in fact multivoltine, the production estimate will be too small by a factor approximately equal to the number of generations per year. In contrast, the production estimate is little affected by deviations from the assumptions of constant year class size, constant rate of growth in length, and uniform distribution of sampling effort throughout the year.

In identifying invertebrates the following were the chief sources used:

Crustacea and Mollusca - Ward and Whipple (1945)

Chironomidae - Usinger (1963) and Roback (1959)

Diptera other than Chironomidae - Usinger (1963)

Ephemeroptera - Edmunds and Allen (1964), Lehmkuhl (1968), and unpublished keys of Lehmkuhl for the mayflies of Oak Creek.

Odonata - Usinger (1963)

Plecoptera - Jewett (1959)

Sialidae - Azam and Anderson (1969)

Trichoptera in our samples were identified by Dr. Norman H. Anderson, Department of Entomology, Oregon State University.

Algae, leaves, diatomaceous slime, and other material in the bottom samples were dried at 70 C for at least two days, weighed, then ashed at 500 C and reweighed, the difference being taken as the organic content of the sample.

RESULTS AND INTERPRETATION

Experimental Temperatures

During the experiment the local area experienced a warm, wet winter (1969-1970), a sunny, warm summer (1970), a second wet but colder winter (1970-1971), and a wet, cool spring and early summer (1971). Heaters were switched on in late November 1969, and a temperature difference was maintained throughout the experiment except for a few days when pumps failed to function. The difference between mean monthly temperatures of control and treatment streams from December 1969 to July 1971 ranged from 3.2 C to 5.0 C with a mean difference of 4.3 C. The diurnal pattern of temperature fluctuation was similar in control and heated streams. Diurnal fluctuation was greatest in summer and least in winter, apparently following the fluctuation in air temperature. There was little overlap of the temperature regimes in the two systems (Figure 4). The control-treatment increment was typically larger than the diurnal fluctuation within a stream.

Except in the fall, temperatures in the control stream generally fell within the range of maximum growth efficiency (growth ÷ food consumption) for coho, as determined by Averett (1969) (Figure 5). Fall temperatures in the control stream were too low for maximum growth efficiency. Temperatures in the heated stream were usually

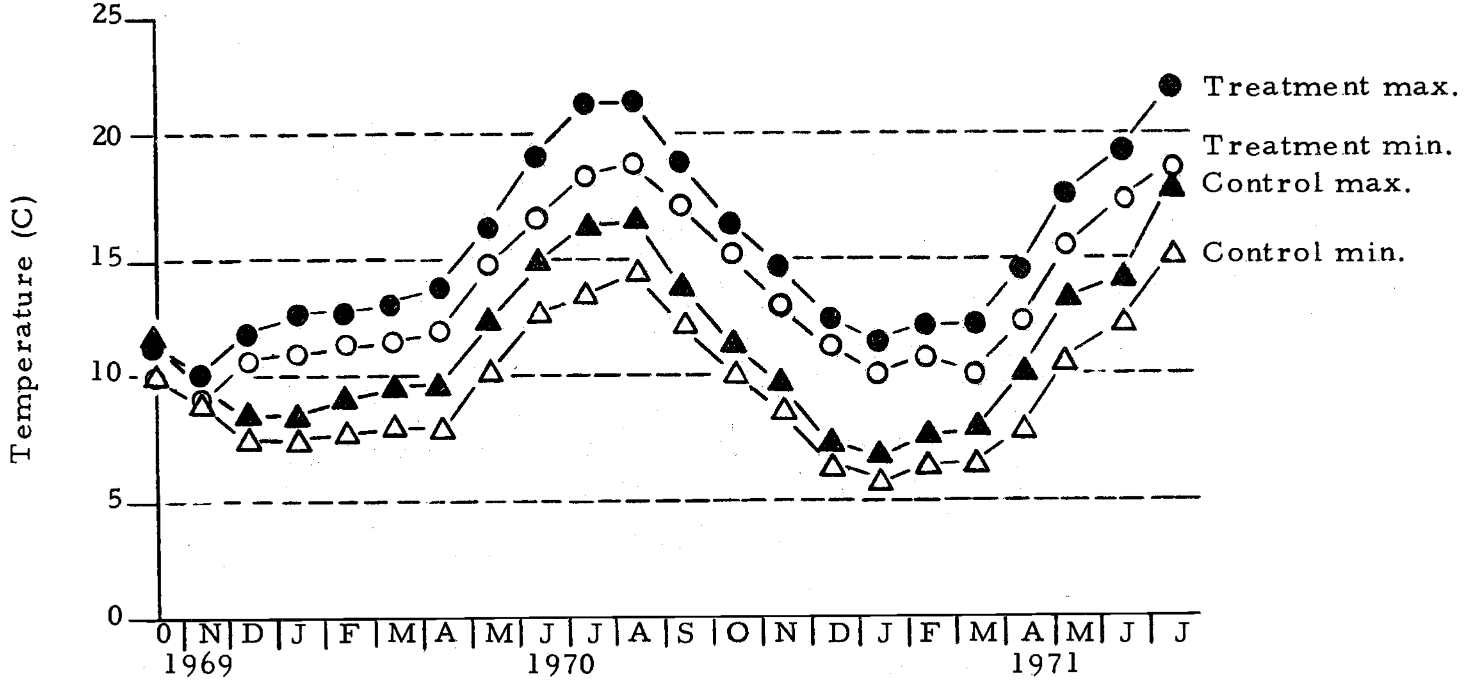


Figure 4. Monthly mean minimum and maximum temperatures for heated and control model streams from 1 October 1969 to 31 July 1971 based upon daily maximum and minimum temperatures.

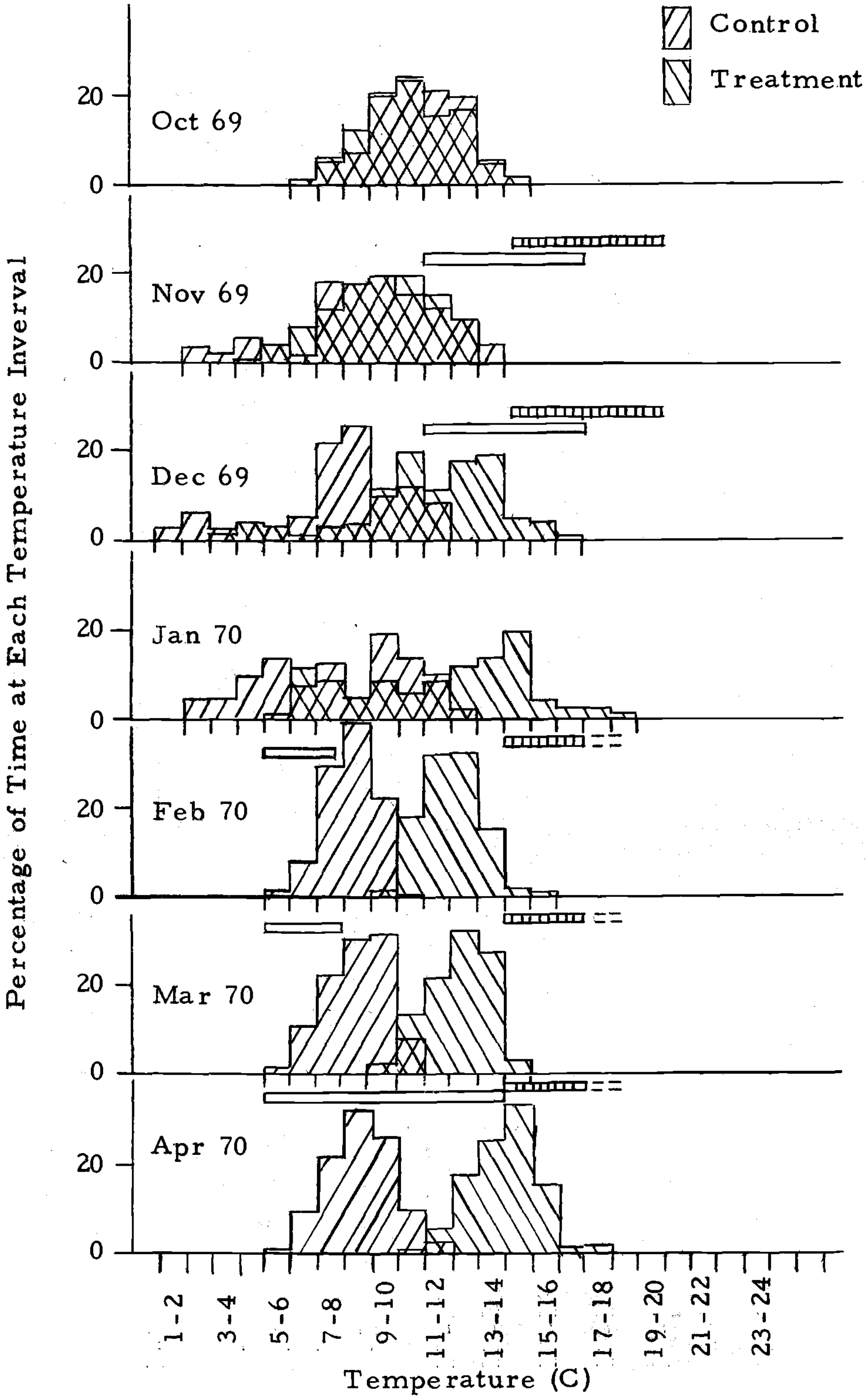
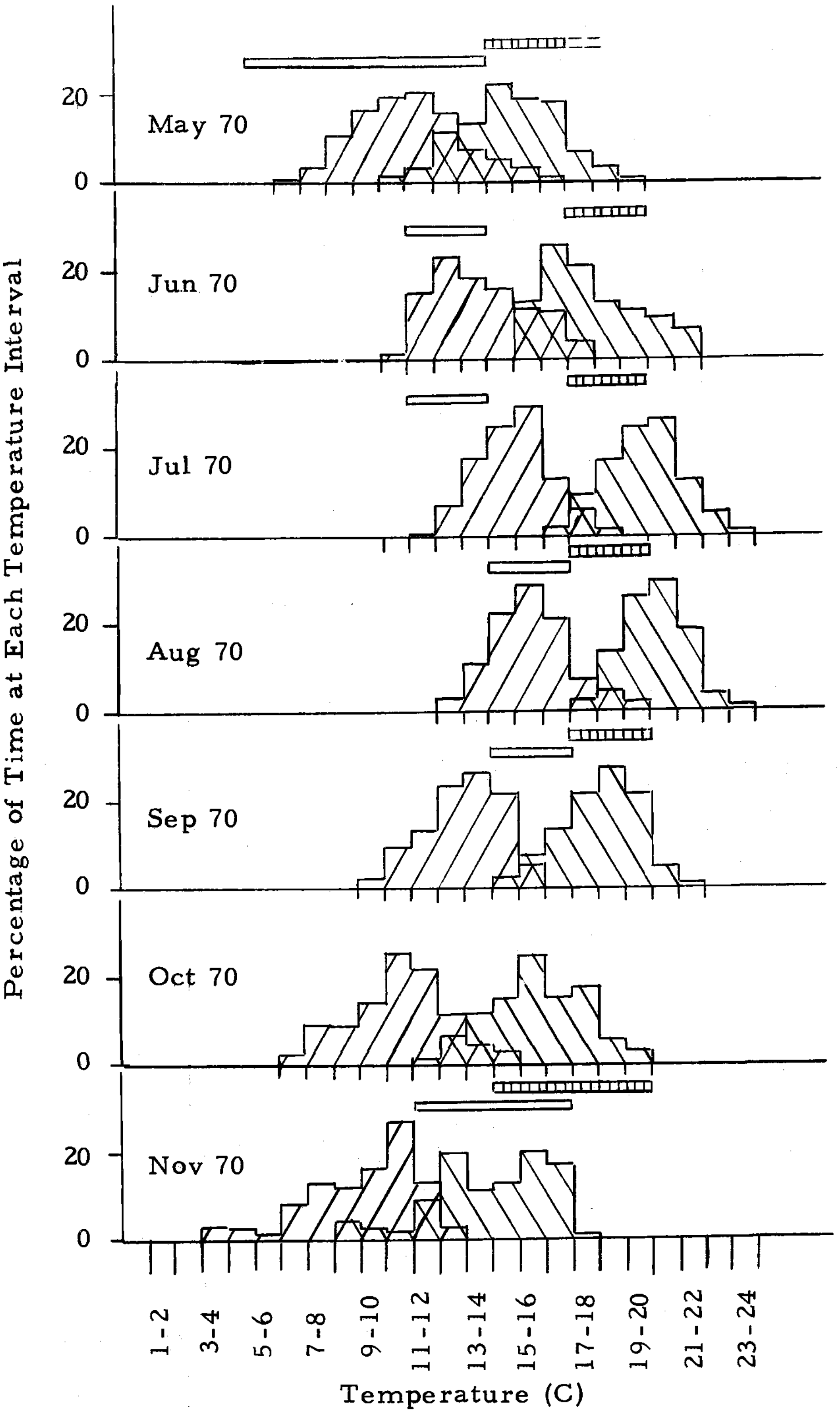


Figure 5. Percentage of time spent at each temperature during each month in the model streams. Solid bars delimit the temperature range for optimal growth efficiency in juvenile coho, as determined by Averett (1969). Broken bars delimit the temperature range permitting maximum food consumption and growth in coho.



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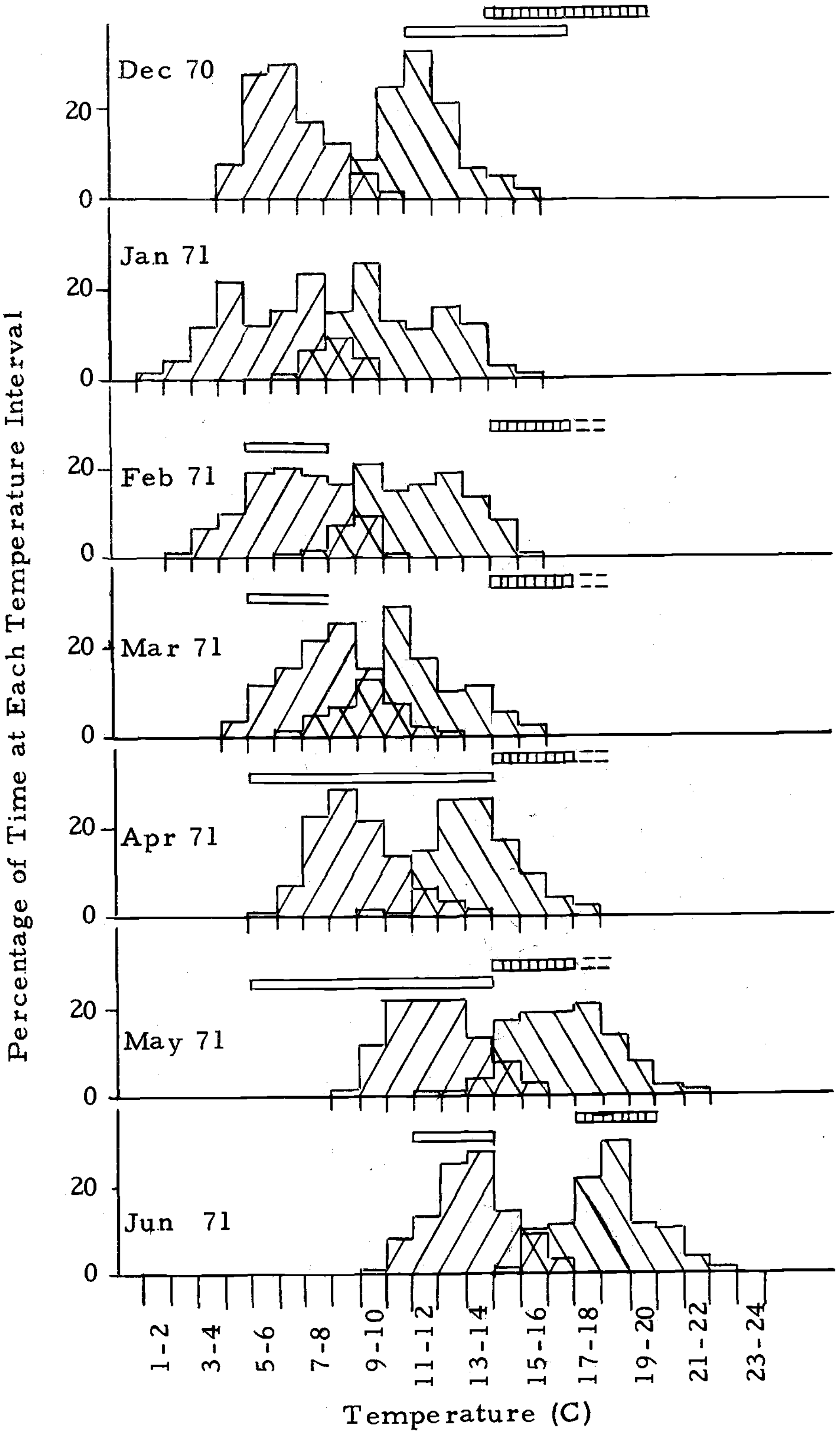

Figure 5. Continued

above the range permitting maximum growth efficiency except in the fall and in part of the spring. Efficiency of food conversion is, however, only one factor in determining growth and production. For instance, while coho kept by Averett at 5-8 C achieved higher food conversion efficiency than fish kept at higher temperatures in his winter experiment, the appetite (as indicated by maximum food consumption) of those fish maintained at higher temperatures was greater. The winter rates of food consumption of coho in both control and heated streams were near the highest consumption levels of Averett's 5-8 C group. The highest growth rates in Averett's winter experiment were at 14-17 C, a temperature range reached only in the heated stream in winter in my experiment. Thus, if sufficient food were available, growth of coho in the heated stream should have exceeded that in the control stream. In the other seasons the temperature distribution in the heated stream continued to coincide with the temperature range of maximum daily food consumption and growth in Averett's experiment. In Averett's February-March and April-May experiments the maximum temperatures at which fish were kept were 17 C and in the June-July and November-December experiments the maximum was 20 C. These were also the temperatures of maximum appetite and growth rate, and higher temperatures might have produced even greater appetite. In his August-September experiment Averett kept one group of coho at 23 C and both growth and food consumption in this group were low, maximum food consumption being about equal to that of the 11 C group and maximum growth rate being much less than for that group. Thus appetite in coho appears to fall off sharply between 20 and 23 C. In my heated stream, a large fraction of the temperature distribution fell in this range in July and August of 1970, with smaller fractions in June of 1970 and 1971 (Figure 5). In summary, temperatures in the heated stream would usually have been favorable for growth at high levels of food availability since appetite would have been less restricted than at the control temperatures. In the control stream, temperatures would have favored growth at low levels of food availability because the efficiency of conversion of food to growth would have been higher than in the heated stream.

Production, Survival, and Behavior of Juvenile Coho

Fish of the 1969 year class grew slowly in both control and heated streams from late fall 1969 until mid-winter 1970. Beginning in January 1970, growth accelerated (Figure 6) so that by February mean weight per fish in the heated stream was approximately triple the late fall value. Mean weight per fish in the control stream lagged behind the treatment value but was approaching it when these fish were removed in March 1970. The late-winter increase in growth rates in both model streams coincided with the emergence of coho fry of Fall Creek origin. These fry were frequently found in

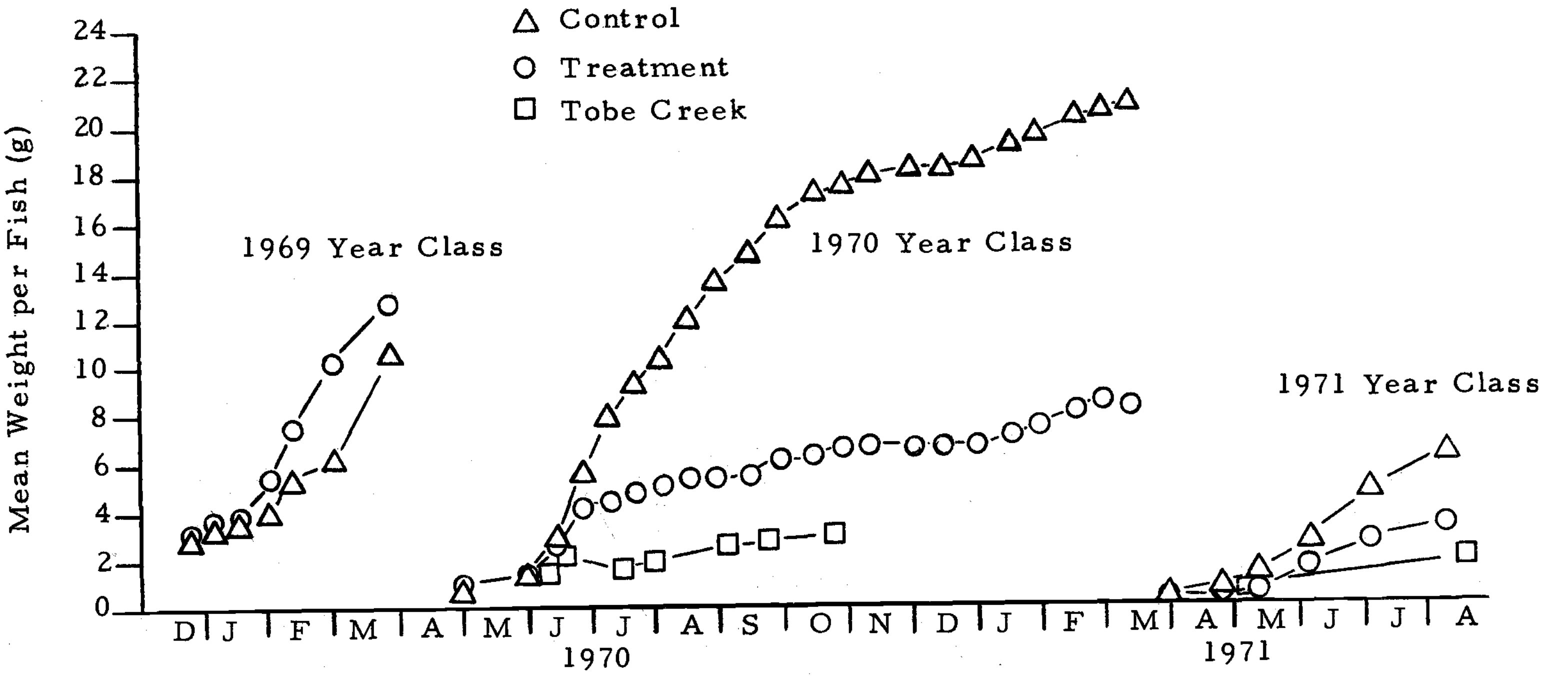

Figure 6. Mean wet weights of juvenile coho salmon in control and heated model streams.

stomachs of yearling coho examined in February, March, and April 1970.

Numbers of coho of the 1969 year class declined quickly from 57 and 51 fish stocked in the control and heated streams respectively to about 40 per stream, then more slowly to about 30 fish each late in the experiment (Figure 7). Initial numbers stocked are not depicted for this or other year classes since these were chosen arbitrarily and were apparently always larger than the streams could support. Also not depicted is the rapid decline in numbers from "stable" levels to zero as fish were removed as smolts in late winter and spring. Here again the criteria for defining fish as smolts and thus suitable for removal from the stream were not rigorous and the rate of removal had no biological significance in itself.

Biomass of coho of the 1969 year class apparently never reached an equilibrium level, although there was some leveling off in the heated stream (Figure 8). Because of the earlier onset of rapid individual growth in the heated stream, coho biomass in this stream began to exceed that in the control stream in early winter and by February 1970 was about half again as large. By March the treatment fish were still larger individually than those in the control stream but their numbers had declined so that biomasses in control and treatment streams were about equal.

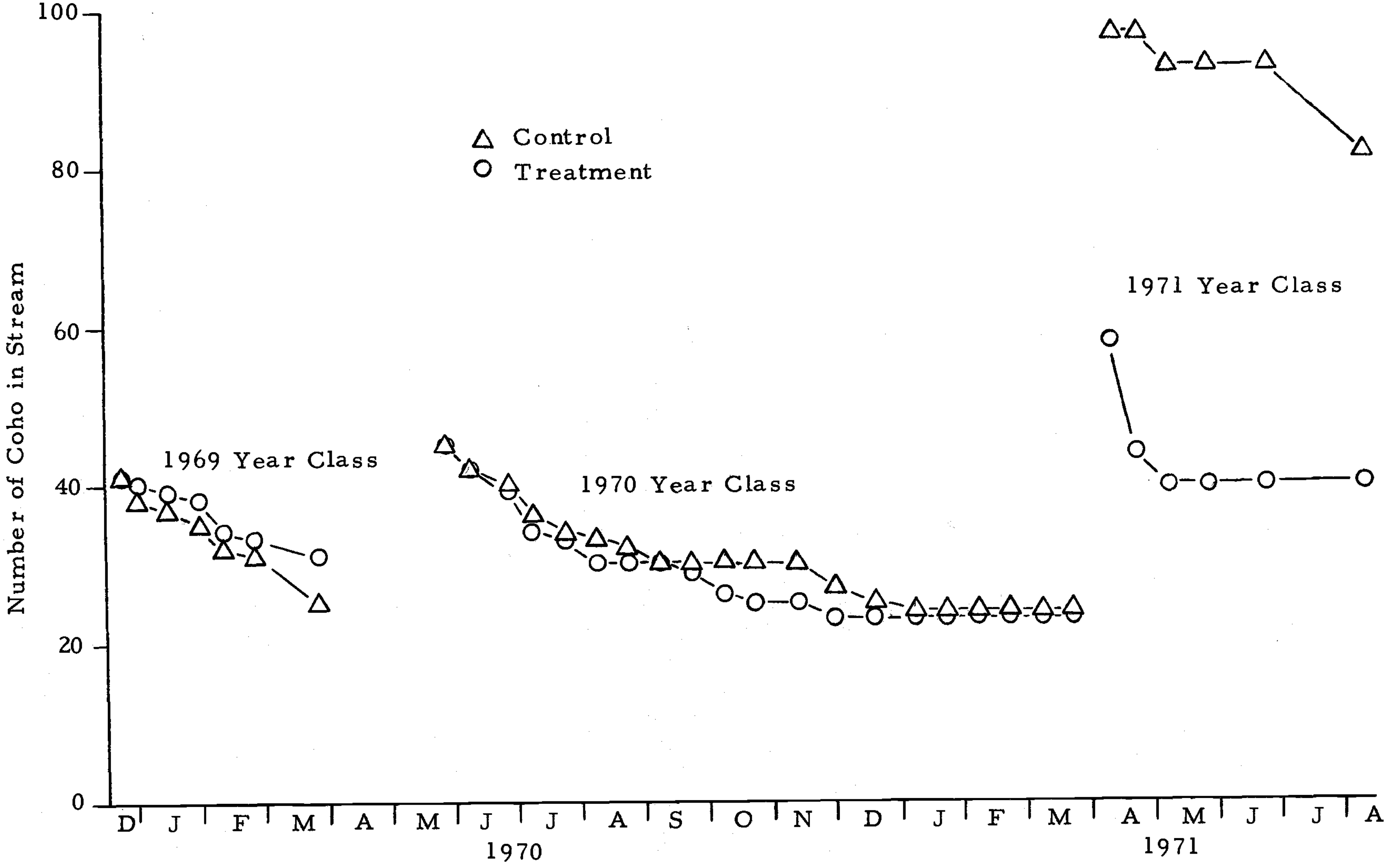

Figure 7. Numbers of juvenile coho salmon resident in the model streams.

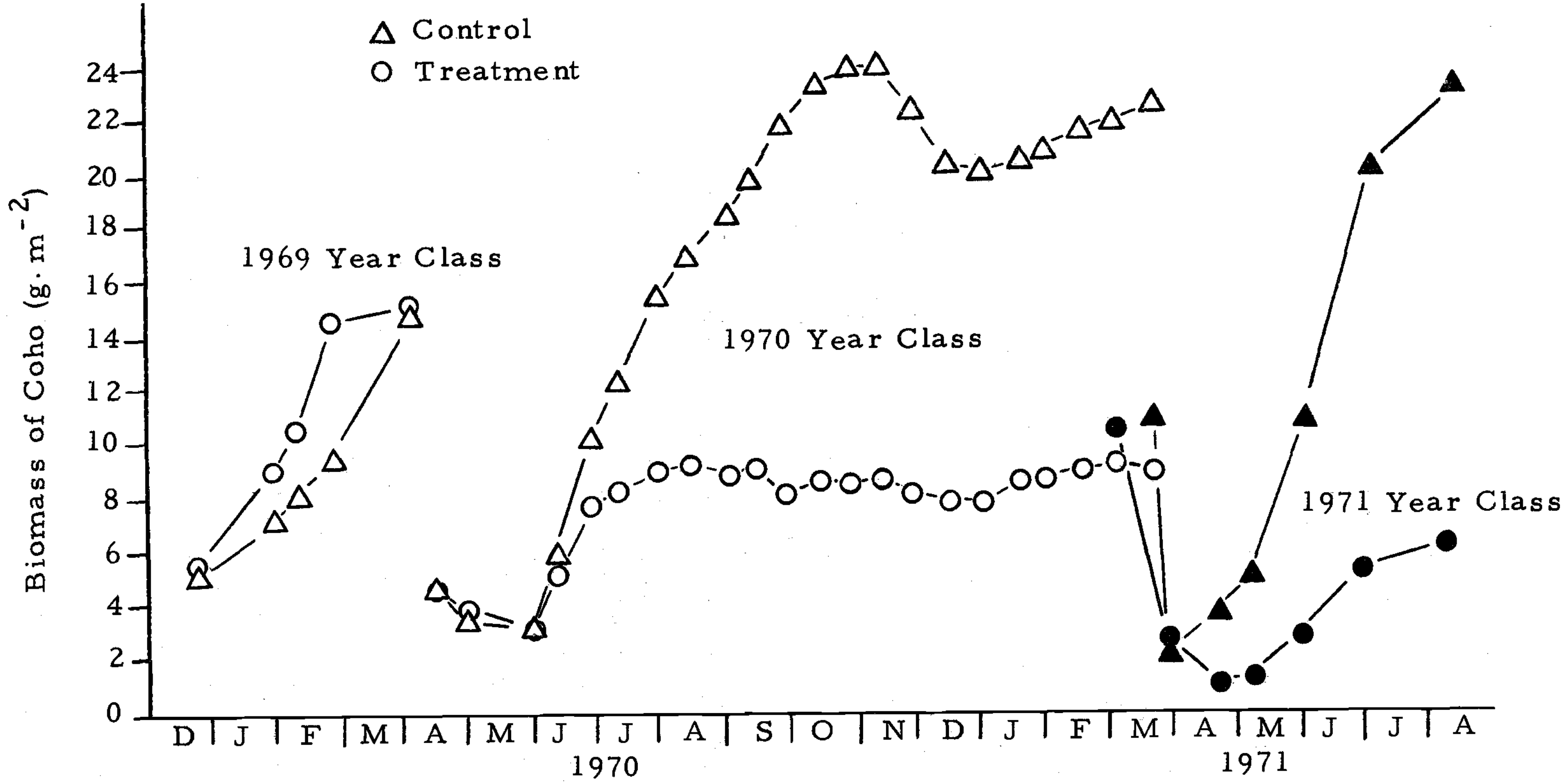

Figure 8. Biomasses of juvenile coho salmon in the model streams.

Production of coho of the 1969 year class in the heated stream exceeded production in the control stream by about one-fourth by May 1970 (Figure 9). Levels of biomass which would have resulted in maximum rates of production may not have been reached in the control stream, but were apparently about 12 $g \cdot m^{-2}$ in the heated stream (Figure 10). The production rate-biomass relationship for the control stream approximated that of the heated stream and may have indicated the same equilibrium biomasses in the two streams if the experiment with the 1969 year class had been prolonged.

Early losses of coho fry of the 1970 year class were much greater in the heated than in the control stream. One cause of losses was a pump failure on 1 May 1970 which permitted an unknown number of fry to leave via the exchange water outflow. For this reason, fry were redistributed on 28 May 1970 so that each stream held 45 fry with mean weights of 1.76 g and 1.77 g in control and treatment streams respectively.

After early June 1970, the mean weight of coho in the control stream grew steadily greater than the treatment mean. The control fish were about twice as heavy by late summer and about 2.5 times as heavy by winter (Figure 6). Fish in both streams were very large compared to fish resident in Tobe Creek. This size advantage was not restricted to the largest, dominant fish in the control stream. Nearly all of the fish in the control population were longer than

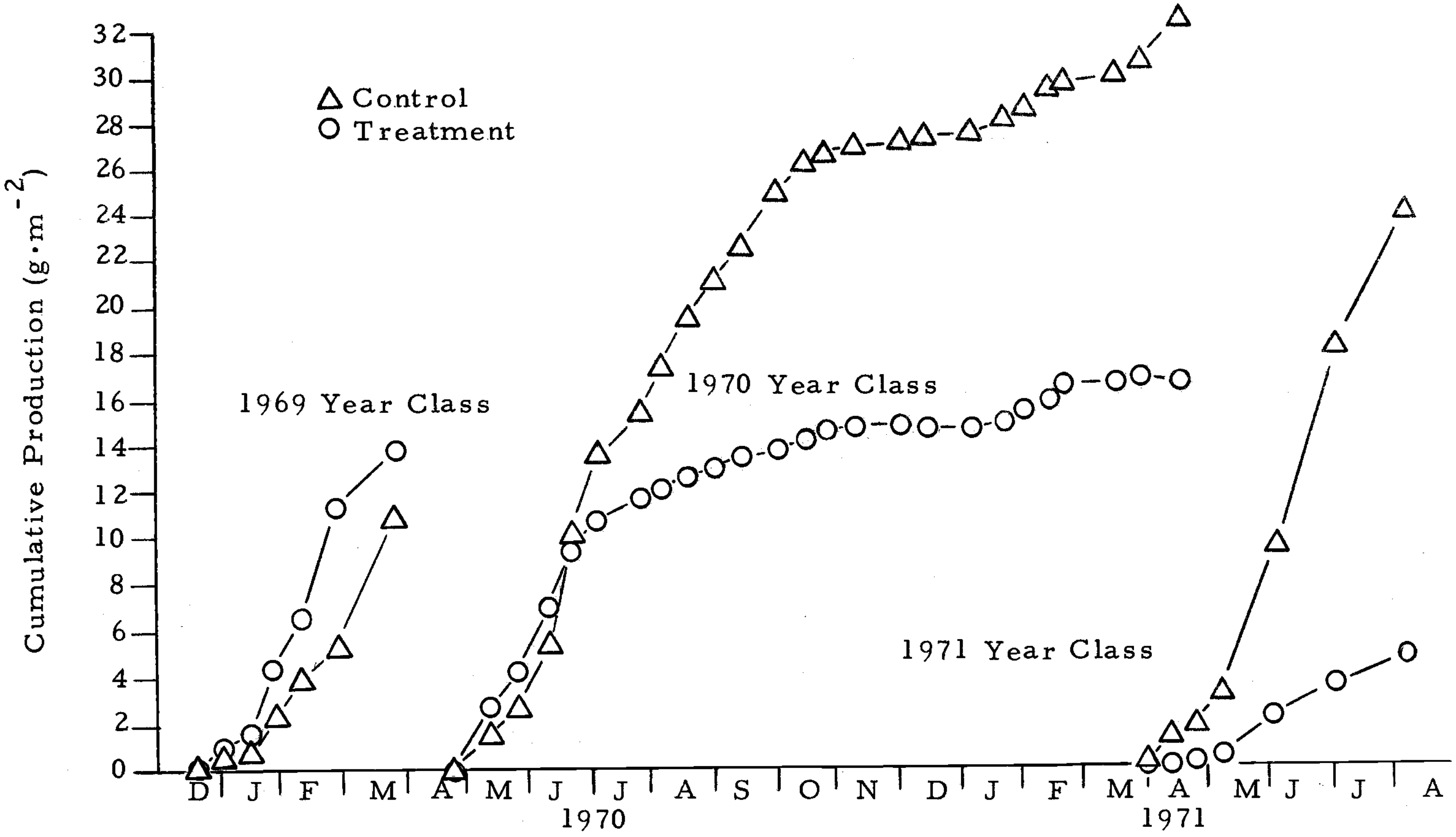

Figure 9. Cumulative production of juvenile coho salmon in control and heated model streams.

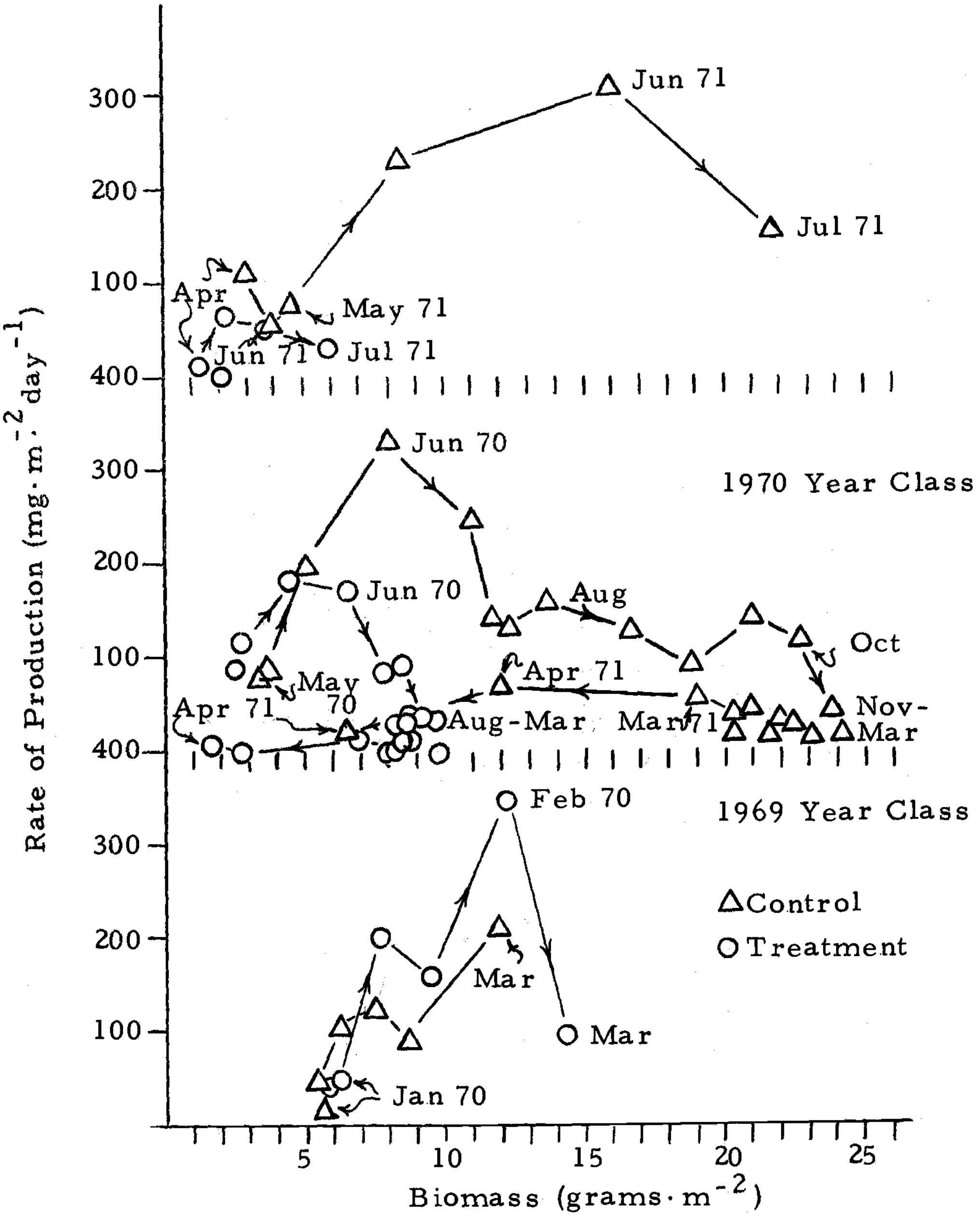

Figure 10. Relationship of coho biomasses and rates of production in control and heated model streams.

treatment fish after the experiment had run for several months (Figure 11). In each stream, there was a wide range in fish size, with a few large fish and a concentration of numbers at the lower end of the length range. This distribution of sizes was also observed in Tobe Creek coho and is typical of stream populations of this species.

In both control and heated streams, all fish surviving to March 1971 were large enough to be potential smolts (Figure 11). Chapman (1965) found that mean lengths of coho taken from downstream traps in the spring ranged from about 75 to 90 mm over four year classes. Thus, by the spring of 1971, coho in the heated model stream had reached a size range typical of outmigrant smolts in small streams, while coho in the control stream reached unusually large size. Not all coho removed from the streams in the spring had the silvery, slender appearance of smolts. Generally, the larger fish removed were obviously smoltlike, while fish below about 100 mm fork length were parr- or smoltlike to various degrees.

Numbers of coho of the 1970 year class in the heated stream remained similar to numbers in the control stream throughout the experimental period (Figure 7). Numbers declined rapidly from the 150 stocked in each stream. This early decline is not depicted. The first sampling date shown in the figure is 28 May 1970, the day when numbers and biomasses in the two streams were made equal.

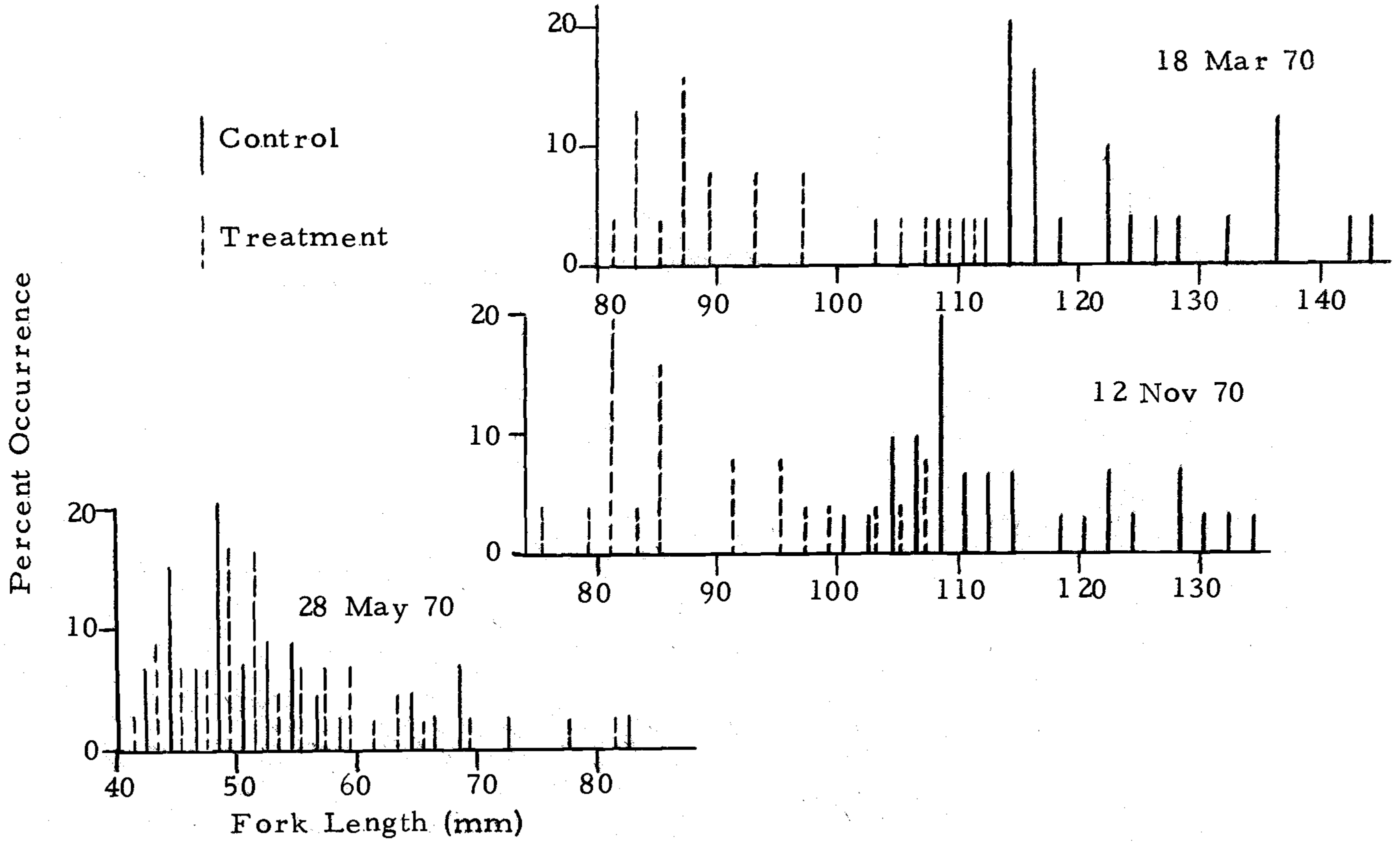

Figure 11. Size distribution of juvenile coho salmon of the 1970 year class in control and heated model streams. Fish are grouped by length intervals of 2 mm.

Since numbers of fish of the 1970 year class did not differ greatly between streams, the great difference in coho biomasses in the two systems (Figure 8) was largely because of the greater mean weight of coho in the control stream. Coho biomass in the heated stream appeared to reach an equilibrium level in early summer 1970 and remained between 8 and 10 $g \cdot m^{-2}$ until smolt removal began in the following spring. The equilibrium biomass of coho in the control stream was less well-established, since the loss of six fish in the autumn reduced the biomass considerably. Control biomass reached its maximum (24.3 $g \cdot m^{-2}$) on 12 November 1970. For the two-week period preceding this sampling date the average relative growth rate of coho reached a very low level (0.05 $percent \cdot day^{-1}$). Thus the equilibrium biomass of coho in the control stream was probably not much larger than 24 $g \cdot m^{-2}$ in 1970.

Average relative growth rates of coho of the 1970 year class were very high in early summer in the control stream, remained fairly high in late summer, approached zero in the fall, and increased slightly in winter (Figure 12). In the heated stream, growth rates were high in late spring but declined rapidly to low levels in summer and fall. Winter growth rates were low but slightly greater than in the control stream. The high winter growth rates of the 1969 year class were not approached by coho of the 1970 year class in either control or heated streams.

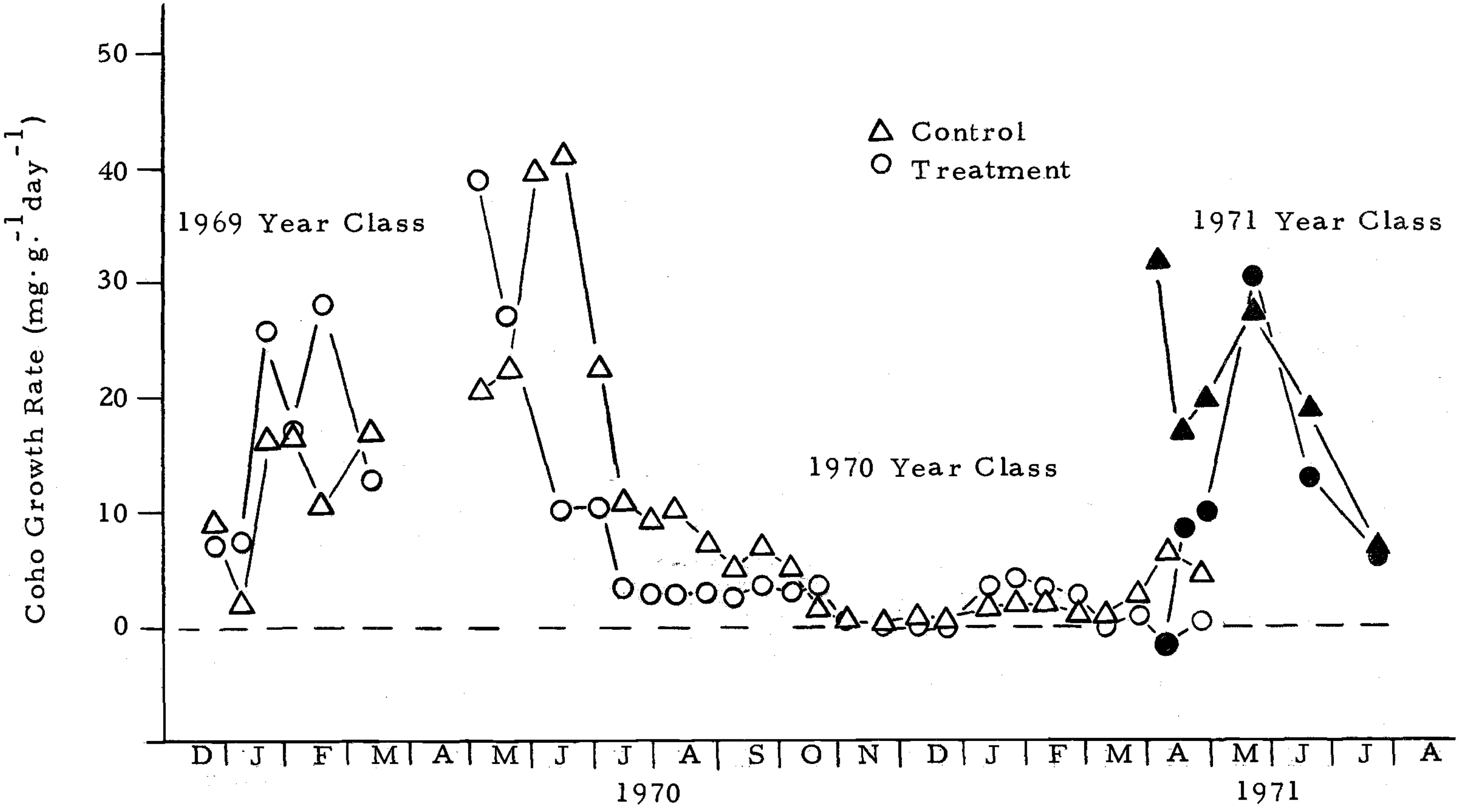

Figure 12. Average relative growth rates of juvenile coho salmon in control and heated model streams.

Total production of coho in the control stream was about twice that of coho in the heated stream for the 1970 year class (Figure 9). Most of this difference resulted from much higher individual growth rate in the control stream between June and October 1970. Before and after this period, production rates in control and heated streams were not greatly different (Figure 10), although the curves of cumulative production began to diverge again in the spring of 1971 (Figure 9).

In the control stream, the level of biomass of coho resulting in the highest production rates for the 1970 year class was about 8 $g \cdot m^{-2}$, reached in June 1970 (Figure 10). At this biomass level, rates of production in the control stream exceeded the highest values for the 1969 year class. Relatively high rates of production were maintained even at extremely high levels of biomass until the fall of 1970, when the capacity for production in this population appeared to decline and to remain at low levels throughout fall and winter, even when biomass was reduced by removal of smolts in the spring of 1971 (Figure 10).

The rate of production of coho was also greatest in June 1970 in the heated stream, at a biomass of about 5 $g \cdot m^{-2}$ (Figure 10). The rate quickly declined to low levels through summer, fall, winter, and spring. As in the control stream, a return in the early spring of 1971 to the biomass levels of June 1970 did not result in increased rate of production, indicating a decline in the productivity of the stream or in some physiological capacity for growth in the fish population. One change in the fish themselves was the great increase in individual size, from about 3-4 g in both streams at the time of maximum rate of production in June to 8-9 g in the heated stream and to over 20 g in the control stream by the end of the experiment. Another change was the onset of the smolt transformation, a process associated with diminished growth rates in salmonids (Wagner, 1971).

Low rates of production in winter in the 1970 year class contrasted with very high rates in coho of the 1969 year class in both streams. The most obvious explanation is that small coho fry were available as food for yearlings of the 1969 year class in the winter and spring of 1970, whereas in the following year fry and yearlings were segregated.

The mean weight of coho of the 1971 year class in the control stream exceeded the mean weight in the heated stream at the earliest measurements, made approximately when fry had reached the buttoned-up stage. The absolute difference in mean weight increased through the experimental period until on 9 August 1971 the control fry were about 90 percent larger on the average than were treatment fry (Figure 6).

Fish of the 1971 year class were considerably smaller in early summer, in both control and treatment streams, than were fish of the

1970 class at the same time of year (Figure 6). In the control stream this may have been associated with the much greater numbers present in the summer of 1971 as compared to the summer of 1970. In the heated stream, however, numbers present in the two years were about equal.

Mean weight of fry taken from the outlet traps was less than that of fry captured in the stream for both control and heated systems (Figure 13). In the heated system, mean weight of trap-caught fry declined through the spring of 1971 and was below 0.4 g for about six weeks. At this weight the fry were clearly starving, and dead, starved fry were removed from the trap throughout March and April. Dead fry, apparently starved, were also observed in the heated stream.

In early March 1971, control coho of the 1971 year class were shorter than treatment fish, the control fish having hatched about ten days later (Figure 14). By July 1971 the length distribution of the control fish was displaced so that the longest coho in the heated stream was shorter than the median length of control coho.

As in the previous year class, numbers of coho fry of the 1971 year class decreased rapidly in both control and heated streams in the winter and spring of 1971. From the 800 eyed eggs placed in each stream, approximately 600 fry in each stream survived to the buttoned-up stage and were released into the lower tanks of the control

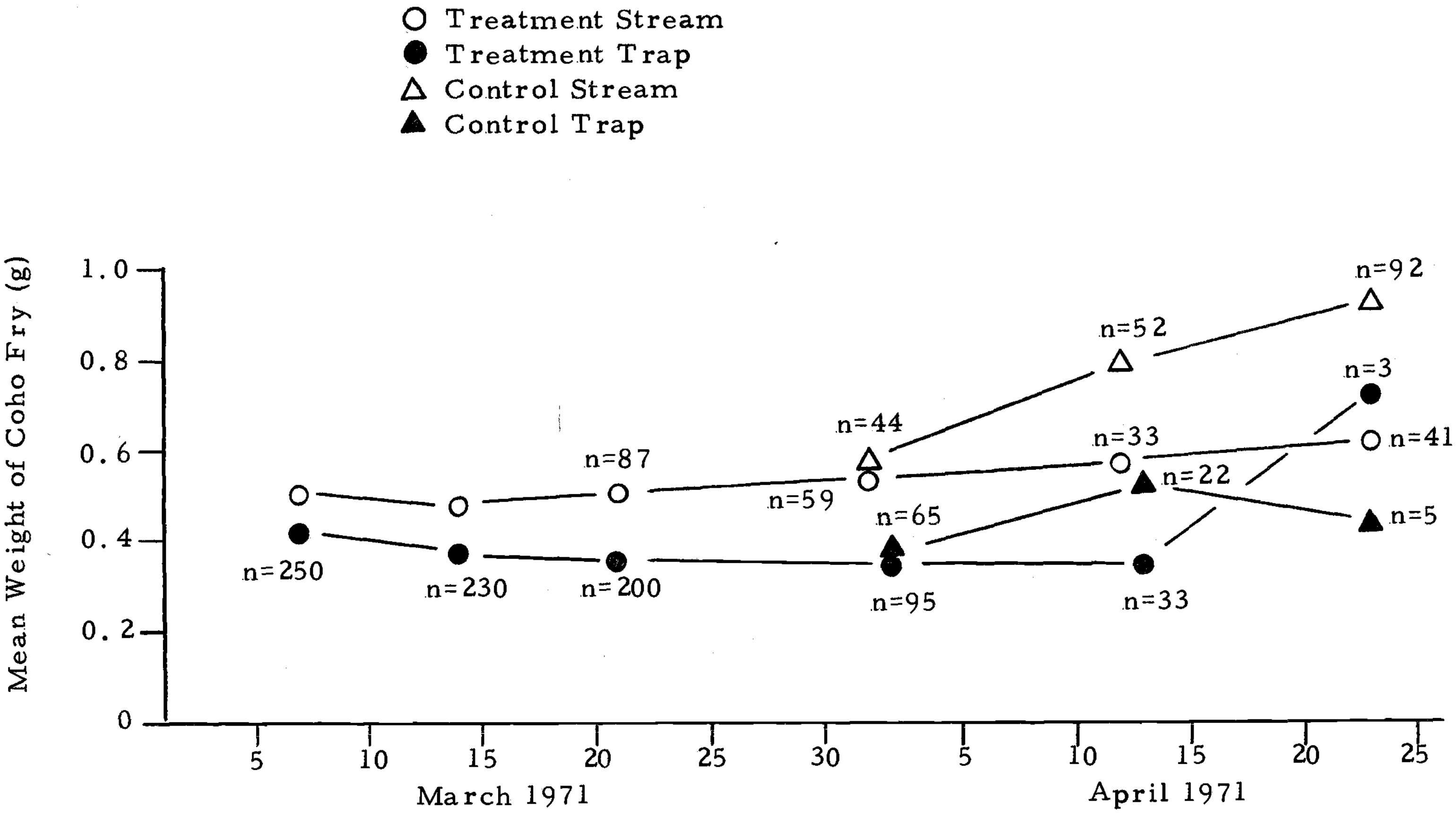

Figure 13. Mean weights and numbers present of coho fry in stream channels and outlet traps.

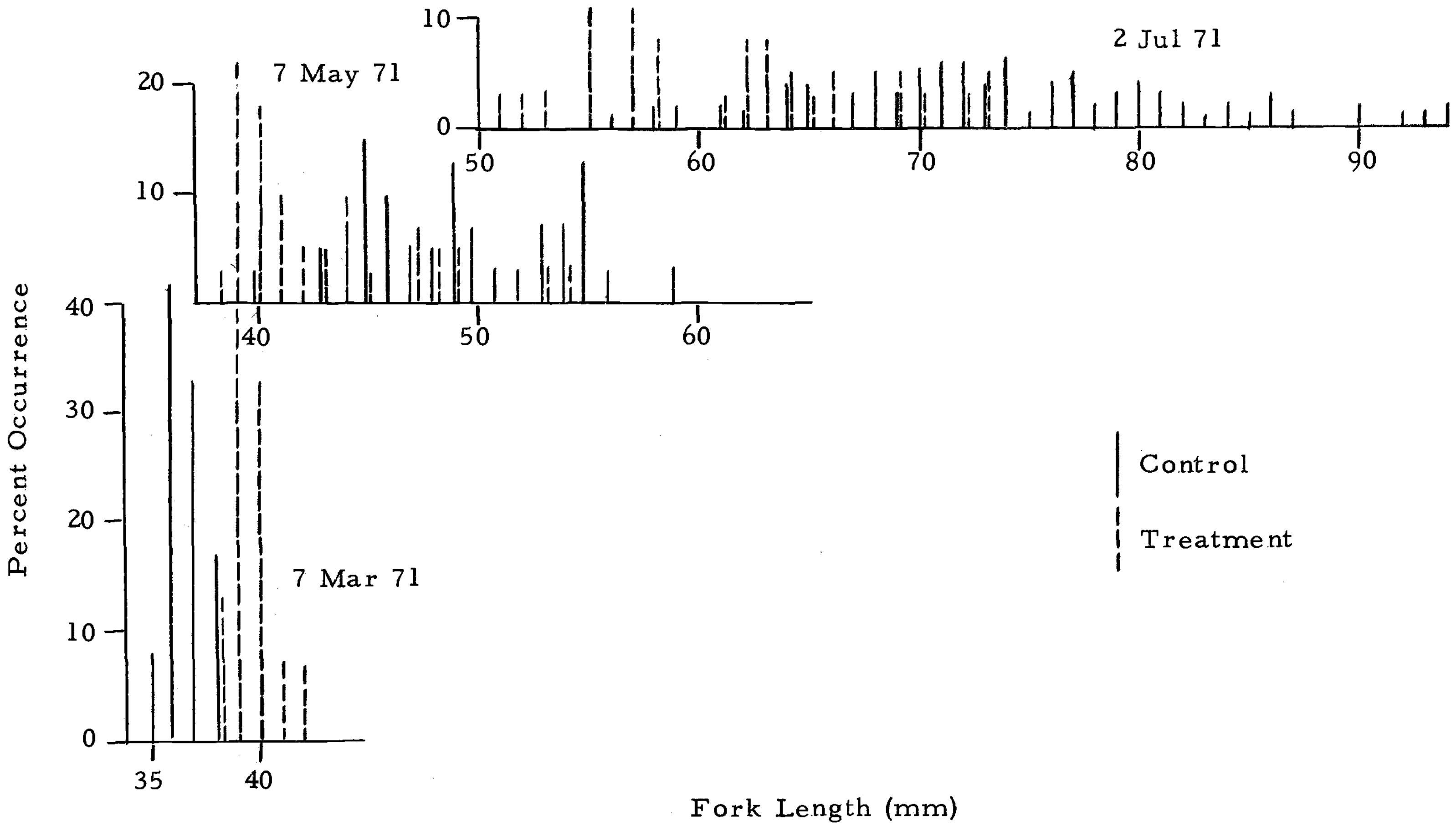

Figure 14. Size distribution of juvenile coho salmon of the 1971 year class in control and heated model streams. Fish are grouped by length intervals of 1 mm.

and heated streams, yearling coho being kept out of these tanks by screens. Releases of fry were made on 18 February 1971 in the heated stream and on 22 March 1971 in the control stream. By 9 August 1971, numbers caught by seining had declined to 82 in the control stream and 40 in the heated stream (Figure 7). The chief cause of the high mortality rate appeared to be starvation, since predation by older coho was not ordinarily possible and there was no evidence of disease.

As was the case for the 1970 year class, biomass of coho of the 1971 year class initially declined below the levels stocked in both control and treatment streams (Figure 8). This resulted largely from starvation and death of large numbers of fry. Growth of survivors in the control stream brought biomass up rapidly until by July 1971 it exceeded the level of July 1970. In the heated stream, biomass of coho fry declined to very low levels in April and May 1970 but by early summer had reached a level typical of wild coho populations in small streams (Chapman, 1965).

In the control stream, coho fry of the 1971 year class exhibited high growth rates throughout the spring of 1971 (Figure 12). In the heated stream, growth rates were relatively low until May, when numbers had greatly declined from earlier levels.

By July 1971, production in the control stream had reached even higher levels than had the production of the previous year class in

July 1970 (Figure 9). In contrast, production in the heated stream was less than half the level it had reached by July of the previous year, and was only about one-third as great as the total for the control stream. Rate of production of coho decreased in the control stream in the last sampling period after having approached the highest level reached in the previous spring (Figure 10). The biomass at which the rate of production was greatest in 1971 was larger than the biomass at which production was maximum during the previous year, indicating an increase in the productivity of the stream. In the heated stream, production rate reached only modest levels and had apparently begun to decline by early summer. The level of biomass associated with the highest production rates was lower than for the 1970 year class.

In all three year classes, initial losses of fish after stocking were considerable, and these apparently were related to the high stocking rates. Most of the fish that died were never recovered. For the 1971 year class starvation was prevalent and presumably this was also an important cause of losses in the other two year classes.

For the 1969 year class, the great majority of coho surviving the first few weeks went on to survive to the spring of 1970 and were removed as smolts (Table 2). Substantial numbers of coho in both control and heated streams were lost and never recovered, and a few jumped out or died from the effects of handling.

Table 2. Fates of marked coho salmon in control and heated model streams.

Year class	Time period considered	Handling losses				Jumped out				Removed as smolts				Not recovered			
		Control		Treatment		Control		Treatment		Control		Treatment		Control		Treatment	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1969	20 Dec 69- 26 Mar 70	1	2	2	5	1	2	0	0	31	76	27	69	8	20	10	26
1970	28 May 70- 1 May 71	1	2	4	9	6	13	1	2	23	51	21	47	15	33	19	42

For the 1970 year class, the experimental period was much longer than for the previous year class. Of the 90 fish present on 28 May 1970, 34 were eventually lost to unknown causes (Table 2). Losses resulting from handling were small in both streams but were more serious in fish from the heated stream, particularly during the period of highest temperature. Losses that occurred when fish leaped from the stream were greatest in the control group, for no apparent reason. In all known cases, fish jumped from the upstream ends of the tanks where water entered. When fish entered these areas they were forced to swim strongly in extremely turbulent water, and it can be hypothesized that a sudden change in water movement might cause a fish to propel itself out of the water.

While it had been thought that disease would lead to losses of fish in the heated stream in summer, no individuals were ever found exhibiting symptoms of the diseases common to juvenile salmonids. A few fish were found in poor condition with abraded tails, but this could have had several causes other than disease. Generally, for all year classes, the control and treatment populations appeared to be composed of healthy individuals once stable population size had been reached. They showed much lower frequency of damaged fins, missing scales, or other lesions than did fish captured in Tobe Creek. The relatively abundant food in the model streams was probably an important factor in maintaining the health of the fish.

Numbers of feeding attempts by coho observed per ten-minute interval were highly variable (Figure 15). Figure 15 compares observations of fish behavior which were made over a six-month period (May-October 1970). The weights of individual fish observed varied from less than 2 g to more than 20 g. Thus, water temperature was probably not the only variable affecting the observed frequencies of feeding attempts. Nevertheless, a temperature-related reduction in feeding activity in the heated stream in summer should have been discernible given the fairly large number of observations. No such reduction was apparent at temperatures up to 22-23 C. On only one occasion was a decrease in activity correlated with high temperature. In the afternoon of 10 August 1970 the temperature of the treatment stream briefly reached 27 C because of failure of exchange water flow. While a standard ten-minute observation was not made, it was obvious that feeding and movements associated with normal social behavior had nearly ceased, with most fish remaining motionless near the bottom.

Effects of heating on feeding activity during winter could not be estimated since the streams were too turbid for consistent observation. At temperatures below about 6-7 C, coho in the control stream behaved rather sluggishly in escaping the seine, sometimes lying against the net where they could be picked up by hand. Since feeding

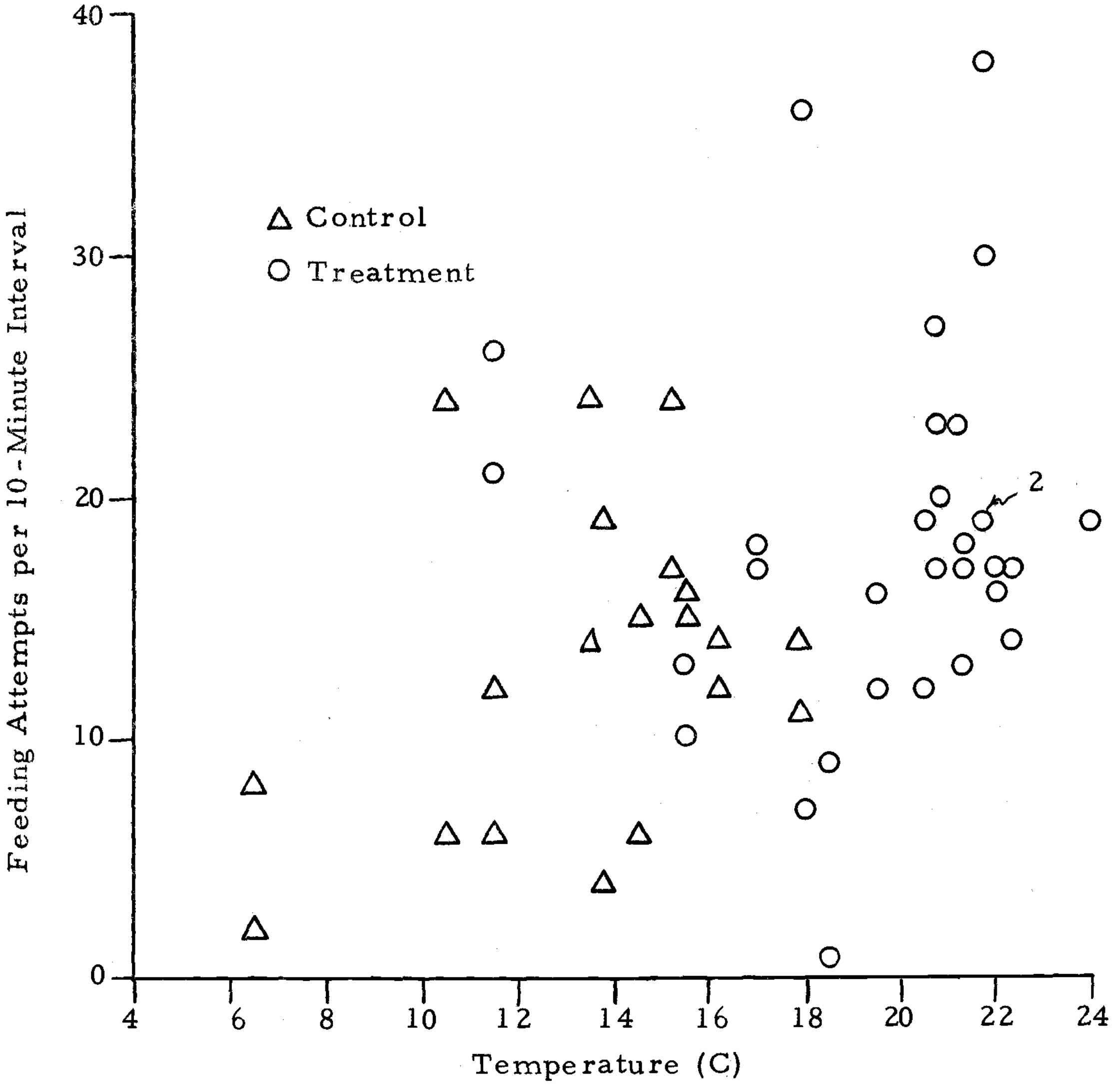

Figure 15. Frequency of feeding attempts per fish per 10-minute interval in the model streams, May-October 1970. Each point represents one fish.

in coho involves quick, well-coordinated pursuit of drifting prey, low winter temperatures may have inhibited feeding success in the control stream.

Abundance, Production, and Drift of Aquatic Invertebrates

Abundance and Community Composition

While the model streams were stocked with invertebrates from Oak Creek and thus presumably contained most of the elements of a diverse benthic community from the beginning, there was some evidence of instability and immaturity in community structure in the early months. Larval cases of the midge Tanytarsus formed dense masses in some riffle areas of both streams through the fall of 1969 and into the winter of 1969-1970. Dominance of the benthos by this organism continued until shortly after systematic sampling of the benthos began in March of 1970.

It was difficult to detect changes in the kinds of invertebrates present during the 16-month period of sampling because taxonomic keys permitting identification of species were not available for most groups. Comparison of community composition in the control and heated streams was difficult for the same reason. The one group present in the model streams for which keys to most species were available were the juvenile mayflies. The keys used were prepared for the mayflies of Oak Creek. The number of species of mayflies did not appear to increase in either stream after the spring of 1970 (Figure 16), although perhaps the sampling period was too short for detection of long-term trends. The mayfly fauna was apparently somewhat less diverse in the heated than in the control stream (Figure 16). This difference can be attributed largely to a lower frequency of appearance of Paraleptophlebia debilis (Walker) and P. temporalis (McDunnough) in samples from the heated stream than from the control stream. Four species of Epeorus were also taken less frequently in the heated stream (Table 3).

In addition to the mayflies, the insect faunas in both model streams included a stonefly fauna of eight known genera, at least three species of dragonfly naiads, two species of Megaloptera, at least four genera of Trichoptera, and an apparently diverse Diptera fauna. Other invertebrates present included Oligochaeta, Cladocera, Copepoda, and molluscs of the families Ancylidae, Planorbidae, and Pleuroceridae.

The most abundant invertebrates in both model streams were the aquatic insects, the Oligochaeta, and the snail Oxytrema silicula (Gould), which made up the bulk of the sampled biomass. No estimate was made of the biomass of the Oligochaeta as it proved impractical to separate these small worms from the substrate, but they were obviously very abundant at times in the pool bottoms.

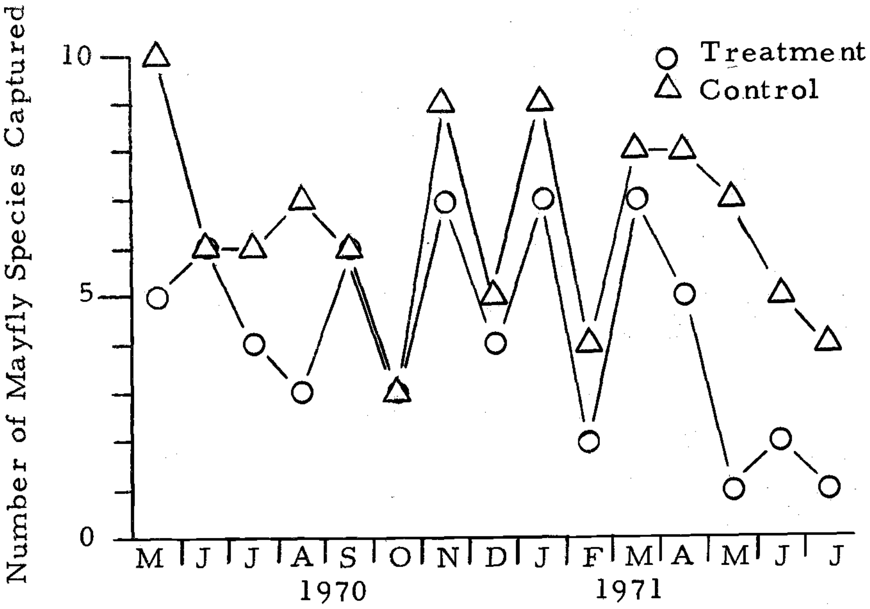

Figure 16. Comparison of the number of mayfly species captured in control and in heated model streams.

Table 3. Occurrence of mayfly species in control (△) and treatment (○) streams, May 1970-May 1971. Symbol indicates that at least one specimen was taken in the month indicated.

	May 70	Jun 70	Jul 70	Aug 70	Sep 70	Oct 70	Nov 70	Dec 70	Jan 71	Feb 71	Mar 71	Apr 71	May 71	Jun 71	Jul 71
Ameletus sp.	△	○					△		△ ○		△ ○	△			
Ameletus A							○								
Ameletus B											△ ○				
Ameletus exquisitus							△ ○		△						
Baetis parvus	△ ○	△ ○	△ ○	△ ○	△ ○	△ ○	△ ○	○	△ ○	△ ○	△ ○	△ ○	△	△	△
Baetis tricaudatus	△ ○	△ ○	△ ○	△ ○	△ ○		△ ○	△ ○	△ ○		△ ○	△ ○	△	△ ○	△ ○
Cinygma	△ ○	△ ○	△ ○	△	△ ○	○	△ ○	△ ○	△ ○		△ ○	△ ○	△	△	△
Epeorus albertae		△	△												
Epeorus longimanus	△								△		△ ○				
Epeorus nitidus	△ ○		△	△ ○	△ ○		△ ○	△ ○	△ ○		△ ○	△	△	△	△
Epeorus n. sp.				△											
Ephemerella A											○				
Ephemerella B												△			
Ephemerella teresa	△	△													
Paraleptophlebia debilis	△ ○	△ ○	△ ○	△	△ ○	△	△	△				△	△	△ ○	
Paraleptophlebia gregalis & sculleni	△						△ ○		○	△			△		
Paraleptophlebia temporalis	△	○		△	△ ○	△ ○	△	△	△ ○	△	△	△	△		

O. silicula, though abundant on the riffles of both streams (Table 4), was unevenly distributed and was not taken at all in many bottom samples. A large fraction of the population of this snail occurred on the walls of the streams and was not subject to routine sampling. Snails of the family Planorbidae were sometimes abundant in bottom samples from the pools. Here again, an apparently large fraction of the population occurred on the walls and was not sampled.

Crustaceans, especially the Ostracoda, sometimes occurred in large numbers in the pool bottoms. Biomasses were usually small (Table 5).

Aquatic insects were the most abundant group other than O. silicula (Tables 4 and 5). Insects were generally more abundant in the control than in the heated stream, in both riffles and pools.

Mayfly nymphs were much more abundant in the control than in the heated stream, particularly in the pools (Figure 17). The mayfly faunas of pools and riffles differed considerably. In both streams the high biomasses of pool mayflies during the spring and summer were made up mostly of P. debilis, which emerges in the fall. Other mayflies abundant in pools of the control stream were Baetis parvus Dodds (fall emergence), Cinygma (probably integrum Eaton) (spring-summer emergence), and P. temporalis (winter-spring emergence). Emergence times were not directly measured by emergence trapping, but were estimated on the basis of the presence of nymphs in the last

Table 4. Biomasses of major groups of invertebrates on riffles of the model streams, in grams per square meter.

Sampling date	Insects		O. silicula[b]		Other molluscs		Crustaceans	
	Control	Treatment	Control	Treatment	Control	Treatment	Control	Treatment
1 Mar 70	8.2	—						
28-29 Mar 70	7.5	6.6	3.1	7.2				
19-20 Apr 70	3.1	1.7	0.4					
5-7 May 70	3.5	5.8	1.5	10.9			<0.1	
21 May 70	7.1	3.4		—			<0.1	
6-9 Jun 70	50.4[a]	14.4[a]	3.8	25.9			<0.1	
2 Jul 70	13.5	5.9	2.2	9.5				
23 Jul 70	17.9	9.0				<.1		<0.1
18 Aug 70	12.5	5.9	29.8	120.9		0.1		
23 Sep 70	12.0	7.5	15.0	—	<0.1	0.6		
3 Nov 70	10.9	4.1	39.4	58.7	<0.1	0.9		
18 Dec 70	11.3	6.6	9.5	46.0	0.1	0.2		
26 Jan 71	11.1	11.3				0.2		
9 Mar 71	12.9	5.0			0.3	0.3	<0.1	<0.1
20 Apr 71	8.9	1.7	6.6	10.0	<0.1	1.7	<0.1	<0.1
21 May 71	5.7	3.4	27.0	50.0	<0.1	0.1	<0.1	
25 Jun 71	7.3	2.4	2.5	4.2	0.5	0.2	<0.1	0.2
26 Jul 71	6.0	2.9	4.2	5.4		0.1	<0.1	0.1

[a] These samples were taken when the pumps were shut off, and the high values probably indicate crowding of insects into the sampling area.

[b] Values shown are for snails dried for at least 48 hours. The shell comprises about 86 percent of the dried weight of O. silicula (Earnest, 1967).

Table 5. Biomasses of major groups of invertebrates in pools of the model streams, in grams per square meter.

Sampling date	Insects		Molluscs		Crustaceans	
	Control	Treatment	Control	Treatment	Control	Treatment
24-26 May 70	30.6	9.4				
28 June 70	18.9	13.3			<0.1	<0.1
31 Jul 70	18.7	8.7		1.5	<0.1	<0.1
5 Sep 70	19.8	1.8		0.5	<0.1	<0.1
8-10 Oct 70	5.0	19.6		6.5		<0.1
16 Nov 70	39.6	3.8	<0.1	3.8	0.5	
14 Jan 71	19.9	11.0	1.8	2.2	0.6	0.3
7-9 Feb 71	19.3	14.9	0.1		1.2	<0.1
6-8 Apr 71	14.8	2.2	1.3	2.2	0.6	0.2
10 May 71	18.4	1.3	2.2	0.7	1.2	0.6
11 Jun 71	11.5	2.0	1.2	3.0	2.6	2.2

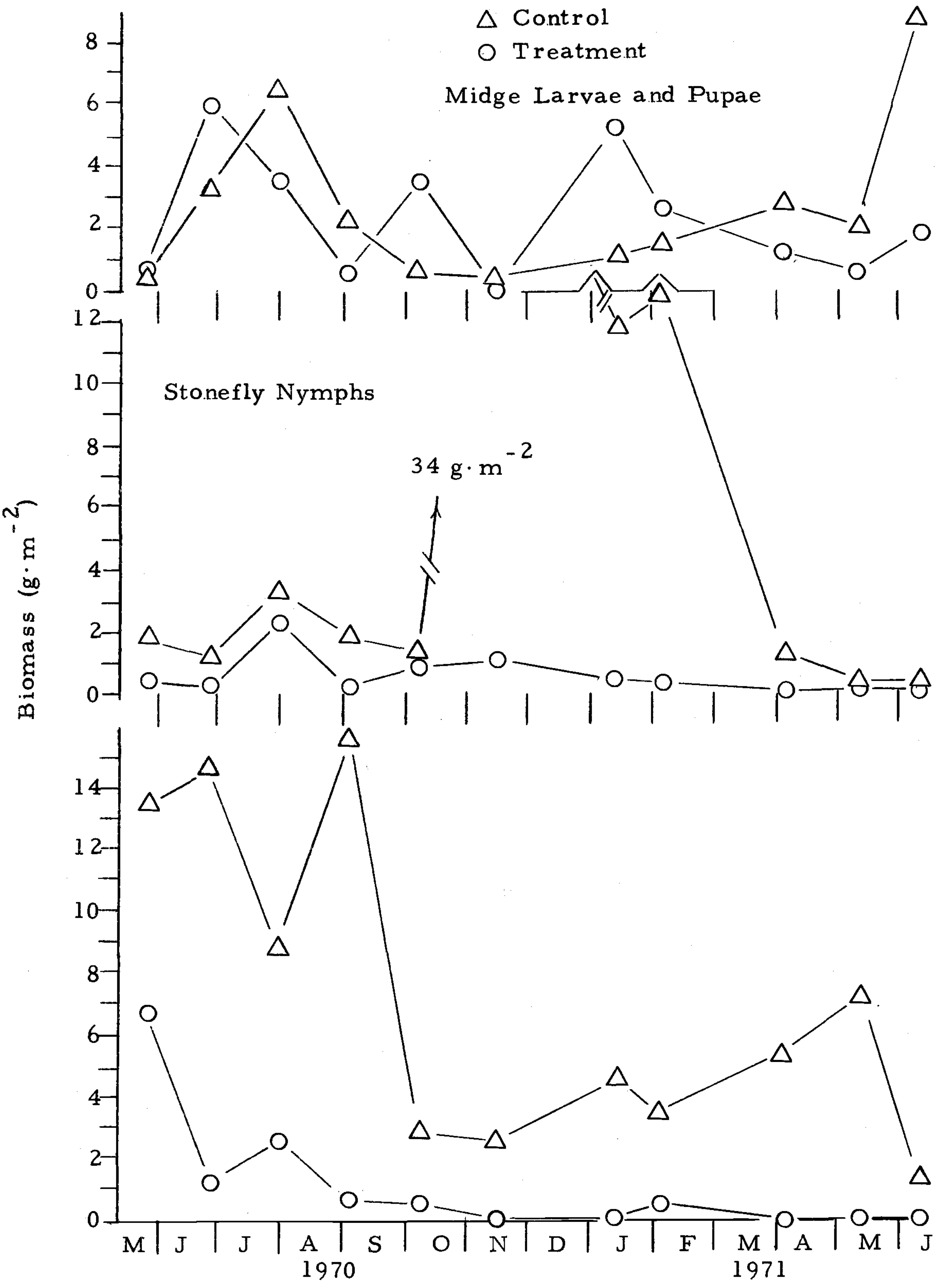

Figure 17. Biomasses of major groups of aquatic insects in pools of the model streams.

nymphal stage, which have black wing pads in many species. All of the four species mentioned above were much less abundant in the heated stream that in the control stream during the period of sampling.

In riffle samples, mayfly biomass exhibited two peaks (Figure 18). In both streams the summer peak was apparently related largely to the growth of *B. parvus* and *Baetis tricaudatus* Dodds, especially the latter. Biomasses fell quickly with the emergence of these species in the fall of 1970. The late-winter and spring peak in the riffle samples can be attributed to growth of the heptageniid mayflies *Cinygma* sp. and *Epeorus* (*Ironodes*) *nitidus* (Eaton). Both of these species, particularly the former, were estimated to be less abundant in the heated stream than in the control.

Fluctuations in stonefly biomass were more difficult to analyze because keys were available for nymphs of only two genera. Within the eight stonefly genera found in the model streams, Kerst (1970) found 27 species in Oak Creek. The genus *Nemoura* (nine species in Oak Creek) was the most abundant stonefly in the model streams, being present during all seasons. The high stonefly biomasses in both riffles and pools in the winter (Figures 17 and 18) were composed mostly of *Nemoura* and the winter stoneflies *Capnia* (including *C. projecta* Frison) and *Brachyptera* (including *B. nigripennis* (Banks)). Extremely high biomasses of these stoneflies were found in pools of the control stream over several months in the fall and winter, but

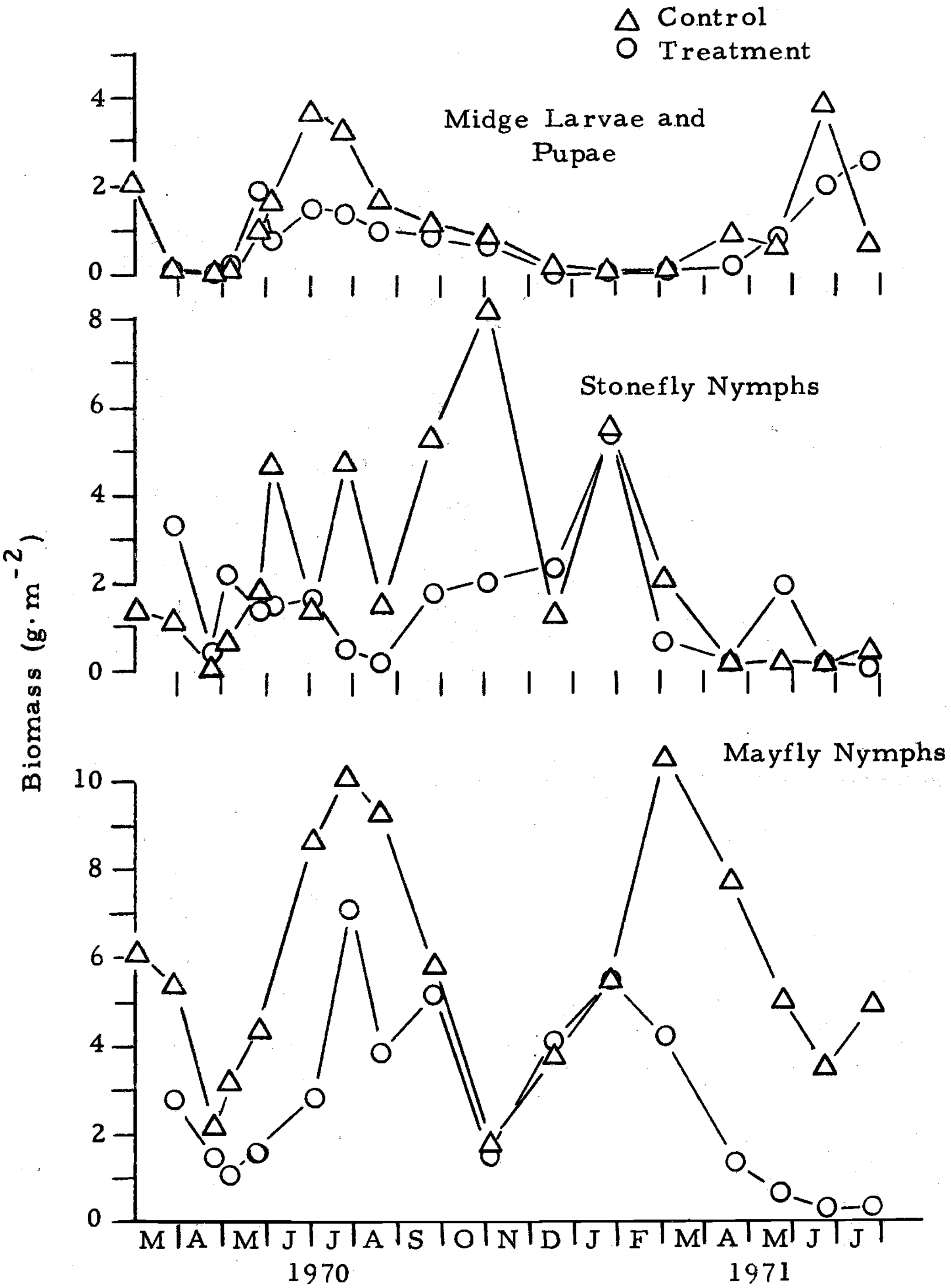

Figure 18. Biomasses of major groups of aquatic insects on riffles of the model streams.

this was not the case in pools of the heated stream, where stonefly biomass remained low throughout the year (Figure 17).

Biomasses of larval and pupal Chironomidae reached summer maxima on the riffles of both control and heated streams (Figure 18). These riffle midges were mostly Brillia, Cricotopus, and others of the subfamily Orthocladiinae, plus some Tanytarsus. In contrast, the pool midges were mostly of the subfamilies Chironominae and Tanypodinae. Seasonal trends in midge abundance were not apparent in the pool samples, nor were biomasses greatly different in control and heated streams.

Several carnivorous forms of juvenile insects occurred in the model streams, and some reached such large size that they could presumably have obtained the same types of food as were used by juvenile coho. Individual carnivorous insects over 10 mm in length were arbitrarily designated "large" carnivores and their mean biomass calculated for the period May 1970-May 1971 (Table 6). In the heated stream their mean biomass for the year was about 10 percent of the "equilibrium" coho biomass of 8-9 $g \cdot m^{-2}$, and in the control stream the value was about two percent of the equilibrium coho biomass of 22-23 $g \cdot m^{-2}$. Conceivably these carnivorous insects could have been a factor in the large difference in coho production between the two streams. Some of these large forms were found in the stomachs of coho yearlings, while others such as the dragonfly naiads were probably too large and fierce to be eaten.

Table 6. Abundance of large carnivorous insects in the model streams. Biomass estimates are averages for the period May 1970-May 1971. Only those individual insects greater than 10 mm in length are included.

Taxonomic group	Estimated biomass $(g \cdot m^{-2})$ Control	Treatment
Plecoptera		
Acroneuria californica	0.036	0.096
Alloperla	0.009	0
Isoperla	0.035	0
Odonata		
Cordulegaster dorsalis	0	0.556
Octogomphus specularis	0.246	0.065
Megaloptera		
Sialis californica	0.065	0.074
S. rotunda	0.007	0.021
Trichoptera		
Psychomyia	0.038	0.043
Total	0.43	0.86

Production

Annual production of aquatic insects (May 1970-May 1971) was much greater in the control than in the heated model stream (Table 7). This was true especially for mayflies and stoneflies, for which annual production values in the two streams differed by a factor of two to three. For mayflies, production was greater in the control stream for all of the six most abundant species, indicating that the entire mayfly fauna may have been adversely affected by high temperature. While production of some of the mayflies, such as *Epeorus* and *Cinygma*, was concentrated in the cooler months, these species still were present in the streams in the summer as eggs or early instars.

Among the stoneflies, only *Nemoura* showed much greater production in the control stream than in the heated stream. Production figures for *Nemoura* probably represent a composite of several species with greatly varying times of hatching and emergence (Kerst, 1970). The winter stoneflies *Brachyptera* and *Capnia* achieved about the same production in the two streams, although values for *Capnia* were so low as to be quite imprecise. Production of these stoneflies appeared to be greatest in coldest months, and very few nymphs were taken before November or after April.

Production was not estimated for the large stoneflies *Acroneuria*, *Alloperla*, *Isoperla*, and *Pteronarcys* because numbers captured were

Table 7. Annual production (May 1970-May 1971) of the most abundant aquatic insects in the model streams, in grams per square meter.

Taxonomic group	Riffle production		Pool production		Total production	
	Control	Treatment	Control	Treatment	Control	Treatment
Ephemeroptera						
Baetis parvus	1.5	0.4	1.9	0.1	3.4	0.5
B. tricaudatus	18.2	14.3	0.1	0.1	18.2	14.3
Cinygma	6.4	1.4	2.9	0.4	9.3	1.8
Epeorus nitidus	6.0	4.9	0.1	0.1	6.0	4.9
Paraleptophlebia debilis	0.2	0.5	22.6	4.0	22.8	4.5
P. temporalis	0.4	0.1	7.5	0.1	7.9	0.1
Totals	32.7	21.5	34.9	4.5	67.6	26.1
Plecoptera						
Brachyptera	8.5	8.5	<0.1	<0.1	8.5	8.5
Capnia	<0.1	0.1	0.8	0.3	0.8	0.3
Nemoura	12.3	5.0	27.8	1.9	40.1	6.9
Totals	20.8	13.5	28.6	2.2	49.4	15.7
Odonata (all)	<0.1	<0.1	1.7	3.6	1.7	3.6
Neuroptera						
Sialis	<0.1	<0.1	2.3	1.7	2.3	1.7
Trichoptera						
(*Psychomyia* only)	<0.1	<0.1	1.0	2.2	1.0	2.2
Diptera						
Chironominae	1.2	1.0	13.8	11.6	15.0	12.6
Orthocladiinae	7.3	4.6	3.5	1.4	10.8	6.0
Tanypodinae	<0.1	<0.1	1.9	1.8	1.9	1.8
Simuliidae	1.5	0.9	<0.1	<0.1	1.5	0.9
Totals	10.0	6.5	19.2	14.8	29.2	21.3
Totals					151.2	70.6

very small. These are all swift-running forms and may have escaped capture more easily than did the smaller stoneflies. Several cast nymphal skins of emergent Acroneuria and Isoperla were found on the wooden superstructures of both streams, suggesting that production may have been considerable.

Production of Diptera was relatively more important in the heated than in the control stream, particularly in the pool fauna. The relative proportions of mayfly, stonefly, and Diptera production were roughly the same for the riffles of the control and heated streams. In contrast, midge production in the pools was much greater relative to production of stonefly and mayfly nymphs in the heated stream than in the control (Table 7). The pool midges were largely of the subfamilies Chironominae and Tanypodinae. This suggests that these groups are relatively tolerant of high temperature.

The sum of production of the large carnivores of the pool bottom (Odonata, Sialis, and Psychomyia) was greatest in the heated streams. Like the biomass data, this may suggest that consumption by carnivores was a more important fate of herbivore production in the heated stream than in the control stream.

Drift

Drift catches were greatest in fall and winter months in both control and heated streams (Figure 19). This was especially true in

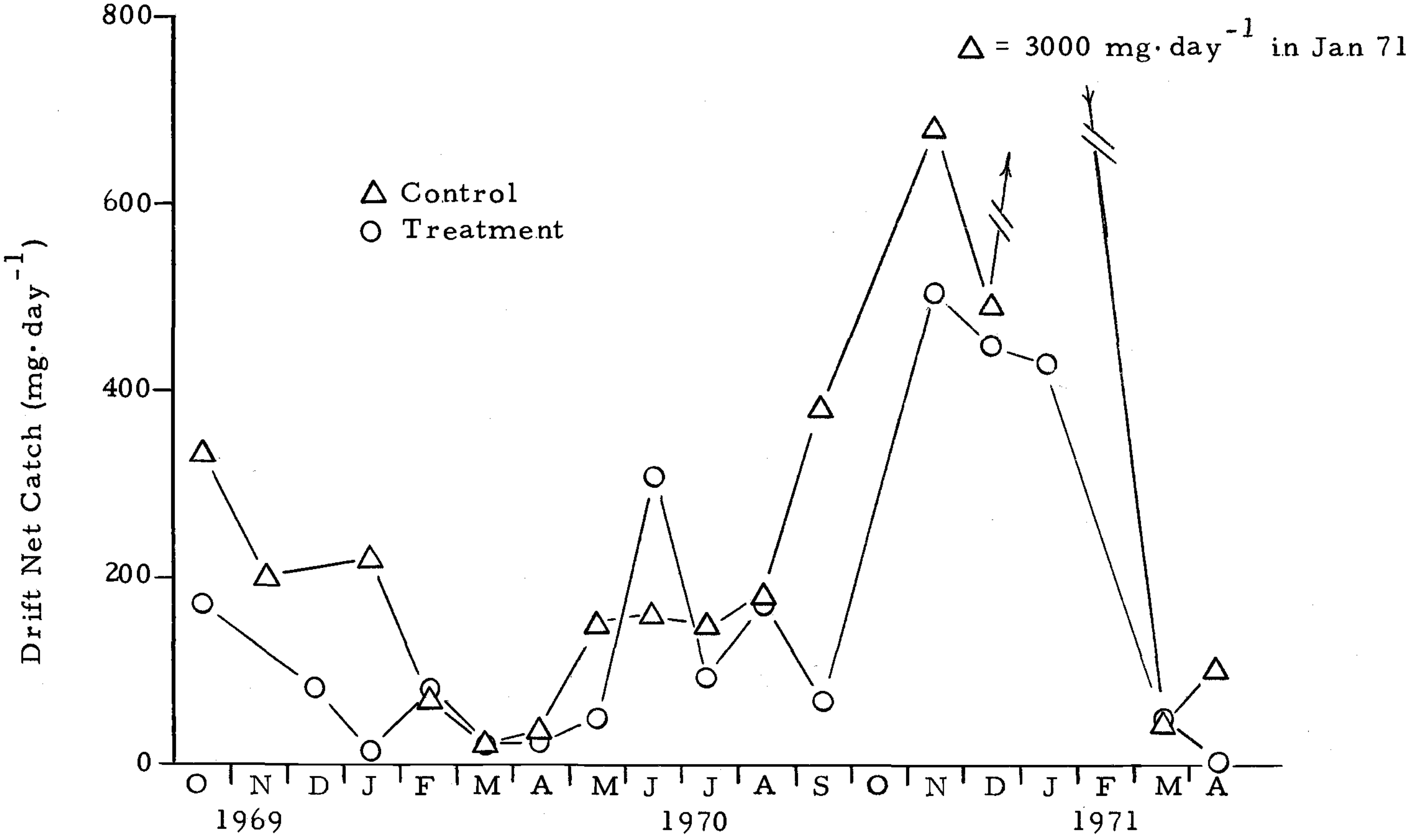

Figure 19. Drift net catches in the model streams. Each point represents the mean catch per day for the month indicated.

the winter of 1970-1971, when drift catches were very large, particularly in the control stream. The composition of drift catches (Figure 20) roughly paralleled that of bottom samples (Figures 17 and 18). Diptera larvae and pupae were important in the summer drift, while stonefly nymphs made up most of the heavy winter drift. The winter drift of stoneflies was composed mostly of *Nemoura* and *Brachyptera*, and included both immature and mature nymphs. Mature and emergent nymphs were more abundant in drift than in bottom samples, relative to abundance of immature nymphs. This was true for mayfly nymphs and for midge larvae and pupae as well. Mayfly drift was composed mostly of the streamlined forms such as *Baetis*, *Paraleptophlebia*, and *Ameletus*. The heptageniid mayflies were seldom taken. Mayfly nymphs were usually more abundant in drift samples from the control stream than from the treatment stream, as was true for bottom samples.

The small catches of drift in summer may have been related to rapid clogging of the net with algae. Use of the large net, however, seemed to permit a long period of net operation (most of a 24-hour period) before clogging was noticeable. Clogging also occurred in fall and winter when alder leaves and catkins entered the streams.

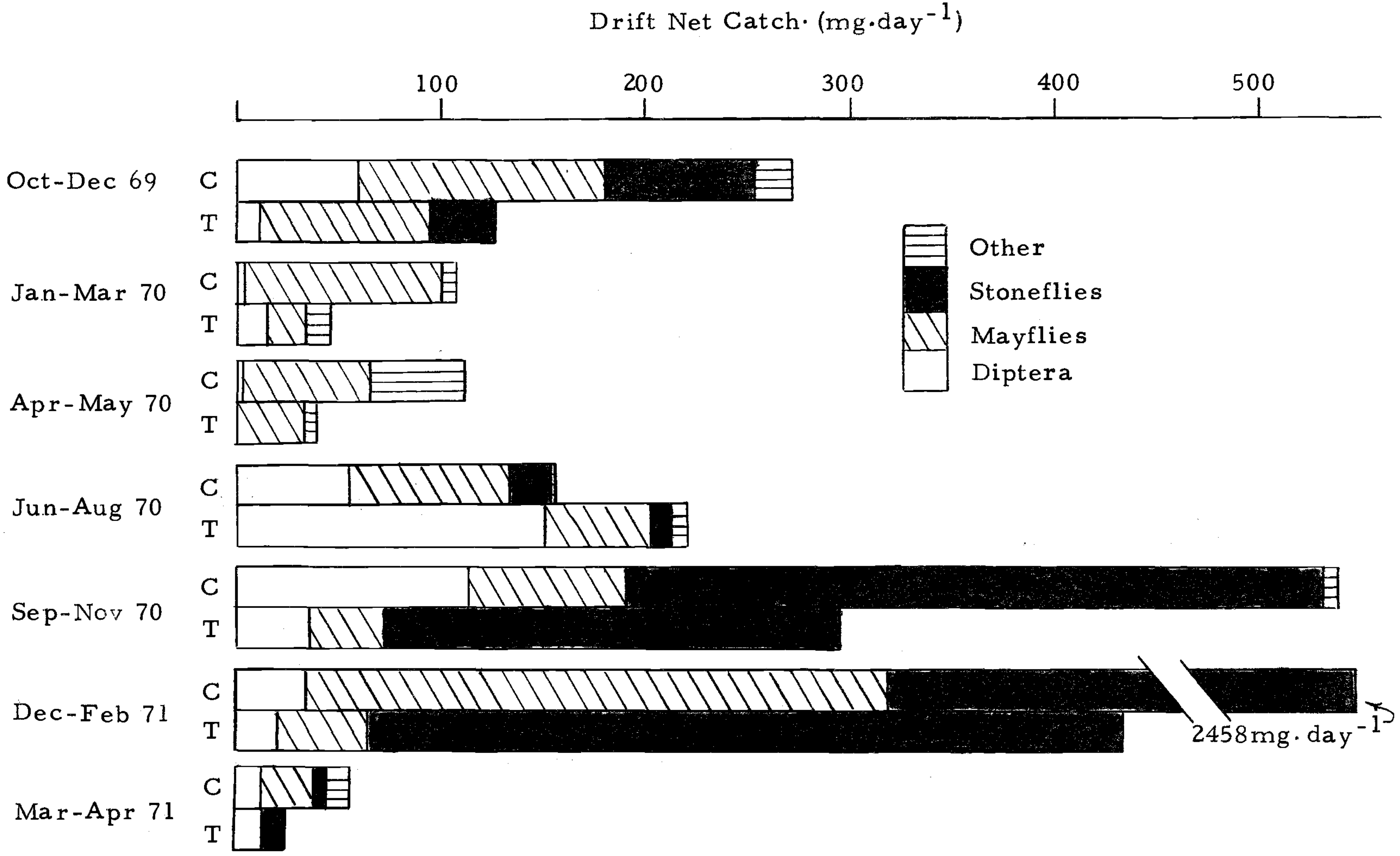

Figure 20. Composition of drift net catches in the control (C) and treatment (T) streams by season.

Food Relationships of Juvenile Coho Salmon

Food Consumption

Rates of food consumption of juvenile coho were estimated on the basis of observed growth rates, using the relationships between growth rate and food consumption rate which were determined by Averett (1969) for juvenile coho kept at various temperatures. Averett's results were rather variable and do not permit the estimation of food consumption rates with any great precision. For this reason, the information presented below is meant only to present general trends rather than precise estimates of food consumption rates.

Daily food consumption by yearling coho of the 1969 year class reached high levels in winter in both control and heated streams (Figure 21). As was noted earlier, a large part of this diet was coho fry, and the high consumption levels were thus something of an artifact of the model systems, which provided little cover for fry compared to that available in natural streams.

Daily food consumption of coho of the 1970 year class was initially low in both streams because of low biomass of coho. As fish biomass increased, food consumption reached high levels in early summer (Figure 21). A high level of consumption was maintained by coho in the control stream until late summer, but summer consumption

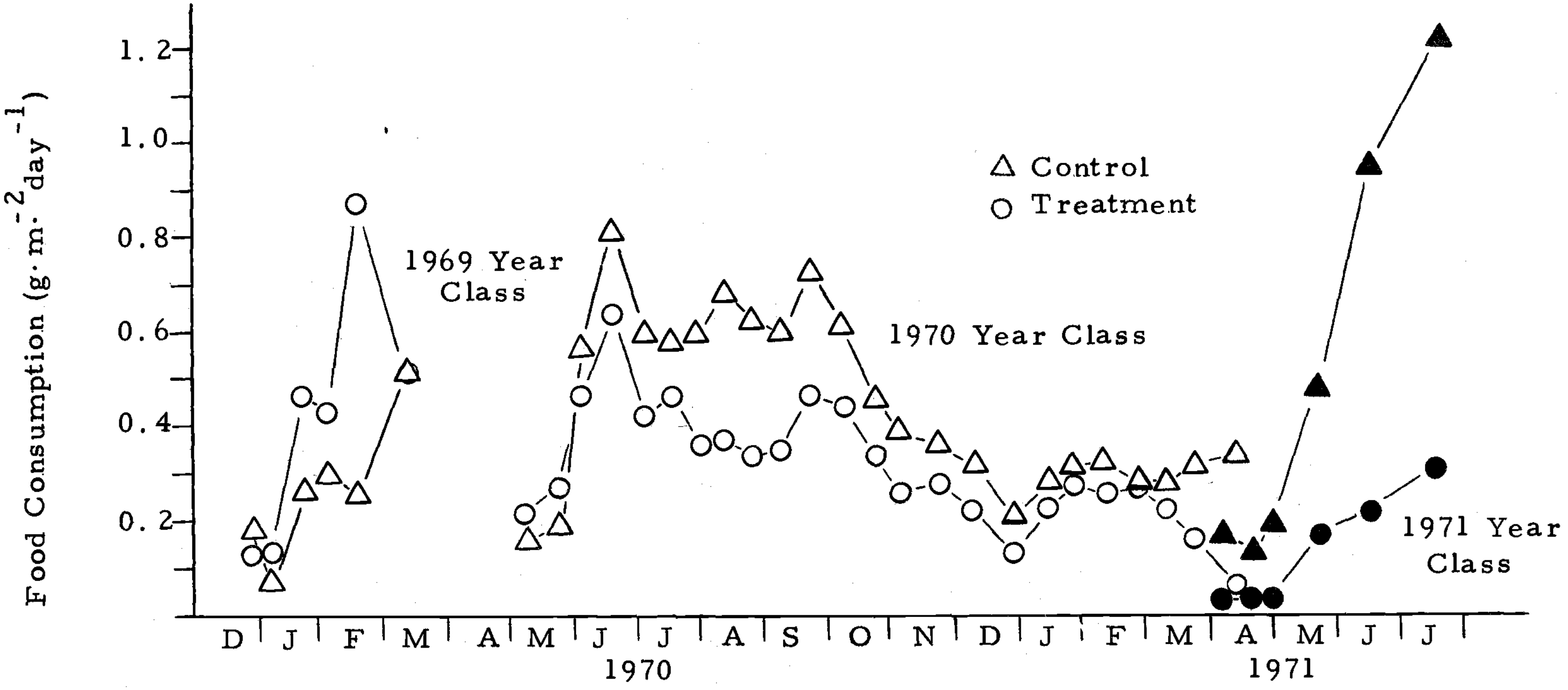

Figure 21. Daily food consumption by juvenile coho in the model streams.

in the heated stream was at lower rates. Consumption in both streams fell to low levels in fall and winter.

Daily food consumption of coho of the 1971 year class followed somewhat the same trends as for the 1970 year class in the control stream. Daily rates increased from a low level in spring to a very high level in early summer. In contrast, food consumption in the heated stream did not approach the early summer levels of the previous year.

When mean daily food consumption rates were computed for the entire period which each year class spent in the model streams, it was seen that rate of food consumption increased with each year class in the control stream, but decreased in the heated stream (Table 8). Total consumption in the control stream was approximately one-third greater than in the heated stream over the entire period of operation of the model streams (Table 8). The ratio of food consumption in the two streams changed over the three year classes from one favorable to the heated stream to the opposite.

Food consumption values for the 1970 year class (Table 8) are given for the period mid-April 1970-May 1971, which is approximately equal to the period over which insect production was estimated (Table 7). Food consumption in the heated stream greatly exceeded estimates of insect production for this period. This discrepancy probably results from an underestimate of insect production. Other factors

Table 8. Food consumption by juvenile coho salmon in the model streams.

Year class	Time period	Food consumption Total ($g \cdot m^{-2}$) Control	Treatment	Daily ($g \cdot m^{-2} \cdot day^{-1}$) Control	Treatment
1969	6 Dec 69- 26 Mar 70	31	44	0.28	0.40
1970	19 Apr 70- 1 May 71	159	113	0.42	0.30
1971	1 Apr 71- 9 Aug 71	93	26	0.71	0.19
Total	6 Dec 69- 9 Aug 71	283	183	0.45	0.30

were the presence of foods other than aquatic insects in the diet, such as planorbid snails, small coho fry, and terrestrial insects. Possibly juvenile coho were able to consume aquatic insects at a rate greater than the rate of insect production, resulting in a reduction of insect biomass. The variation in estimated insect biomass was too large to permit identification of any such trend, but there was some evidence of a reduction in insect biomass during the period from the winter of 1970-1971 to the summer of 1971 (Tables 4 and 5). This, however, may have been a reflection of insect life cycles rather than of predation by fish.

Daily food consumption per unit of coho biomass was usually higher in the heated than in the control stream for coho of all three year classes (Figure 22). The generally lower rates of growth of coho in the heated stream (Figure 12), even when the rates of food consumption were higher than in the control stream, can be attributed, at least in part, to the higher costs of standard metabolism associated with the elevated temperatures of the heated stream. The higher food consumption per unit area by the coho population in the control stream than in the heated stream was the result of the greater biomass of coho in that stream, which more than compensated for the lower rate of food consumption per unit of biomass.

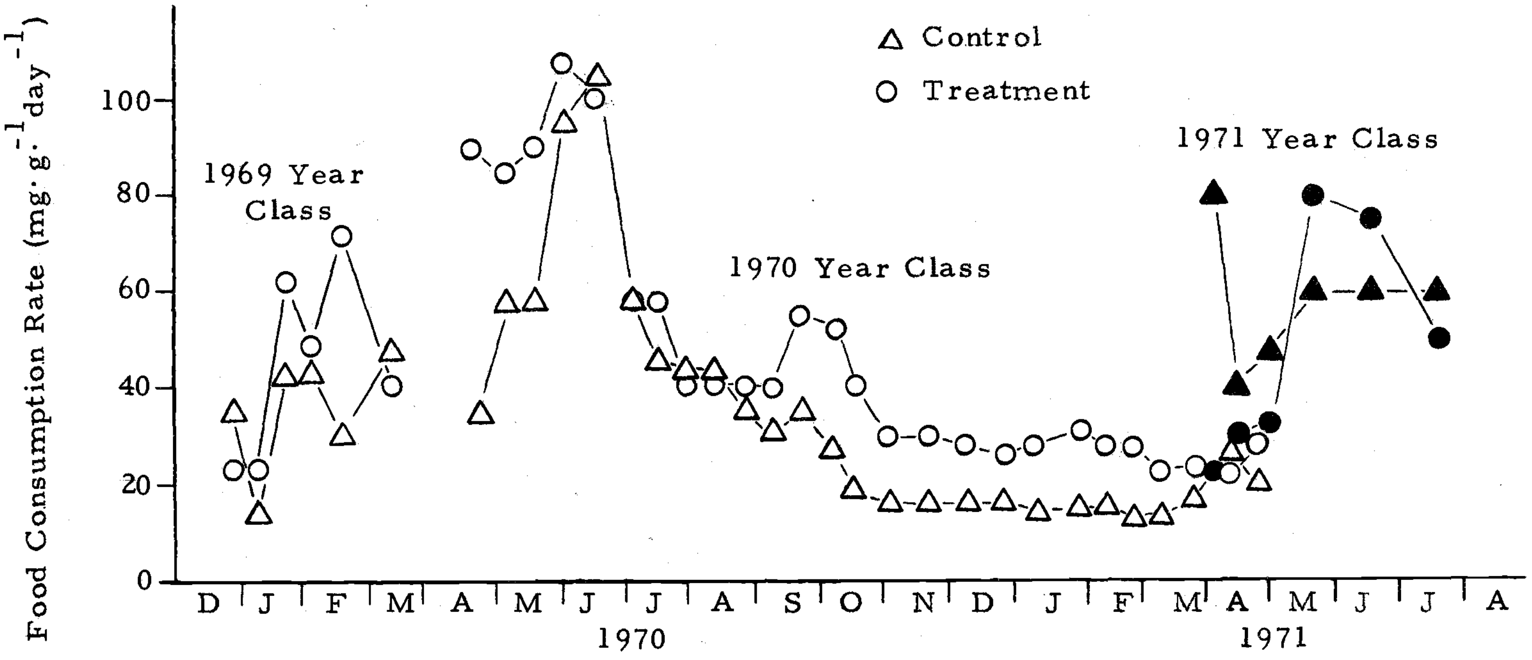

Figure 22. Daily food consumption per unit of biomass of juvenile coho in the model streams.

Diet

Dietary composition was not quantified for coho of the 1969 year class because coho fry of the 1970 year class were available as food and made up a large part of the diet of yearlings after January 1970.

In coho of the 1970 year class, composition of the diet varied greatly with season and also differed between the two streams (Figure 23). Analysis of food habits involved examination of stomachs of a rather small number of fish, so the results should not be interpreted as highly precise. In the control stream, mayflies were important in the diet of coho fry in the spring and summer of 1970, and again became important in the following spring when these fish were yearlings. Stoneflies were important in the diet in fall and winter, reflecting their abundance in the benthos and drift. In the heated stream, mayflies were important in the diet in spring and early summer though less so than in the control stream. Diptera, principally Chironomidae, were more important in the diet in summer in the heated stream, perhaps as a result of the relatively high share of total production made up by Diptera in the heated stream. Stoneflies were never an important component of stomach contents even in winter.

Dietary composition in the 1971 year class in the control stream was rougly similar to that of the previous spring, with mayflies greatly predominating (Figure 23). In ~~the~~ heated stream, mayflies were not

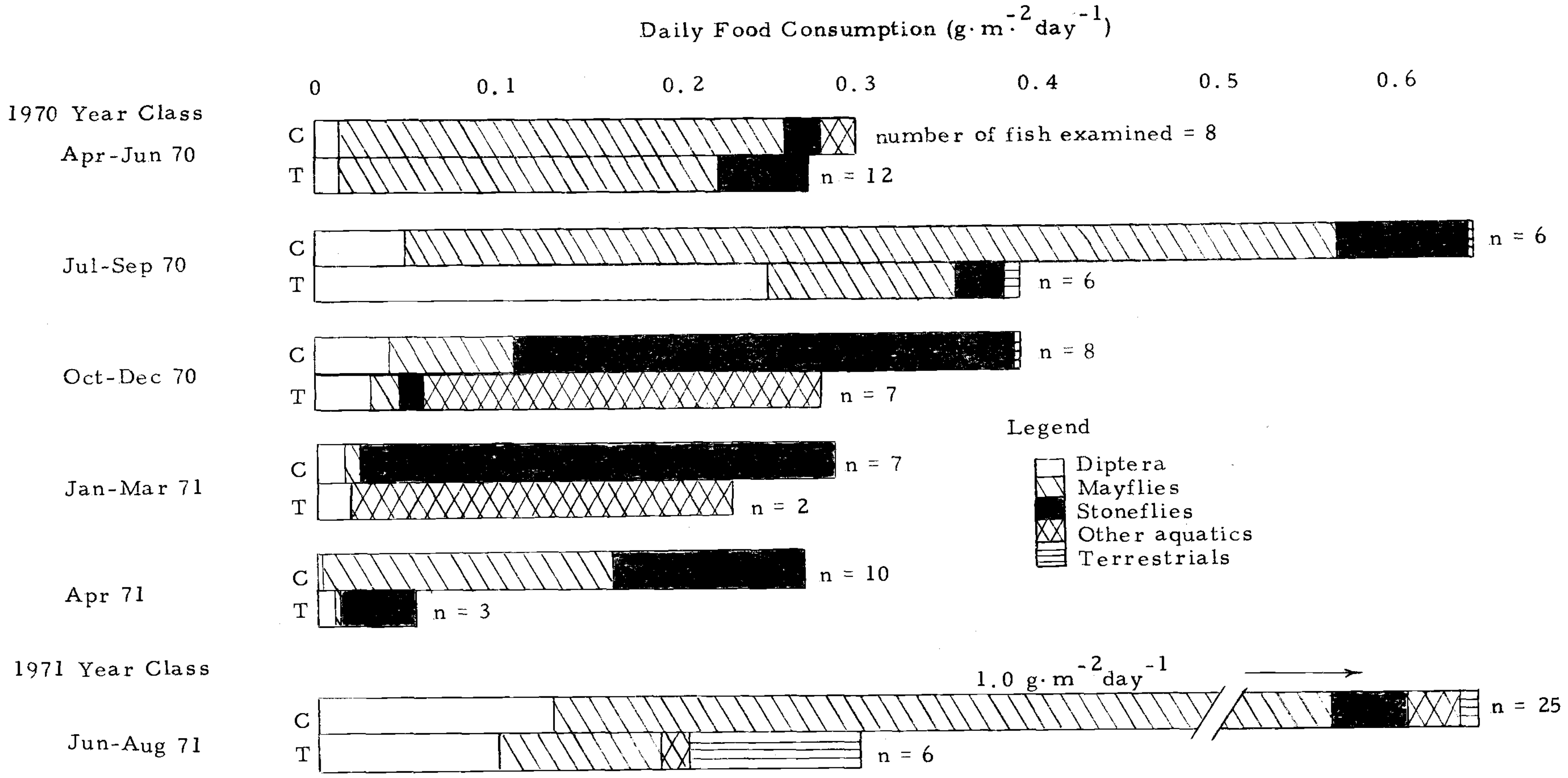

Figure 23. Composition of the diet of juvenile coho in the control (C) and treatment (T) model streams.

so important in the diet as in the previous spring, and much food was of non-aquatic origin.

Juvenile coho apparently selected those mayfly and stonefly nymphs which were in the last nymphal instar or which had undergone or were undergoing the metamorphosis to the winged adult form. In the control stream, 83 percent of the mayfly biomass consumed by the 1970 and 1971 year classes combined were mature nymphs or winged forms. For stoneflies the figure was 60 percent, and in the heated stream the figures were 92 percent and 56 percent, respectively. These proportions of mature and emergent insects were higher than for either the drifting or benthic mayflies and stoneflies.

Factors Influencing the Use of the Food Resource by Coho

The abundance of food organisms maintained in the control stream was higher at all seasons than in the heated stream, as was the biomass of coho (Figure 24). Daily drift was also generally higher in winter in the control than in the heated stream (Figure 19). Clearly, the high levels of biomass and of total production of coho in the control stream were associated with the abundant food present in that stream. Nevertheless, a density-dependent relationship wherein an increase in the biomass of a predator over time results in a decreased biomass of prey was not clearly demonstrated in either stream, although there was some evidence that such a relationship existed during at least

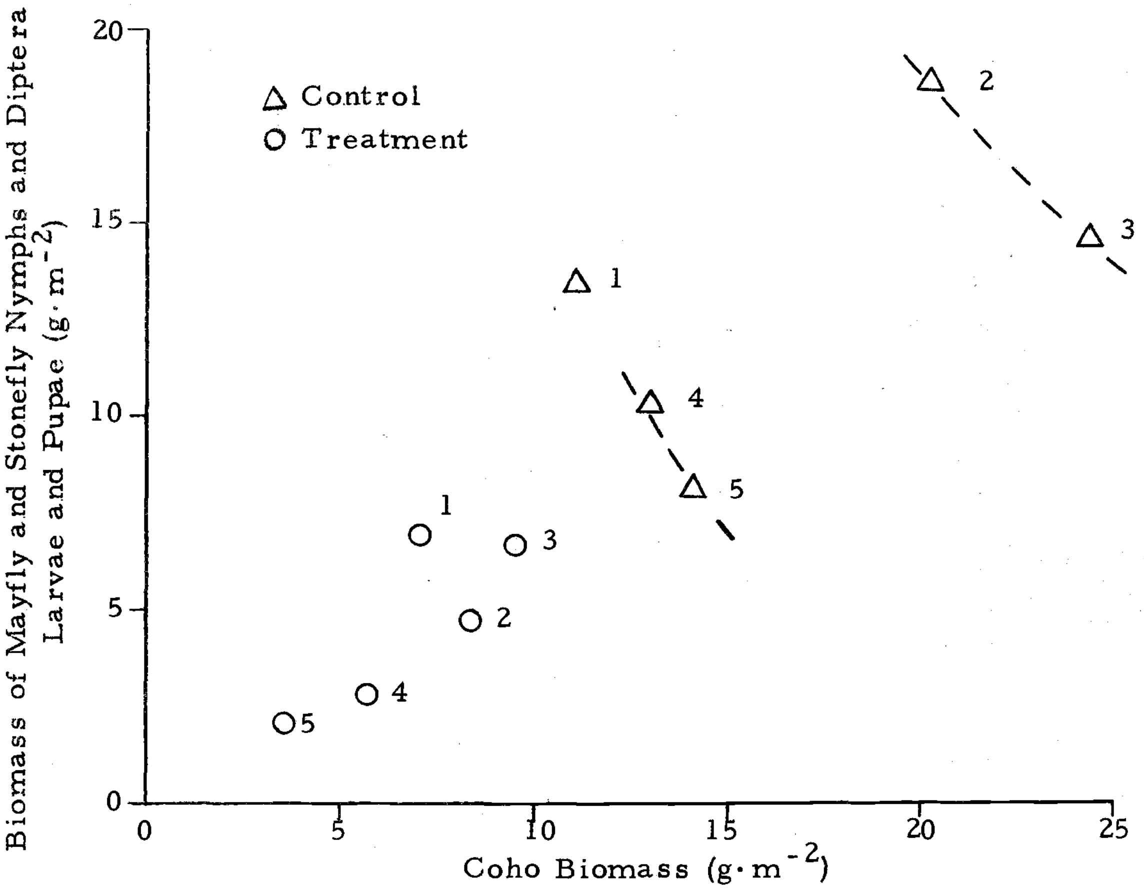

Figure 24. Relationship of biomass of the major food types to biomass of juvenile coho in the model streams. Insect biomass values are means of riffle and pool samples for the following periods:

1 = 28 May 70-3 Sep 70
2 = 3 Sep 70-3 Dec 70
3 = 3 Dec 70-4 Mar 71
4 = 4 Mar 71-1 May 71
5 = 7 May 71-9 Aug 71

some seasons (dotted lines, Figure 24). No well-defined relationships existed between drift rate and daily food consumption per unit area, daily food consumption per unit of coho biomass, or coho growth rate. Rates of food consumption and growth were low for coho of both streams during the period of highest daily drift (fall 1970 and winter 1971). Factors such as high turbidity and reduced day length may have combined to reduce the availability of winter drift to coho in both streams. Physiological factors associated with the parr-smolt transformation may have caused reduced feeding activity or may have altered the relationship between food consumption and growth. The lowest drift rates occurred simultaneously with the highest levels of daily food consumption by coho (in summer 1970), a reversal of the winter situation. Under summer conditions of clear water and increased day length plus many clear, moonlit nights, coho may have been so efficient in feeding that they reduced drift to low levels. High efficiency in feeding may also account for the scarcity in the drift of such large forms as mature nymphs of Cinygma, which sometimes made up a large share of the stomach contents of coho. Bishop and Hynes (1969) attributed the scarcity of drifting imagines in the Speed River, Ontario, to predation by fish. I have no evidence as to whether such large forms would ever have entered the drift in important numbers in the model streams, and they may in fact have been captured by the fish as they moved about on the bottom, particularly in their last hours of aquatic life when they leave the protected undersides of stones and climb up an emergent stone or other object in order to moult into the winged form. Coho are primarily drift feeders but about 12 percent of the feeding attempts which I observed were directed toward the bottom, and there was some indication that these were more frequently successful than were attempts directed at the drift.

DISCUSSION

Factors Limiting Abundance and Production of Coho

Estimates of food consumption indicate that juvenile coho in the control stream had available to them more abundant food than did coho in the heated stream, at least for the 1970 and 1971 year classes. It cannot, however, be assumed that food density or availability was the only ecological factor influencing population density and annual production of coho in the two streams. Factors other than food availability may act to limit the density of a stream population of a territorial species like the coho. Chapman (1966) suggested that space may be a limiting resource for such a species, since some minimal distance between individuals may be required to inhibit transfer of pathogens or to avoid attracting predators. At different times of year different components of the total available space may be limiting. In spring and summer the limiting components of space might be feeding areas at the lower ends of riffles and places to hide from large trout or birds. In winter shelter from freshets might be limiting. In the model streams winter freshets did not occur nor was predation, except for cannibalism, a factor. If the need for space was in fact less limiting in the model streams than in nature, the food resource in the model streams may have been unusually important in limiting the coho population. The poor growth of coho in Tobe Creek relative to their growth in either the heated or control model streams (Figure 6) indicates an even more important limiting role for food in that stream than in the model streams. Mason and Chapman (1965) found that a greater supply of drifting food to one of two experimental channels containing juvenile coho resulted in greater biomass and greater numbers remaining in that channel. Chapman (1966) believed that these results indicated that space requirements are not fixed in coho but can be modified by food supply. Still, Chapman suggested that winter population densities in streams subject to freshets are fixed by the amount of available shelter rather than by food supply. If this is the case, increased temperature might increase carrying capacity by enhancing swimming performance of fish although heated discharges might have little effect on the temperatures of streams at high flow.

Direct Effects of Temperature on Coho

Direct physiological effects of temperature on juvenile salmonids have been studied extensively in the laboratory. It would be desirable to separate out these direct effects of temperature on the growth of fish from the effect on growth of an alteration in the abundance of food resources caused by increased temperature. These growth effects are difficult to separate since they interact. A change in temperature to a more nearly optimal level may result in an increase in biomass of fish, in turn altering the quantity of food available to each individual.

Rates of food consumption per unit of coho biomass were usually higher in the heated than in the control stream (Figure 22). Thus, had the food consumption rates been artificially kept equal in the control and treatment streams, other circumstances being unchanged, the diminution of growth in the heated stream should have been even greater than that observed in the experiment.

It is not necessary to assume that all aspects of the physiology of an animal are affected in the same way by temperature change nor that they all exhibit the same temperature optimum. Brett (1971) found that maximum metabolic scope for activity, maximum sustained swimming speed, maximum active cardiac work and other physiological maxima occurred at about 15 C in juvenile sockeye salmon, yet voluntary food intake was maximized at 17 C, and burst speed was apparently independent of temperature. As with Averett's (1969) findings for coho, Brett found that optimal temperature for growth declined with diminishing ration size. My study emphasized growth rather than survival, and the ratio of total production in the two streams, or of smolt production, might have been different if large predacious fish, extreme fluctuations in water level, or other hazards to survival had been present. Brett, for example, found that maximum sustained swimming speed was attained at 15 C, the same temperature at which highest growth rate was attained by fish fed to repletion but higher than the optimal temperature for growth of fish on restricted rations, as they usually are in nature. If the same relationship between performance and temperature holds for juvenile coho, fish in the heated stream might have been at some advantage in the winter if large predators or high flows had been present. Coho in the heated stream exhibited obviously superior swimming performance in the coldest parts of the winter. In the simplified environment of the model streams this conferred no survival advantage nor, in the winter of 1970-1971, was there much growth advantage over the control group. During this season the fish were apparently unable to consume drifting insects in quantities proportional to the abundance of these food organisms.

Food Relationships

Limitation of abundance of a prey species by its predators is theoretically the general case for herbivores (Hairston, Smith, and Slobodkin, 1960). A negative relationship between the biomass of predator and prey has been demonstrated for juvenile sockeye feeding on zooplankton (Brocksen, David, and Warren, 1970) and for juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), feeding on aquatic insects (Lichatowich, 1970). Warren (1971) discusses other examples. While there was some indirect evidence that juvenile coho were able to reduce the insect drift rate in the model streams under summer conditions of clear water, there was no apparent reduction in the benthic biomass of insects even at the extremely high levels of coho biomass and food consumption reached in the control stream. This apparent lack of control of abundance of the insects by fish may have been related to the mode of feeding in coho. Since prey must apparently be visible and moving to elicit an attack by coho (Chapman, 1966), the majority of insects in the substrate would be normally safe from coho predation. Another factor in the fish-insect relationship was the constantly changing composition of the insect community. A species of insect particularly vulnerable to fish predation might emerge and be replaced by another species which could grow and increase its biomass with little predation by coho. Certainly no equilibrium appeared to be reached in the benthic biomass of either model stream. Instead, biomass fluctuated seasonally with the growth of the several dominant insect species. In summary, while density-dependent relationships between the coho and their prey could not be clearly demonstrated, there was evidence that a temperature-related reduction in benthic biomass contributed to reduced growth of coho in the heated stream. In all seasons from March 1970 to August 1971, the heated stream supported smaller biomasses of juvenile coho and of their principle food organisms than did the control stream (Figure 24). A similar relationship may have existed between the temperature regime and the production of coho and of invertebrates. Total production of coho of the 1970 year class was approximately twice as great in the control stream as in the heated stream (Figure 9), and production of aquatic insects over the same time period was approximately twice as great in the control as in the heated stream (Table 7).

Temperature and the Invertebrate Community

My results indicate that biomass and annual production were reduced in many insect species in the heated stream, particularly among the mayflies and stoneflies. There was also some reduction in the number of species present at any given time, at least among mayflies. Sprules (1947) and Ide (1935) found that numbers of mayfly species increased with increasing temperature in a downstream direction in Ontario streams. These streams, however, were located in a region where very low winter temperatures inhibited growth. Species which could not reach the emergent stage in the short growth season available would not occur, so the fauna became poorer with upstream decline in the length of the growth season (Hynes, 1970a). In contrast, my model streams were located in an area of mild winters and occasionally high summer temperatures. Lehmkuhl (1968) surmised that Epeorus (Iron) longimanus (Eaton) and E. (Iron) albertae (McDunnough) are cold water forms which cannot tolerate temperatures above about 18 C and so are near the limit of their range in Oak Creek. While to my knowledge neither experimental studies of temperature tolerance nor field studies of distribution in relation to temperature are available for any of the invertebrate species of the model streams, it may be largely a cool water fauna of hill streams which is unable to maintain high levels of production under conditions of increased temperature.

As cold-adapted forms were reduced in numbers and biomass in the heated stream, forms more tolerant of high temperature might have been expected to move into the system and to utilize the excess resources. The nearest natural habitat for such forms probably would have been several miles down Oak Creek, where it flows slowly through pastures and is exposed to the sun. Lehmkuhl (unpublished material, 1969) collected such mayflies as Hexagenia limbata (Upholt), Trichorythodes fallax Traver, and Heptagenia sp. in lower Oak Creek and in the Marys River to which Oak Creek is a tributary. None of these mayflies was taken in the model streams or by Lehmkuhl in upper Oak Creek. Kerst (1970) found great differences between lower and upper Oak Creek in the relative abundance of different stoneflies. These downstream areas differ from the model streams and from upper Oak Creek in flow rate, substrate type, and other factors in addition to temperature, which could make colonization of the model streams difficult for species adapted to such different conditions. For weak-flying forms such as mayflies and stoneflies, distance may be a factor limiting colonization.

The duration of the temperature study may have been too short for faunal additions and a resultant increase in the productivity of the heated stream to appear. Hynes (1970a) reported on a long-term study of a small stream in which the mayfly fauna was dominated for three years by *Rhithrogena* whereupon for no apparent reason *Baetis* became the most abundant mayfly for the next three years, with *Rhithrogena* rather uncommon. Perhaps important changes in faunal composition and productivity can only be measured over many years.

Maturation, in the sense of Margalef (1963), is a long-term process which would result in less excess production being available to the top carnivore as more information (more species) enters the community, either naturally or artificially introduced. It is difficult to say how far this process has gone in the model streams. Presumably they have already received most elements of the fauna of the small stream from which exchange water is drawn. The high level of production of coho salmon is, however, an indication that the stream communities are still relatively immature. This is to some extent artificial as other fish species have been excluded. The lack of winter freshets should contribute to the development of maturity, as these have been shown to have drastic simplifying effects on stream communities (Hynes, 1970a). On the other hand, pump failures could have had the same effect as a drought, leaving the riffles bare for short periods.

Increased temperature should have a simplifying effect on the stream communities, presumably by removing information during the summer through eliminating the less tolerant individuals. If tolerant species were available to utilize the energy resource in the model streams, the energy supply exported from the invertebrate component of the community to the fish should be increased, according to Margalef. The growth of fish in turn would depend on their ability to function at increased temperature and to utilize the increased food supply.

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APPENDICES

Appendix Table I. Biomasses of invertebrates in riffles of the control (C) and treatment (T) model streams based upon samples collected between March 1970 and June 1971. Values are given for each taxonomic group in grams per square meter.

Taxon	Sampling Data Mar 70		19-20 Apr 70		5 May 70		21 May 70		6 June 70		2 Jul 70		23 Jul 70		18 Aug 70		23 Sep 70		3 Nov 70		18 Dec 70		26 Jan 71		9 Mar 71		20 Apr 71		21 May 71		25 June 71		26 Jul 71	
	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T
Ephemeroptera	6.02	2.78	2.23	1.54	3.28	3.26	4.40	1.57		12.26	8.65	2.82	10.17	7.10	9.31	3.97	5.80	5.17	1.79	1.53	3.81	4.15	5.52	5.54	10.52	4.20	7.73	1.42	4.99	0.64	3.50	0.32	4.89	0.39
<u>Ameletus</u>	0.22		0.04		0.52					0.06														<0.01	0.15			0.15			0.02			
<u>Baetis parvus</u>					0.14		0.05		0.54	0.27	0.03	0.02	0.03	0.21	0.31	0.22	0.43	0.11	<0.01	0.02		0.02	<0.01	0.01	0.10	0.01	0.96	0.15	1.27		0.04		1.22	
	4.25	0.05	0.07	0.11																														
<u>B. tricaudatus</u>					0.04	0.05	0.55	0.14	0.50	0.29	2.57	2.46	8.53	6.80	6.93	3.25	4.95	4.65	0.51	0.67	0.27	0.13	0.39	0.55	0.62	0.09	0.85	0.04	0.45	0.33	1.72	0.32	1.77	0.39
<u>Cinygma</u>	0.91	2.35	2.12	1.37	2.34	1.08	2.13		41.80	10.82	5.72	0.34	1.27	0.08	0.25		0.15	0.02	0.14	0.08	0.14	0.21	0.09	0.56	4.14	0.35	5.32	1.09	2.63	0.26	1.65		0.34	
<u>Cinygmula reticulata</u>	0.61																																	
<u>Epeorus albertae</u>									0.86		0.32																							
<u>E. longimanus</u>							0.09																0.11		0.15	0.08								
<u>E. nitidus</u>	0.02	0.04		0.03	0.05		1.47	1.43					0.34		1.20	0.50	0.26	0.37	1.10	0.76	3.40	3.78	4.88	4.41	4.99	3.56	0.03		0.65	0.10	0.06		1.56	
<u>E. n. sp.</u>															0.62																			
<u>Ephemerella</u>	0.61						0.10		0.17																	0.09	0.01							
<u>Paraleptophlebia debilis</u>				0.04	0.19	2.12			0.33	0.80			0.01		0.62																0.01		<0.01	
<u>P. temporalis</u>					0.01					<0.01							0.15	0.15	0.03				0.05		0.35		0.56							
Plecoptera	1.20	3.27	0.14	0.44	0.58	2.28	1.81	1.37	4.76	1.50	1.39	1.60	4.74	0.52	1.48	0.22	5.28	1.78	8.25	2.02	7.22	2.38	5.49	5.41	2.08	0.66	0.10	0.10	0.19	1.91	0.03	0.07	0.54	0.04
<u>Acroneuria</u>			0.05										0.10																	1.45			<0.01	
<u>Brachyptera</u>																			0.09		2.51	0.53	4.03	5.18	0.08	0.53								
Capniidae																			0.06	0.18	0.06	0.01	<0.01											
Chloroperlinae				<0.01	0.01		<0.01							0.01					0.02						<0.01		0.02	<0.01						
<u>Isogenus</u>								<0.01																0.01										
<u>Isoperla</u>	0.85	0.03	0.12		0.16	0.28	0.48		0.03	0.02		<0.01									0.16	0.01	0.44	0.05	0.47	0.02	0.03		0.06				<0.01	
<u>Nemoura</u>	0.34	3.18	0.02	0.44	0.40	1.91	1.33	1.36	4.73	1.48	1.39	1.59	4.63	0.51	1.48	0.22	5.27	1.76	8.09	1.85	4.47	1.83	1.00	0.14	0.73	0.11	0.05	0.09	0.11	0.51	0.03	0.07	0.44	0.04
<u>Pteronarcys</u>							0.09																		0.80				0.02	0.03			0.10	

Appendix Table I. Continued

Taxon	Sampling Data																																	
	Mar 70		19-20 Apr 70		5 May 70		21 May 70		6 June 70		2 Jul 70		23 Jul 70		18 Aug 70		23 Sep 70		3 Nov 70		18 Dec 70		26 Jan 71		9 Mar 71		20 Apr 71		21 May 71		25 June 71		26 Jul 71	
	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T
Trichoptera	0.37	0.50	0.03	0.15	0.14		0.30			0.32			0.15			0.75		<0.01		0.01		0.01	<0.01	0.09	0.12		0.01			0.01				
Hydroptilidae																				<0.01		0.01	<0.01		0.12		0.01							
<u>Neophylax</u>	0.37	0.50	0.03	0.15	0.14		0.30			0.32			0.15			0.71								0.09										
<u>Psychomyia</u>																0.04				<0.01										0.01				
Diptera	2.14	0.08	0.05	0.02	0.02	0.20	1.03	1.93	1.63	0.68	3.68	1.53	3.34	1.40	1.69	0.98	1.23	0.79	0.85	0.57	0.26	0.02	0.11	0.24	0.16	0.15	0.91	0.21	0.60	0.86	3.81	2.03	0.59	2.51
Chironomidae larvae																																		
Chironominae	0.58					<0.01			0.12	0.09	0.57	0.37	1.55	0.32	0.03	0.02		0.11	<0.01	0.01	<0.01		<0.01	0.21	0.05	0.10	0.07	0.01		0.23	0.21	0.06	<0.01	<0.01
Orthocladiinae	0.07	0.07	0.05	0.02	0.02	0.20	1.01	1.90	1.11	0.57	2.53	0.93	1.09	0.27	0.11	0.20	0.30	0.43	0.80	0.51	0.21	0.02	0.06	0.01	0.10	0.02	0.76	0.20	0.51	0.58	3.01	1.72	0.33	2.16
Tanypodinae													<0.01													<0.01	0.03							
Chironomidae pupae	<0.01		0.01					<0.01	0.39	0.02	0.46	0.13	0.01	0.02	0.01	0.02	0.02	0.04	0.03	0.02	0.03		<0.01		<0.01	0.03	0.06		<0.01	0.06	0.11		<0.01	0.12
Simulidae larvae							0.03	<0.01			0.12	0.16	0.34	0.70	1.49	0.75	0.67	0.17	0.02	0.02	0.02	<0.01	0.04	0.03					0.03	0.04	0.43	0.05	0.26	0.23
Simulidae pupae														0.07	0.03		0.22	0.03	<0.01	<0.01											0.05			
Tipulidae larvae												<0.01		0.02	<0.01		0.02																	
Tipulidae pupae																													0.01					<0.01

Appendix Table II. Biomasses of invertebrates in pools of the control (C) and treatment (T) model streams based upon samples collected between March 1970 and June 1971. Values are given for each taxonomic group in grams per square meter.

	Sampling Date																					
	19-26 May 70		28 Jun 70		31 Jul 70		31 Aug 70-5 Sep 70		8-10 Oct 70		16 Nov 70		12-14 Jan 71		7-11 Feb 71		6-8 Apr 71		10 May 71		11 Jun 71	
Taxon	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T
Ephemeroptera	13.38	6.88	14.64	1.17	8.70	2.53	15.63	0.58	2.83	0.54	2.57	<0.01	4.69	0.09	3.53	0.47	5.39	0.01	7.08	0.05	1.25	0.05
Ameletus											0.11	<0.01	0.05									
Baetis parvus			0.15		0.28	0.03	0.38		0.87		0.03		0.07	0.03	0.11	0.06	0.34		1.35		<0.01	
B. tricaudatus							0.21	0.05						0.02								
Cinygma	0.33	0.63	1.77		0.36		0.04			0.03	0.38		0.10	0.04	0.58	0.41			4.16		0.03	
Paraleptophlebia debilis	11.95	6.25	12.72	1.17	8.06	2.50	15.21	0.82	1.96	0.48	0.67		0.68				0.06	0.01	0.55	0.05	1.22	0.05
P. gregalis	0.74													<0.01	0.01				0.41			
P. temporalis	0.28								<0.01	0.04	1.39		3.78		2.84		4.96		0.53			
Odonata		1.67		6.03						14.09			0.15			9.15	5.12		6.90		1.10	
Cordulegaster dorsalis		1.23		6.03						12.81						9.15						
Libellulidae		0.44																				
Octogomphus specularis										1.28			0.15				5.12		6.90		1.10	
Plecoptera	1.97	0.33	1.15	0.19	3.34	2.22	1.98	0.17	1.34	0.87	34.47	1.09	11.93	0.41	12.99	0.32	1.22	0.06	0.30	0.04	0.34	
Acroneuria californica															1.78							
Brachyptera			0.06	0.19				0.16			0.36		0.48	0.11								
Capniidae									0.21	0.29	2.01	0.41	0.31				0.05		0.02		0.01	
Chloroperlinae			0.32			0.10								0.13	0.42							
Isoperla							0.19		0.07	0.06	0.86	0.20					0.70					
Nemoura	1.89	0.22	0.77		2.60	2.13	1.79	0.01	1.05	0.39	31.24	0.48	11.14	0.17	8.24	0.32	0.48	0.01	0.28	0.04	0.33	
Pteronarcys californica															2.56							

Appendix Table II. Continued.

	Sampling Date																					
	19-26 May 70		28 Jun 70		31 Jul 70		31 Aug 70- 5 Sep 70		8-10 Oct 70		16 Nov 70		12-14 Jan 71		7-11 Feb 71		6-8 Apr 71		10 May 71		11 Jun 71	
Taxon	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T
Megaloptera					0.18	0.41		0.46	0.14		1.94	1.76	1.96	1.74	0.82		0.03	0.64				
Sialis californica					0.18	0.41		0.46	0.14		1.02	0.75	1.96	1.74	0.82		0.03	0.64				
S. rotunda											0.92	1.01										
Trichoptera							0.09			0.38	0.07	0.85			0.46	2.28	0.11	0.06	2.04	0.56		
Hydroptilidae										0.26	0.04	0.02			0.15	0.02						
Psychomyia										0.08	0.03	0.83		1.66	0.31	2.27	0.11	0.06	2.04	0.56		
Diptera	0.29	0.74	3.16	5.88	6.44	3.50	2.14	0.54	0.68	3.51	0.45	0.08	1.09	5.26	1.49	2.68	2.87	1.11	2.08	0.66	8.79	1.82
Chironomidae larvae																						
Orthocladiinae	0.21	0.28	0.83	0.54	0.46	0.79	0.24	<0.01	0.27	1.22	0.05	<0.01	0.19	0.12	0.46	0.11	0.39	<0.01	0.73	0.19	2.87	0.32
Chironominae	0.08	0.09	1.38	3.13	5.19	1.13	1.24	0.42	0.27	1.51	0.18		0.18	0.24	0.28	1.34	0.86	0.15	0.13	0.24	4.19	0.60
Tanypodinae			0.30	0.17	0.15		0.07	0.07	0.10	0.67	0.19	0.08	0.71	2.00	0.87	0.73	0.74	0.82	0.78	0.22	0.19	0.53
Chironomidae pupae		0.30	0.64	2.02	0.32	0.34	0.27	0.04	0.05	0.11	0.04		0.01		0.02	0.38	0.43	0.13	0.34	<0.01	1.27	0.37
Tipulidae larvae														2.74								
Tipulidae pupae						0.33				0.01				0.15								

Appendix Table III. Mean weights of drifting invertebrates in the control (C) and treatment (T) streams based upon samples collected between October 1969 and April 1971. Values are given for each taxonomic group in milligrams of drift per day.

	Oct 69		Nov 69	Dec 69	Jan 70		Feb 70		Mar 70		Apr 70		May 70		Jun 70		Jul 70		Aug 70		Sep 70		Nov 70		Dec 70		Jan 71		Mar 71		Apr 71	
Taxon	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T	C	T
Ephemeroptera			131.4	11.5	266.4		61.9	30.3	18.4	24.8	39.4	24.4	87.1	42.1	120.5	63.5	20.2	3.7	75.3	84.3	121.8	26.4	32.8	45.5	90.3	6.0	379.6	62.1	15.0	0.8	44.2	3.9
Ameletus	9.5	152.0			160.8		48.4		11.5				24.9										6.3	3.0		2.0	173.6	0.5	1.8	0.7	0.7	
Baetis parvus									3.4		39.4	5.4	5.7	5.4		2.9	0.5	2.6	0.3	5.1	25.5	1.0		3.0			0.5	2.2	0.1		2.6	
	101.4	30.4	125.6	11.5																												
B. tricaudatus							12.5	6.8	3.5				1.0		1.7	0.1	0.9		45.8	79.3	91.8	15.2	1.9	19.5	25.4		55.6	38.1	5.6	0.1	2.8	
Cinygma		121.6	5.7		105.6								55.5		67.6				26.0					8.3		1.0						
Epeorus																								11.4				21.0			3.6	
Paraleptophlebia debilis								23.5						36.7	51.2	13.3 2.1	18.8	1.1	3.1 0.1				0.6		35.0							
P. temporalis																							22.8		29.9		149.9	0.3	0.8		24.6	
Unidentified subimagoes										24.8		19.0									4.5	10.2							6.7		11.3	
Plecoptera	106.4		39.1	67.0	0.9					1.0		5.2	1.0	5.4	16.0	18.2	13.5	7.4	26.6	0.5	87.3	3.9	592.3	437.2	354.3	420.4	3029.7	340.7	9.1	19.2	0.9	
Brachyptera																							26.9	8.8	32.6	103.3	615.3	290.3	6.0	16.9		
Capniidae																					0.5		154.4	224.9	60.8	9.7	180.7	4.6		1.0		
Isoperla																6.3							1.7	15.5			19.1					
Nemoura			39.1	23.0						1.0		5.2	1.0	5.4	16.0	11.8	13.5	7.4	26.6	0.5	86.8	3.9	409.2	186.6	251.9	307.4	2214.1	45.6	3.0	1.3	0.9	
Trichoptera									7.7	26.8														20.6	2.4	4.0		1.5		3.5		
Coleoptera			2.3		2.8																		2.5		2.0			4.0		2.0	32.3	
Diptera	84.7	6.0	34.8		17.6	16.1	0.7	20.5	0.4	3.0		0.2	0.2	1.1	28.8	254.5	99.8	66.9	61.9	80.2	165.1	37.4	61.6	33.9	39.7	21.6	33.2	21.3		22.3	24.5	1.4
Chironomidae larvae																																
Orthocladiinae					6.1	0.7				0.9		0.2	0.2	0.6	5.1	15.1	26.3	11.5	11.1	2.9	17.6	4.3	5.8	3.0	8.8	0.5	4.6	0.2		1.0	2.2	
	4.1	1.2																														
Chironominae					0.7	2.1									6.3	10.8	14.8	14.2	16.6	10.7	31.9	3.9		0.2				0.1				
Chironomidae pupae & adults	43.0	1.9	29.5		7.8	14.3	0.3	20.5	0.4	1.9				0.5	17.4	220.6	17.7	37.8	27.8	58.5	97.6	26.6	55.7	30.0	30.4	15.8	18.7	16.4		21.0	8.5	
Simulidae larvae	6.1				3.0																1.6	2.1		0.4	0.3	3.3	7.8	3.3			8.8	
Terrestrial insects	12.2	1.9			13.4								90.0		1.5	4.8	0.5	5.0	13.5	5.0												

Appendix Table IV. Percentage composition of stomach contents of juvenile coho in control (C) and treatment (T) model streams.

	Apr-Jun 70		Jul-Sep 70		Oct-Dec 70		Jan-Mar 71		Apr-May 71		Jun-Aug 71	
	C	T	C	T	C	T	C	T	C	T	C	T
Ephemeroptera	89	77	79	18	22	6	4		58	6	79	29
Baetis	1	2	24	13	7	3	4		16		5	29
Cinygma	20	13	10						12		65	
Epeorus									12			
Paraleptophlebia	67	60	46		14	3			18		9	
Unidentified	2	3		5						6		
Plecoptera	6	16	11	3	65	14	92	100	40		4	
Acroneuria									40			
Brachyptera					1		41	100				
Capniidae					3	1						
Isoperla	4					1						
Nemoura	2	16	11		61	8	51				4	
Unidentified				3		4						
Diptera	5	7	8	46	13	10	5		1	16	13	32
Chironomidae larvae	3	2	7	31	6	5	2		1	1	9	10
Chironomidae pupae and adults	2	5	1	7	7	5	3			14	3	19
Other Diptera				8						1	1	3
Terrestrial insects			1	33		1				78	1	35
Molluscs						58					2	
Crustaceans						11					1	5

Appendix Table V. Seasonal values of biomasses and drift rates of invertebrates and seasonal values of biomasses, growth rates, and rates of food consumption of juvenile coho in the control (C) and treatment (T) model streams.

Time period	Mean biomass of food resources[a] ($g \cdot m^{-2}$)		Mean drift rate ($mg \cdot day^{-1}$)		Mean coho biomass ($g \cdot m^{-2}$)		Coho growth rate ($mg \cdot g \cdot day^{-1}$)		Rate of food consumption by coho ($mg \cdot g \cdot day^{-1}$)	
	C	T	C	T	C	T	C	T	C	T
28 May 70- 3 Sep 70	13.5	7.0	157	220	11.2	7.1	15.8	11.6	57.0	64.7
3 Sep 70- 3 Dec 70	18.7	4.7	428	302	20.4	8.5	3.2	2.2	25.0	39.0
3 Dec 70- 4 Mar 71	14.5	6.7	2458	441	24.5	9.6	1.3	2.1	12.6	24.4
4 Mar 71-[b] 1 May 71	10.3	2.8	58	25	13.1 5.7	5.7 0.6	3.5 17.5	0.0 3.3	24.2 38.8	21.0 15.0
7 May 71- 9 Aug 71	8.1	2.1	-	-	14.2	3.6	12.2	13.2	51.2	69.5

[a] These values include mayflies, stoneflies, and Diptera from both riffles and pools.

[b] The upper line of statistics on coho refers to the 1970 year class, the lower line to the 1971 year class.