

ENERGETIC RESPONSE OF JUVENILE COHO SALMON (*ONCORHYNCHUS
KISUTCH*) TO VARYING WATER TEMPERATURE REGIMES IN NORTHERN
CALIFORNIA STREAMS

by

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ABSTRACT

ENERGETIC RESPONSE OF JUVENILE COHO SALMON (*ONCORHYNCHUS KISUTCH*) TO VARYING WATER TEMPERATURE REGIMES IN NORTHERN CALIFORNIA STREAMS

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Bioenergetic modeling of growth was assessed as an approach for investigating the effects of differing temperature regimes on the energetic response of juvenile coho salmon in northern California streams. A bioenergetic model was developed and calibrated which simulated the growth of juvenile coho salmon in stream environments. The model predicted independent observations of coho salmon weight gain in 10 of 16 experimental laboratory data sets from three laboratory studies of fish between two and ten grams wet weight during the summer growth period. Results indicate that the final calibrated model may adequately represent growth of juvenile coho salmon.

Energetic analysis of growth from coho salmon populations studied revealed that losses from respiration (average standard and activity metabolism) was the single greatest energy expenditure for stream-dwelling juvenile coho salmon, averaging 52.2% and 60.6% of consumption in 1998 and 1999, respectively. Energetic losses from specific dynamic action and waste products were far less. The proportion of consumed energy allocated to growth ranged between 3% and 29% in streams over both years of study.

Calculated food conversion efficiency in streams characterized as having cool

temperature regimes (15.1-17°C daily average temperatures) was higher than in streams characterized as having either cold (12-15°C) or warm (>17°C) temperature regimes. The energetic analysis performed in this study indicated that the proportion of consumed energy allocated to growth was maximum when daily average water temperatures ranged from 14.7°C to 15.7°C. These results indicate that juvenile coho salmon growth efficiency and growth rates may decrease as daily average water temperatures increase past 15.7°C in the absence of unlimited food resources.

ACKNOWLEDGMENTS

This Master's Thesis is the culmination of over five years of difficult, time consuming, and often frustrating field and office work. However, I consider my experience to have been a good one, due in part to the contributions of advice, time, and encouragement from many people who helped make this project possible. I wish to thank my major advisor, Dr. Walter Duffy, for having patience with me and for letting me work on this project on my own time schedule. His experience with graduate projects and subsequent advice about my project in particular, made this thesis much better than I alone could have ever made it. I also wish to thank my other committee members, Dr. David Hankin and Dr. Terry Roelofs for their comments and help with text editing. Several landowners were extremely helpful by facilitating the acquisition of permits and keys and for allowing access to study streams located on private or state owned land. The list of landowners includes: Mr. Jeff Barrett, Pacific Lumber Company; Mr. Steve Horner, Barnum Timber Company; Mr. Aaron Nadig, Mendocino Redwood Company; Mr. Norm Henry, California Department of Forestry, Jackson State Demonstration Forest; and Mr. Jim Timmonds. I also appreciate California Department of Fish and Game for their efforts to coordinate sampling between their coho research and the work presented in this thesis. Their work was greatly appreciated as it significantly increased both the sample size and geographic distribution of streams sampled in northern California.

I am greatly indebted to several individuals who took the time to help me collect the field data which was necessary for this project. I am especially grateful for the superior work provided by David Grant and Seth Ricker who, at times, were willing to sacrifice class time or take time away from their jobs to work around my field sampling schedule. Their contributions of time and labor during several long days of field data collection made this project possible.

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INTRODUCTION

Water temperature is one of the most important environmental factors affecting fish (Fry 1967, Lantz 1969, Fry 1971). Fish are poikilothermic and do not regulate their internal body temperature to maintain a state of constant thermal equilibrium. Instead, the body temperature of a fish approximates the temperature of the water it lives in. The inability of fish to regulate their body temperature has a direct influence on metabolic processes. Metabolism and other energetic processes increase when external water temperature is warm and decrease when it is cold.

Water temperatures are especially important to species of Pacific salmon and trout (*Oncorhynchus* spp.) in the Pacific Northwest region of North America. Salmonid fishes require clean, cool water to successfully migrate, reproduce, and grow. Because of the importance of water temperature to salmonid fishes, a great deal of research has been conducted on how temperature affects their life history characteristics (Brett 1952, Bottom et al. 1985, Sullivan et al. 2000). Several authors have provided excellent reviews of salmonid temperature requirements, including optimum or “preferred” temperature ranges as well as both upper and lower lethal tolerance limits for most Pacific salmonid species (Brett 1952, Beschta et al. 1987, Bjornn and Reiser 1991, Brungs and Jones 1977, Becker and Genoway 1979, Konecki et al. 1995). Although water temperature is known to be important in regulating growth rates and production in salmonid fishes, its effect in regulating growth of fish cannot be easily predicted under

field conditions. Research on thermal tolerance of salmonid fishes suggests that they respond positively to increased stream temperatures to a certain point; beyond that point, as temperatures approach lethal limits, they become physiologically stressed (Bisson and Davis 1976, Brett 1976, Brett et al. 1982, Brungs and Jones 1977, Oregon Department of Environmental Quality 1995). As a result, it is currently thought that fish populations exposed to a gradient of temperatures will show improved growth rates as temperatures increase up to some optimum temperature (Figure 1). If temperatures continue to increase beyond this optimum, however, sub-lethal stress-induced detrimental physiological and behavioral effects will begin to manifest themselves (Figure 2) (Wedemeyer 1973, Brett et al. 1982, Beschta et al. 1987, Bjornn and Reiser 1991).

Research on the growth of salmonid fishes at elevated water temperatures has often produced inconclusive or conflicting results. High summer water temperatures are believed to reduce growth and thus production of salmonids, as has been reported from laboratory studies (Brett 1952, Coutant 1973) as well as in natural streams systems (Bottom et al. 1985; Martin et al. 1986; Reeves et al. 1989). Conversely, other researchers have reported evidence that fish productivity in summer increased after stream water temperatures increased in both laboratory experiments (Brett 1971, Bisson and Davis 1976, Hokanson et al. 1977) and under natural stream conditions (Beschta et al. 1987, Holtby 1988, Bisson et al. 1988).

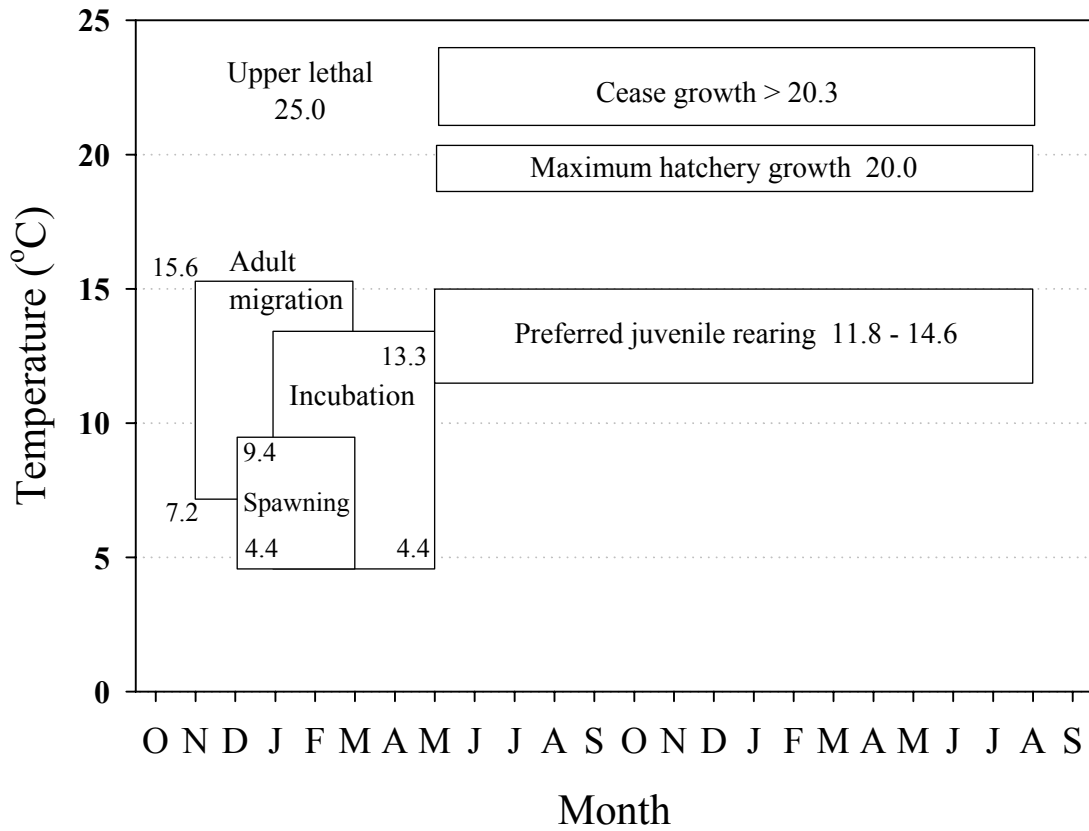


Figure 1. Temperature requirements of coho salmon by life history stage (from Reiser and Bjornn 1979 and Brett 1952). Figure adapted from Oregon Department of Environmental Quality (1995).

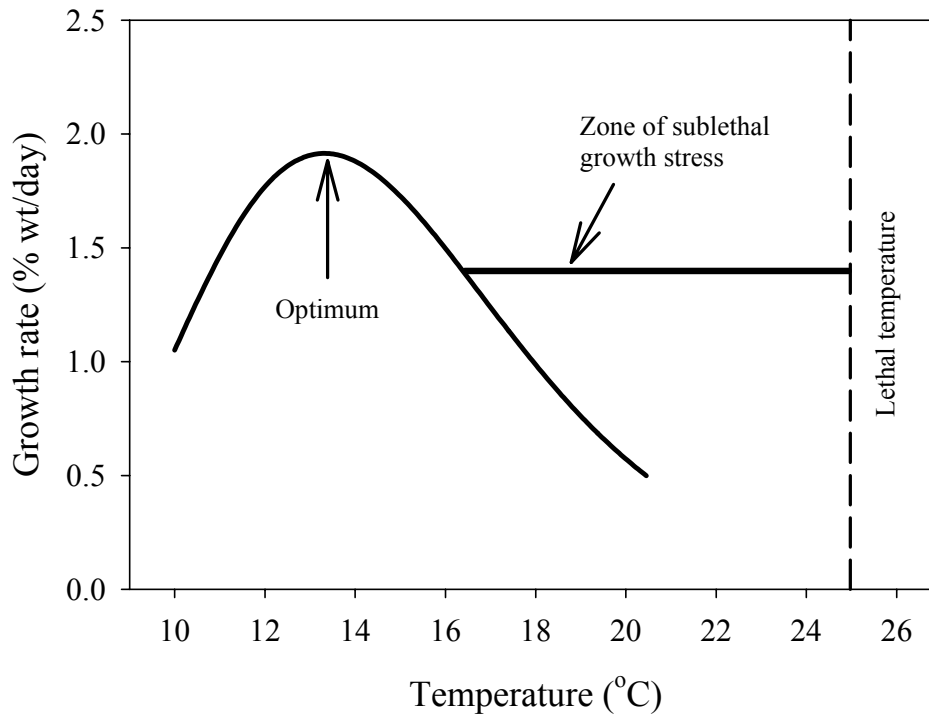


Figure 2. Theoretical relationship between growth rate and temperature for salmonids fed sub-optimal rations thought to correspond to food availability in British Columbia streams (figure adapted from Brett et al. 1982).

Variability in the growth of salmonids to water temperature may result from moderating habitat, biological interactions or behavior. This variability may be attributable to some form of compensation, such as low predation rates, reduced intra- or interspecific competition rates, high food production, or possibly genetic adaptation that leads to higher than expected population success (Armour 1991). Growth variability may also be attributed to other site-specific phenomena that are not well understood.

Observed variability in salmonid fish growth at elevated water temperature likely reflects our failure to accurately determine temperatures at which growth and other physiological processes become negatively affected (Thomas et al. 1986). We simply do not have a full and precise understanding of how elevated water temperatures affect salmonid growth and survival under natural conditions. If the goal is to better understand the growth of salmonid fishes at elevated temperature regimes, it is clear that further research must be performed to clarify temperature - growth relationships.

Coho salmon (*O. kisutch*) are an excellent candidate for the study of relationships between elevated temperatures and growth in Pacific salmon. Coho salmon are adapted to cold water stream habitats, are sensitive to water temperatures greater than 16°C, and are considered the most temperature intolerant of the Pacific salmon species (Brett 1952). Because they are adapted to streams with cold water and presumably initiate thermal stress at only moderate water temperatures (>16°C), effects of temperature on coho salmon growth may be seen over the range of temperatures typically encountered in northern California streams. Furthermore, juvenile coho salmon typically remain in selected stream habitats throughout the summer and their growth reflects environmental conditions in relatively discrete areas (Burns 1971, Nielsen 1992). These characteristics make coho salmon ideal for the study of temperature effects on growth during the summer period.

Bioenergetic modeling can be used to study the interaction of temperature effects on fish growth and has become an increasingly important and useful tool for gaining

insights into a variety of natural resource problems (Brandt and Hartman 1993, Cho et al. 1982, Hansen et al. 1993, Ney 1993). The bioenergetic approach has had an extensive record of previous applications in research and management and has been used in a variety of modeling situations to investigate several resource problems, including studies of growth responses of fishes to changing environmental conditions such as temperature (Brandt et al. 1992, Kitchell et al. 1977, Hanson et al. 1997, Ney 1993). Excellent reviews of bioenergetics approaches to modeling situations can be found in Adams and Breck (1990), Brett (1971), Brett and Groves (1979), Hewett (1989), Hewett and Johnson (1992), Hansen et al. (1993), and Hewett and Kraft (1993).

The purpose of this study was to investigate how elevated stream water temperatures affect growth of juvenile coho salmon in northern California streams. The primary objective of this research was to develop and test a bioenergetic model that would simulate the growth of juvenile coho salmon in these streams during the summer rearing period (June through October).

This thesis describes the development and subsequent implementation of such a bioenergetic model. I present a bioenergetic model for stream dwelling coho salmon that can provide a basis for understanding the effects of elevated stream temperature on growth processes in these fish. Bioenergetic model development is discussed in two phases: 1) model development and parameter selection, and 2) model calibration. The final calibrated model was then used to analyze the energetic response of juvenile coho salmon populations exposed to varying water temperature regimes in eight northern

California streams. The outcome of this research should shed light on the problem of how juvenile coho salmon respond energetically to elevated stream water temperatures.

METHODS

To investigate how stream-dwelling juvenile coho salmon energetically react to elevated water temperatures in stream environments, I constructed a bioenergetics model that simulated the energetic response (consumption rate, metabolic losses, and growth) of juvenile coho salmon to water temperature during the period of summer freshwater residence. Model development was based on an existing bioenergetics model that was modified to incorporate juvenile coho salmon physiological information obtained from the literature. The model was then calibrated against the energetic response of juvenile coho salmon to temperature and food consumption data obtained from laboratory studies. This research was completed under Humboldt State University Institutional Animal Care and Use Committee Approval No. 98/99.F.38B.

Stream-specific data on water temperature, invertebrate species presence and abundance, and juvenile coho salmon growth was obtained from field studies conducted in several northern California stream systems in 1998 and 1999. Data collected from study streams were used as input parameters in the bioenergetics model. By integrating growth as a function of fish size and water temperature obtained from stream-specific field studies, the bioenergetics model was used to calculate an energy budget for each coho salmon population studied. Energy losses (metabolism and waste products) and net energy gains (growth) were then related to the temperature regime experienced by each population studied.

Study Sites

Streams selected for this project were chosen based on the status of native coho salmon populations, temperature regimes, geographic representation, and habitat characteristics. The primary criteria for selection was that the stream possessed relatively healthy populations of juvenile coho salmon that were likely to maintain a minimum population of at least 25 fish per 100 meter sampling reach during the period of study. The second criterion was that streams selected would reflect a range of temperature regimes typically encountered in the coastal and inland regions of northern California. A third criterion was geographic location. Streams selected for study were intended to be representative of the coastal zone of northern California influenced by marine fog, as well as the higher temperature and drier climate characteristic of the Mediterranean temperate climate inland from the fog influence. The final criterion used in stream selection was the lack of recent stocking of hatchery coho salmon within the stream system so as to avoid genetic influences that could affect growth rates.

In 1998, I sampled five streams representing three thermal regimes, based on daily average summer water temperature ranges. These included two cold streams (12-15°C), two cool streams (15.1-17°C), and one warm stream (>17°C) (Table 1). The inclusion of an additional warm stream was planned for this project, however no other warm water streams were found that could support the coho salmon population required for this study.

Table 1. Summary of watershed characteristics and habitat variables measured in sampling reaches of eight northern California streams during 1998 and 1999. All measurements were collected according to methods described in Flosi et al. 1998.

	S.F. Broken Kettle	Lindsay	Sharber	Freshwater	Pollack	W.F. Sproul	Hollow Tree	Caspar
<u>Watershed characteristics</u>								
County	Del Norte	Humboldt	Trinity	Humboldt Humboldt	Humboldt	Humboldt	Mendocino	Mendocino Pacific
Drainage basin	Illinois R.	Mad R.	Trinity R.	Bay	S.F. Eel R.	S.F. Eel R.	S.F. Eel R.	Ocean
Latitude	41 58 27	40 55 28	40 53 48	40 56 7	40 05 39	40 02 29	39 48 45	39 20 57
Longitude	123 44 17	124 01 59	123 33 51	124 02 58	123 54 38	123 52 2	123 45 32	123 45 37
Drainage area (km ²)	5.8	42.0	15.7	20.6	7.1	14.3	78.0	18.5
<u>Habitat variables</u>								
Reach length sampled (m)	60	117	50	60	60	100	100	100
Elevation (m)	486.0	4.5	500.0	19.8	80.0	65.5	92.0	6.0
Gradient (%)	1.0	1.4	1.0	1.8	2.4	2.4	1.3	2.2
Mean wetted width (m)	1.79	1.57	1.58	2.90	1.92	1.55	4.49	2.90
Mean pool depth (m)	0.23	0.68	0.26	0.42	0.38	0.49	0.82	0.45
Area in pools (%)	92	47	68	34	84	57	61	59
Instream cover (%)	30	25	36	34	18	85	65	62*
Canopy cover (%)	81	45	68	80	77	85	65	70
Mean discharge (m ³ /s)								
1998	--	0.133	--	0.045	--	0.078	0.174	0.043
1999	0.011	0.080	0.014	0.026	0.004	0.016	0.136	0.028
Mean water temperature (°C)								
1998	13.5	15.7	12.4	15.5	15.9	14.8	18.1	13.6
1999	12.9	15.2	11.2	14.9	15.2	13.4	17.3	13.5

* Several pieces of Large Woody Debris (LWD) (>40 ft. long and >12 in. in diameter) were added to the sampling reach of Caspar Creek during 1999. The instream cover value reported here represents cover after LWD addition.

In 1999, three additional streams were sampled. These streams were sampled cooperatively by the California Cooperative Fish Research Unit, Humboldt State University and the California Department of Fish and Game (CDFG). The CDFG also made data available from their monitoring performed in 1998 as part of the California Anadromous Salmonid Project (Jong, W. 1999. Personal Communication, California Department of Fish and Game, Arcata, California). The addition of streams from the CDFG cooperative study increased the geographic coverage of sampling sites (Table 1). All eight streams sampled were either second- or third-order, as determined from 1:24,000 U.S. Geological Survey maps, and were oriented in an east to west direction. Elevations at sampling reaches ranged from 5-6 m for Lindsay and Caspar Creeks, to 486-500 m for South Fork Broken Kettle and Sharber Creeks. Drainage areas above the downstream point of the sampling reaches ranged from 6.5 to 78 km², and stream gradients within the reaches ranged from 1.0% to 2.2%. All streams had similar substrate characteristics derived from their similar parent geologies. Pools ranged from 34 to 92% by area and, except in Lindsay Creek, canopy cover was greater than 65% in all stream reaches sampled (Figures 3-6). Summer discharges varied threefold across sites in 1998 and fourfold across sites in 1999 (Table 1).

Characterizing the Thermal Regime

Continuously recording temperature data loggers were placed in each 100-m study reach to accurately characterize the thermal regime of each stream. Three HOBO

(Onset Instrument Corp., Pocasset, MA) temperature data loggers were located in each study reach as follows: 1) in a pool, 2) in a pool tail out, and 3) in a run or glide. All thermographs were attached to pieces of iron rebar that had been securely driven into the streambed at selected habitat units (Figure 7). Each thermograph was suspended approximately 10 cm from the stream bottom and was positioned in a location that minimized prolonged exposure to direct sunlight to avoid excessive artificial radiation (Forest Science Project 1998). Prior to field installation, temperature data loggers were



Figure 3. Typical habitat units selected for juvenile coho salmon sampling in Freshwater Creek during 1998 and 1999.



Figure 4. Typical habitat units selected for juvenile coho salmon sampling in Caspar Creek during 1998 and 1999.



Figure 5. Typical habitat units selected for juvenile coho salmon sampling in West Fork Sproul Creek during 1998 and 1999.

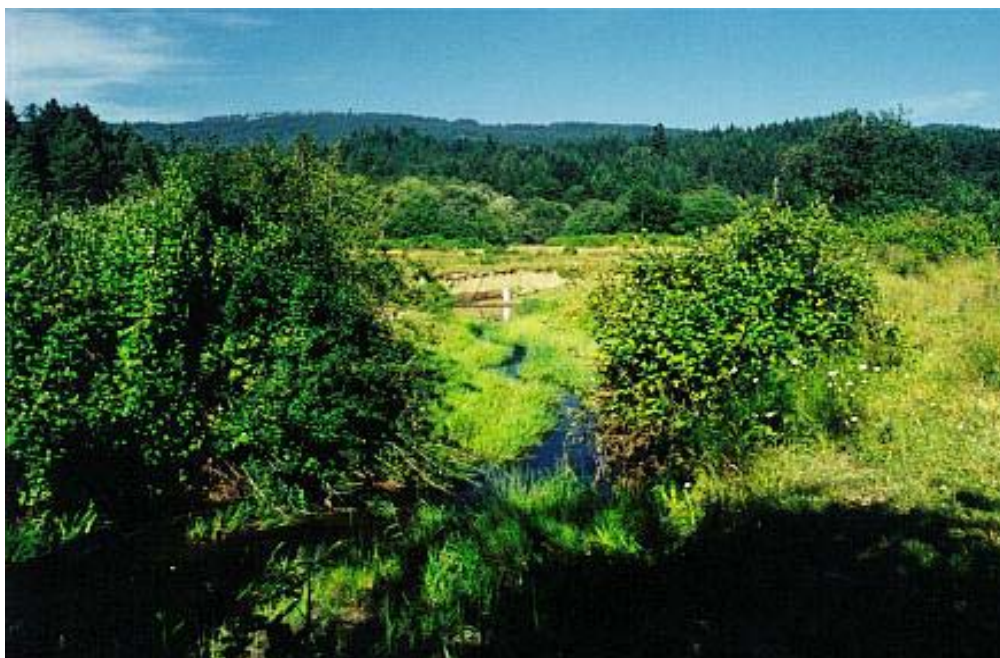


Figure 6. Typical habitat units selected for juvenile coho salmon sampling in Lindsay Creek during 1998 and 1999.

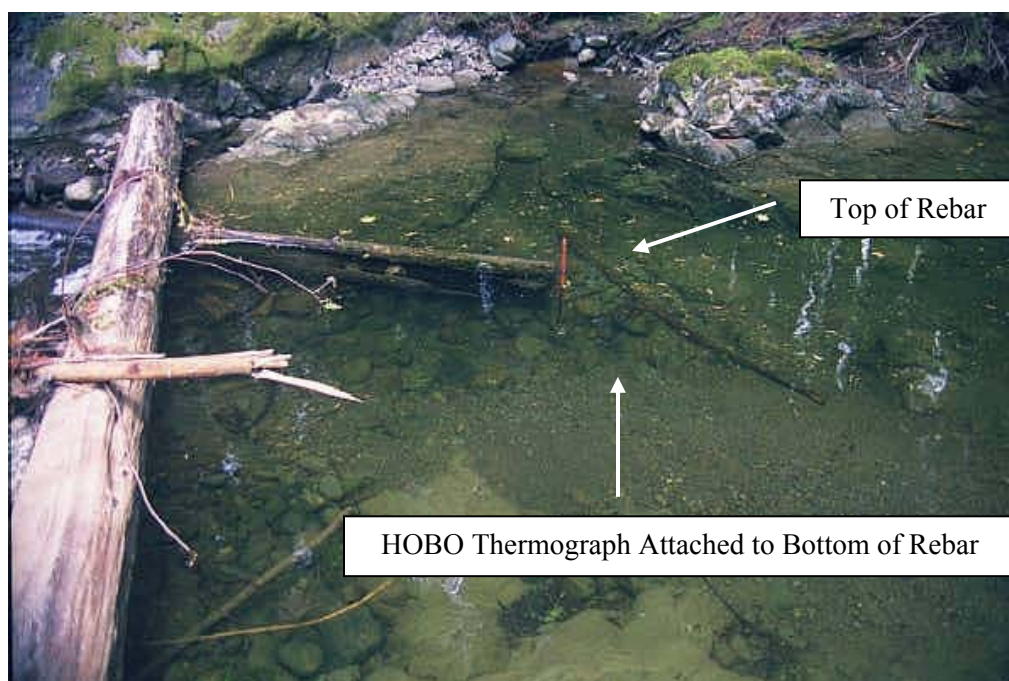


Figure 7. Typical installation of HOBO thermograph within pool habitat units in all study streams sampled.

calibrated in the laboratory according to the manufacturer's calibration procedures and were programmed to collect temperatures at 1.6 hour intervals (15 measurements per day) for a period of four months (June to October).

The continuously recorded stream water temperature data were downloaded from the HOBO data loggers and sent to the Forest Science Project at Humboldt State University in Arcata, California, for subsequent analysis and data summarization. The Forest Science Project screened the raw temperature data and removed any temperature discrepancies that were observed in the temperature data sets (e.g. periods immediately prior to and after probe immersion in the water when temperature spikes were recorded by the probe during periods when the probe was out of the water). The temperature data for each thermograph were then summarized for daily average temperature (DAT) for the entire study period of June through October for both years of study.

Sampling Protocol

One study reach was selected for sampling within each stream. Sampling reaches within study streams were chosen based on recommendations from California Department of Fish and Game fisheries biologists, ease of accessibility, and location within known coho salmon spawning and rearing areas. Where possible, sampling reaches corresponded with juvenile coho salmon sampling reaches used for the CDFG inland fisheries monitoring program (i.e. Freshwater, W. F. Sproul, and Pollack Creeks). Each stream study reach was sampled twice, once in June or July and again in September or October, during two consecutive years. Lengths of stream reaches sampled ranged

from 60 to 150 m, and average wetted width ranged from 1.5 to 4.5 m (Table 1). Stream study reaches were habitat typed using methods described in Flosi et al. (1998).

Important stream physical features were also measured (depth, width, surface area, instream structure, pool focal velocities, and mean discharge) to characterize the available habitat for fish.

After the study reaches were delineated and measured, fish within the study reach were sampled by electroshocking with a 24-volt Smith-Root Model 12-A POW backpack electroshocker (Smith Root Inc., Vancouver, Washington). Each stream study reach was block netted and a two- or three-pass removal estimate (Zippin 1958) was made of the population for both coho salmon and steelhead trout in each study reach. All other



Figure 8. Electroshocking habitat units during juvenile coho salmon sampling in Freshwater Creek.



Figure 9. Sampling juvenile coho salmon using beach seines in deep pool habitat units in Freshwater Creek.

species captured during electroshocking were separated from the coho salmon and steelhead and counted. In 1999, a 9.1 by 1.2 m beach seine was used to sample deep pool habitats after electroshocking was conducted, since electrofishing was not efficient in these habitats (Figures 8-9). Juvenile coho salmon collected were anesthetized with tricaine methanesulfonate (MS-222), measured for fork length (FL) (± 1 mm) and weight (± 0.1 g), then marked. Marking during 1998 was accomplished by completely removing the adipose fin with small clipping shears. Marking during the 1999 season was conducted by injecting phosphorescent paint of different colors between the skin and fatty tissues in several different locations in the fish (e.g. snout, behind the eye, base of

pectoral fin, etc.) (Kelly 1967, Pauley and Troutt 1988). After marking, fish were allowed to recover for approximately 1-2 hours and were then released back into the study reach from which they were originally captured. To ensure that marked coho salmon did not immediately migrate out of the study reach after their release, block nets were left at the upstream and downstream ends of the study reach for approximately one hour after their release.

Invertebrate drift was collected in each study reach. Invertebrate drift samples were used to determine which taxa were present and to obtain relative proportions for each taxa present in the drift. Two replicate 0.9 m² invertebrate drift sample nets were installed in the thalweg of riffle habitat units upstream of the study reaches 30 minutes before fish sampling began and were removed 4-6 hours later. Estimates of invertebrate drift rates for each stream ($\text{mg} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$) were calculated by averaging the 2 replicate samples. Organisms were washed from drift nets and were stored in isopropyl alcohol until they could be sorted and counted in the laboratory. All organisms were counted under 15x magnification, identified to order and categorized by percentage total occurrence to obtain a representation of taxa available as food. Organisms sampled in drift nets were weighed to the nearest 0.001 g blotted wet weight using an Ohaus Model AS200 balance, to get an estimate of total weight of the drift from each stream. Energy density values ($\text{Joules} \cdot \text{g}^{-1}$ wet weight) for specific invertebrate taxa were obtained from the literature (Cummins and Wuycheck 1971, Hanson et al. 1997) and used, with

percentage occurrence and average weight, to calculate an average energy density value for drift in each stream.

To observe which habitat units were used by marked juvenile coho salmon, each site was visited once or twice during the period between summer and fall sampling. Fish observations during these visits consisted of snorkeling each reach and recording habitats used by marked fish (i.e. pools, runs, or riffles). Water clarity in each stream reach was sufficient to allow for reliable detection of marked fish while snorkeling. These observations were made to determine the appropriate habitat unit that would be most representative of the thermal regime that would subsequently be used in characterizing the water temperatures experienced by juvenile coho salmon in the bioenergetics model.

In September or early October, each study reach was sampled using the same protocols used in June. Each study reach was electroshocked to recapture as many marked coho salmon as possible. Beach seining was also performed in several habitat units within and downstream of the study reach to increase the number of recaptured fish. Similar to the initial sampling in June, all coho salmon were anesthetized, measured and weighed. Steelhead trout (*O. mykiss*), threespine sticklebacks (*Gasterosteus aculeatus*), speckled dace (*Rhinichthys osculus*), Sacramento pikeminnow (*Ptychocheilus grandis*), Sacramento sucker (*Catostomus occidentalis*) and sculpins (*Cottus* ssp.) were only counted. All fish captured were subsequently released alive back into the streams from which they were caught.

My analysis focused on growth of age 0+ coho salmon. To ensure that only age 0+ coho salmon were included in calculating average starting size, only fish <75 mm FL in June were used in calculations. This eliminated from the analysis any age 1+ pre-smolts that may have been captured prior to migration and that would have lead to an overestimate of initial starting size for 0+ salmon. In October, only those coho salmon possessing a mark were used when calculating average size at the end of the summer growth period. Marked fish that were captured during the October sampling period were assumed to have remained in the study reach for the entire duration of the summer rearing period. Juvenile coho salmon without marks were not included in average size calculations in October because they were not captured in the study reach during the initial June sampling period and therefore could not be considered as study reach residents for the entire study period. Unmarked fish were considered to be immigrants into the sampling reach or may have been present in the reach but were simply not captured during electroshocking in June.

Growth was expressed as both (a) the average absolute gain in weight (g) between the initial and final sampling periods, and (b) as the average mass-dependent specific growth rate (SGR) ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$). Growth rates were estimated from the difference in mean weight between sampling dates in June and October of each year. Specific growth rates were calculated using the following formula (Busacker et al. 1990):

$$SGR = \frac{(W_2 - W_1)}{0.5 \cdot (W_2 + W_1) \cdot \Delta T}$$

where, W_2 and W_1 represent the average final and average initial fish weights (blotted wet weight), respectively, and ΔT represents the time (days) between samples.

Certain biotic variables were analyzed for interactions that could affect growth in the study streams. Biotic variables of concern were density of fish in stream reaches (coho salmon and total fish density) and the drift rate of prey organisms. Fish densities may affect the food available to individual fish via inter- and intraspecific competition for feeding sites and prey. These variables were regressed against growth to determine if relationships existed that could negatively interact with growth of coho salmon. Density of juvenile coho salmon and total fish density were computed as the means of the June and October densities ($\text{No} \cdot \text{m}^{-2}$).

Bioenergetic Modeling

I chose to compare growth of juvenile coho salmon among streams using a bioenergetics model. The model I developed was a modification of a model for coho salmon in Fish Bioenergetic 3.0 (Hewett and Johnson 1992, Hanson et al. 1997), widely referred to as the Wisconsin Model. This model incorporates early work on fish bioenergetics by Winberg (1956) as well as later improvements by Warren and Davis (1967), Elliot (1976) and Kitchell et al. (1977).

The Wisconsin Model includes mathematical algorithms designed to mimic physiological processes in fish. Flexibility is incorporated by allowing the user to select between or among algorithms designed to represent processes in warm, cool or cold

water species. The Wisconsin Model assumes that inputs, gains and losses of energy can be balanced. In the balanced energy equation, consumption is the energy input, growth is the net energy gain, and all other uses are losses. The balanced energy equation is represented by the following formula (Kitchell et al. 1977, Warren and Davis 1967):

$$C = G + R + S + F + U$$

where, C = rate of energy consumption, G = somatic and reproductive tissue elaboration, R = standard metabolic rate, S = metabolic rate increase from specific dynamic action (heat increment), F = waste losses due to egestion (feces), and U = waste losses due to excretion (urine)

The model accounts for the energy intake and use by fish by balancing the equation as a fish grows over time as simulated by species-specific algorithms (Brandt and Hartman 1993). The model calculates each component of the energy budget based on species-specific growth coefficients and parameters that have been derived by prior laboratory experimentation and physiological research. More importantly, the model accounts for the non-linear effects on these parameters and coefficients due to variables such as temperature and feeding rates (Hanson et al. 1997).

Although the Wisconsin Model has been criticized for its complexity, few inputs are required to run a model after physiological responses have been defined. Site-specific inputs include the initial and final size of fish, water temperature, diet composition and prey energy content. It is important to note that the Wisconsin Model simulates the

growth of an average fish within a population and that population data are projected from that average individual.

Model Development and Parameter Selection

Model development was accomplished by first selecting equations that mathematically represent energetic processes occurring in juvenile coho salmon. Rates of energy consumption, respiration, egestion and excretion can all be expressed as non-linear functions of fish weight and water temperature. Temperature is an important factor in all energetic processes and all the equations used to represent the energetic components of the Wisconsin Model are regulated by temperature.

When algorithms representing the individual components of consumption, respiration, excretion, egestion and energy density are combined, they define the flow of energy through a fish. Most parameters used in the bioenergetic model are species-specific physiological parameters that are dependent on fish size and water temperature. Table 2 provides a complete list of values for all parameters and coefficients used in the bioenergetic model developed for this project.

Considerable effort was made to obtain the most applicable data pertaining to juvenile coho salmon energetics. I initially obtained values for selected model parameters and coefficients by searching the published literature relating to coho salmon energetics. Physiological parameters based on laboratory experimentation using juvenile coho salmon were selected for the bioenergetic model, when available. These values

Table 2. Juvenile coho salmon consumption, respiration, egestion, excretion, and energy density parameters and coefficients used in the bioenergetic model.

Parameter	Modeled Value	Description	Source	Species
$C = C_{\max} \cdot p \cdot f(T)_C$		Specific consumption rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$)		
a_C	0.303	Intercept of the allometric mass function.	Hanson et al. (1997)	Coho
b_C	-0.275	Slope of the allometric mass function.	Hanson et al. (1997)	Coho
CQ	5	On the ascending portion of the consumption temperature dependence function curve – the lower water temperature at which consumption is a small fraction ($CK1$) of the maximum rate.	Hanson et al. (1997)	Coho
CTO	15	On the ascending portion of the consumption temperature dependence function curve – the water temperature corresponding to 98% of the maximum consumption rate.	Hanson et al. (1997)	Coho
CTM	18	On the ascending portion of the consumption temperature dependence function curve – the water temperature (> CTO) at which dependence is still 98% of the maximum.	Hanson et al. (1997)	Coho
CTL	26	On the ascending portion of the consumption temperature dependence function curve - the water temperature at which dependence is some reduced fraction ($CK4$) of the maximum rate.	Hanson et al. (1997)	Coho
$CK1$	0.42	On the ascending portion of the consumption temperature dependence function curve – a small fraction of the maximum rate.	This study	Coho
$CK4$	0.03	On the ascending portion of the consumption temperature dependence function curve – a small fraction of the maximum rate.	This study	Coho
$R = a_R W^{a_R} \cdot f(T)_R \cdot ACT$		Specific respiration rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$)		
a_R	0.0046	Intercept of the allometric mass function.	White and Li (1985)	Chinook
b_R	-0.217	Slope of the allometric mass function.	Hanson et al. (1997)	Coho
RQ	2.1	Approximation of Q_{10} value over lower water temperature.	This study	Coho

Table 2 (concluded).

Parameter	Modeled Value	Description	Source	Species
RTO	18	The water temperature at which respiration is highest (optimum).	Brett (1952)	Coho & Sockeye
RTM	26	The maximum (lethal) water temperature.	Brett (1952)	Coho & Sockeye
ACT	2	The activity multiplier.	Kitchell et al. (1997)	Various Species
SDA	0.172	Specific dynamic action	Hanson et al. (1997)	Various Species
$F = a_F T^{a_F} \cdot e^{(G_F \cdot p)} \cdot C$		Egestion rate dependent on mass, temperature and ration.		
a_F	0.212	The intercept of the proportion of consumed energy egested versus water temperature.	Hanson et al. (1997)	Coho
b_F	-0.522	The coefficient of water temperature dependence of egestion.	This study	Coho
G_F	0.631	The coefficient for feeding level dependence of egestion.	Hanson et al. (1997)	Coho
$U = a_U T^{a_U} \cdot e^{(G_U \cdot p)} \cdot C - F$		Excretion rate dependent on mass, temperature and ration.		
a_U	0.0214	The intercept of the proportion of consumed energy excreted versus water temperature.	This study	Coho
b_U	0.380	The coefficient of water temperature dependence of excretion.	This study	Coho
G_U	-0.299	The coefficient for feeding level dependence of excretion.	Hanson et al. (1997)	Coho
$ED = \alpha + \beta W$		Predator energy density ($J \cdot g^{-1} \cdot d^{-1}$).		
α	4111	The intercept of the allometric mass function ($J \cdot g^{-1}$).	This study	Coho
β	155	The slope of the allometric mass function.	This study	Coho
Weight cutoff	10	Weight (g) at which the predator energy density equation switches from α and β , to α_2 and β_2 .		
α_2	7602		Hanson et al. (1997)	Coho
β_2	0.5266		Hanson et al. (1997)	Coho

were used in place of those derived for adult coho salmon for which the model was originally developed. However, published data for juvenile coho salmon were limited, so when available, model parameters were borrowed from experimental data for similar juvenile salmonid species such as chinook salmon. Borrowing parameters from similar species is a commonly accepted practice in bioenergetic model development when specific parameters or coefficients are not available. Once these values were obtained for the model, the remaining parameters were taken from adult coho salmon values from the

Fish Bioenergetics for Windows 3.0 Software (Appendix 3 of Hanson et al. 1997) or were estimated from experimental laboratory data during the calibration phase of model development. Many of the temperature-dependent functions for consumption, respiration, egestion, and excretion are based on an empirical fit of laboratory data which were obtained during model calibration. Equations that describe the energy budget of a fish are described below.

Consumption

Predator consumption rates are modeled based on the assumption that an individual fish cannot consume more than its stomach can contain, digest, and pass. The equation for specific consumption rate (C) is:

$$C = C_{\max} \cdot p \cdot f(T)_C$$

where C_{\max} = the maximum specific consumption rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$), p = proportion of maximum consumption actually realized, and $f(T)_C$ = the temperature dependence

function for consumption. Predator feeding rate is therefore bounded by C_{\max} , an allometric function of individual predator weight and ambient water temperature as:

$$C_{\max} = a_c W^{b_c}$$

The Wisconsin Model uses C_{\max} to calculate the proportion of maximum ration consumed over the interval modeled (p), given body size and temperature constraints experienced by the fish. All individual model parameters (e.g. a_c and b_c) are defined and their values are presented Table 2.

The temperature dependence function for consumption ($f(T)_c$) is the product of two sigmoid curves,

$$f(T)_c = KA \cdot KB$$

One curve describes the ascending limb and another describes the descending limb of the temperature dependence function for consumption (Thornton and Lessem 1978). This function is considered to provide a better fit for cold water species (Hanson et al. 1997).

In this algorithm, the ascending limb is described by the equation for KA:

$$KA = \frac{CK1 \cdot e^{(G1 \cdot (T - CQ))}}{1 + CK1 \cdot (e^{(G1 \cdot (T - CQ))} - 1)}$$

where

$$G1 = \frac{1}{CTO - CQ} \cdot \ln\left(\frac{0.98 \cdot (1 - CK1)}{CK1 \cdot 0.02}\right)$$

The descending limb is described by the equation for KB:

$$KB = \frac{CK4 \cdot e^{(G2 \cdot (T - CQ))}}{1 + CK4 \cdot (e^{(G2 \cdot (T - CQ))} - 1)}$$

where

$$G2 = \frac{1}{CTL - CTM} \cdot \ln\left(\frac{0.98 \cdot (1 - CK4)}{CK4 \cdot 0.02}\right)$$

The temperature dependence function largely determines the hyperbolic shape of the consumption algorithm.

Respiration

Respiration (R), the energy loss resulting from fish metabolism, was modeled using a species-specific function of predator weight, temperature and activity:

$$R = a_R W^{a_R} \cdot f(T)_R \cdot ACT$$

The temperature dependence function for respiration $f(T)_R$ is:

$$f(T)_R = V^X \cdot e^{(X \cdot (1-V))} \text{ where}$$

$$V = \frac{RTM - T}{RTM - RTO} \text{ and}$$

$$X = \frac{(\ln(RQ) \cdot (RTM - RTO))^2 \cdot \frac{(1 + (1 + 40)^{0.5})^2}{\ln(RQ) \cdot (RTM - RTO + 2)}}{400}$$

An activity multiplier (ACT) is incorporated in bioenergetic models to specify metabolic rates above standard metabolism that result from the activity of fish. The ACT is a constant that is multiplied by the resting metabolism. I chose an ACT multiplier of 2.0 to represent the activity component of the balanced energy equation for juvenile coho salmon in streams. The ACT multiplier of 2.0 essentially indicates that energy expenditure for activity is approximately equal to that allocated for standard metabolism.

The assumption that spontaneous activity metabolism is twice standard metabolism is supported by previous research (Winberg 1956, Kerr 1971, Kitchell et al. 1977, Hewett and Johnson 1992).

The metabolic cost of digesting and assimilating ingested food is the energy expenditure for the post-absorptive processes that follow ingestion of food (Beamish and Trippel 1990). The proportion of assimilated energy lost to specific dynamic action, SDA (S) is defined as:

$$S = SDA \cdot (C - F)$$

Although Beamish and Trippel (1990) found that there was wide variation in SDA values for different fish species and that these values tend to change with temperature, I modeled SDA as a constant proportion of assimilated food, and selected a value of 17.2% (0.172) as the fixed proportion of the total consumption. This value has been used to model a variety of fish species (Stewart et al. 1983, Hanson et al. 1997) and bioenergetics models have been determined to be relatively insensitive to SDA (Bartell et al. 1986).

Egestion and excretion

Egestion and excretion components of energy budgets are commonly incorporated into bioenergetic models to express the loss of energy due to assimilated and nonassimilated waste products. These parameters are often modeled as a constant proportion of ingested energy, however, I chose to model these parameters as a function

of temperature (see Elliott 1976 and Jobling 1980). The algorithm I applied for specific egestion rate (F) was:

$$F = a_F T^{a_F} \cdot e^{(G_F \cdot P)} \cdot C$$

The algorithm I applied for specific excretion rate (U) was:

$$U = a_U T^{a_U} \cdot e^{(G_U \cdot P)} \cdot C - F$$

Elliott (1976) and Persson (1979) demonstrated that temperature has a moderate effect on the proportion of food that is excreted and egested over time. Therefore, I elected to include the moderating effects of temperature on egestion and excretion in the model.

Predator energy density

If results obtained from bioenergetic models are to be accurate, estimates of energy density of predators as well as prey species are required for specific seasons and fish sizes (Hartman and Brandt 1995). The seasonal and size derived energy density (ED) for coho salmon was calculated as:

$$ED = \alpha + \beta W$$

Energy density is the weight specific amount of energy contained in the tissues of an organism. Energy density was expressed in units of Joules \cdot g⁻¹ wet weight to be applicable for the modeling approach selected for this project. The relationship between coho salmon wet weight (g) and energy density (Joules \cdot g⁻¹) was obtained by regressing the observed energy density for individual coho salmon (from laboratory bomb calorimetry data) against initial coho salmon wet weight data obtained from laboratory studies (Carline 1968, Averett 1969, Everson 1973, Hutchins 1974). Values of α and β

were estimated from the regressed data presented in Figure 10. Energy budget studies for fish must take into account differences in energy density between predator and prey species as well as seasonal or ontogenetic changes in energy density of predators and prey (Stewart et al. 1983, Hewett and Stewart 1989).

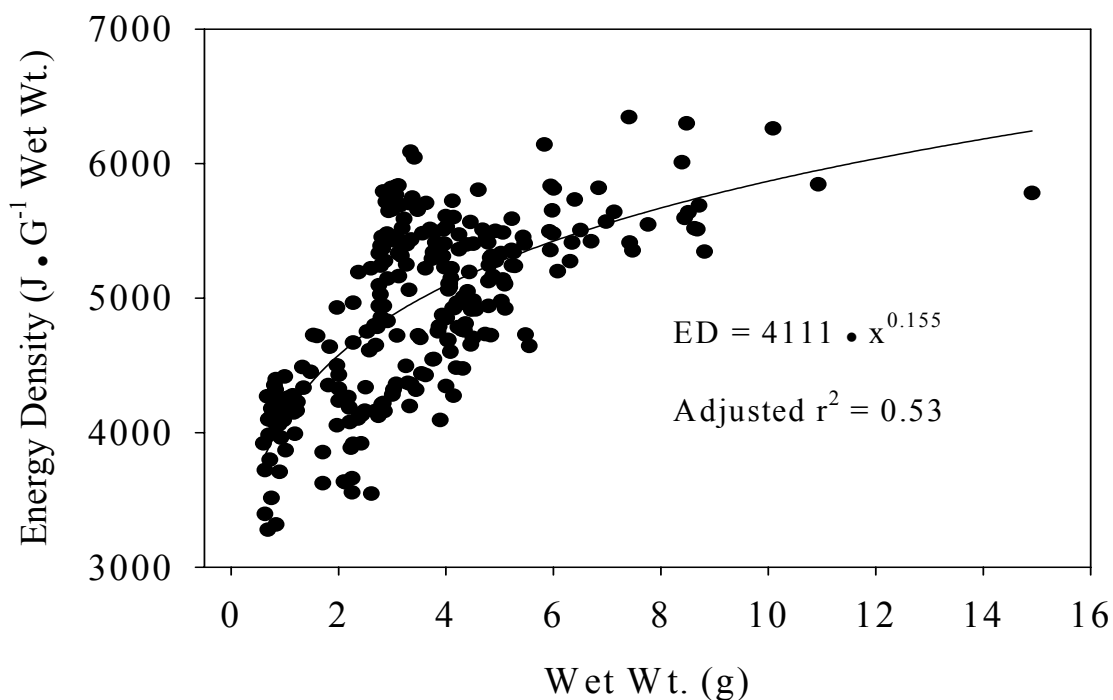


Figure 10. Curvilinear regression of coho salmon energy density versus wet weight for juvenile fish between 0.5 and 15 grams wet weight. Energy density and wet weight values were obtained from experimental fish by bomb calorimetry. Regression equation was used to refine coefficients in bioenergetic model energy density equation. Data taken from Carline 1968, Averett 1969, Everson 1973, and Hutchins 1974.

Model Calibration

The bioenergetic model was calibrated by comparing model estimates with observed laboratory growth-consumption curves for juvenile coho salmon from laboratory studies reported in the literature. I used experimental data that met the following criteria: experimental fish ranged between one and ten grams wet weight, the fish were fed a known amount of food (g), energy in the food fed to test fish ($\text{Joules} \cdot \text{g}^{-1}$) could be calculated, experiments were of ten or more days duration, test fish never swam faster than 2.0 body lengths per second, and the temperature regime could be determined for the entire length of the experiment. Three laboratory studies satisfying these criteria (Carline 1968, Everson 1973, Hutchins 1974) were selected for model calibration. All three used similar techniques, similar laboratory facilities and reported a total of 16 separate experimental trials involving juvenile coho salmon growth versus consumption.

For each of the 16 experimental trials I determined the average weight gain and calculated the mass-dependent specific rate of growth ($\text{Joules} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) realized by individual fish during each experimental period. I then set external variables (duration of trial, water temperature, food consumption rate, fish size, and energy content of food) in the bioenergetic model to match those of each trial and modeled the growth of individual fish. Six of the 26 total parameters used in the model could not be derived from a literature search of coho salmon energetics nor could they be borrowed from other juvenile salmonid species. These six unknown parameters were varied iteratively until

mean predicted consumption, respiration, egestion, and excretion rates were similar to means reported for laboratory trials.

I tested model accuracy by comparing observed fish final mean wet weight for each of the 16 laboratory data sets and fish mean wet weight predicted from the bioenergetic simulations on individual fish. Both the observed and model predicted mean fish weights were compared quantitatively using F-tests for equal variances (Snedecor and Cochran 1980). A paired two-sample t-test (Zar 1984) was then performed to determine if observed and predicted wet weight means were equal. Although visual comparisons of model predictions to observed data are inadequate (Smith and Rose 1995), I also plotted bioenergetic simulation results and experimental laboratory growth curves to graphically compare goodness-of-fit of model predictions with laboratory observations (Appendix A).

After I determined that the model provided a satisfactory simulation of juvenile coho salmon growth, and all values for bioenergetic parameters were finally selected (Table 2), I performed sensitivity analysis on these parameters. Sensitivity analysis were performed to determine how errors in estimated model parameters might influence estimates of mean fish mass and growth rates predicted by the model. Sensitivity of growth to model parameters were analyzed as suggested by Kitchell et al. (1977) by using the following equation:

$$S_x(p) = \frac{p \cdot \Delta X}{X \cdot \Delta p}$$

where $S_x(p)$ is the sensitivity of output parameter x to deviations of input parameter p , p is the nominal value of parameter p , Δp is the input deviation of parameter p , X is the nominal value of output parameter x from a model simulation, and ΔX is the deviation of output parameter X due to Δp . Single parameter values were increased or decreased by a constant fraction ($\pm 10\%$ nominal values) while remaining parameters were fixed at their nominal values. Relative changes in selected model predictions (fish weight and specific growth rate) were used to assess sensitivities of changes in consumption, respiration, egestion and excretion parameters after a model run. This technique is commonly used to identify those parameters in bioenergetic models that are most sensitive to change (Stewart et al. 1983, Bartell et al 1986).

Energetics Analysis of Coho Salmon in Streams

As a means of assessing temperature effects on growth of coho salmon, the energetic components of the balanced energy equation were analyzed in relation to stream water temperatures. An energy budget was calculated for each population studied in 1998 and 1999 by entering initial and final mean weights, daily mean water temperature, and duration, then running the bioenergetics model using the “Fit-to-end-weight” option. Bioenergetics model results recorded for each model run included energy allocated to each component (i.e. consumption, respiration, SDA, egestion, excretion, and growth) of the balanced energy equation for each stream sampled each year.

I analyzed the effect of stream temperature on juvenile coho salmon growth by evaluating the efficiency with which coho salmon were able to convert consumed food into body mass. Conversion efficiency varies with energy losses and these energy losses, particularly metabolic rate, vary with water temperature experienced by the fish. Comparing conversion efficiencies among streams that exhibit a range of water temperature regimes should reveal those streams in which water temperature is near optimum for growth. I calculated conversion efficiency following Brett et al. (1982) as:

$$CE = \frac{G}{C}(100)$$

where, CE = conversion efficiency, G = total energy allocated to growth, and C = total energy consumed.

RESULTS

There was a marked difference between years in the number of fish caught. A total of 133 coho salmon were captured and marked in five streams during June 1998 (Table 3). In June 1999, 981 juvenile coho salmon were captured and 809 were marked in eight study streams (Table 4).

Most juvenile coho salmon were captured in pools in all streams sampled. Snorkel surveys conducted between July 10 and August 20 of both years verified that the majority of juvenile coho salmon were using pools. For both years combined, 72% of juvenile coho salmon observed were occupying pool habitat units. Pool water velocity measurements taken in fish rearing locations indicated that juvenile coho salmon were positioning themselves in areas with low, <2 body lengths per second (BLS) velocities. Average pool velocities ranged from 1.6 BLS in Hollow Tree Creek to 0.4 BLS in West Fork Sproul Creek.

Recapture rates for marked fish were low in 1998. The percentage of marked coho salmon recaptured ranged from 7.4% in Hollow Tree Creek to 31.8% in Lindsay Creek and averaged 15.9% for all streams (Table 3). Coho salmon recapture rates were greater in 1999 and ranged from 27.6% in Hollow Tree Creek to 54.9% in Sharber Creek (Table 4). Mean recapture rate in 1999 was 38.3%.

Size of juvenile coho salmon varied among study streams and between years. In June 1998, average weight of coho salmon ranged from 1.73 g to 2.67 g among study

Table 3. Sampling dates, number of fish captured, mean length and weight, and growth for all juvenile coho salmon sampling sites in northern California streams during 1998. Numbers in parentheses are standard deviations.

	S.F. Broken			Freshwater	Pollack	W.F.	Hollow	Caspar
	Kettle	Lindsay	Sharber			Sproul	Tree	
<u>Start date</u>	--	6/12/98	--	6/30/98	--	6/18/98	6/26/98	6/15/98
Coho salmon caught		22		31		24	27	29
Coho salmon marked		22		31		24	27	29
Mean wet weight (g)		2.20 (0.8)		2.67 (0.6)		1.73 (0.6)	2.08 (0.7)	2.23 (0.7)
Mean fork length (mm)		52.8 (6.8)		59.0 (4.1)		50.8 (5.7)	53.1 (6.3)	55.2 (4.9)
<u>End date</u>		10/3/98		10/24/98		10/10/98	10/20/98	10/6/98
Coho salmon caught		18		17		11	8	19
Marked recaptures		7		3		2	2	4
Recapture %		31.8		9.7		8.3	7.4	13.8
Mean wet weight (g)		8.60 (1.6)		5.22 (0.9)		6.17 (1.4)	4.11 (0.6)	6.56 (1.8)
Mean fork length (mm)		98.2 (4.8)		74.6 (3.7)		77.6 (5.2)	70.9 (4.1)	79.9 (7.5)
<u>Change</u>								
Elapsed days		113		116		114	116	116
Absolute growth (g)		6.40		2.55		4.44	2.03	4.33
Absolute growth rate (g/d)		0.057		0.022		0.039	0.018	0.039
Specific growth rate ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$)		0.0104		0.0056		0.0098	0.0056	0.0085

Table 4. Sampling dates, number of fish captured, mean length and weight, and growth for all juvenile coho salmon sampling sites in northern California streams during 1999. Numbers in parentheses are standard deviations.

	S.F. Broken Kettle	Lindsay	Sharber	Freshwater	Pollack	W.F. Sproul	Hollow Tree	Caspar
<u>Start date</u>	6/30/99	6/27/99	6/24/99	6/21/99	7/7/99	6/18/99	6/26/99	6/17/99
Coho salmon caught	101	92	133	238	96	204	29	101
Coho salmon marked	101	92	133	135	96	135	29	101
Mean wet weight (g)	3.27 (0.92)	2.79 (0.9)	2.40 (1.1)	1.36 (0.6)	1.63 (0.8)	1.26 (0.7)	2.70 (0.4)	1.74 (0.65)
Mean fork length (mm)	63.5 (5.3)	60.8 (6.1)	57.1 (7.4)	48.4 (6.0)	50.4 (7.0)	45.9 (7.3)	59.3 (3.0)	51.1 (5.4)
<u>End date</u>	10/5/99	10/10/99	9/22/99	10/9/99	9/29/99	10/2/99	10/6/99	9/26/99
Coho salmon caught	88	91	287	173	116	135	16	87
Marked recaptures	52	34	73	49	30	61	8	33
Recapture %	51.5	37.0	54.9	36.3	31.3	45.2	27.6	32.7
Mean wet weight (g)	4.23 (1.7)	6.67 (1.7)	2.59 (1.3)	1.92 (0.7)	2.19 (1.2)	2.86 (1.4)	3.10 (0.3)	3.20 (0.9)
Mean fork length (mm)	71.0 (8.4)	80.6 (6.7)	63.6 (8.7)	57.4 (7.6)	56.4 (8.0)	60.6 (1.4)	65.0 (3.0)	62.4 (4.7)
<u>Change</u>								
Elapsed days	98	106	91	111	85	107	103	102
Absolute growth (g)	0.96	3.88	0.19	0.56	0.56	1.60	0.40	1.46
Absolute growth rate (g/d)	0.010	0.037	0.002	0.006	0.007	0.015	0.004	0.014
Specific growth rate (g·g ⁻¹ ·d ⁻¹)	0.0026	0.0077	0.0008	0.0031	0.0035	0.0072	0.0013	0.0060

streams (Table 3). In June 1999, average coho salmon weight among the eight streams ranged from 1.26 g in West Fork Sproul Creek to 3.27 g in South Fork Broken Kettle Creek (Table 4). However, differences in both mean weight and mean length were greater among populations in September and October than in June during both years.

Both specific and absolute growth rates calculated for fish in the coldest and warmest sites varied between years and among streams (Tables 3, 4). Coho salmon in Lindsay Creek, Caspar Creek and West Fork Sproul Creek achieved greater specific and absolute growth rates than they did in Freshwater Creek and Hollow Tree Creek during both years (Tables 3, 4). Comparisons between years could not be made in Sharber, South Fork Broken Kettle or Pollack Creeks which were only sampled in 1999. Growth rates exhibited by coho salmon in these three streams were similar to those calculated for Freshwater and Hollow Tree Creeks. Specific growth rate ranged from $0.0104 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ (6.40 g absolute growth) in Lindsay Creek to $0.0056 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ (2.03 g absolute growth) in Hollow Tree Creek during the summer rearing period in 1998 (Table 3). Both specific growth rates and absolute weight change were lower in all streams sampled during 1999 than in 1998. During 1999, specific growth rates ranged from $0.0077 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ (3.88 g absolute growth) in juvenile coho salmon from Lindsay Creek to $0.0008 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ (0.19 g absolute growth) in Sharber Creek (Table 4).

Coho salmon and steelhead were the dominant species at all sites, but Sacramento pikeminnow were relatively abundant in Hollow Tree Creek, the warmest site studied. Sharber Creek as well as South Fork Broken Kettle Creek were the only streams sampled

that contained juvenile coho salmon almost exclusively. No inter-specific competition was therefore assumed for these creeks although the chances of intra-specific competition were increased due to the high coho salmon densities found in these stream systems.

Density of coho salmon increased in 1999, relative to 1998. In 1998, coho salmon density ranged from 0.025 m^{-2} in Hollow Tree Creek to 0.175 m^{-2} in Freshwater Creek. In 1999, coho salmon densities ranged from 0.04 m^{-2} in Hollow Tree Creek to 3.18 m^{-2} in Sharber Creek. Overall, coho salmon density in most streams was about four times higher in 1999 than in 1998 (Bonferroni adjusted t-test, $t = -2.75$, $df = 7$, $P = 0.028$; Table 5).

Total fish density also increased in 1999 relative to 1998. Among all streams, density of all species was, on average, 2.5 times greater in 1999 than in 1998 (Bonferroni adjusted t-test, $t = -2.63$, $df = 7$, $P = 0.034$). Total fish densities for the five streams studied in 1998 ranged from 0.16 m^{-2} to 1.26 m^{-2} , whereas total fish densities in 1999 for these same streams were 0.21 m^{-2} to 2.23 m^{-2} . The highest estimates of total fish density come from Sharber and Pollack Creeks with densities of 3.26 m^{-2} and 3.45 m^{-2} , respectively (Table 5).

Average size of coho salmon within study streams in September and October was related to density of coho salmon, density of total fish and invertebrate drift rate. The relationship between coho salmon density (X) and average wet weight, $Y = 5.5689 e^{(-.3835 * X)}$, was significant ($P = 0.0341$) but explained only 29% of the variation in average wet weights (Figure 11). The relationship between total fish density (X) and wet weight,

$Y = 5.525 e^{(-.2080 * X)}$, was not significant ($P = 0.128$) and explained only 12% of the variation. The relationship between invertebrate drift rate (X) and average coho salmon wet weight, $Y = 2.3717 + 0.9857(X)$, was significant ($P = 0.05$) but only explained 24% of the variation in average wet weights (Figure 12).

Table 5. Biotic factors measured for each 60-m to 100-m sampling reach in eight northern California streams used for corroborating the bioenergetic model in 1998 and 1999. Total fish density includes coho salmon and steelhead (for all streams) and pike minnows for Hollow Tree Creek. Coho salmon density, total fish density, and rates are June through invertebrate drift October averages for the two years of study used in the analysis. Standard error for density estimates are in parentheses. Sharber, S. F. Broken Kettle, and Pollack Creeks were not intensively studied in 1998, California Department of Fish and Game provided the data on fish densities from these three creeks.

Stream Name	Coho Density (fish · m ⁻²)		Total Fish Density (fish · m ⁻²)		Invertebrate Drift Rate (g · m ⁻² · hr ⁻¹)	
	1998 ¹	1999	1998 ¹	1999	1998	1999
Lindsay Creek	0.15 (0.04)	0.62 (0.08)	0.57 (0.14)	1.54 (0.23)	2.92	4.54
Caspar Creek	0.10 (0.03)	0.37 (0.10)	0.49 (0.06)	0.84 (0.14)	2.31	1.98
West Fork Sproul Creek	0.15 (0.19)	0.74 (0.05)	0.51 (0.09)	1.16 (0.07)	3.18	1.95
Hollow Tree Creek	0.02	0.04 (0.01)	0.21	0.16 (0.03)	1.02	0.55
Freshwater Creek	0.17 (0.05)	1.45 (0.29)	1.26 (0.20)	2.23 (0.32)	2.59	2.73
Sharber Creek	0.89	3.18 (0.20)	1.18	3.26 (0.19)	--	1.05
South Fork Broken Kettle Creek	0.41	0.49 (0.11)	0.57	0.55 (0.16)	--	0.39
Pollack Creek	0.02	2.29 (0.29)	0.37	3.45 (4.27)	--	1.66

¹ Standard error in not provided for Hollow Tree Creek in 1998 because only one electrofishing pass was performed in this creek during this year. Data was not available to calculate standard error for Sharber, S.F. Broken Kettle, and Pollack Creeks in 1998.

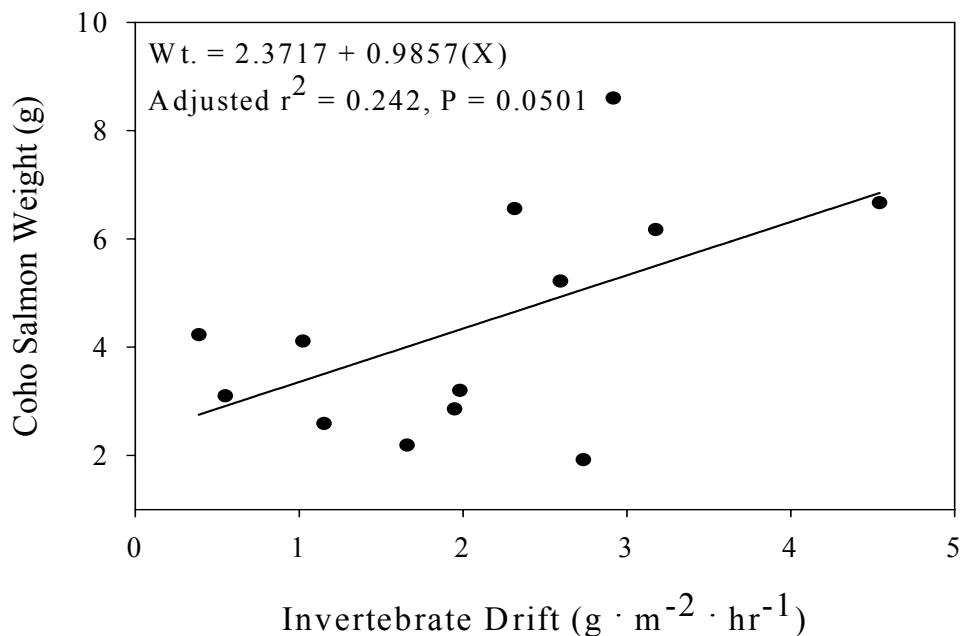


Figure 11. Regression of juvenile coho salmon density ($\text{No} \cdot \text{m}^{-2}$) against coho salmon wet weight (grams) for all streams sampled in September and October of 1998 and 1999.

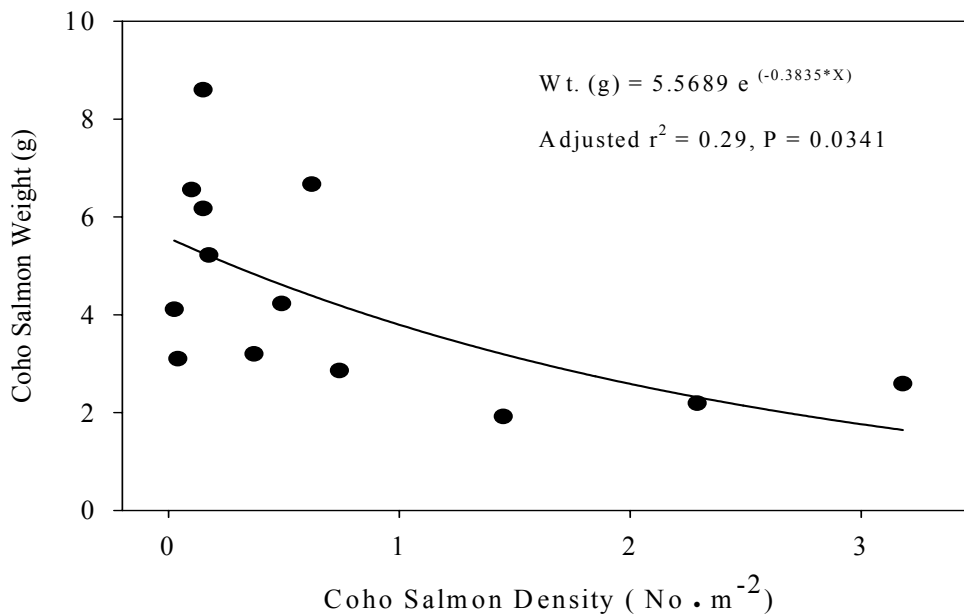


Figure 12. Regression of invertebrate drift rate ($\text{g} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$) against juvenile coho salmon wet weight (grams) for all streams sampled in 1998 and 1999.

Invertebrate Drift

Among streams sampled in both years, drift biomass was greater in 1998 than in 1999 (Table 5). Lindsay Creek, Freshwater Creek and West Fork Sproul Creeks had the greatest invertebrate drift rates of all streams sampled with rates ranging from 2.59 - 3.18 $\text{g} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ in 1998 and 1.95 - 4.54 $\text{g} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ in 1999. Drift rates in Hollow Tree and Caspar Creeks ranged from 1.02 - 2.31 $\text{g} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ in 1998 and 0.55 - 1.98 $\text{g} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ in 1999. Drift rates in the additional streams sampled in 1999 ranged from 0.39 $\text{g} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ in South Fork Broken Kettle Creek to 1.05 $\text{g} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ in Sharber Creek.

Twenty-two invertebrate taxa (categorized by order) were identified in drift samples. Chironomidae (Diptera larvae) and Ephemeroptera nymphs were the most abundant taxon by number in the drift for all streams. Diptera from both aquatic and terrestrial sources dominated the drift biomass (Table 6). Ephemeroptera nymphs were the second greatest category of drift biomass. Emergent Tricoptera and Diptera were the primary adult invertebrates sampled, while Diptera and Tricoptera larvae, as well as adult and larval aquatic Coleoptera were common in samples. Of the aquatic taxa, larval chironomids comprised 23.6% and adult chironomids represented 8.1% of the biomass in all samples. Chironomidae and Ephemeroptera exuvia made up a large proportion of samples at some sites. Dipterans and coleopterans were common terrestrial invertebrates

Table 6. Average percent contribution by weight of organisms collected in drift samples within study reaches in 1998 and 1999. Drift samples for Sharber and Pollack Creeks were collected by personnel from the CDFG during 1999 only. Drift samples were collected from S.F. Broken Kettle Creek in 1999 but were not identified.

Prey Type	Lindsay Creek	Caspar Creek	W.F. Sproul Creek	Hollow Tree Creek	Freshwater Creek	Sharber Creek	S.F. Broken Kettle Creek	Pollack Creek	Average
<u>Aquatic Invertebrates</u>									
Chironomidae larvae and pupa	28.4	26.0	15.4	36.4	16.0	29.1	--	13.8	23.6
Chironomidae Adults	11.0	14.0	7.3	5.4	5.0	3.5	--	10.6	8.1
Chironomid and Ephemeroptera exuviae	8.4	12.0	3.6	24.0	26.0	15.6	--	8.9	14.1
Ephemeroptera (Mayflies)	12.4	22.1	16.8	9.2	16.6	7.0	--	18.6	14.7
Plecoptera (Stoneflies)	3.5	0.8	6.1	--	2.3	--	--	0.8	2.7
Tricoptera (Caddisflies)	5.9	10.7	13.4	--	6.2	0.3	--	0.9	6.2
Coleoptera larvae (Immature Beetles)	6.0	2.5	6.2	3.0	4.0	--	--	7.8	4.9
Odonata (Dragonflies)	--	0.4	0.8	--	1.0	--	--	0.5	0.7
Total Aquatic Invert Percentage	75.6	88.5	69.6	78.0	77.1	55.5	--	61.9	72.3
<u>Terrestrial Invertebrates</u>									
Dipterans (Adult flies and gnats)	8.1	5.1	21.4	8.1	2.1	18.5	--	14.2	11.1
Homopterans (Leaf hoppers)	1.5	--	--	--	0.6	--	--	--	1.1
Coleoptera (Adult Beetles)	3.7	1.0	6.2	11.2	8.6	5.4	--	11.8	6.8
Hemiptera (Water bugs)	0.8	1.2	--	2.0	2.4	--	--	--	1.6
Arachnida (Spiders and mites)	3.0	--	2.4	0.7	--	8.2	--	1.5	3.2
Hymenoptera (Bees and Wasps)	--	--	--	--	0.8	--	--	--	0.8
Other Terrestrial (Worms, Copepods etc)	7.3	4.2	0.4	--	8.4	12.4	--	10.6	7.2
Total Terrestrial Invert Percentage	24.4	11.5	30.4	22.0	22.9	44.5	--	38.1	27.7
Sample Size ¹	8	8	8	8	8	2	0	2	

¹ One sample was considered to be one 0.9 m² drift net set for a 4-6 hour period.

in drift samples, comprising 11.1% and 6.8% of the biomass respectively. However, hemipterans were an important component of the terrestrially derived drift in many of the drift samples. Similarly, spiders and mites (Arachnida) were also an important terrestrial taxon. Among all streams 72.3% of invertebrates sampled were derived from aquatic sources, while the remaining 27.7% came from terrestrial sources.

Water Temperature

Water temperatures were warmer in all streams during 1998 than in 1999 (Figures 13, 14). For streams studied, coldest water temperatures were always recorded in pool habitats, although water temperatures in pools and pool tail-outs in most streams were similar (Table 7). Warmest water temperatures were recorded in glides, although these too showed little temperature difference between those located in pools (Table 7). These results, coupled with the fact that coho salmon were observed in highest densities in pool habitats, suggested that temperature regimes for each study reach would be most accurately represented by the thermographs located in pool habitats. Therefore, temperature regimes recorded by pool habitat thermographs were used in the bioenergetic model for all study streams.

The summer period bracketed the warmest water temperatures in study streams during both years. Seasonal patterns of water temperature were similar in all streams, although temperature ranges differed substantially between streams. Water temperatures were initially similar, rose to a peak between 15 August and 1 September, then decreased

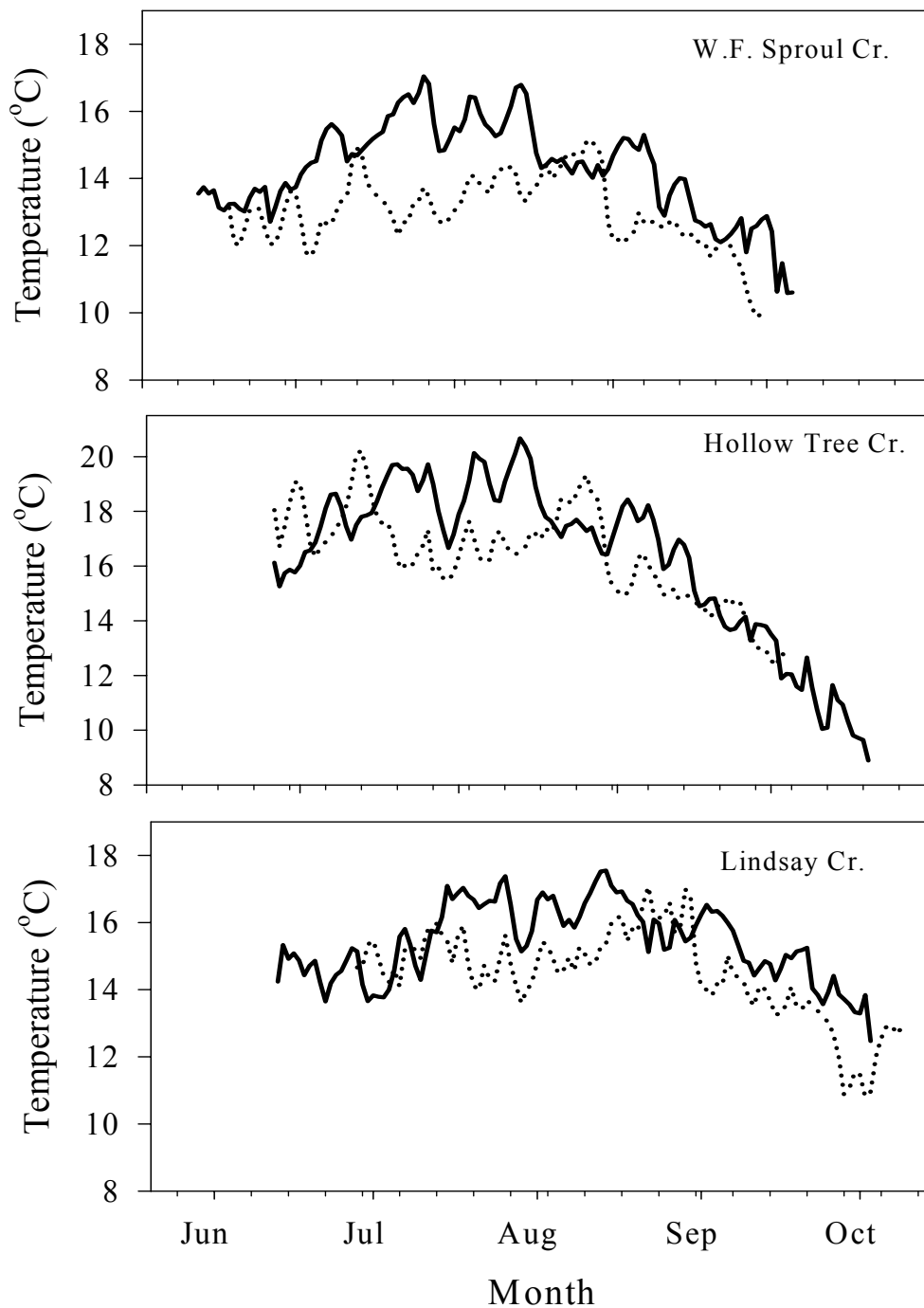


Figure 13. Daily mean water temperature ($^{\circ}\text{C}$) in West Fork Sproul Creek (top), Hollow Tree Creek (middle) and Lindsay Creek (bottom), California during summer 1998 (solid line) and 1999 (dotted line).

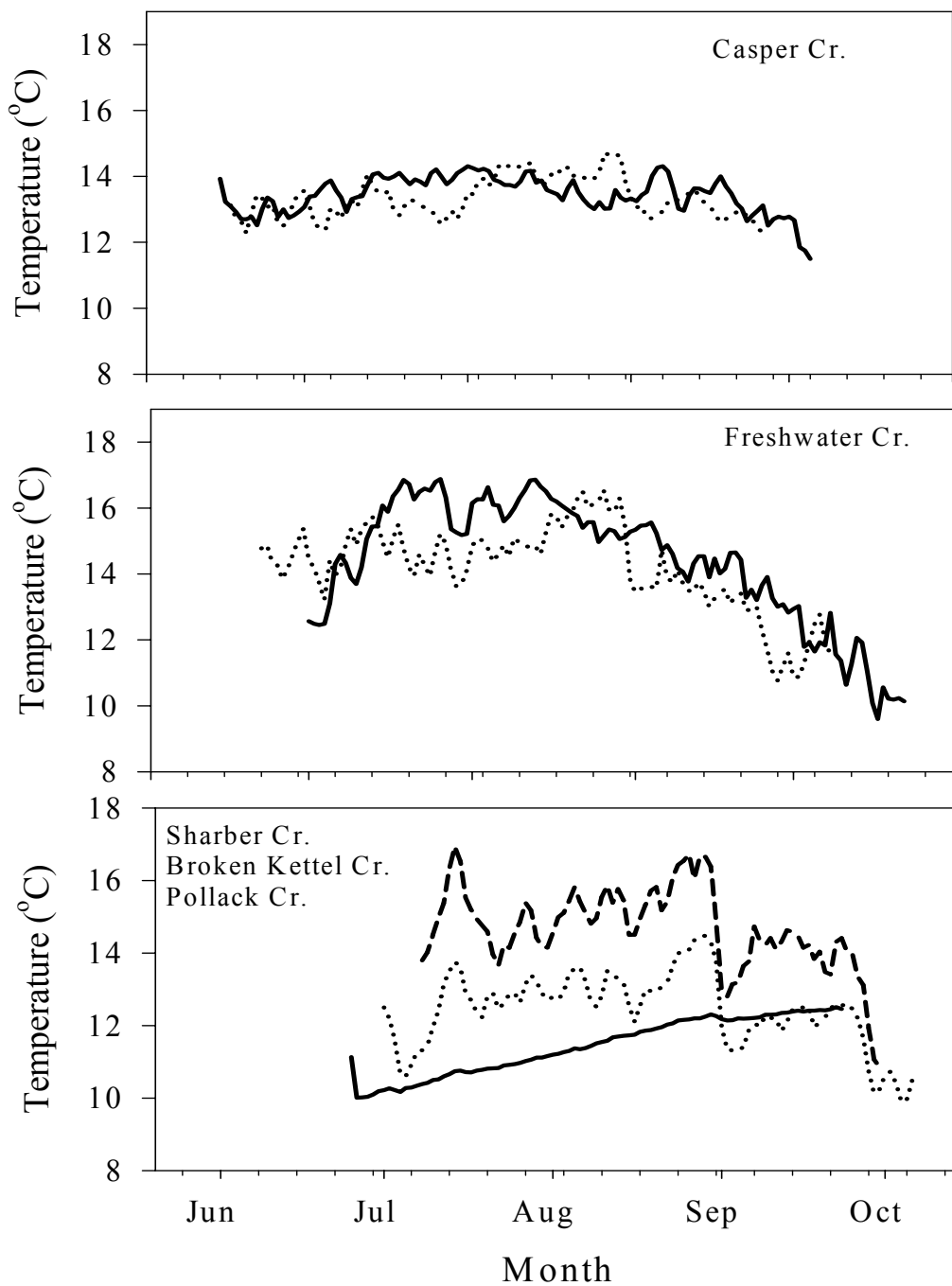


Figure 14. Daily mean water temperature ($^{\circ}\text{C}$) in Casper Creek (top) and Freshwater Creek (middle), California during summer 1998 (solid line) and 1999 (dotted line). Bottom figure is mean daily water temperature for Sharber (solid line), Broken Kettle (dashed line) and Pollack (dotted line) Creeks, California during 1999 only.

Table 7. Minimum, maximum and average water temperatures recorded by temperature data loggers located in pool, pool tail-out, and run or glide habitat types within stream study reaches on August 13, 1998.

Habitat Type	Lindsay Creek (°C)	Freshwater Creek (°C)	W.F. Sproul Creek (°C)	Hollow Tree Creek (°C)	Caspar Creek (°C)
<u>Pool</u>					
Minimum	15.91	15.12	15.75	18.95	13.25
Maximum	20.08	18.95	17.66	22.39	15.43
Average	17.52	16.86	16.71	20.67	14.17
<u>Pool Tail-out</u>					
Minimum	15.91	15.12	15.75	19.11	--
Maximum	20.40	19.15	18.31	22.73	--
Average	17.59	16.94	17.08	20.98	--
<u>Run or Glide</u>					
Minimum	15.75	15.27	--	18.95	13.28
Maximum	20.76	20.24	--	22.56	15.88
Average	17.61	17.00	--	20.79	14.74

substantially in late September (Figures 13, 14). Hollow Tree Creek was the warmest stream in both 1998 and 1999, followed by Lindsay Creek and Freshwater Creek. Caspar Creek was the coldest stream in the first year of sampling, but Sharber and South Fork Broken Kettle Creeks were found to be even colder when they were included in 1999 sampling. Water temperatures exhibited by the three coldest streams (Sharber, South Fork Broken Kettle, and Caspar Creeks) sampled in 1999 appeared to have more uniform

temperatures than other streams and did not change substantially through the course of the summer period.

Bioenergetic Modeling Results from Calibration Data

Model predictions of final mean wet weight did not differ statistically from observations of growth in most experiments compared (Table 8). All experimental and simulated data sets were found to have equal variances except for Everson's Experiment 2 data set which was found to possess unequal variance between the observed and predicted values. Bioenergetic model predictions of average coho salmon final weights were not distinguishable from observed values, given the variation in the observed data. The refined model successfully predicted experimental observations in 10 out of 16 experimental laboratory data sets ($P = <0.0001$ to 0.3892) (Table 8).

Model Sensitivity Analysis

An analysis of the model's sensitivity to adjusted parameters and coefficients suggests that the model is accurately representing juvenile coho salmon growth. The percentage of error in modeled final mass (grams wet weight) and specific growth rate ($\text{Joules} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) was $<5\%$ for all parameters analyzed after a $\pm 10\%$ change in modeled input parameters (Table 9). The two most sensitive parameters to perturbation were activity (ACT) and specific dynamic action (SDA), but response of neither exceeded 5%.

Table 8. Information on data sets employed to calibrate the bioenergetic model, including conditions experiments were conducted under and results of statistical tests to determine equality of means between experimentally derived (observed) juvenile coho salmon weights and simulations (predicted) of fish weights from the bioenergetic model. Statistical analysis used was the paired two-sample t-test. Data was analyzed using the alpha = 0.05 level of significance.

Data Set	Temperature (°C)	Experiment Duration (days)	Number of fish in data set	Observed Mean Initial Weight (g)	Observed Mean Final Weight (g)	Predicted Mean Final Weight (g)	t-Statistic	Probability
<u>Everson (1973)</u>								
Experiment 1	14.5	30	19	1.68	2.67	2.90	1.764	0.0945
Experiment 2	18.6	30	17	2.23	2.71	3.49	3.843	0.0014
Experiment 3	20.8	30	15	1.74	2.54	2.68	1.589	0.1343
Experiment 4	15.6	30	20	1.76	2.31	2.14	1.501	0.1496
Experiment 5	18.8	30	17	1.62	1.98	1.61	9.004	<0.0001
Experiment 6	22.0	30	17	1.83	2.00	1.40	7.126	<0.0001
<u>Carline (1968)</u>								
Experiment 1	9.0	12	17	4.09	4.31	4.22	0.975	0.3440
Experiment 2	9.6	14	18	6.31	7.33	6.96	8.838	<0.0001
Experiment 3	5.9	13	22	5.13	5.51	5.38	6.392	<0.0001
Experiment 4	7.2	13	25	0.81	0.90	0.86	1.525	0.1401
Experiment 5	12.3	14	17	0.94	1.11	1.07	1.383	0.1856
<u>Hutchins (1974)</u>								
Experiment 3	15.0	11	39	3.63	3.98	3.96	0.871	0.3892
Experiment 4	15.0	10	24	2.73	3.04	3.25	6.686	<0.0001
Experiment 5	15.0	10	18	2.56	2.85	2.82	1.487	0.1552
Experiment 6	15.0	12	34	3.12	3.60	3.63	1.942	0.0606
Experiment 7	15.0	12	21	3.76	4.50	4.61	1.460	0.1598

Table 9. Sensitivity analyses of coho salmon model estimates of final weight (grams) and specific growth rate ($J \cdot g^{-1} \cdot d^{-1}$). Data are percent change from nominal values after a perturbation of $\pm 10\%$ using the equation $S_x(p) = (p \cdot \Delta X) / (X \cdot \Delta p)$ as described in text (see Kitchell et al. 1977). Parameter notations are after Hewett and Johnson 1992.

Parameter*	Nominal Value	Percent change in model output with a $\pm 10\%$ change in nominal value			
		Final Weight (grams)		Specific Growth Rate ($J \cdot g^{-1} \cdot d^{-1}$)	
		-10%	10%	-10%	10%
P-value	0.2843	0.343	0.323	1.590	1.510
CA	0.303	0.061	0.046	0.285	0.210
CB	-0.275	0.022	0.025	0.055	0.067
CQ	5	0.009	0.011	0.040	0.050
CTO	15	0.025	0.025	0.114	0.117
CTM	18	0.159	0.152	0.010	0.010
CTL	26	0.159	0.158	0.010	0.010
RA	0.00354	0.149	0.168	0.738	0.737
RB	-0.217	0.061	0.058	0.260	0.250
RQ	0.06818	0.110	0.108	0.468	0.498
RTO	0.0234	0.013	0.013	0.057	0.057
RTL	25	0.010	0.010	0.010	0.010
ACT	2	2.330	2.540	4.760	4.620
BACT	0.0305	0.162	0.162	0.252	0.252
SDA	0.172	1.237	1.285	3.830	3.720
FA	0.212	0.060	0.060	0.293	0.293
FB	-0.522	0.079	0.069	0.370	0.330
FG	3	0.540	0.570	0.860	0.880
UA	0.0214	0.080	0.076	0.167	0.179
UB	0.38	0.048	0.050	0.101	0.098
UG	-0.299	0.240	0.240	0.590	0.630

Modeling Results

Allocation of consumed energy to components of the bioenergetic equation varied among study streams and between years (Table 10). The greatest energetic costs to juvenile coho salmon were from respiration (standard + activity metabolism) and heat increment (SDA). Average respiration costs for all populations during 1998 were 52.2%, while in 1999 respiration costs averaged 60.6% of consumption. SDA costs varied little and averaged 16.2% during both years. Energetic losses due to egestion and excretion were relatively low in both years, ranging from 11% to 15% of consumed energy.

Proportion of consumed energy allocated to growth (conversion efficiency) varied between years and among streams. Among all streams, average energy allocated to growth in 1998 was 20.6% (range 12.06 - 29.32%, Table 10). In 1999, average energy allocated to growth was 11.9% (range 4.40 - 23.56%). The greatest proportion of consumed energy directed to growth was found in fish from Lindsay Creek during both years (Table 10). In contrast, fish from Sharber Creek directed the least energy to growth during both years.

Conversion efficiency consistently varied with water temperature during both years. Greatest average food conversion efficiency was found in streams classified as cool (daily average water temperatures 15.1 - 17°C) (Figure 15). Streams categorized as cold (12 - 15°C) had the next highest food conversion efficiencies. Hollow Tree Creek, the only stream categorized as warm (>17°C), had the lowest food conversion efficiency in both years.

Table 10. Energy allocation in Joules for six components of the balanced energy equation from eight study streams sampled in 1998 and 1999. Energy values for consumption, respiration, specific dynamic action (SDA), egestion, excretion, and growth were obtained as output values from bioenergetic model simulation runs for each stream sampled using the "Fit-to-end-weight" option of the model. Temperature (°C) was obtained by averaging daily average water temperatures over the simulation period.

Stream Name	Allocation of Energetic Components					Daily Avg. Temperature (°C)
	Consumption (Joules)	Respiration (%)	SDA (%)	Egestion and Excretion (%)	Growth (%)	
1998						
Lindsay Creek	109,131	43.33	16.20	11.15	29.32	15.71
Caspar Creek	80,964	46.91	16.15	11.21	25.72	13.56
W.F. Sproul Creek	77,893	45.65	16.17	11.19	26.99	14.76
Freshwater Creek	67,561	54.83	16.19	11.15	17.83	15.53
Hollow Tree Creek	56,071	56.13	16.24	11.08	16.54	18.07
Sharber Creek	44,688	60.61	16.15	11.18	12.06	12.42
S.F. Broken Kettle Creek	16,722	59.96	16.15	11.19	12.70	13.46
Pollack Creek	77,757	49.72	16.23	11.10	22.96	15.90
1999						
Lindsay Creek	80,079	49.10	16.18	11.16	23.56	15.22
Caspar Creek	39,737	56.32	16.17	11.15	16.36	13.47
W.F. Sproul Creek	36,626	53.44	16.15	11.20	19.20	13.44
Freshwater Creek	28,248	64.18	16.21	11.08	8.53	14.92
Hollow Tree Creek	40,908	68.33	16.28	11.00	4.40	17.32
Sharber Creek	26,458	69.42	16.11	11.26	3.21	11.15
S.F. Broken Kettle Creek	45,426	62.78	16.14	11.20	9.88	12.87
Pollack Creek	25,535	63.20	16.22	11.06	9.52	15.20

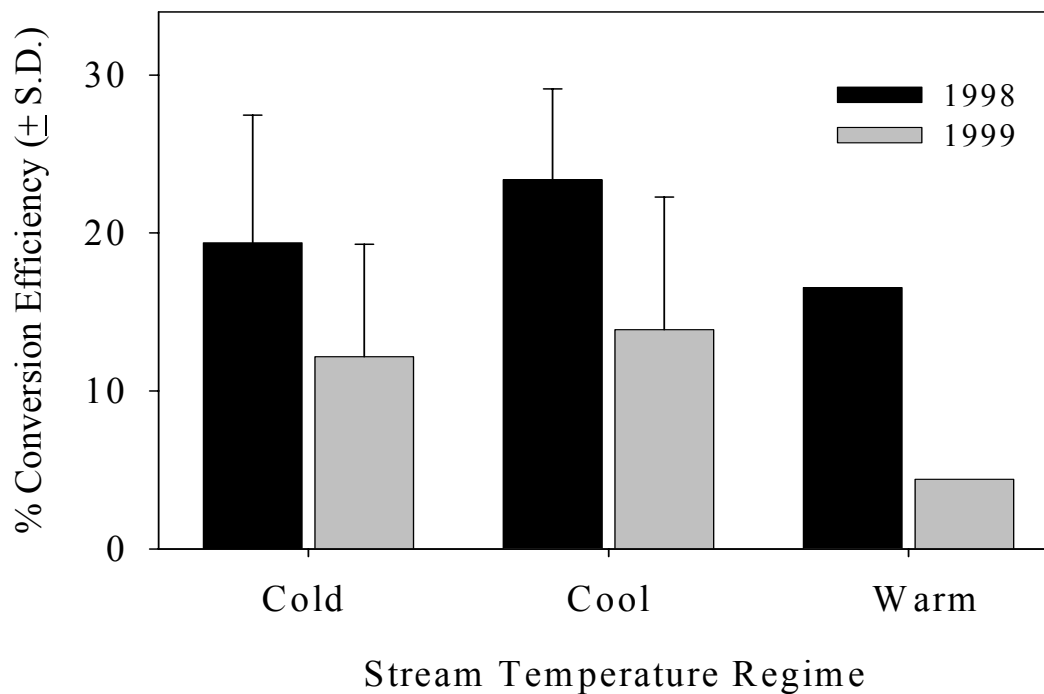


Figure 15. Average food conversion efficiency (%) of juvenile coho salmon in study streams grouped by water temperature regime. Temperature regimes included in each are defined in the text. Cold streams included Casper, W.F. Sproul, S.F. Broken Kettle and Sharber Creeks. Cool streams included Lindsay, Freshwater and Pollack Creeks. Hollow Tree Creek was the only stream classified as warm.

DISCUSSION

The bioenergetics model I developed for juvenile coho salmon contained 26 parameters, less than the maximum number of 30 possible in Wisconsin models, but twice the minimum number. My decision to model egestion and excretion as a function of water temperature rather than as a percentage of consumption increased the number of model parameters. Modeling errors tend to increase with an increase in the number of variables included in the model (Hansen et al. 1993, Hartman and Brandt 1993). Conversely, models with too few variables can be overly simplistic and not be sufficiently detailed to provide accurate results. I attempted to apply an appropriate number of variables in the bioenergetic program that would provide sufficient modeling detail while avoiding being overly complex. The adaptability of the bioenergetic modeling software used for this project (Hanson et al. 1997) allowed me to include variables that I felt were appropriate and exclude those that I felt were not appropriate for inclusion in the final model.

I was unable to derive all model parameters and coefficients from published research on juvenile coho salmon. Physiological information relating specifically to many aspects of juvenile coho salmon is lacking. Six of the model parameters I used were modified from an adult coho salmon model by using data specific to juvenile coho salmon (Carline 1968, Averett 1969, Hutchins 1974). Others were taken from adult coho salmon (Hanson et al. 1997), juvenile sockeye salmon (Brett 1952), and juvenile chinook

salmon (White and Li 1985). The only parameters incorporated in the model that were not specific to salmonids were the Activity (ACT) (Winberg 1956, Kitchell et al. 1977) and Specific Dynamic Action (SDA) components of the model (Table 2). Although bioenergetics models are recognized as being robust, the practice of transferring parameter and coefficient values from one species to another or even from one size class to another within a species, is not the preferred method of developing a model (Ney 1993). Error introduced by amalgamation of parameters derived from different taxa and complicated by error in experimental measurements within taxa could bias model simulations. Parameter amalgamation or transfer was therefore used with caution and only when necessary.

The primary assumption incorporated into this model was that active metabolism was double the standard metabolic rate. Activity metabolic rates reported range from 1 – 3.9 standard metabolic rates (Boisclair and Leggett 1989, Boisclair and Sirois 1993). These results suggest that assuming activity rates are a constant multiple of standard metabolic rates, as I did, may not accurately represent this energetic cost. Most criticisms of this approach, however, have been drawn from research performed on actively foraging fish in pelagic environments. Activity in pelagic species should be greater than in a lotic species such as drift feeding juvenile coho salmon that occupy slow flowing, energy-efficient positions within stream channels. Mason (1976) found that the metabolic scope for growth of coho salmon was reduced due to the slow-flowing habitat selected by these fish. Finally, previous work also supports the assumption of spontaneous activity

metabolism being double standard metabolism (Winberg 1956, Kerr 1971, Kitchell et al. 1977, Hewett and Johnson 1992).

Sensitivity analysis results confirmed that parameters in the final calibrated model were not sensitive enough to contribute to accumulated errors. I found, as have others (Rice et al. 1983, Bartell et al. 1986), that the juvenile coho salmon bioenergetics model was relatively insensitive to energy density, egestion and excretion variables. Parameters and variable coefficients that have typically been demonstrated to be most sensitive in bioenergetics models are those associated with the estimation of the realized fraction of maximum consumption rate (p-value) and allometric parameters for consumption (CA and CB), and respiration (RA and RB) (Bartell et al. 1986, Kerr and Dickie 1985, Stewart et al. 1983). My sensitivity analysis results indicated that the latter parameters were the most sensitive parameters in the model, along with SDA and ACT parameters (Table 9). All of these values were extremely low, however, indicating that little error would be attributable to changes in these parameters. The sensitivity analysis suggests that a high degree of confidence can be placed in model simulation results from this research on juvenile coho salmon and that the model would not produce spurious results due to overly sensitive model parameters.

Model Application

The bioenergetics model I developed has promise in evaluating growth of juvenile coho salmon relative to stream water temperature. The percentage of consumed energy

juvenile coho salmon allocated to growth exceeded 20% in five of the 16 stream-by-year combinations that I evaluated (Table 10). Average daily water temperature in these five streams ranged from 13.6 - 15.9°C, suggesting a narrow temperature range for optimum growth in the wild. In 9 of the 11 stream-by-year combinations where energy allocated to growth was < 20%, average daily water temperature was either $\leq 13.5^{\circ}\text{C}$ or $\geq 17.3^{\circ}\text{C}$ (Table 10).

These results are only partially consistent with previously published results of juvenile coho salmon growth in relation to water temperature. Stein et al. (1972) reported that the growth rate of coho salmon fry was high in the temperature range of 9.0 - 13.0°C, and decreased considerably near 18°C in the Sixes River, Oregon. Similarly, Brungs and Jones (1977) reported that the greatest growth in coho salmon occurred in the temperature range of 10.0 - 17.0°C. Averett (1969) reported that the scope for growth of juvenile coho salmon from western Oregon during August and September was greatest at water temperatures of 14.0°C and 17.0°C. Water temperature ranges associated with increased growth in the latter two reports compare somewhat favorably with the temperature range at which model results suggested most energy was devoted to growth in California streams from this study. They also compare well with empirical data used to calibrate the model (Everson 1968, Carline 1968, and Hutchins 1974, Appendix A). The report of high growth at water temperatures of 9.0 - 13.0°C from work performed in Oregon is not consistent with conclusions drawn from my modeling results for California streams. I found that less energy was generally devoted to growth in cold streams.

The water temperature at which growth of juvenile coho salmon is greatest varies with food consumption as well as water temperature (Averett 1969), and has been reported to increase, within limits, with increasing food consumption (Brett et al. 1969, Elliott 1976). Food consumed by fish is a function of the amount of food available and the number or biomass of competitors for that food. I found that in streams where energy devoted to growth in juvenile coho salmon was $> 20\%$, total fish density was generally low ($\leq 0.64 \text{ fish} \cdot \text{m}^2$) and drift biomass was high ($> 2.30 \text{ g} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$). The sole exception was Freshwater Creek, where energy devoted to growth was $< 20\%$ during both years even though water temperature was moderate, drift was relatively high and total fish density was intermediate.

When food is limited, as it often is in the wild, growth of coho salmon has been reported to decrease at higher water temperatures (Iverson 1972). In laboratory studies, juvenile coho salmon required twice the amount of food to grow at 17°C than at 5°C (Averett 1969). Wurtsbaugh and Davis (1977) reported that the maintenance ration in rainbow trout increased from 2.7% of body weight per day to 7.5% body weight per day as water temperature was increased from 6.9°C to 22.5°C . Thus, maintaining productivity at elevated temperatures requires that the food supply be increased enough to compensate for the increased metabolic requirements (Beschta et al. 1987). My results suggest that low summer growth rates appear to result from food consumption being inadequate to meet fish metabolic demands at higher water temperatures.

Interpreting growth of juvenile salmonids during summer solely on the basis of water temperature may be misleading (Railsback and Rose 1999). Railsback and Rose (1999) attributed variation in growth of age 1+ trout more to variation in apparent consumption than to water temperature. They cautioned that bioenergetic assessments where a change in temperature is not accompanied by an change in consumption could result in the model overestimating growth. When water temperatures exceed the temperature range at which C_{\max} is high, the effects of changes in consumption may be more important to fish growth than the direct effect of the temperature change (Railsback and Rose 1999). Partially for this reason, I modeled bioenergetics of juvenile coho salmon using the fit-to-end-weight option, which adjusts consumption to water temperature.

Density of fish is assumed to influence growth of stream salmonids through both inter- and intraspecific competition for food resources. Growth rates of juvenile coho salmon have been reported to be inversely proportional to density and, therefore, strongly influenced by density-dependant factors (Fraser 1969, Harvey and Nakamoto 1996). However, at low densities often found in streams, competition was reduced. Fraser (1969) considered low natural stream densities to be $0.24 \text{ fry} \cdot \text{m}^{-2}$, while Harvey and Nakamoto (1996) suggested that $1.5 \text{ total fry} \cdot \text{m}^{-2}$ was the natural range for fish densities in their experiments. During this study, I found that densities of total fish ranged from $0.16 - 3.45 \text{ fish} \cdot \text{m}^{-2}$, and only four of 16 stream-by-year combinations exceeded $1.5 \text{ fish} \cdot \text{m}^{-2}$ (Table 5). Density of juvenile coho salmon and other fish was generally low in

most streams I studied. However, density of total fish in 1999 averaged 2.5 times the density observed in 1998 and a density-dependent effect on growth was apparent (Figure 12). It is possible that changes in density resulted in social interactions (inter- and intraspecific competition) that influenced growth of juvenile coho salmon (Carline 1968).

As water temperature increases beyond the temperature considered optimal, energy devoted to physiological processes for maintenance in fish increases. Continually increasing water temperatures eventually produces sub-lethal stress and eventually death. Sub-lethal growth stress in fish has been defined to take place when water temperature exceeds 20% of the optimum (Brett et al. 1982, Armour 1991). Following this definition and using the water temperature range at which I found greatest growth efficiency, the onset of sub-lethal growth stress in coho salmon could occur at temperatures ranging from 16.3 - 19.1°C. Growth stress could result in further detrimental physiological responses such as increased susceptibility to disease or predation or may lead to behavioral modifications such as emigration from the stream system. Streams that exhibit temperature regimes within the zone of sub-lethal stress, as did Hollow Tree Creek, do not provide fish with suitable conditions for growth and survival, resulting in poor salmonid fish populations.

Temperature tolerance limits for Pacific salmonids have generally been identified from laboratory conditions, where the fish are held at constant elevated temperatures for long periods (Brett 1952). Although these conditions are not natural, streams may display sizeable fluctuations in water temperature over diel periods and maximum

temperatures may exceed the reported lethal threshold for some time daily. Hence, the direct application of laboratory derived temperature limits to field conditions is tenuous (Beschta et al. 1987). However, growth of coho salmon has been reported to cease at water temperatures $\geq 20.3^{\circ}\text{C}$ (Bell 1973). Interestingly, in the bioenergetics model I developed for juvenile coho salmon, growth ceases at 20.3°C (Appendix, Figure B-1). Lethal temperatures experienced by fish are, however, modified by acclimation temperature, feeding rate, and population level genetic adaptations. Salmonids have been reported to withstand periodic, short-term exposure to temperatures exceeding those defined as lethal without displaying acute negative impacts (Bisson et al. 1988, Schrank et al. 2003). Finally, salmonids appear to have the ability to reduce the temperature they are exposed to, the duration of exposure, or both through behavioral adaptations or by utilizing thermal refugia (Nielsen et al. 1994, Berman and Quinn 1991, Kaya et al. 1977).

The bioenergetics model I developed partitioned energy consumed into metabolism, SDA, egestion, excretion and growth. Metabolism represented the greatest energy cost, while about 27% of consumed energy was consistently lost to SDA and waste. Metabolism costs averaged 52% of consumed energy in 1998 (range 43.3 – 60.6%) and 60% in 1999 (range 49.4 – 69.4) (Table 10). Brett and Groves (1979) estimated that metabolism in an average carnivore would consume 44% of the energy consumed. Similarly, metabolic costs associated with the estuarine migration of juvenile chum salmon were estimated to be about 47% of energy consumed (Wissmar and Simenstad 1988). The higher metabolic rates reported here are not particularly alarming

since juvenile coho salmon occupy flowing water and feed on small prey that requires greater activity costs than predators consuming larger prey. Also, metabolic activity during estuarine migration should be less than during juvenile residency, since fish are not swimming to overcome water currents.

Benefits of the Project

The development of a bioenergetic model that accurately simulates coho salmon growth as a function of temperature offers several benefits. The model developed could be useful as a predictive tool to forecast coho salmon growth rates in streams where water temperature regimes change due to management decisions or natural phenomena. For example, if a timber harvest plan near a stream containing juvenile coho salmon is being considered that would result in increased stream temperatures, the model could be employed to estimate how this modified temperature regime might impact or modify coho salmon growth rates. If the model predicts normal growth patterns these activities may be considered for approval; however, if the model predicts negative impacts on coho salmon growth rates, these activities should be scrutinized more closely.

The model could also be used by regional managers in evaluating which watersheds should receive priority for limited restoration dollars by predicting potential success of restoration projects on improving or maintaining fish communities in watersheds which typically experience elevated temperatures in summer. Recommendations derived from these options may be applied to streams that are or will

be affected by channel modifications, diversions, reservoir releases, or adjoining land-use practices such as vegetation removal, all of which may alter temperature regimes (Beschta and Taylor 1988).

Not only were insights gained into the energetic requirements of juvenile stream-dwelling salmonids as a result of elevated temperatures, but additional information was gained from the development and refinement of a potentially useful bioenergetic model for such fish. It is hoped that further research and refinements can be made to this initial modeling effort to increase the accuracy and ultimately the usefulness of this model.

Recommendations

Components of bioenergetics models could be improved if information was incorporated as it became available (Beamish and Trippel 1990) or, in some cases, if the existing but often incomplete information base was included. Although temperature dependence functions have been incorporated into the majority of the energetic components of this bioenergetic model, other components such as SDA and ACT variables of respiration have not incorporated the influence of temperature (Beamish et al. 1986). This model and others have assumed that these variables are independent of temperature and as a result may inaccurately estimate the true contribution of energy expenditure. In future iterations of this model and others, the importance of the temperature dependence function should be evaluated for all model components.

Model parameters and coefficients can be further refined to better simulate growth of small fish. I was uncertain if the bioenergetics model I developed accurately approximated growth of juvenile coho salmon < 2.0 g wet weight. Future modeling work should address small juvenile fish.

This research appears to indicate that reduced growth in juvenile coho salmon begins to occur in warm streams that have average summer temperatures greater than 15.9°C. However, the sample size for warm streams for this project was limited to one (Hollow Tree Creek) that was sampled over two consecutive years. Further research should be conducted on additional warm streams in the north coast region of California in order to better define the temperature-growth relationship at higher temperatures.

Bioenergetics models applied using the fit-to-end-weight option allow the user to estimate consumption by fish, but do not allow the user to forecast consumption. Modifying bioenergetics models to allow forecasting consumption would broaden the possible applications of these models. Needless to say, any attempt to forecast consumption should also include improvements in methods for data collection to accurately determine what prey are available to fish and what they eating.

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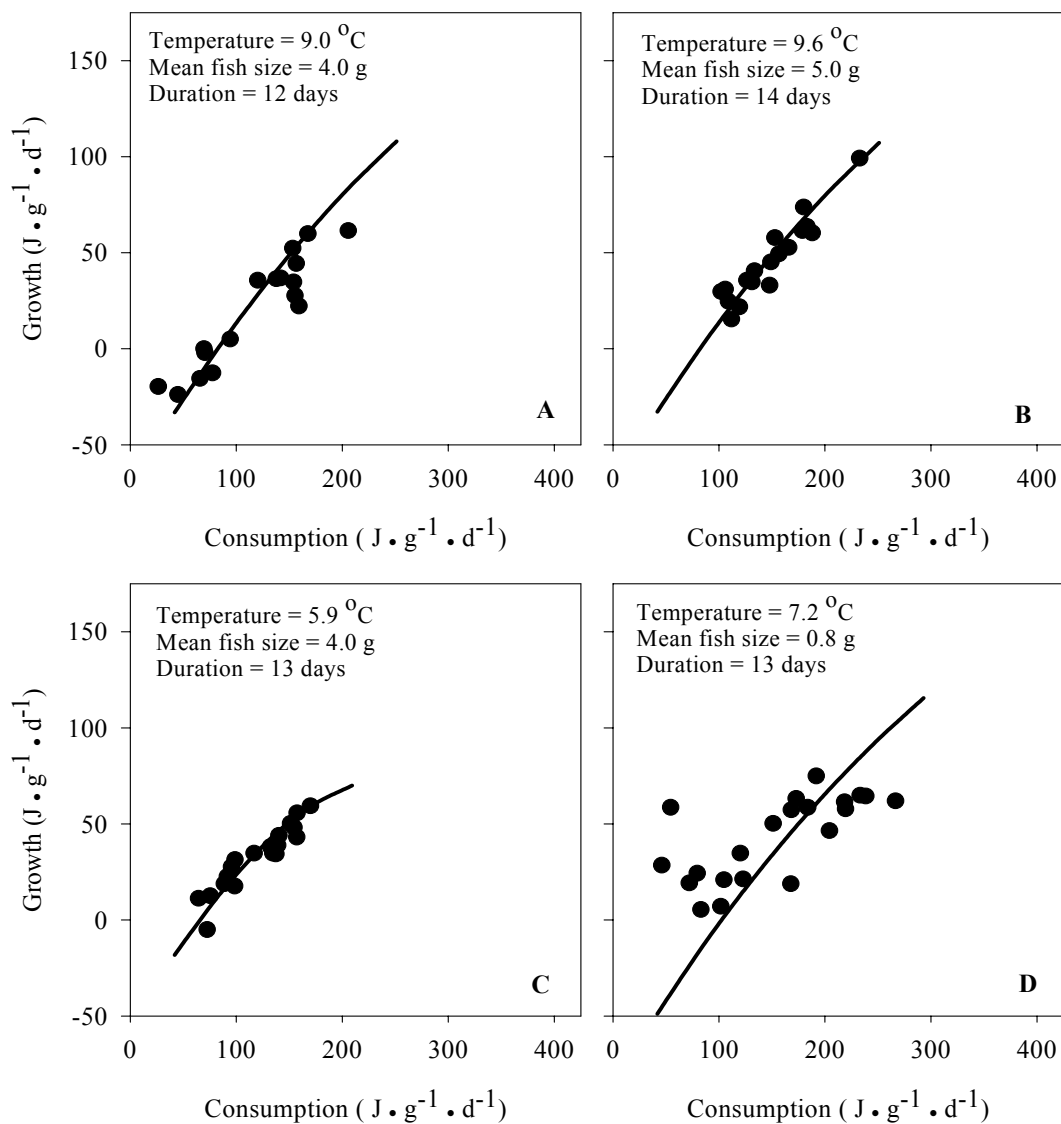
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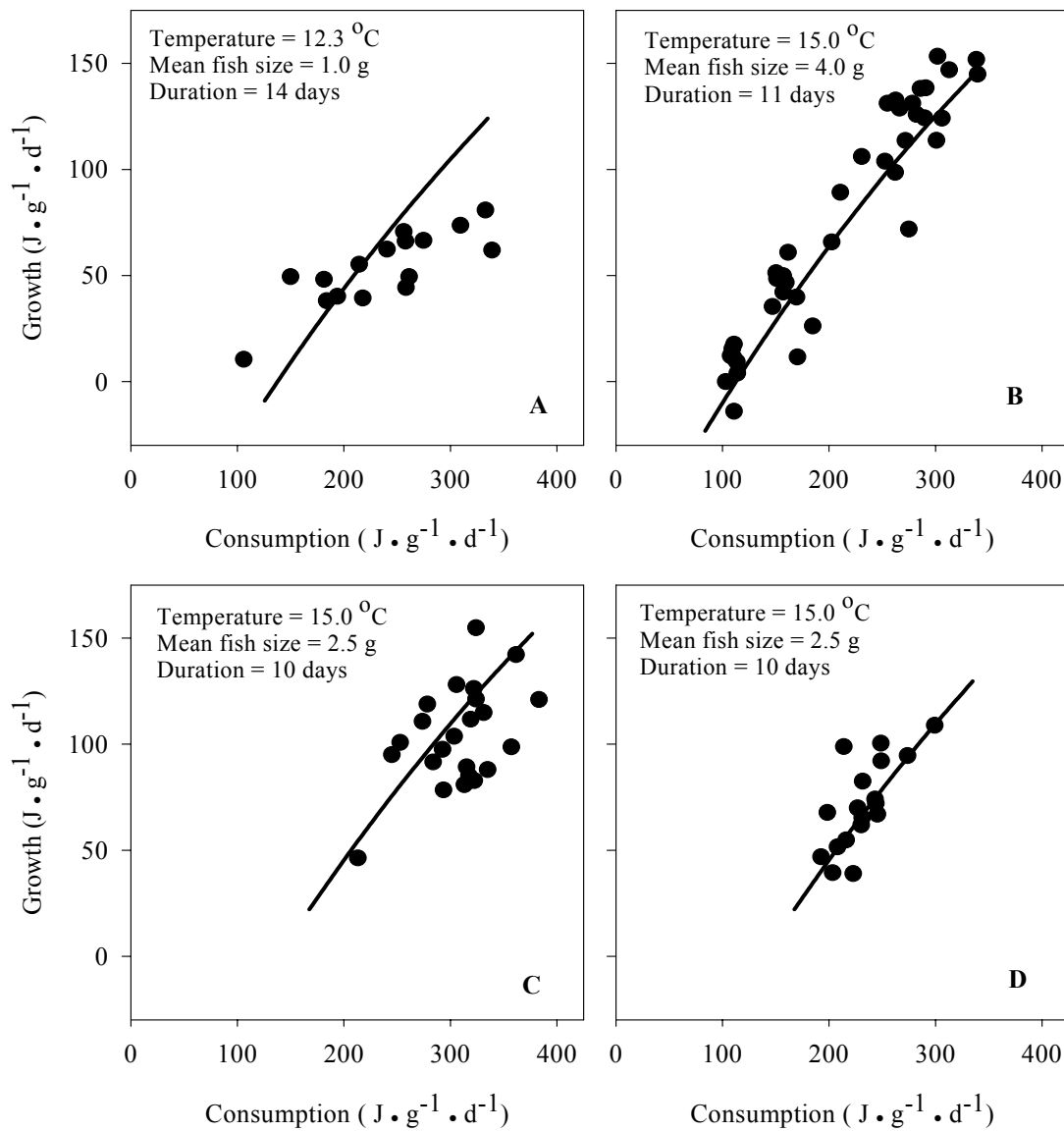
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APPENDICES

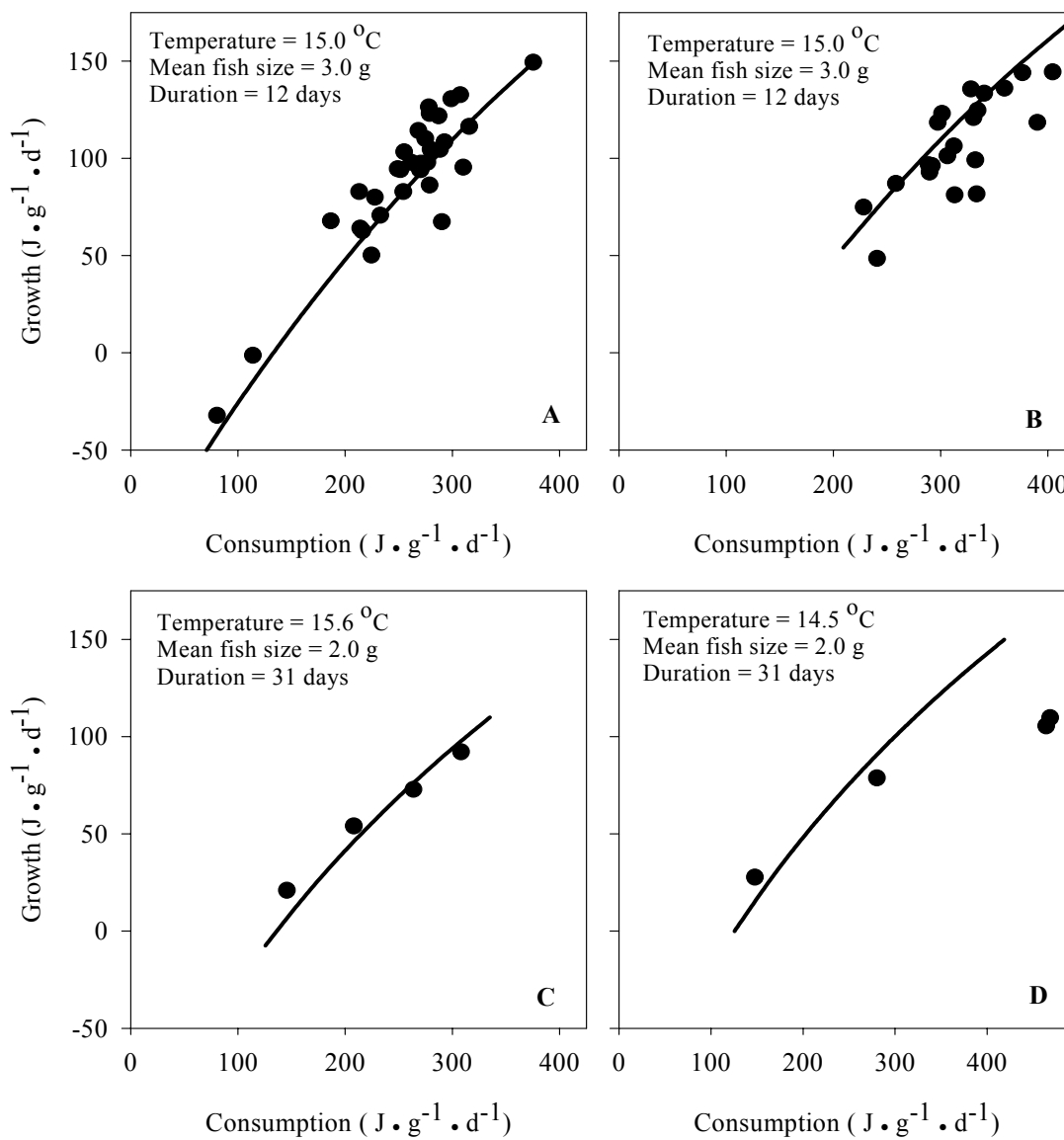
Appendix A. Modeled consumption rate (solid line) in relation to consumption rates measured in laboratory experiments (solid circles). Data from Carline (1968).



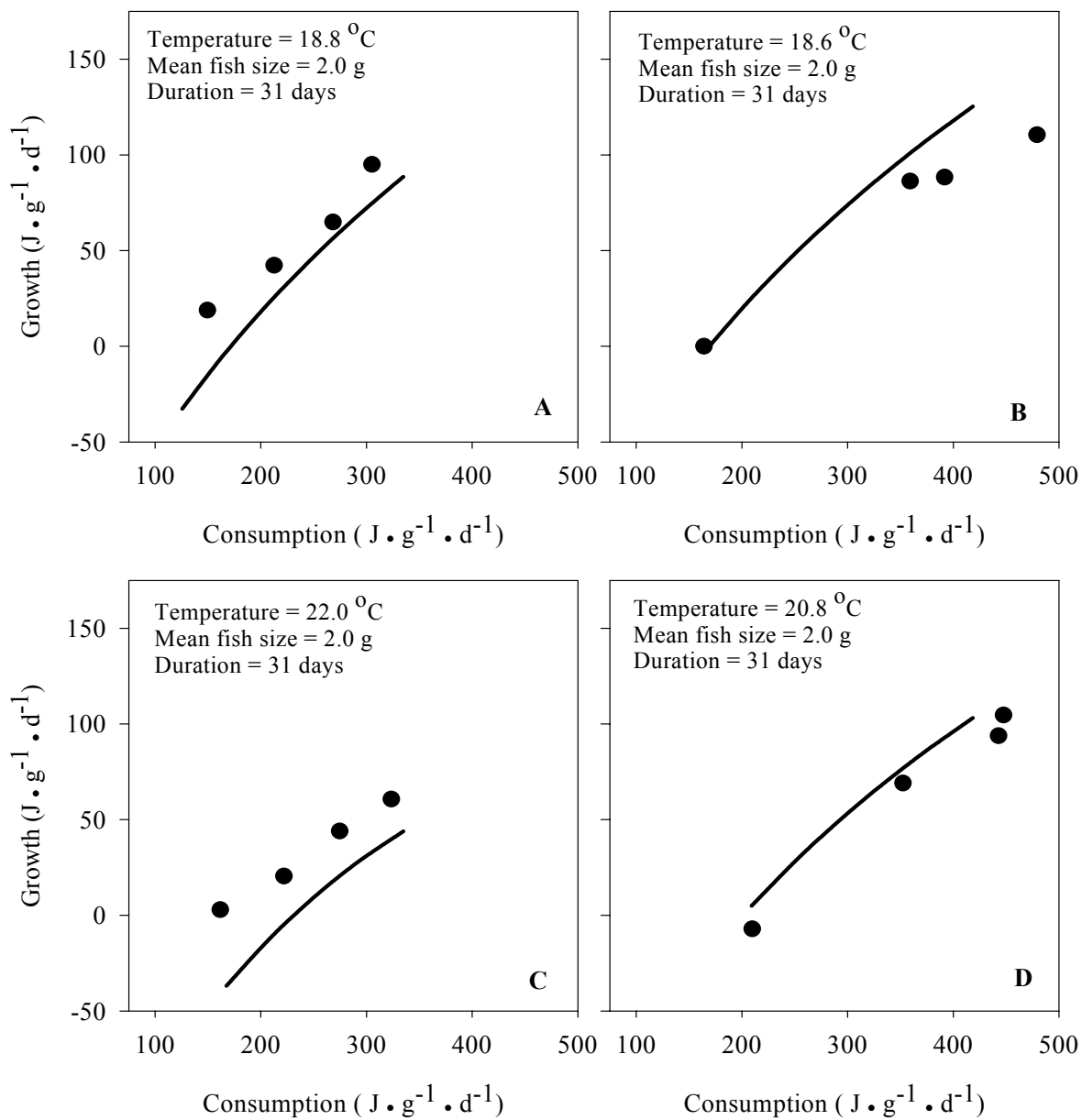
Appendix B. Modeled consumption rate (solid line) in relation to consumption rates measured in laboratory experiments (solid circles). Data for figure A are from Carline (1968) and for figures B-D are from Hutchins (1974).



Appendix C. Modeled consumption rate (solid line) in relation to consumption rates measured in laboratory experiments (solid circles). Data for figure A-B are from Hutchings (1974) and for figures C-D are from Everson (1973).



Appendix D. Modeled consumption rate (solid line) in relation to consumption rates measured in laboratory experiments (solid circles). Data are from Everson (1973).



Appendix E. Juvenile coho salmon bioenergetics model output of energy consumption and losses in response to water temperature.

