

Linking Habitat Quality with Trophic Performance of Steelhead along Forest Gradients in the South Fork Trinity River Watershed, California

SARAH G. MCCARTHY*

University of Washington, School of Aquatic and Fishery Sciences,
Box 355020, Seattle, Washington 98105-5020, USA

JEFFREY J. DUDA AND JOHN M. EMLÉN

U.S. Geological Survey, Western Fisheries Research Center,
6505 Northeast 65th Street, Seattle, Washington 98115, USA

GARTH R. HODGSON

U.S. Forest Service, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, California 95521, USA

DAVID A. BEAUCHAMP

U.S. Geological Survey, Washington Cooperative Fish and Wildlife Research Unit,¹
School of Aquatic and Fishery Sciences, Box 355020, Seattle, Washington 98105-5020, USA

Abstract.—We examined invertebrate prey, fish diet, and energy assimilation in relation to habitat variation for steelhead *Oncorhynchus mykiss* (anadromous rainbow trout) and rainbow trout in nine low-order tributaries of the South Fork Trinity River, northern California. These streams spanned a range of environmental conditions, which allowed us to use bioenergetics modeling to determine the relative effects of forest cover, stream temperature, season, and fish age on food consumption and growth efficiency. Evidence of seasonal shifts in reliance on aquatic versus terrestrial food sources was detected among forest cover categories and fish ages, although these categories were not robust indicators of *O. mykiss* condition and growth efficiency. Consumption estimates were generally less than 20% of maximum consumption, and fish lost weight in some streams during summer low-flow conditions when stream temperatures exceeded 15°C. Current 100-year climate change projections for California threaten to exacerbate negative growth patterns and may undermine the productivity of this steelhead population, which is currently not listed as endangered or threatened. To demonstrate the potential effect of global warming on fish growth, we ran three climate change scenarios in two representative streams. Simulated temperature increases ranging from 1.4°C to 5.5°C during the summer and from 1.5°C to 2.9°C during the winter amplified the weight loss; estimated average growth for age-1 fish was 0.4–4.5 times lower than normal (low to high estimated temperature increase) in the warm stream and 0.05–0.8 times lower in the cool stream. We conclude that feeding rate and temperature during the summer currently limit the growth and productivity of steelhead and rainbow trout in low-order streams in the South Fork Trinity River basin and predict that climate change will have detrimental effects on steelhead growth as well as on macroinvertebrate communities and stream ecosystems in general.

The ability of streams to support fish populations depends on several factors, including temperature, flow, seasonal variability, predators, trophic competitors, food availability, anthropogenic impacts on habitat, and natural disasters (Moyle 1994; Beecher et al. 1995; Arrington et al. 2002). Since salmonids can

consume more than 80% of benthic prey production in streams (Huryn 1996), feeding rate is a critical factor for survival during the stream-rearing and subsequent life history stages. Feeding rate can be influenced by food supply, temporal–spatial access to the food supply, and other factors that could inhibit access to or efficient acquisition of food resources, such as predation risk, competition, dominance hierarchies, and environmental stressors. Territorial fish choose stream positions that maximize net energy acquisition while minimizing costs associated with holding position, territorial defense, and predator avoidance (Hill and Grossman 1993; Hughes 1998). Environmental changes related to seasonal temperature shifts, fluctuation in

* Corresponding author: sarahpdr@yahoo.com

¹ The Washington Cooperative Fish and Wildlife Research Unit is jointly sponsored by the U.S. Geological Survey, the University of Washington, the Washington Departments of Ecology, Fish and Wildlife, and Natural Resources, and the Wildlife Management Institute.

Received March 4, 2008; accepted January 8, 2009

Published online May 4, 2009

feeding rate (affected by prey abundance and prey accessibility), and flow variability can easily upset this delicate balance (Brandt et al. 1992; Nakano and Murakami 2001).

Individual fitness is related, in part, to the efficiency with which the fish takes in and expends energy (Arrington et al. 2002). Several factors affect the assimilation of energy into body mass, including temperature, prey energy density, activity, and metabolism (Hanson et al. 1997; Morinville and Rasmussen 2003). Energy acquisition in streams can vary dramatically in response to different environmental conditions that affect prey accessibility, such as thermal regime, predation threat, high flows, or density-dependent competition for space and food (Sweka and Hartman 2001). Bioenergetics modeling is a useful approach for estimating the implications of changes in feeding rate, thermal experience, diet, or activity on energy gains and losses and how these effects are ultimately expressed as net growth (Hanson et al. 1997). These models provide species-specific functional relationships among growth, feeding rate, food quality, and temperature, based on allometric and temperature effects on metabolism and maximum consumption rate. Because the model simultaneously accounts for temporal changes in temperature (on a daily time step), diet composition, and the associated energetic value of the ingested prey, the relative importance of temperature, feeding rate, and prey quality can be evaluated for the unique combinations of conditions offered by different streams (or other habitats) during different periods.

The decline of stream-dwelling anadromous fishes in California is a result of environmental and anthropogenic effects such as watershed degradation, diversions and dams, pollution, invasive species, and overharvest (Moyle 1994). Steelhead *Oncorhynchus mykiss* (anadromous rainbow trout) are commonly reared in freshwater habitats for 2 years before migrating to sea (Busby et al. 1994). This extended freshwater residence makes steelhead more reliant on seasonal patterns in stream productivity than many other anadromous salmonids. Klamath Mountains Province steelhead are the only distinct population segment (DPS) of steelhead in California that was not listed as endangered or threatened under the Endangered Species Act (ESA) as of 2008. Though not currently listed, this DPS is indeed at risk of decline owing to the same pressures affecting steelhead runs along the West Coast. Each year, steelhead belonging to the Klamath Mountains Province DPS return to the South Fork Trinity River in northern California and spawn in its tributaries. Accurate and extensive baseline data on the

habitat requirements of this sensitive species is essential for conservation and recovery efforts.

Smolt-to-adult survival of anadromous salmonids is related in part to the size they achieve in freshwater habitats (Zabel and Achord 2004). Habitat elements such as temperature, prey supply, and feeding rate, directly affect acquisition and expenditure of energy by stream-dwelling fish. Therefore, a bioenergetics analysis of seasonal energy gains and losses provides a basis for linking habitat characteristics to steelhead growth and survival. It is important to understand limiting factors in fish populations to ascertain whether critical thresholds in energy balance are in danger of being reached. Bioenergetics modeling can be used to determine whether these stocks are on the margin of falling into negative growth regimes during critical periods of their life history. These analyses also may be used to inform research and recover efforts for ESA-listed steelhead in California, Oregon, and Washington.

Our objectives were to determine whether seasonal and age-specific growth of steelhead and resident rainbow trout (herein collectively referred to as *O. mykiss*) in the South Fork Trinity River watershed varied among predominant forest types or thermal regimes, and whether seasonal patterns of invertebrate production, fish diet composition, and temperature associated with these forest-temperature categories affected food consumption, growth, and growth efficiency. We examined the variability of these factors among stream categories that occurred along a vegetative-thermal gradient, from conifer-dominated forest at higher elevations to small hardwood forest at lower elevations. Based on theoretical bioenergetics modeling results using the Wisconsin bioenergetics model (Hanson et al. 1997) and steelhead parameters from Rand et al. (1993), we hypothesized that fish condition, consumption, and growth efficiency should vary predictably along this gradient, with higher values in the cooler conifer-dominated streams. We expected *O. mykiss* to be more sensitive to temperature at lower feeding rates, and for smaller fish that tend to have higher growth rates to respond more dramatically to changes in consumption or temperature. Comparisons of condition and growth were used to identify significant factors affecting efficient energy acquisition for *O. mykiss* in this region.

Study Site

The Trinity River in northwestern California is the largest tributary of the Klamath River. Construction of the Trinity Dam in 1962 (Mills et al. 1997) blocked upstream passage of anadromous fishes. The South Fork Trinity River drains a 2,538-km² watershed (Figure 1) and meets the Trinity River downstream

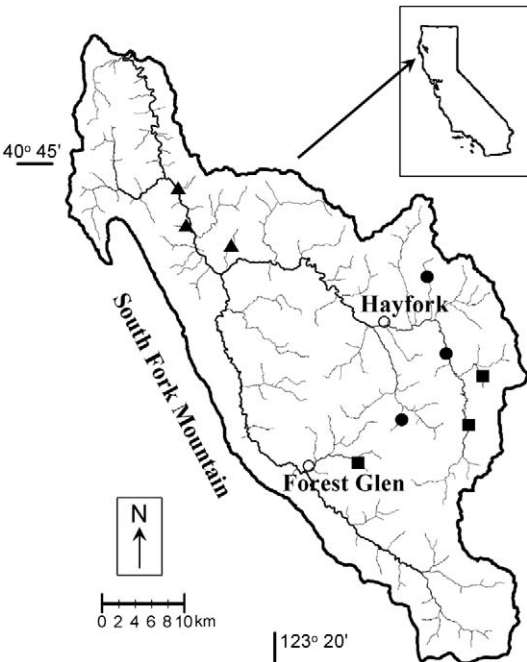


FIGURE 1.—The South Fork Trinity River watershed and sampling locations. Symbols depict late-seral mixed (squares), hardwood (triangles), and conifer (circles) forest categories.

from the Trinity Dam, leaving the entire reach of the South Fork Trinity River accessible to anadromous fish populations such as spring- and fall-run Chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, and summer and winter steelhead.

A companion project to ours, designed to describe the multiscale habitat relationships of herpetofauna across the South Fork Trinity River watershed, was initiated in 2000. The design and implementation of this project was based upon results obtained from other

studies in the same ecoregion (Welsh and Hodgson 1997; Welsh and Lind 2002). Ordination of physical and environmental variables across three spatial scales allowed the 60 stream basins to be categorized into four groups, characterized by dominant vegetation type (H. H. Welsh and G. R. Hodgson, U.S. Forest Service, Redwood Sciences Laboratory, unpublished data). *Oncorhynchus mykiss* occurred in 23 of these streams and are believed to be a mix of resident (rainbow trout) and anadromous (steelhead) life histories based upon otolith microchemistry (J. J. Duda, unpublished data). We selected three streams from each of the three fish-bearing stream groups to study intensively as part of this investigation. Stream selection was based on fish capture success in 2002. The study by Welsh and Hodgson also provided fish density data for our project (Table 1).

Methods

We used the Wisconsin bioenergetics model (Hanson et al. 1997), parameterized for steelhead (Rand et al. 1993), to determine the expected growth responses of juvenile *O. mykiss* to different feeding rates, temperatures, and energetic qualities of prey (Beauchamp, in press) to provide context for interpreting the relative profitability of seasonal, size-specific, growing conditions among tributaries with differing thermal regimes and forest cover types in the South Fork Trinity River drainage. Expected daily growth rates ($g \cdot g^{-1} \cdot d^{-1}$) were computed for factorial combinations of temperature (1–25°C) and feeding rate (15, 50, and 100% of the theoretical maximum consumption rate, hereafter termed C_{max}) for 1-g (representing age-0) and 10-g (representing age-1) steelhead. The growth simulations assumed that steelhead fed on an invertebrate diet with a composite energy density averaging 3,000 J/g wet weight, which emulated a diet of

TABLE 1.—Temperature regime and forest type categories (SH = low elevation, small hardwood; LS = late seral, mixed; CON = conifer dominated) of nine tributaries of the South Fork Trinity River, California. Streams were placed into five vegetative-thermal categories for bioenergetics modeling analyses. Fish/m² was calculated from double-pass electrofishing of 18 habitat units (9 fast and 9 slow). Area was calculated as length × width, which was used to convert relative abundance to relative density. Elevation is that of the study site (downstream end of unit), and basin area is the size of the subwatershed. Number of pools was calculated in 2001 as the number of slow-water habitats in each study reach (Hawkins et al. 1993).

Study stream	Temperature regime	Forest type	Number of pools	Fish/m ²	Elevation (m)	Basin area (ha)
Monroe Creek	Cool	SH	57	0.59	463	391.5
Underwood Creek	Cool	SH	49	0.29	315	1,134.5
Olsen Creek	Cool	SH	48	0.24	740	926.5
Chancellula Creek	Cool	LS	27	0.18	1,000	703.9
Barker Creek	Cool	CON	33	0.16	890	1,286.3
West Twin Creek	Warm	LS	37	0.34	940	396.2
Potato Creek	Warm	LS	25	0.51	960	1,240.2
Carrier Gulch	Warm	CON	30	0.86	800	488.5
Ditch Gulch	Warm	CON	19	0.89	880	1,674.6

predominantly immature aquatic invertebrates. Simulations for the lowest feeding rate (15% $C_{\max}$) were repeated using an average prey energy density of 5,000 J/g to emulate a diet containing higher proportions of adult aquatic and terrestrial insects.

To describe the role of various environmental variables in *O. mykiss* energy acquisition and growth efficiency, we assigned nine streams to combinations of dominant forest cover type and temperature regime (Table 1). Streams with average daily summer temperatures regularly exceeding 17°C were categorized as warm and those that never exceeded 17°C during the summer were categorized as cool (Table 1). We then used the bioenergetics model to estimate the consumption and growth efficiency of juvenile *O. mykiss* among the five vegetative–thermal categories based on observed age-specific growth, diet, and environmental data from each stream as inputs for the model simulations. We sampled within a previously delineated 300-m reach in each stream (Welsh and Hodgson 1997).

Physical attributes and invertebrate composition.—We deployed HOBO Temp temperature loggers in the nine study streams from April to October 2003 and year-round (April 2003 to May 2004) in three secure sites (Barker Creek, Carrier Gulch, and West Twin Creek). The temperature loggers, which were calibrated simultaneously, recorded temperature every 20 min (accuracy, $\pm 0.7^\circ\text{C}$ at 21°C). We compared average daily temperatures between streams in the three forest cover categories and among seasons. We recorded the duration and magnitude of periods when temperatures approached or exceeded 20°C (temperatures above 20°C lead to precipitous declines in growth; see Figure 2) and used average daily temperatures during summer low flow (late June–early September) to assign streams to a cool or warm temperature category.

Stream sampling dates in 2003 were 25–26 April, 11–20 June, 12–18 August, and 9–17 October, and each stream generally took 1 d to fully sample. In each sampling reach, we measured a bank-full cross-sectional profile of depth and water velocity (using a meter stick and a Global Flow Probe current meter) in June, August, and October 2003 and calculated stream discharge for the estimation of prey availability (Orth 1983; McMahon et al. 1996). We then compared mean discharge among streams in each vegetative–thermal category by season, and overall mean discharge among seasons using analysis of variance (ANOVA) and Tukey's multiple comparisons (Zar 1999).

We sampled stream drift to determine the relative abundance of aquatic and terrestrial invertebrates in the water column and to estimate the type and composition of allochthonous input. Our goal was to determine the

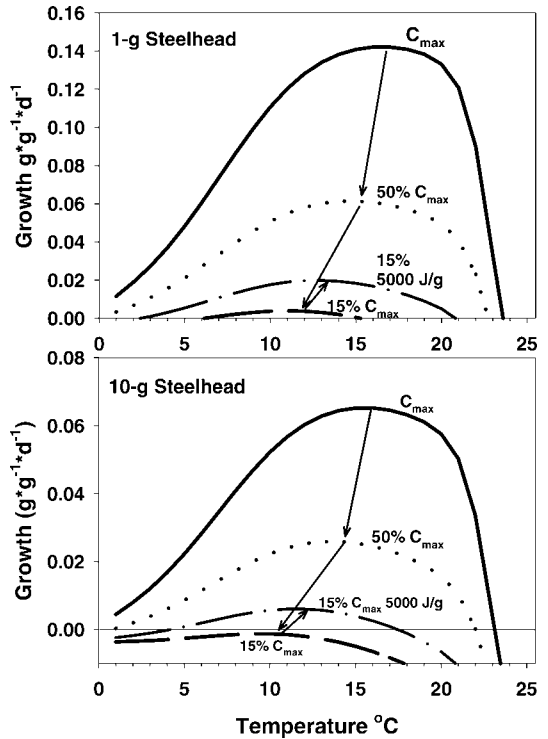


FIGURE 2.—Temperature-dependent daily growth responses by 1-g and 10-g *O. mykiss* feeding at 100%, 50%, and 15% $C_{\max}$ on a diet with a composite energy density of 3,000 J/g wet weight. If the same biomass of a higher-quality diet (e.g., 5,000 J/g at 15% $C_{\max}$) was consumed, growth increased and the range of temperatures that support growth widened. The arrows indicate the highest temperatures for optimal growth given the feeding rate and energy density of the prey.

energy density and relative contribution of different prey types to total prey abundance in different stream types. Two drift nets were deployed in each stream, one in a riffle and one in the head of a pool. The drift samplers, constructed from two interlocking polyvinyl chloride (PVC) tubes, had circular openings with a cross-sectional area of 62.1 cm². We used nylon stockings (mesh size when stretched, approximately 450 μm) inserted into the PVC tubes as drift nets. The nets were submerged and anchored in the substrate before dusk and retrieved after dawn to capture evening and morning peaks in invertebrate activity (Rabeni 1996). Drift sampling always occurred the evening before the stream was sampled for fish. Average stream depth at the drift sampling sites was 9 cm. The volume of invertebrates captured in each drift sample, the area of the drift sampler, and the stream discharge measurement (m³/s) were used to quantify invertebrate biovolume for the stream. Energy density was

TABLE 2.—Stream invertebrate energy density determined by bomb calorimetry (except where indicated otherwise). Invertebrates were captured in drift nets, and, where necessary, pooled by functional group to attain sufficient dry weight for bomb calorimetry (na = no data available).

Prey type	Wet : Dry weight ratio	Energy density (J/g)
Aquatic larvae, soft-bodied ^a	na	2,746
Aquatic larvae, rigid body ^b	0.21	4,272
Aquatic nymphs ^c	0.13	3,076
Aquatic other ^d	na	2,789
Winged insects ^e	0.18	4,225
Coleoptera adults	0.29	6,387
Hymenoptera adults	0.24	5,134
Orthoptera adults	0.22	4,228

^a Diptera (Cummins and Wuycheck 1971).

^b Coleoptera and Trichoptera.

^c Ephemeroptera, Plecoptera, Trichoptera, and Diptera.

^d Gastropoda and Annelida (Cummins and Wuycheck 1971).

^e Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Neuroptera.

measured in J/g wet weight for each invertebrate category in the drift samples, and samples were frozen immediately after retrieval to preserve specimens for bomb calorimetry (Table 2). We compared the volumetric proportions of each invertebrate functional group in the drift-net samples by season (June, August, October), forest cover type (conifer, mixed, hardwood), and temperature regime (cool or warm summer temperatures) using multivariate analysis of variance (MANOVA) on the square-root-transformed taxonomic proportions in each drift sample (Zar 1999).

Leaf litter and other organic material in the drift net samples were separated from invertebrates, and then biovolumes (in milliliters) of available invertebrate prey were measured by means of volumetric displacement. Invertebrates found in the drift samples were identified to order and blotted wet weights were measured for each order in the sample. We dried samples of each order for 3 to 6 d at 55°C to obtain a constant dry weight. When necessary to obtain sufficient dry weights (0.2–0.02 g) for bomb calorimetry, we pooled orders into functional groups so that we could at least obtain energy densities for these composite groups. Each functional group was ground into a fine powder, dried again at 55°C to a constant weight, pressed into small pellets, and burned in the bomb calorimeter to obtain an energy density value (as cal/g dry weight). Values were converted to obtain the correct units (J/g wet weight) for bioenergetics modeling.

Fish sampling.—Using a two-pass method and a backpack electrofisher (Smith-Root Model 12B set at 60 Hz, 6 ms, and 400–600 V), we electrofished pools and riffles within each 300-m stream reach until a minimum of 20 fish were captured. Electrofishing

commenced in the morning and continued for the majority of the day and fish were processed within 15 min of capture. We minimized current and voltage during electrofishing to reduce trauma while facilitating capture (Reynolds 1996). We anesthetized all *O. mykiss* over 30 mm fork length (FL) using dissolved tricaine methanesulfonate (MS-222 [50 mg/L; Bowser 2001], measured FL and weight (Anderson and Neumann 1996), removed stomach contents using a nonlethal stomach lavage technique (Giles 1980), and preserved the contents in 90% solutions of ethanol (Bowen 1996). We attempted to standardize the minimum size of invertebrates captured by using the same nylon material used in the drift net as a sieve to collect stomach contents. Scales were collected from the preferred region of the fish below and posterior to the dorsal fin, placed on numbered gummed cards, and pressed into acetate impressions for age and growth analysis (Devries and Frie 1996). Fish sampling began approximately 2 h after sunrise and generally took all day. All fish were placed in freshwater to recover from anesthesia and released alive.

Diet analysis.—For each stomach lavage sample, we measured the blotted wet weight for each invertebrate order represented. Invertebrate orders were combined to describe the fish diet in terms of the percentage composition by weight of each functional group within each stomach (Table 2). We used MANOVA to compare how the weight proportions of each invertebrate functional group in the diet varied by season, forest cover, temperature regime, and age-class (Zar 1999). We computed electivity indices for key taxa found in the stomach contents using Manly's α (Manly et al. 1972; Chesson 1983); however, no pattern in electivity emerged, so the results were not reported.

Age and growth analysis.—We aged fish using scale annuli following DeVries and Frie (1996). Relative weight (W_r) was used for comparisons of fish condition. Growth and W_r for the three *O. mykiss* age-classes (ages 0, 1, and 2) were compared among seasons, forest cover types, and temperature regimes. We converted fork lengths to total lengths (TL, mm) for all *O. mykiss* from a regression of 10 pairs of fork and total lengths ($r^2 = 0.999$, $P < 0.001$), then calculated length-specific standard weight W_s (Wege and Anderson 1978) for lotic rainbow trout using the standard weight equation from Simpkins and Hubert (1996) ($\log_{10} W_s = -5.023 + 3.024 \log_{10} TL$). We calculated W_r ($W_r = [W/W_s] \times 100$) for each fish, where W was the wet weight (g) of the fish and W_s was the standard weight for a fish of the same TL (Table 3). For each season, we tested for significant differences in W_r among forest cover types and between temperature regimes using ANOVA (Zar 1999).

TABLE 3.—Mean weight (W ; g), SD of W , mean relative weight (W_r), SD of W_r , and sample size (N) of age-0, age-1, and age-2 *O. mykiss* during June, August, and October 2003 in streams categorized by forest cover and temperature regime.

Regime and month	Age 0					Age 1					Age 2				
	N	W	SD	W_r	SD	N	W	SD	W_r	SD	N	W	SD	W_r	SD
Conifer-cool															
Jun	12	1.4	0.4	94.3	13.0	5	11.1	2.0	94.3	13.9	1	18.0		124.3	
Aug	11	2.2	1.0	80.2	9.0	2	13.0	4.2	97.6	5.5	5	21.8	9.2	86.6	7.4
Oct	16	3.0	1.0	104.7	19.6	2	13.8	6.0	93.8	6.1	2	23.5	7.8	86.0	4.5
Conifer-warm															
Jun						16	9.6	2.7	110.2	9.6	14	19.1	3.8	106.1	8.8
Aug	26	2.6	1.9	96.2	14.6	6	9.5	4.8	93.0	9.3	6	21.2	6.4	90.0	11.1
Oct	23	2.7	0.7	110.9	15.7	8	10.5	4.0	82.5	10.1	2	37.0	12.7	96.7	16.5
Mixed-cool															
Jun						7	7.2	2.7	122.0	17.0	6	20.3	8.5	129.1	18.0
Aug	14	1.7	1.0	95.5	15.9	3	10.0	1.8	100.4	8.3	1	23.0		95.8	
Oct	19	2.0	0.9	90.3	13.4	2	9.8	1.0	83.4	4.8					
Mixed-warm															
Jun	8	0.6	0.1	110.3	27.5	25	7.1	2.4	110.6	13.0	6	14.0	1.9	94.8	12.2
Aug	28	1.8	0.9	93.8	11.7	11	8.6	2.0	97.1	8.6	8	27.2	14.6	92.1	7.2
Oct	22	2.4	1.1	108.6	11.7	12	8.4	2.9	102.1	7.7	4	34.1	20.1	84.8	11.7
Hardwood-cool															
June	3	0.7	0.2	98.2	18.5	10	8.6	3.3	105.8	12.3	10	20.3	5.2	105.2	16.7
August	16	3.1	0.7	98.6	8.5	17	10.9	4.3	95.7	12.8	21	29.3	10.2	94.3	7.4
October	15	3.6	1.0	93.9	9.1	21	10.9	4.0	93.7	7.2	22	31.1	13.7	92.7	12.7

Bioenergetics modeling.—We used the Wisconsin bioenergetics model (Hanson et al. 1997) with the fish sampling data from the streams in different forest cover types and thermal categories to estimate the necessary energy required (i.e., consumption, C [g]) for *O. mykiss* to achieve the growth rates observed over specified time intervals (1–4 seasons). The model estimated C from the sum of somatic growth (G), metabolism (M ; activity, respiration, and specific dynamic action), and waste (W). The physiological parameters (including energetic costs associated with metabolism and waste production) for *O. mykiss* were taken from Rand et al. (1993). Thermal experience for *O. mykiss* was input as the average daily temperature from field measurements from each stream during April–October 2003, and from just Barker Creek and Carrier Gulch during October 2003–May 2004. Bomb calorimetry results from drift-net invertebrate samples provided input values for prey energy density (J/g wet weight), except for a literature-derived value for dipteran larvae (Table 2; Cummins and Wuycheck 1971).

We ran bioenergetics model simulations for each age-class in each stream during the summer growing season to compare the consumption and growth efficiency of fish among forest cover types and temperature regimes. For each stream, we used average diet and body mass data for each age-class during June, August, and October as inputs for stream- and age-specific simulations. We separated fish into age-classes based on scale data and estimated seasonal growth in each stream by taking the difference in average weight between sampling events in June, August, and October

2003. Owing to the small sample sizes, we excluded 3- and 4-year-old fish, and in most cases age-0 fish in June and age-2 fish in October, from the analysis.

We estimated the seasonal and annual consumption rates of each prey category for individuals of each age-class using the bioenergetics model. We also estimated consumption C as a proportion ($p = C/C_{\max}$) of the theoretical maximum consumption rate given the current temperature and body mass of the consumer. These values indicated whether feeding rate was limited; low feeding rates could result from limited prey supply or from restricted access to existing prey because of spatial–temporal separation, predation risk, dominance hierarchies, competition, or other factors. In addition, the incremental weight gain for each age was divided by the corresponding consumption rate for each season to estimate seasonal or annual growth efficiency. These metrics allowed comparisons of prey-specific consumption, feeding rate, and growth efficiencies among age-classes, seasons, and streams.

We also conducted year-round model runs for two streams in the conifer-dominated category (Barker Creek [cool] and Carrier Gulch [warm]) that had year-round temperature measurements. Projections of climate change in California, using a range of global climate change models, suggest increased winter flows and decreased summer flows, with a shift in the hydrograph towards earlier peak flows (Maurer and Duffy 2005). Coupled with the changing hydrological conditions, which could have direct and indirect ecological consequences on fish communities, would be temperature increases, which would affect the

bioenergetics performance of *O. mykiss*. Temperature increases are expected, as a range of different global climate change model scenarios predict an increase in air temperature by 2100 ranging from 1.7°C to 5.8°C in California (Cayan et al. 2006a). Predicting stream temperatures from projected future air temperatures is potentially confounded by local conditions, including vegetation and geology, as well as nonlinear responses due to climate change-related changes in groundwater, riparian vegetation, and hydrology (reviewed by Webb et al. 2008). Nevertheless, recent work has suggested that a linear response in the range of 0.86 would be an estimate of water temperature change with rising air temperature.

To determine the effects of projected climate change on fish growth, we conducted three climate change scenarios (low, medium, and high) for Barker Creek and Carrier Gulch and used the model to estimate growth based on consumption rates and fixed values of p from the previous nominal model runs for these two streams. We modified average daily stream temperatures according to summer and winter climate change projections (corrected for water temperature by a factor of 0.86) for northern California (Cayan et al. 2006b). Low, medium, and high projections for summer (June–August: +1.4, +3.2, and +5.5°C, respectively) and winter (December–February: +1.5, +2.0, and +2.9°C) were used, and spring (March–May) and fall (September–November) temperature modifications were derived as the averages of summer and winter projections (+1.4, +2.6, and +4.2°C).

Results

Expected Size-Specific Growth Responses to Different Feeding Rates and Temperatures

The bioenergetic model simulations indicated that optimal growth and thermal tolerance differed between sizes of steelhead (Figure 2). At $C_{\max}$, the optimal growth of an age-0, 1-g steelhead would be 14.2% of their body weight per day ($0.142 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) at 16–17°C, but optimal growth declined to $0.061 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ at 14–15°C at 50% $C_{\max}$ and was only $0.004 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ at 11°C at 15% $C_{\max}$. However, if the composite energy density of the diet increased from 3,000 to 5,000 J/g, growth would rebound to $0.020 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ when feeding at 15% $C_{\max}$. Thermal tolerance, defined here as the range of temperatures that support positive growth at a given feeding rate, also shifted with changes in feeding rate and the energetic quality of the diet. Positive growth could be supported up to 23°C when feeding at $C_{\max}$ and up to 2°C at 50% $C_{\max}$, but only to 15°C at 15% $C_{\max}$; however, by increasing the energy density of prey from

3,000 to 5,000 J/g, thermal tolerance increased to 20°C (Figure 2).

The simulated growth responses for 10-g steelhead resulted in lower optimal growth rates, lower temperatures corresponding to optimal growth at a given feeding rate, and lower thermal tolerances than for 1-g steelhead (Figure 2). At $C_{\max}$, the optimal daily growth of an age-1, 10-g steelhead was 6.5% of their body weight ($0.065 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) at 15–16°C, but declined to $0.026 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ at 13–14°C when feeding at 50% $C_{\max}$. The 10-g steelhead lost weight at all temperatures if only feeding at 15% $C_{\max}$; however, if the composite energy density of the diet increased from 3,000 to 5,000 J/g, positive growth could be supported in 5–17°C temperatures and was optimum at $0.006 \text{ g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ in 11–12°C (Figure 2). When feeding at 50–100% $C_{\max}$, the upper thermal tolerance (22–23°C) was very similar between 1-g and 10-g steelhead; however, at 15% $C_{\max}$, 10-g steelhead required the higher energy diet (5,000 J/g) to sustain positive growth.

Physical Attributes and Invertebrate Composition

Fish density was highest ($>0.85 \text{ fish/m}^2$) in the conifer–warm category (Carrier and Ditch gulches), and the number of pools was highest in the hardwood–cool streams (Table 1). In the cool streams, the average stream temperature was 6.4°C (SD = 1.2) during winter (Barker Creek only), 13.8°C (1.8) during early June—early September, and never exceeded 17°C, whereas the mean temperatures in warm streams were higher during the summer and more variable (5.5°C [1.5] during winter in Carrier Gulch and West Twin Creek and 15.0°C [2.2] during early June—early September, regularly exceeding 17°C). Maximum daily temperatures in one warm–mixed stream (Potato Creek) exceeded 20°C for 12 d in late July.

Within each forest cover category and month, mean stream discharge did not differ among streams (ANOVA: $P > 0.58$), nor did it differ between cool and warm streams (two-sample t -test: $P > 0.11$ for all months; Figure 3). However, overall mean stream discharge in April was significantly higher than mean discharge in later months (ANOVA: $P < 0.001$; Tukey's test: $P < 0.001$).

Overall, total invertebrate biovolume (mL/h) did not vary according to month (ANOVA: $P = 0.208$) or stream type ($P = 0.187$; Figure 3). The biovolume of individual prey types did not vary significantly among stream types or months except during April in the hardwood–cool category, when the volume of aquatic invertebrate nymphs was significantly higher than in August or October (ANOVA: $P = 0.034$; Tukey's test:

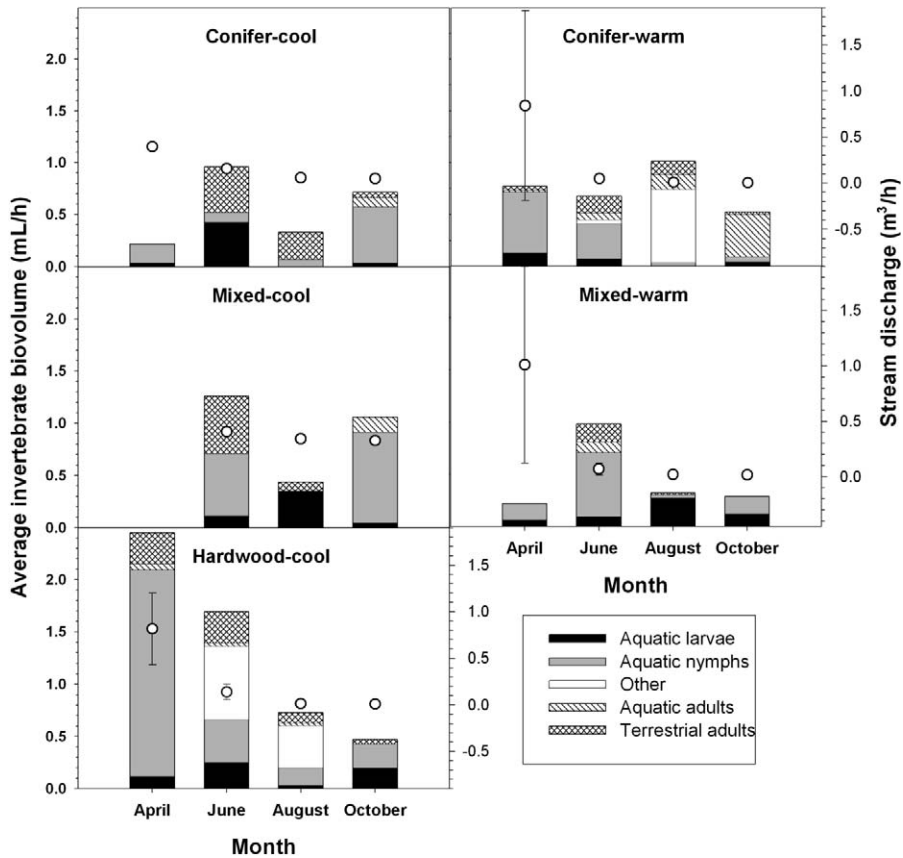


FIGURE 3.—Average invertebrate biovolume from drift-net sampling (columns) and stream discharge measurements (small circles; the vertical lines represent 2 SEs) during April, June, August, and October 2003, by habitat type.

$P < 0.032$). Higher prey volumes in April were associated with higher stream discharges.

Diet Analysis

The proportion of aquatic nymphs and adult insects (of both aquatic and terrestrial origins) in the diet varied by month, forest cover, stream temperature, and fish age, whereas other prey types showed no pattern (Figure 4). The proportion of aquatic nymphs in the diet was significantly lower in August than in June and October (ANOVA: $P < 0.001$; Tukey's test, $P < 0.002$), and the proportion of adult insects (aquatic and terrestrial origin) in the diet was significantly higher in August than in June and October (ANOVA: $P < 0.006$; Tukey's test: $P < 0.023$) for comparisons across thermal-vegetative categories and within cool streams for all forest cover categories. The dietary proportion of adult insects was significantly higher in mixed-cool streams than in mixed-warm (ANOVA: $P = 0.001$; Tukey's test: $P = 0.039$) and conifer-warm streams (ANOVA: $P = 0.001$; Tukey's test: $P = 0.001$). In

general, the proportion of aquatic nymphs in the diet decreased with age, while the proportion of adult aquatic and terrestrial-origin invertebrates increased in the diet with age (Figure 4). For all comparisons, age-0 fish consumed a higher proportion of aquatic nymphs than fish of ages 1 and 2 (ANOVA: $P < 0.001$; Tukey's test: $P < 0.007$), and age-2 fish consumed a higher proportion of adult insects than did those of ages 0 and 1 (ANOVA: $P < 0.001$; Tukey's test: $P < 0.021$).

Age and Growth

The age distribution of *O. mykiss* in each month, forest cover category, and temperature regime indicated that age-0 fish were not fully recruited in all streams by June 2003. However, age-0–2 fish samples from all stream types were reasonably represented in August (Table 3). Body weights did not differ among stream types by month (ANOVA: $P > 0.169$), except that age-1 fish exhibited higher weights during June in the conifer-cool and conifer-warm streams than in mixed-

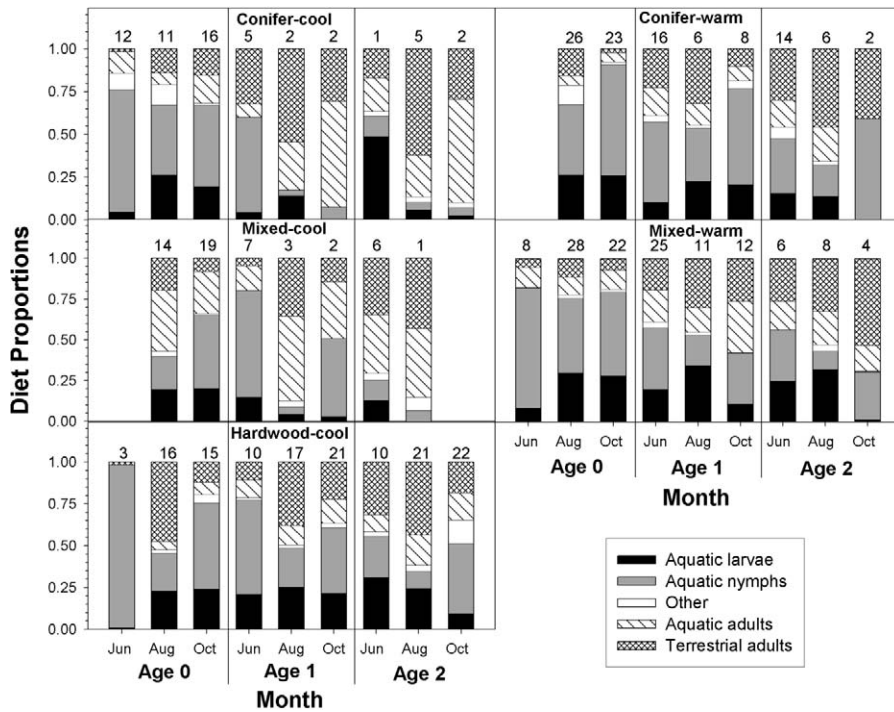


FIGURE 4.—Diet proportions for age-0, age-1, and age-2 *O. mykiss* during June, August, and October 2003. Streams were categorized by forest cover and temperature regime. Prey items were pooled to create five broad prey types: aquatic larvae (Diptera, Trichoptera, and Coleoptera), aquatic nymphs (Ephemeroptera, Plecoptera, and Diptera), aquatic other (Ostracoda, Gastropoda, Isopoda, Crustacean, and Acarina), aquatic adults (Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Neuroptera), and terrestrial insects (Hymenoptera, Coleoptera, Orthoptera, and Arachnid).

warm streams (ANOVA: $P = 0.008$; Tukey's test: $P < 0.042$). For all months combined, body weights were higher in conifer-cool and hardwood-cool streams for age-0 *O. mykiss* (ANOVA: $P < 0.007$; Tukey's test: $P < 0.031$; Table 3).

In most cases, fish condition (W_r) did not differ significantly among forest cover types and temperature regimes (ANOVA: $P > 0.078$), except among thermal-vegetative combinations in June (ANOVA: $P = 0.021$) and among age-classes in October ($P < 0.001$; Table 3). For age-1 *O. mykiss* in June, W_r was lower in the conifer-cool streams than in the conifer-warm streams (Tukey's test: $P = 0.041$) and in both the mixed-cool and mixed-warm streams ($P < 0.033$). In October, W_r for age-0 *O. mykiss* was significantly higher than for age-1 (Tukey's test: $P = 0.003$) and age-2 ($P = 0.007$) fish for all streams combined (excludes the mixed-cool category).

Bioenergetics Modeling of Feeding Rate, Consumption, and Growth Efficiency

In model simulations, seasonal *O. mykiss* consumption ranged from 6% to 45% of maximum consumption

and averaged less than 25% among the tributaries from June to October (Table 4). Model-derived growth efficiency was generally higher during June–August and declined during the August–October simulations. Total model-derived consumption (during 3-month simulations) was low (<50 g) in most cases, with the exception of age-2 *O. mykiss* in Potato Creek and the hardwood-cool streams (range, 6.2–141.9 g). *Oncorhynchus mykiss* generally consumed more in the hardwood-cool streams than in the other forest cover types (Figure 5). Terrestrial and adult aquatic invertebrates represented important fractions of the prey biomass consumed for most age-classes in all streams during June–October (5–41% for age-0, 9–84% for age-1, and 27–92% for age-2 fish; Figure 5), and terrestrial insects represented 4–51% of the total energy budget during this period. For age-2 fish in the hardwood-cool streams, there was less reliance on terrestrial and aquatic adults (30–52%) than in the conifer and mixed categories, with fish having higher overall consumption rates (>50 g).

Field measurements suggested that most of the growth occurred outside the presumed growing season

TABLE 4.—Bioenergetics model output for *O. mykiss* in individual streams during June, August, and October 2003. Growth efficiency (GE) was calculated by dividing the average growth over each simulation period by the model estimate of consumption (*C*). *P* is the ratio of *C* to maximum consumption.

Location, age, and month	<i>C</i> (g)	<i>P</i>	GE (%)
Conifer-cool			
Barker Creek			
Age 0			
Jun–Aug	9.13	0.20	8.90
Aug–Oct	10.80	0.18	7.73
Age 1			
Jun–Aug	27.73	0.16	6.85
Aug–Oct	26.00	0.14	2.89
Age 2			
Jun–Aug	47.88	0.20	7.94
Aug–Oct	42.71	0.16	3.98
Conifer-warm			
Carrier Gulch			
Age 0			
Aug–Oct	10.06	0.15	−0.79
Age 1			
Jun–Aug	28.17	0.15	−2.31
Aug–Oct	26.48	0.16	3.27
Age 2			
Jun–Oct	201.01	0.32	9.70
Ditch Gulch			
Age 0			
Aug–Oct	9.49	0.19	7.22
Age 1			
Jun–Aug	24.28	0.16	0.31
Aug–Oct	16.83	0.12	−7.28
Age 2			
Jun–Aug	46.75	0.16	−0.36
Mixed-cool			
Chanellula Creek			
Age 0			
Aug–Oct	6.21	0.14	4.93
Age 1			
Jun–Aug	24.98	0.20	11.04
Aug–Oct	19.03	0.13	−1.05
Age 2			
Jun–Aug	39.04	0.16	7.04
Mixed-warm			
Potato Creek			
Age 0			
Jun–Aug	8.41	0.25	9.76
Aug–Oct	6.81	0.16	3.67
Age 1			
Jun–Aug	38.22	0.24	6.51
Aug–Oct	8.51	0.06	−41.95
Age 2			
Jun–Aug	141.94	0.45	15.22
Aug–Oct	83.86	0.21	6.36
West Twin Creek			
Age 0			
Jun–Aug	13.94	0.35	15.38
Aug–Oct	13.32	0.20	8.40
Age 1			
Jun–Aug	26.06	0.19	4.24
Aug–Oct	21.48	0.16	3.40
Age 2			
Jun–Aug	30.93	0.15	−3.77
Aug–Oct	26.01	0.13	2.56

TABLE 4.—Continued.

Location, age, and month	<i>C</i> (g)	<i>P</i>	GE (%)
Hardwood-cool			
Monroe Creek			
Age 0			
Aug–Oct	11.34	0.15	5.29
Age 1			
Jun–Aug	33.83	0.18	5.95
Aug–Oct	35.42	0.18	4.53
Age 2			
Jun–Aug	65.54	0.21	3.69
Aug–Oct	86.17	0.25	7.06
Olsen Creek			
Age 0			
Jun–Aug	14.24	0.32	13.22
Aug–Oct	15.45	0.21	9.49
Age 1			
Jun–Aug	36.65	0.25	7.27
Aug–Oct	25.11	0.16	1.64
Age 2			
Jun–Aug	78.28	0.27	9.69
Aug–Oct	45.40	0.15	−2.72
Underwood Creek			
Age 0			
Jun–Aug	15.58	0.33	15.95
Aug–Oct	11.06	0.25	−0.90
Age 1			
Jun–Aug	29.12	0.18	−2.14
Aug–Oct	17.95	0.13	−12.16
Age 2			
Jun–Aug	112.49	0.32	9.73
Aug–Oct	82.72	0.21	−0.64

of June–October simulated here, especially for age-0 and age-1 fish. The higher observed weight gain between April and June was accompanied by higher consumption rates (over 25% $C_{\max}$) in Barker Creek and 23–44% $C_{\max}$ in Carrier Gulch, and higher growth efficiencies (Table 5). Simulated temperature increases ranging from 1.4°C to 5.5°C during the summer and from 1.5°C to 2.9°C during the winter caused reduced growth in both conifer-dominated streams that were modeled year-round. During the summer (June–August), age-1 fish grew more slowly (low-temperature simulation) and lost weight (medium- and high-temperature simulations) in the conifer-warm stream (Carrier Gulch; summer growth was 0.4–4.5 times lower than normal) than in the conifer-cool stream (Barker Creek; summer growth was 0.05–0.8 times lower) during the summer (Figure 6). The growth curve during the subsequent winter was steeper in the conifer-warm stream than in the conifer-cool stream (Figure 6).

Discussion

Our bioenergetic simulations demonstrated that summer growth of *O. mykiss* in the nine study streams was limited by feeding rate and elevated temperatures (Brandt et al. 1992). Consumption estimates during

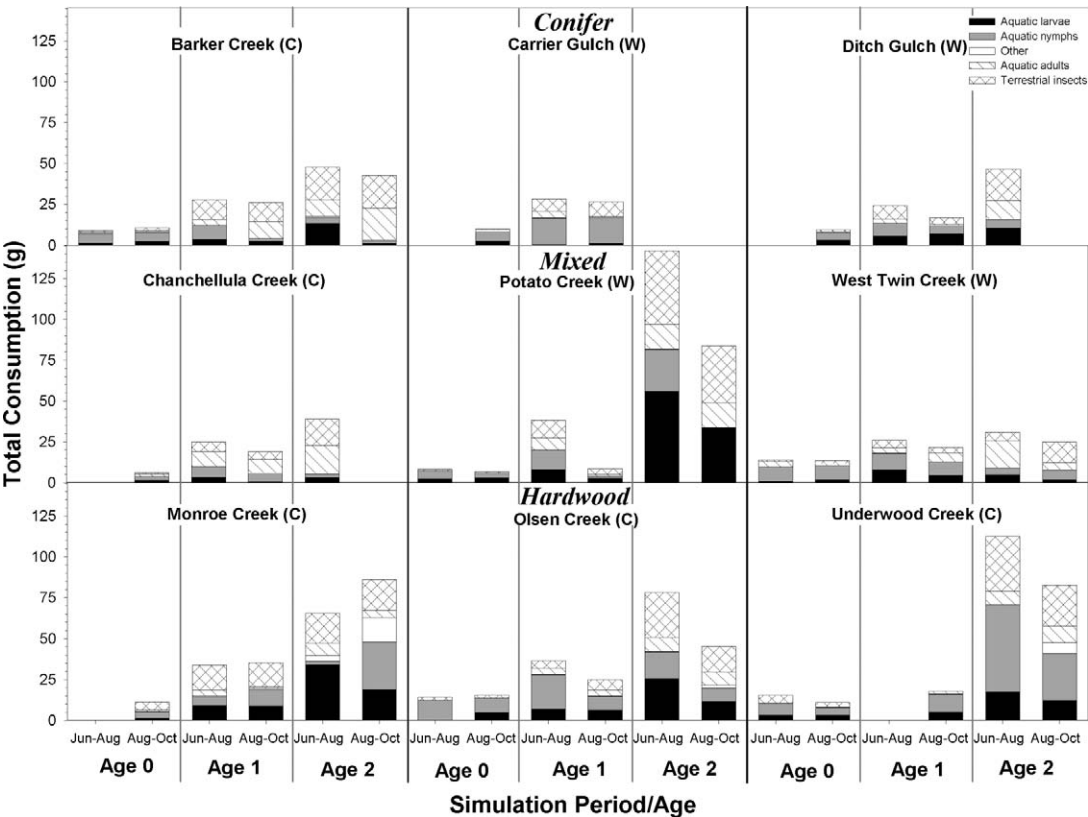


FIGURE 5.—Bioenergetics model estimation of total consumption (biomass) of five prey types over 2-month simulation periods (June–August and August–October) for age-0, age-1, and age-2 *O. mykiss* in cool (C) and warm (W) streams in three forest cover categories. See Figure 4 for prey types.

June–October were routinely less than 25% of the physiological maximum consumption rate for fish of comparable size under the prevailing temperature regimes, which is low compared with steelhead in other systems (Godby et al. 2007). As predicted by theoretical bioenergetics model runs (Figure 2), a low ration accentuated the detrimental effects of high stream temperatures, even though temperatures remained well below the lethal range for the species.

For the two streams with year-round temperature data (Carrier Gulch and Barker Creek), our modeling results showed a rapid increase in growth during spring (April to June), with higher proportions of maximum consumption during this period (Figure 6). During the spring, these streams experienced both lower temperatures and higher flows. Higher stream flow probably increased habitat and prey availability, and lower temperatures reduced the effect of thermal stress on *O. mykiss*. The simulated reductions in *O. mykiss* growth under three climate change scenarios further emphasized the effect of low feeding rate on

temperature-dependent growth. Though temperatures did not exceed 20°C, low consumption rates caused the optimal temperature for growth to decrease and the result was low or negative growth (Figure 2). Recent trends in global climate change suggest increased temperatures are likely for our study region, which will result in river and stream temperatures becoming warmer (Eaton and Scheller 1996; Cayan et al. 2006a, 2006b). These predicted increases in stream temperatures could restrict *O. mykiss* growth in many West Coast streams, as demonstrated by our bioenergetics modeling. Other species of salmonids may be similarly affected, as stream temperatures and precipitation patterns vary outside of their historical ranges. Further, temperature fluctuations associated with climate change have the capacity to alter macroinvertebrate community structure, including species diversity, abundance, survival, and emergence timing (Hogg and Williams 1996; Harper and Peckarsky 2006).

In addition to the differences in *P*-values between spring and our June–October simulation period, our

TABLE 5.—Bioenergetics model output for *O. mykiss* in two conifer-dominated streams (Barker Creek and Carrier Gulch). Temperature measurements from April 2003 to April 2004 were used to model consumption for 2 years of growth (August age 0 to August age 2).

Location, age, and month	C (g)	P	GE (%)
Conifer-cool			
Barker Creek			
Age 0			
Aug–Oct	10.82	0.18	7.67
Oct–Jun	65.68	0.26	16.50
Age 1			
Jun–Aug	35.01	0.19	5.42
Aug–Oct	26.14	0.14	2.87
Oct–Jun	95.88	0.20	4.43
Age 2			
Jun–Aug	51.20	0.19	7.42
Conifer-warm			
Carrier Gulch			
Age 0			
Aug–Oct	10.13	0.15	−0.79
Oct–Apr	25.10	0.24	6.45
Age 1			
Apr–Jun	40.57	0.44	16.59
Jun–Aug	30.40	0.15	−2.14
Aug–Oct	26.67	0.16	3.26
Age 2			
Oct–Jun	95.31	0.23	6.21

field measurements of *O. mykiss* growth indicated that age-0 fish approximately tripled in weight between October and the following June. Size-selective or density-dependent mortality is a possible explanation for this result (Marschall and Crowder 1995; Keeley 2003). If the smallest fish at the end of the summer do

not survive through the winter, then the apparent growth that resulted from sampling the larger surviving age-1 fish in June would overestimate the true growth rate during October–June. However, we did not see the size-selective truncation of the length frequency histogram for age-1 fish that would suggest such pressure. The more likely explanation for increased growth during winter and spring was improved growing conditions due to lower stream temperatures, increased feeding rate, or both. This hypothesis was supported by the higher growth efficiencies estimated during these periods. The already low consumption rates and growth efficiencies during June–August generally declined even further during the August–October simulation periods. In situ prey production often decreases through the summer as stream temperatures increase (Nakano and Murakami 2001). Therefore, fish simultaneously experience lower prey availability and higher thermal stress, which leads to reduced growth efficiency.

Because a higher proportion of *O. mykiss* diet consisted of adult invertebrates in mixed-cool streams than in conifer-warm and mixed-warm streams, we may expect higher growth rates in the cool streams. Previous research has determined a link between thinner riparian cover and increased average stream temperature and temperature fluctuation (Bourque and Pomeroy 2001; Macdonald et al. 2003). In the cool streams, the moderate temperatures may result in part from thick forest cover providing shade. More vegetation over the streambed would probably cause higher levels of allochthonous input, including high-

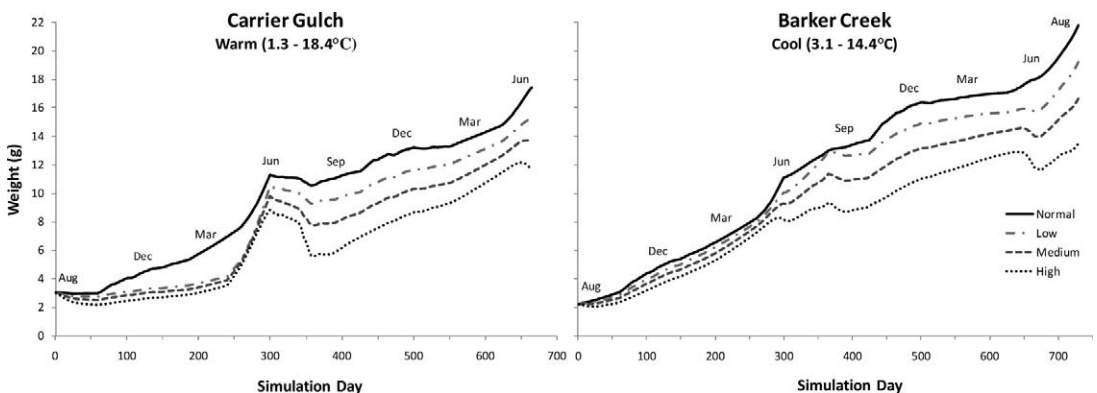


FIGURE 6.—Bioenergetics model output of daily growth for age-0, age-1, and age-2 *O. mykiss* under three climate change scenarios in two conifer-dominated streams. Growth was estimated using consumption rates from the initial modeling for these streams (solid lines). Average daily stream temperature was modified according to summer and winter climate change projections for northern California (Cayan et al. 2006b). Low, medium, and high projections were used for summer (June–August; low: +1.4°C, medium: +3.2°C, high: +5.5°C) and winter (December–February; +1.5°C, +2.0°C, +2.9°C); the average summer and winter projections were then used to modify the spring (March–May) and fall (September–November) temperatures (+1.4°C, +2.6°C, +4.2°C).

quality adult invertebrate prey sources (Edwards and Huryn 1996; Nakano et al. 1999). However, fish growth may not be obviously higher in shaded streams than in more exposed streams. Though thick forest cover offers many advantages to stream-dwelling fish, such as bank stabilization, large woody debris input, and increased allochthonous input, increased light exposure (e.g., from logging practices) can increase primary production, which thereby increases aquatic prey production (Bilby and Bisson 1987). Vegetation type may also affect the type and amount of allochthonous (terrestrial) invertebrate input. Previous research documented higher biomass of terrestrial invertebrate input in streams dominated by deciduous (alder) cover compared with coniferous (hemlock and spruce; Allan et al. 2003). However, there were no clear patterns in drift or diet composition among vegetative stream categories.

Of the food choices experienced by fish in streams, aquatic invertebrates (including larvae and nymphs) were less energy-rich than terrestrial or adult aquatic insects owing to differences in water content. Based on our bomb calorimetry results and on previous research, we expected older fish that consumed more adult or terrestrial invertebrates to exhibit better body condition than younger fish that consumed more immature forms of aquatic invertebrates (Mason and Macdonald 1982; Filbert and Hawkins 1995; Wipfli 1997). However, no significant difference in W_r was detected among age-classes. However, using standard weight (W_s) for nonanadromous rainbow trout could lead to bias in age-2 or older steelhead that may have begun the smoltification process. Further, because growth rate is a significant determinant for smoltification to occur, fish that grew fastest may have tended to leave the system as smolts at a younger age, thereby truncating the growth curves (Weatherley and Gill 1995).

Age-0 fish in conifer-cool and mixed-cool streams exhibited higher initial weights in June than age-0 fish in mixed-warm streams. Though warm streams would normally be associated with earlier emerging fry, the thermograph for our study streams suggested that the "cool" streams experienced more moderate fluctuations from minimum to maximum temperature over the year than did the "warm" streams, which showed sharper increases in temperature from winter lows to summer highs. Since the cool streams appeared to stay slightly warmer through the winter of 2002–2003, the fry in these streams probably developed faster and were able to emerge earlier. The earlier-emerging fish have the opportunity to establish feeding territories sooner than fish that emerge later (Jones et al. 2003) and will grow larger than later-emerging fish (Chandler and Bjornn 1988). Since growth conditions apparently

degraded significantly during the summer, earlier emergence during the higher growth period in the spring could confer a significant selective advantage in these streams, if early spring floods do not select against early emergence (Jensen and Johnsen 2002). Alternatively, adult spawning time may be adapted to localized thermal regimes, so differences in adult spawning time among streams may affect fry emergence time.

Significant differences in diet among seasons should indicate seasonal differences in drift composition; however, we did not detect many significant differences in invertebrate drift composition. Our sampling technique may have overrepresented immature aquatic invertebrates and undersampled adult aquatic and terrestrial insects because adult invertebrates (especially aquatic adult stages) were probably floating on the surface and may have evaded our drift samplers (Leung et al. 2009). In future studies, it would be useful to deploy rectangular drift samplers during the day. The samplers should only be partially submerged so that the surface drift and submerged cross-section can be quantified and translated into unbiased estimates of surface and water column drift.

Future research should include an investigation of the effects of habitat suitability as well as inter- and intraspecific competition for prey and feeding territories in the streams. Habitat suitability (e.g., low prey supply, high fish density, and the presence of predators) may drive fish to move among habitat units or streams, thereby causing changes in densities, feeding rate, and fish growth. Fish that tend to emigrate have been found to grow more (Kahler et al. 2001). *Oncorhynchus mykiss* density or occurrence of other species (e.g., herpetofauna) that compete for similar prey types might also affect growth efficiency among streams.

Our direct measurements of growth, bioenergetics modeling, and climate change scenarios suggest that interannual variation in temperature or global warming could push this food-limited population further into negative growth patterns and reduce productivity of the freshwater rearing habitat. The implications for a population likely to become endangered or threatened in the foreseeable future are grave. Although current consumption levels are presumably sufficient during the summer growing season to maintain current stock productivity, our modeling suggests that even minor reductions in ration or increases in temperature could diminish the stock considerably. Future research may include looking at individual fish to determine which portions of the population are most vulnerable.

This approach could be applied to predict how other West Coast steelhead populations would react to climate change. Proper forest and stream management

for sensitive, threatened or endangered salmonid stocks is essential for future conservation and recovery efforts. Since consumption rates were severely constrained in our study streams, forest practices that maximize riparian vegetation shading to reduce solar input and increase allochthonous prey input may keep streams closer to the optimal temperature for *O. mykiss* growth as well as provide greater nutritional benefits for stream-dwelling salmonids.

Acknowledgments

We thank Hartwell Welsh of the U.S. Forest Service's Redwood Sciences Laboratory in Arcata, California, as well as John Lang and Jim Fitzgerald of the U.S. Forest Service's ranger station in Hayfork, California, for background research, local insight, field support, and supplementary data. Funding and support was provided by the U.S. Geological Survey, Western Fisheries Research Center, the University of Washington, Cooperative Fish and Wildlife Research Unit, and the U.S. Forest Service's Redwood Sciences Laboratory. Additional assistants and volunteers included Evelyn Chia, Daniel O'Donnell, Adam Van Mason, Catherine Chambers, Christina Galitsky, Jeremy Steinbacher, Jim Matilla, Chris Sergeant, and Steve Damm. This paper benefited from reviews by Walt Duffy, Scott Vanderkooi, and journal peer reviewers. The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Government of any product or service to the exclusion of others that may be suitable.

References

- Allan, J. D., M. S. Wipfli, J. P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. *Canadian Journal of Fisheries and Aquatic Sciences* 60:309–320.
- Anderson, R. O., and R. M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447–481 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Arrington, A. A., K. O. Winemiller, W. F. Loftus, and S. Akin. 2002. How often do fishes "run on empty"? *Ecology* 83:2145–2151.
- Beauchamp, D. A. In press. Bioenergetics ontogeny: linking stage-specific feeding and growth to life cycle survival of salmon. American Fisheries Society, Special Publication, Bethesda, Maryland.
- Beecher, H. A., J. P. Carleton, and T. H. Johnson. 1995. Utility of depth and velocity preferences for predicting steelhead parr distribution at different flows. *Transactions of the American Fisheries Society* 124:935–938.
- Bilby, R. E., and P. A. Bisson. 1987. Emigration and production of hatchery coho salmon (*Oncorhynchus kisutch*) stocked in streams draining an old-growth and clear-cut watershed. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1397–1407.
- Bourque, C. P. A., and J. H. Pomeroy. 2001. Effects of forest harvesting on summer stream temperatures in New Brunswick, Canada: an intercatchment, multiple-year comparison. *Hydrology and Earth System Sciences* 5(4):599–613.
- Bowen, S. H. 1996. Quantitative description of the diet. Pages 513–531 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Bowser, P. R. 2001. Anesthetic options for fish. Pages xx–yy in R. D. Gleed and J. W. Ludders, editors. *Recent advances in veterinary anesthesia and analgesia: companion animals*, volume A1412.0701. International Veterinary Information Service, Ithaca, New York.
- Brandt, S. B., D. M. Mason, and E. V. Patrick. 1992. Spatially explicit models of fish growth rate. *Fisheries* 17(2):23–31,34–35.
- Busby, P. J., T. C. Wainwright, and R. S. Waples. 1994. Status review for Klamath Mountains Province steelhead. NOAA Technical Memorandum NMFS-NWFSC-19.
- Cayan, D., A. Luers, M. Hanemann, G. Franco, and B. Croes. 2006a. Scenarios of climate change in California: an overview. California Climate Change Center, Report CEC-500-2005-186-SF, San Diego.
- Cayan, D., E. Maurer, M. Dettinger, M. Tyree, K. Hayhoe, C. Bonfils, P. Duffy, and B. Santer. 2006b. Climate scenarios for California. California Climate Change Center, Report CEC-500-2005-203-SF, San Diego.
- Chandler, G. L., and T. C. Bjornn. 1988. Abundance, growth, and interactions of juvenile steelhead relative to time of emergence. *Transactions of the American Fisheries Society* 117:432–443.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297–1304.
- Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *International Association of Theoretical and Applied Limnology Communications* 18.
- DeVries, D. R., and R. V. Frie. 1996. Determination of age and growth. Pages 483–512 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. *Limnology and Oceanography* 41:1109–1115.
- Edwards, E. D., and A. D. Huryn. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia* 337(1–3):151–159.
- Filbert, R. B., and C. P. Hawkins. 1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. *Transactions of the American Fisheries Society* 124:824–835.
- Giles, N. 1980. A stomach sampler for use on live fish. *Journal of Fisheries Biology* 16:441–444.
- Godby, N. A., Jr., E. S. Rutherford, and D. M. Mason. 2007. Diet, feeding rate, growth, mortality, and production of

- juvenile steelhead in a Lake Michigan tributary. *North American Journal of Fisheries Management* 27:578–592.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. *Fish Bioenergetics 3.0*. University of Wisconsin, Sea Grant Institute, Madison.
- Harper, M. P., and B. L. Peckarsky. 2006. Emergence cues of a mayfly in a high-altitude stream ecosystem: potential response to climate change. *Ecological Applications* 16(2):612–621.
- Hill, J., and G. D. Grossman. 1993. An energetic model of microhabitat use for rainbow trout and rosyside dace. *Ecology* 74(3):685–698.
- Hogg, I. D., and D. D. Williams. 1996. Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. *Ecology* 77(2):395–407.
- Hughes, N. F. 1998. A model of habitat selection by drift-feeding stream salmonids at different scales. *Ecology* 79(1):281–294.
- Hurn, A. D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. *Limnological Oceanography* 41:243–252.
- Kahler, T. H., P. Roni, and T. P. Quinn. 2001. Summer movement and growth of juvenile anadromous salmonids in small western Washington streams. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1947–1956.
- Keeley, E. R. 2003. An experimental analysis of self-thinning in juvenile steelhead trout. *Oikos* 102:543–550.
- Jensen, A. J., and B. O. Johnsen. 2002. The functional relationship between peak spring floods and survival and growth of juvenile Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). *Functional Ecology* 13(6):778–785.
- Jones, M., A. Laurila, N. Peuhkuri, J. Piironen, and T. Seppä. 2003. Timing an ontogenetic niche shift: responses of emerging salmon alevins to chemical cues from predators and competitors. *Oikos* 102:155–163.
- Leung, E. S., J. S. Rosenfeld, and J. R. Bernhardt. 2009. Habitat effects on invertebrate drift in a small trout stream: implications for prey availability to drift-feeding fish. *Hydrobiologia* 623:113–125.
- Macdonald, J. S., E. A. MacIsaac, and H. E. Herunter. 2003. The effect of variable-retention riparian buffer zones on water temperatures in small headwater streams in subboreal forest ecosystems of British Columbia. *Canadian Journal of Forest Research* 33(8):1371–1382.
- Manly, B. F. J., P. Miller, and L. M. Cook. 1972. Analysis of a selective predation experiment. *American Naturalist* 106:719–736.
- Marschall, E. A., and L. B. Crowder. 1995. Density-dependent survival as a function of size in juvenile salmonids in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 52:136–140.
- Mason, C. F., and S. M. Macdonald. 1982. The input of terrestrial invertebrates from tree canopies to a stream. *Freshwater Biology* 12(4):305–311.
- Maurer, E. P., and P. B. Duffy. 2005. Uncertainty in projections of stream flow changes due to climate change in California. *Geophysical Research Letters* 32:L03704.
- McMahon, T. E., A. V. Zale, and D. J. Orth. 1996. Aquatic habitat measurements. Pages 83–120 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Mills, T. J., D. R. McEwan, and M. R. Jennings. 1997. California salmon and steelhead: beyond the crossroads. Pages 91–111 in D. J. Stouder, P. A. Bisson, and R. J. Naiman, editors. *Pacific salmon and their ecosystems: status and future options*. Chapman and Hall, New York.
- Morinville, G. R., and J. B. Rasmussen. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 60:401–410.
- Moyle, P. B. 1994. The decline of anadromous fishes in California. *Conservation Biology* 8:869–870.
- Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* 80(7):2435–2441.
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the USA* 98:166–170.
- Orth, D. J. 1983. Aquatic habitat measurements. Pages 61–111 in L. A. Nielsen and D. L. Johnson, editors. *Fisheries techniques*. American Fisheries Society, Bethesda, Maryland.
- Rabeni, C. F. 1996. Invertebrates. Pages 335–352 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Rand, P. S., D. J. Stewart, P. W. Seelback, M. L. Jones, and L. R. Wedge. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. *Transactions of the American Fisheries Society* 122:977–1001.
- Reynolds, J. B. 1996. Electrofishing. Pages 221–253 in B. R. Murphy and D. W. Willis, editors. *Fisheries techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Swaka, J. A., and K. J. Hartman. 2001. Effects of turbidity on prey consumption and growth in brook trout and implications for bioenergetics modeling. *Canadian Journal of Fisheries and Aquatic Sciences* 58:386–393.
- Weatherley, A. H., and H. S. Gill. 1995. Growth. Pages 103–151 in C. Groot, L. Margolis, and W. C. Clark, editors. *Physiological ecology of Pacific salmon*. UBC Press, Vancouver.
- Webb, B. W., D. M. Hannah, R. D. Moore, L. E. Brown, and F. Nobilis. 2008. Recent advances in stream and river temperature research. *Hydrological Processes* 22:902–918.
- Wege, G. J., and R. O. Anderson. 1978. Relative weight (W_t): a new index of condition for largemouth bass. Pages 79–91 in G. D. Novinger and J. G. Dillard, editors. *New approaches to the management of small impoundments*. American Fisheries Society, North Central Division, Special Publication 5, Bethesda, Maryland.
- Welsh, H. H., Jr., and G. R. Hodgson. 1997. A hierarchical strategy for sampling herpetofauna assemblages along small streams in the western U.S., with an example from northern California. *Transactions of the Western Section of the Wildlife Society* 33:56–66.
- Welsh, H. H., Jr., and A. J. Lind. 2002. Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou region of California and Oregon. *Journal of Wildlife Management* 66:581–602.

- Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1259–1269.
- Zabel, R. W., and S. Achord. 2004. Relating the size of juveniles to survival within and among populations of Chinook salmon. *Ecology* 85(3):795–806.
- Zar, J. H. 1999. *Biostatistical analysis*, 4th edition. Prentice Hall, Upper Saddle River, New Jersey.