SEASONAL PATTERNS OF ANABOLISM AND CATABOLISM IN JUVENILE STEELHEAD: ENERGY PARTITIONING IN GROWTH

by

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ABSTRACT

Seasonal Patterns of Anabolism and Catabolism in Juvenile Steelhead: Energy Partitioning in Growth

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I examined growth patterns in young of the year steelhead trout in two northern California streams with different temperature regimes. Carr Creek served as the warm water stream and Barker Creek served as the cold water stream. Measurements of steelhead length, weight and lipid content were recorded on 7 sampling events over a 1 year period. The relationship between growth rates and several environmental variables (photoperiod, stream discharge and temperature) were investigated. Early spring was identified as a period of rapid anabolism in all types of growth, with preference to weight allocations. It appeared that high water temperatures imparted stress on steelhead in Carr Creek, as evidenced by the use of lipid stores, population declines and limited somatic growth during summer. In contrast, steelhead in the cooler water of Barker Creek exhibited summer growth in length, weight and lipid stores at some of the highest rates observed during the study in that stream. In the mild winter climate of northern California, water temperatures averaged 6^{o} C and rarely dipped below 4^{o} C. During early winter, steelhead trout in both streams showed no somatic growth and loss of lipid stores. Models investigated in this study suggest that the combination of regular flood events, lower water temperatures and shortened day length may draw upon energy reserves during winter.

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INTRODUCTION

The energetics of fish reflect the compilation of environmental opportunities and constraints with inherent and adapted tactics to maximize survival. Energy consumed by stream fishes is partitioned into various components. These include standard and active metabolism, digestion, somatic growth or energy storage (i.e. lipids) and waste. The allocation of consumed energy is a function of pre-determined behavioral and developmental strategies, and tactics in response to environmental conditions (Wootton 1984). There are trade-offs in the allocation of energy consumed by fish, energy devoted to one function or behavior, such as predator avoidance, is not available to other functions such as somatic growth or lipid storage. Varying seasonal environmental conditions impose differing stresses and resource limitations on stream fishes. Energy allocation strategies change throughout the year in response to local environmental conditions, prey availability and predation pressures (Forsman and Lindell 1991, Berg et al. 2000, Berg and Bremset 1998) with corresponding changes in physiology.

Pacific salmon physiology has been examined (Groot et al. 1995) most extensively in production or experimental hatcheries. Denton and Yousef (1976) observed specific periods of fat and protein increases in rainbow trout over a 14 month hatchery experiment, with rapid initial decreases in fat stores during 45-days of starvation. Hatchery experiments have documented positive relationships between feeding and temperature (Larsen et al. 2001). Other studies have shown that lipid metabolism may be related to the size of fish under stressful conditions (Connolly and Petersen 2003).

Detailed information on the seasonal energetics of wild fish is limited, with much of the work for salmonids focused in climates with harsh winter conditions and long periods of ice cover (Berg et al. 2000, Berg and Bremset 1998, Post and Parkinson 2001, Cunjak et al. 1987, Rikardsen and Elliott 2000). Although population-specific patterns are locally determined, lipids and protein are generally accumulated during warmer months and lipids are depleted during harsher winter months. Energy allocations to growth and lipid stores are size dependent, with implications for survival. The conflict among ways to allocate growth energy is greatest for the smallest fish of the youngest age groups during their first growing season. These small fish are most vulnerable to predation pressures that can be offset by greater size, but have the least amount of stored energy. It appears that, in spring, smaller fish give priority to increases in size, therefore reducing predation risk, rather than devoting energy to fat for energy storage (Post and Parkinson 2001). Larger fish tend to have greater lipid and protein stores than smaller fish, and therefore experience greater losses of protein and fat during winter (Berg and Bremset 1998). With the onset of spring, all sizes of fish are quick to resume growth. Energy allocations to growth and lipid stores are also growth rate dependent. Post and Parkinson (2001) found that slower growing individuals have lower lipid stores than faster growing fish of the same size.

It is clear that juvenile salmonids exhibit marked differences in proximate composition through the year, and that these differences are determined by environmental and population characteristics. Beckman et al. (2000) described the integrated seasonal pattern of physiological states in juvenile Chinook salmon to include four distinct phases:

1) anabolism in summer-fall in which fish gain size and increase lipid concentrations, 2) catabolism in winter in which growth ceases and lipids are depleted, 3) anabolism in early spring in which growth replenishes energy reserves and 4) a combination of anabolism and catabolism during late spring in which size increases but lipids decrease. Most studies on the topic report this general pattern, yet differ in the timing and magnitude of physiological changes.

In the more southern portion of their range, both summer and winter may be stressful periods for juvenile steelhead trout. In northern California streams, three periods of growth (in terms of change in mean fish length over time) have been described for juvenile steelhead: high initial spring growth, slowed growth during low flow summer months, and increased growth following fall rains (Reeves 1979, Allen 1986). It is believed that winter growth is minimal in northern California. Little information is available about the physiological condition of salmonids throughout summer and winter in this area.

The objectives of this descriptive field study were to describe seasonal changes in body size and lipid stores of young-of-the-year steelhead trout in two streams with differing thermal regimes and relate these changes to differences in environmental conditions. I hypothesized that higher summertime water temperatures in Carr Creek would be more taxing on juvenile steelhead trout than cooler summertime water temperatures of Barker Creek. I hypothesized that physiology would reflect this stress through limited somatic growth and depletion of lipid stores. I also hypothesized that shortened day length of winter months, combined with high-flows and low-temperatures would impart stress on young-of-the-year steelhead in both streams.

STUDY AREA

This study was carried out on Carr and Barker creeks. These streams are located in neighboring watersheds in the upper South Fork Trinity Basin of northern California (Figure 1). This region is characterized by cool, wet winters and hot, dry summers. Steelhead trout abundance was high in the region in the early 20th century, but has since declined. Study reaches were selected in these two streams because they are similar in watershed characteristics, yet differ in summertime water temperature regime. Carr Creek (19.0 ^{o}C maximum mean weekly temperature, Jim Fitzgerald, 2001 US Forest Service unpublished data) was selected as representative of high water temperature streams in the region. Barker Creek (14.1 ^{o}C maximum mean weekly temperature, Jim Fitzgerald, 2001 US Forest Service unpublished data) was selected as representative of low water temperature streams in the region. A water diversion below the study reach on Carr Creek withdraws most of the stream's flow during later summer and most likely prevents fish movement at that time. During the study, steelhead trout dominated the fish community in both streams. Other species commonly observed in both streams include lamprey ammocetes (*Lampetra spp.)*, yellow-legged frog *(Rana boylii),* pacific giant salamanders *(Dicamptodon tenebrosus),* and crayfish species.

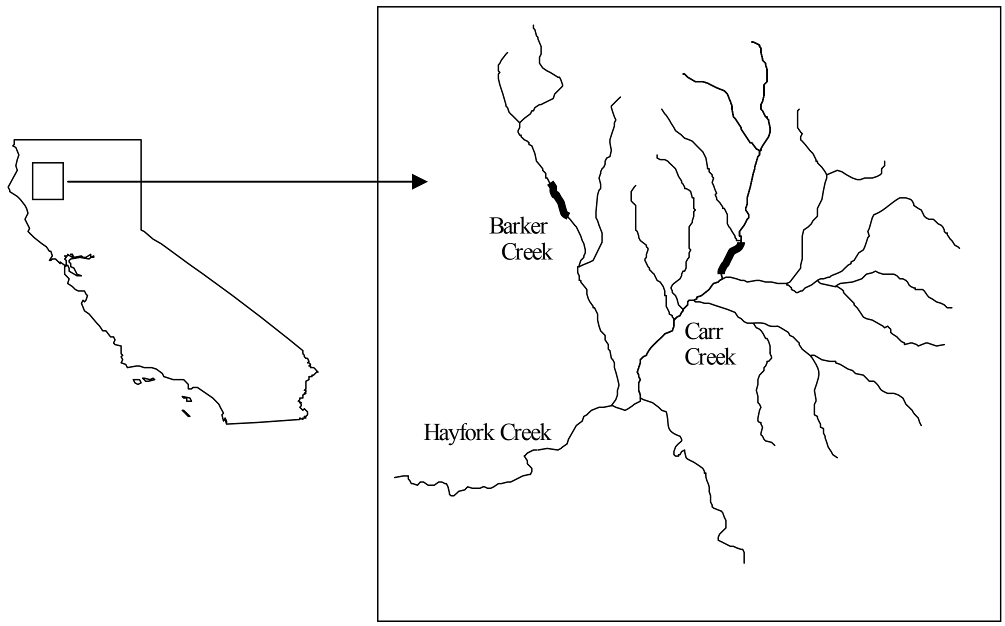

Figure 1. Location of study sites in Barker Creek and Carr Creek in the upper South Fork Trinity River basin in northern California. One kilometer study reaches are indicated as bolded segments. The lower end of the sample reach in Barker Creek was 40° 36’ 09.94” N, 123 ° 06’ 52.99” W, and in Carr Creek was 40 ° 35’ 02.65” N, 123 ° 04 25.15” W.

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MATERIALS AND METHODS

Study Design

One kilometer stream segments selected as study reaches in each stream were sampled in July, September, and November of 2002 and January, April, June and August of 2003. Sampling periods were based on photoperiod, expected flow conditions and water temperature. Data collected during each sampling period consisted of habitat typing, steelhead trout abundance estimation, fish size measurements and selection of individual fish to sacrifice for lipid analysis.

High winter flows prevented implementing the full sampling protocol during January. Stream measurements and abundance estimates were not conducted during the January sampling, but steelhead were collected for lipid analysis to examine the possibility of an early winter metabolic deficit (Cunjak et al. 1987). Steelhead were collected from throughout the reach where flows allowed safe access to the stream. Length and weight of collected steelhead were recorded.

Stream Measurements

Stream temperature was monitored in each stream for the duration of the study with temperature data loggers (Onset Corporation, Pocase, Massachusetts). Water temperature metrics calculated include total degree days and mean daily range in temperature for each stream during each sampling interval. Discharge was measured during each sampling interval at both creeks. Stream flow for each creek was then estimated using the Maintenance of Variance Extension, Type 1 (MOVE.1) equation (Hirsch, 1982) with Grass Valley Creek serving as the long term dataset. Equations used in this method are set to maintain the sample mean and variance and have been found to minimize bias in comparison with other methods (Hirsch 1982). Stream flow metrics calculated included mean discharge and variance of discharge for each sampling interval. Daily photoperiod was estimated at 40.5 degrees latitude using a Java Applet available at http://www.geoastro.de/astro/astroJS/decEoT/index.htm.

During each sampling period, stream habitat units were classified into one of four habitat strata. Runs, riffles, or pools were separated using methodologies outlined in Bison et al. (1982). Units considered unsuitable for electrofishing due to extreme large woody debris, or shallow cascades were classified as "complex". Habitat units were numbered sequentially beginning at the downstream end of the reach to allow for individual identification. Small habitat units with a width to depth ratio less than 1 were included in the upstream habitat unit. The thalweg length, maximum depth, and the width and average depth at 1/3 and 2/3 of the unit length were recorded.

Abundance Estimation

Within one week of habitat typing, multiple pass depletion electrofishing was used to determine steelhead abundance in pools, runs and riffles. Habitat units were randomly selected in each habitat strata and at least 25% of the units in each stratum were sampled. Selected habitat units were blocked with 6 mm mesh netting at the upstream and downstream boundaries. Units were electrofished with a Smith Root Model 12

(Smith-Root, Inc., Seattle, Washington) backpack electrofisher starting at the downstream end and shocking up to the top and back again to complete one pass. Each unit was electrofished with at least two passes. If the number of steelhead caught on the second pass was greater than 25% of the number caught on the first pass, a third pass was performed. The amount of time spent on each subsequent pass was at least 90% of the first pass to ensure equal effort among passes. The number of steelhead caught on each pass was recorded. Abundance was estimated in each habitat type using the bias adjusted jackknife estimator:

$$\hat{y}_J = \sum_{i=1}^{m-1} C_i + \frac{C_m}{\hat{p}},$$

where $\hat{y}_J$ is steelhead abundance in each unit, C_i denotes the number of steelhead caught on pass i, m refers to the number of passes $\hat{p}$ is an estimate of capture probability, which was estimated as:

$$\hat{p} = 1 - \frac{\sum_{k=1}^{n} \sum_{i=1}^{m} C_{ik} - \sum_{k=1}^{n} C_{1k}}{\sum_{k=1}^{n} \sum_{i=1}^{m} C_{ik} - \sum_{k=1}^{n} C_{mk}},$$

where C_{ik} is the number of steelhead caught on all passes, C_{1k} is the number caught on the first pass, C_{mk} is the number caught on the final pass and k is the number of habitat units (1,2,3….n).

Fish abundance in each strata in the reach was estimated using surface area as an auxiliary variable with the equation:

$$\hat{t}_y = t_z \frac{\sum_{k=1}^{n} \hat{y}_J}{\sum_{k=1}^{n} z_k}$$

where $\hat{t}_y$ is the total number of fish in each strata, t_z is the total surface area of all units in the reach in that strata, and z_k is the sum of the area of the units sampled in each strata. Variance for the $\hat{t}_y$ estimator was calculated using the equation:

$$\hat{V}(\hat{t}_y) = N^2 \frac{(1-n/N)}{n} \frac{\sum_{k=1}^{n} z_k^2 (\hat{\bar{y}}_k - \hat{\bar{\bar{y}}})^2}{n-1} + \frac{N}{n} \sum_{k=1}^{n} \hat{V}(\hat{y}_k),$$

where N equals the total number of units in each strata in the reach, n equals the number of units sampled in each strata, $\hat{\bar{y}} = \hat{y}_k / \hat{z}_k$, $\hat{\bar{\bar{y}}} = \sum_{k=1}^{n} \hat{y}_k / \sum_{k=1}^{n} z_k$, and $\hat{V}(\hat{y}_k) = m(m-1)C_m$.

The total number of fish in the reach, $\hat{t}$, was estimated as the sum of $\hat{t}_y$ for all strata. The variance for the reach was estimated as the sum of $\hat{V}(\hat{t}_y)$ for all strata. Confidence intervals for the population estimate were estimated as $\hat{t}_y \pm 2\sqrt{\hat{V}(\hat{t}_y)}$.

Fish Sampling

Biological data were collected on all steelhead trout captured. For all fish captured, fork length was measured to the nearest mm and wet weight measured to the nearest 0.01 g. Scales were collected from a total of 530 steelhead, or 33% of the 1,619 steelhead captured during the study. Scale samples for age determination were collected from approximately 50 steelhead in each stream during each sample period. Systematic random sampling was used to select fish for scale collection. The interval for scale collection was based upon the number of fish collected from the previous sample period.

Additional scales were collected from fish that were at the expected tail ends of the age class histogram, estimated from the distribution of steelhead from the previous sampling period. Age determination from scales was as outlined in Devries and Frie (1996). A second individual confirmed ages on 25% of all scales read.

To assign unaged fish to the appropriate age class, length histograms were created that included all fish sampled and aged fish for each sampling period in each stream (Figures 2, 3). Upper and lower length limits were assigned to an age class based on histograms. These length limits were used to assign un-aged fish to an age class. Length histograms were good estimators of age class because they showed fairly discrete age classes that were confirmed by aged fish. During some sampling periods, the length frequency distributions overlapped at the upper and lower ends of an age class. However, scales were collected from all steelhead at the tail ends of the length distribution when overlap occurred.

During each sampling period, a minimum of six steelhead were selected for lipid analysis at each site using systematic random sampling. Scales were collected on all sacrificed steelhead. Sacrificed steelhead were immediately placed on ice in the field and then stored in a super cooled freezer at –80 ^{o}C until analysis. Lipid analysis was conducted by ABC Research Corporation, Gainesville, Florida. Lipid analysis was determined using an acid hydrolysis method for determining total fat in steelhead (Association of Official Analytical Chemists, 1975). Whole steelhead samples were pulverized to uniform consistency. Samples were dried and then weighed (W_1). Petroleum spirits were added to the Soxhlet Extraction Apparatus and heated to boiling

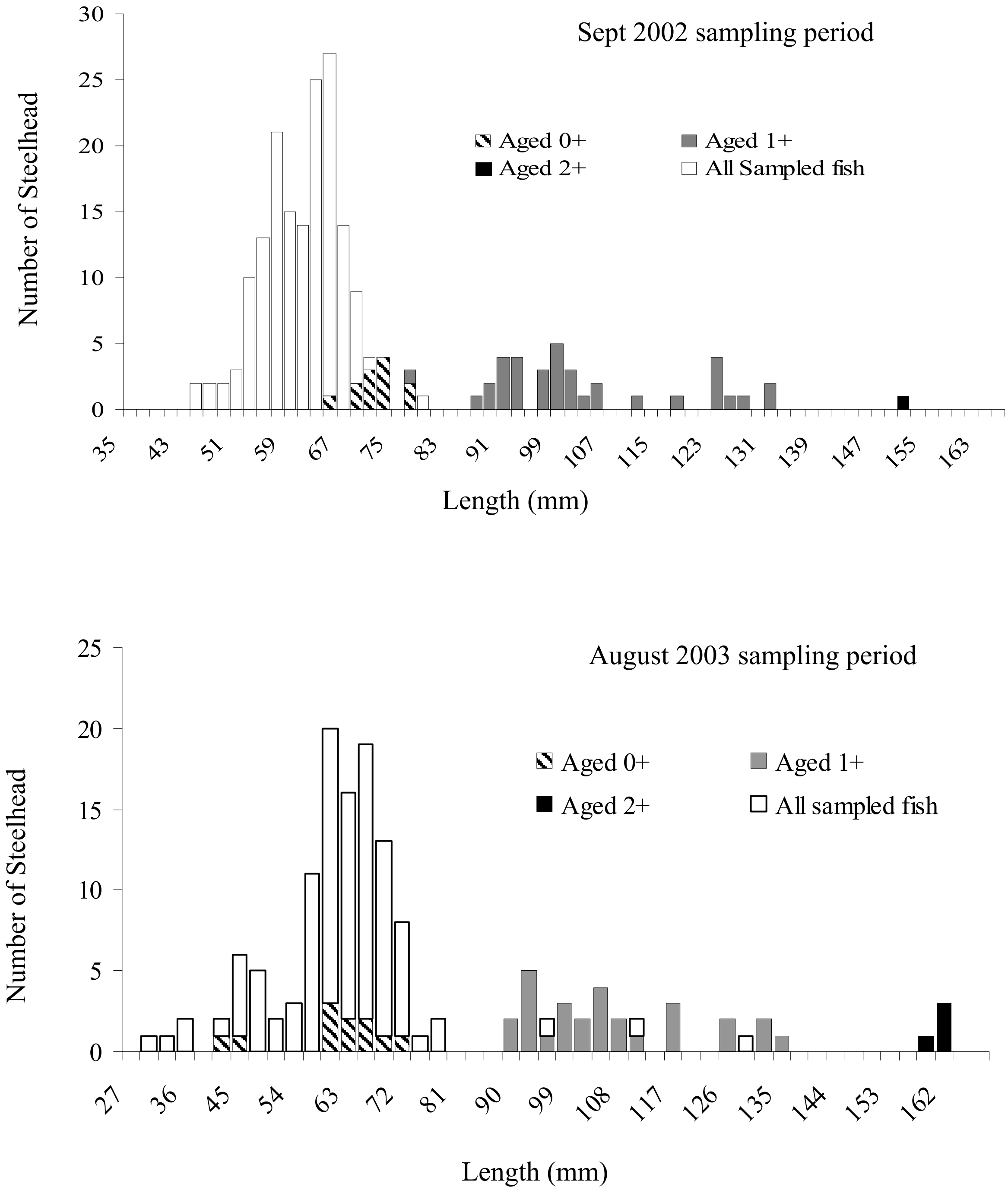

Figure 2. Number of steelhead sampled and number of steelhead aged as 0+ or 1+ cohorts in 2 millimeter size classes during September 2002 and August 2003 sampling periods in Barker Creek, Trinity County, California.

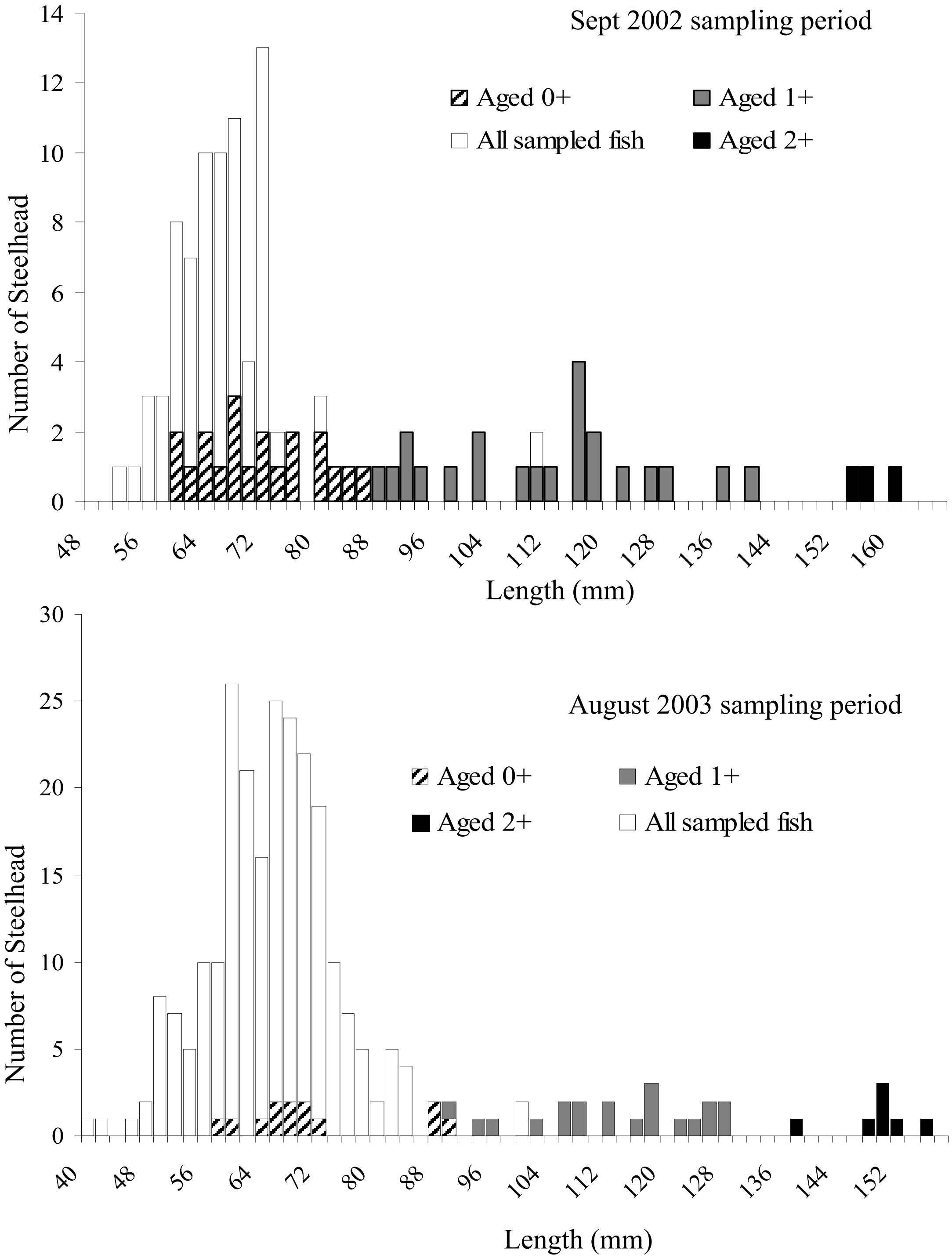

Figure 3. Number of steelhead sampled and number of steelhead aged in 0+ or 1+ cohorts in 2 millimeter size classes during September 2002 and August 2003 sampling periods in Carr Creek, Trinity County, California.

so that the solvent dripped from the condenser into the sample. Extraction of the sample continued for 6 hours. Samples were then dried and weighed again (W_2). Total lipid content was then calculated as (W_2/W_1)*100.

Statistical Analysis

I investigated growth patterns for the 2002 cohort throughout the study. All data were $\log_e$ transformed prior to analysis. Length measurements were assumed to be accurate. The weight measurements on a small number of fish appeared to not be accurate. To examine if these data points should be rejected as outliers, I first fit a linear regression of log weight verses log length for each stream during each sample period. Data points were considered outlier candidates if predicted values of log weight given log length exceeded the 95% predicted confidence intervals. I then calculated studentized residual values and R-student values (Kuehl, 2000) for each data point. All fish removed from length and weight analysis exceeded the 95% confidence interval for predicted log weight given log length, had studentized residual values greater than 4 or less than -4, and R-student values greater than 4 or less than -4.

A two tailed t-test was used, following a two sample F-test for equality of variance, to determine if the length and weight distributions of lipid analysis steelhead trout were similar to the sampled population for each age class. For the 2002 cohort, patterns of growth in mean length and mean weight were examined with ANOVA and Student-Newman-Keuls multiple comparison test (Kuehl, 2000).

Relative growth rates were calculated as:

$$RG_z = \frac{[(Z_2 - Z_1)/Z_1)]*100}{t_z}$$

where Z_1 and Z_2 are the mean of the length, weight or lipid growth parameters at the beginning and end of the period, respectively. Since sampling intervals varied in duration, relative growth rates were divided by the number of days (t_z) in the interval to allow for comparison among intervals. Analysis of variance was used at a significance level of 0.05 with season nested within stream to determine if mean length, mean biomass and mean lipid measures differed significantly between streams for each sampling period. Student-Newman-Keuls analysis was used to identify differences among specific sampling periods within streams. Lipid content of juvenile steelhead trout was presented as lipid weight to consider absolute lipid reserves. Lipid content was also presented as percent lipid to consider relative lipid stores.

Production estimates between streams were compared. Production for the age-0 cohort during each sampling interval was estimated using the instantaneous growth method (Warren and Doudoroff (1971). The instantaneous growth method estimates production from the product of daily instantaneous growth and mean population biomass:

$$P_i = G_i * \overline{B}_i$$

where

$$G_i = \frac{\ln(Wt_{t2}) - \ln(Wt_{t1})}{t2 - t1}$$

Wt = the average weight of an age 0 steelhead at time t and $\overline{B}$ = the mean of population biomass measured at time t1 and t2. Population biomass of age 0 steelhead trout was calculated as the product of average weight and abundance, as described on page 8.

Production was calculated for each sampling interval. To eliminate potential bias in the amount of habitat sampled between the two streams, production estimates were divided by surface area of the study reach measured during each sampling period in each stream and as expressed as $g/d/m^2$. In Barker Creek, one sampling unit 4 feet long was considered complex during habitat typing and was excluded from this analysis.

The relationship between lipid and environmental variables was examined using an information-theoretic approach suggested by Burnham and Anderson (2002). Seven multiple regression models relating lipid content with environmental variables were examined (Table 1). All data were $\log_e$ transformed for analysis. Summary statistics of environmental conditions for a sampling interval were independent variables used to predict lipid weight for the sampling period at the end of the sampling interval (e.g. summary statistics for environmental variables from July – September were matched with lipid values from the September sampling period). Significant multicollinearity existed among many of the environmental variables. Thus, variables were considered for inclusion in a model only when Pearson's correlation coefficients were less than 0.75 (Appendices A, B). R-squared values, Akaike's Information Criterion (AIC) and relative AIC weights (w_i) were used to assess the relative merits of models describing the relationship between fat reserves and environmental conditions.

Table 1. Models used to assess the relationship between lipid content and environmental variables in 2002 cohort steelhead trout in Carr and Barker creeks, Trinity County, California. Input parameters are abbreviated as MT - Mean Temperature, RANG - Mean daily range in temperature, HR - Mean hours of daylight, MQ - Mean estimated discharge.

Model	Rationale
MT	Lipid accumulation and depletion has been found to be related to temperature (Berg and Bremset 1998, Beckman et al. 2000)
RANG	Changing water temperatures is energetically demanding (Cunjak et al. 1987) and may affect lipid content (Spigarelli et al. 1982)
HR	Increase in lipids may be due to greater forage opportunities for visual feeders (Burke et al 2005)
MQ	Activity costs associated with higher flows may influence lipid content (Rennie et al. 2005)
MQ, MT	The combination of low temperatures and high flows in winter months may limit lipid accumulation.
MQ,HR	The combination of high flows and limited daylight for visual feeders in winter months may limit lipid accumulation.
MQ, RANG	The combination of fluctuating water temperatures and low flows in summer months may limit lipid accumulation.

Length-weight relationships of young of the year steelhead trout were investigated with condition factor, calculated as:

$$a = \frac{\log_e(W)}{\log_e(L)^b} \text{ x } 10^5$$

where a is the condition factor, W is weight, L is length and b is the slope of the fitted linear regression of $\log_e$(W) versus $\log_e$(L). To test the isometric growth assumptions in Fulton's condition factor, a t-test was used to determine if slopes did not significantly differ from 3. If slopes did differ from 3.0, comparisons were made to determine if slopes differed from each other using Analysis of covariance. When a common slope was achieved, condition factor of 2002 cohort steelhead trout was compared between streams for each sampling period. An alpha level of 0.05 was used to detect significance in all statistical analyses. All analyses were conducted using SAS software version 6.12 (SAS Institute Inc., Cary, North Carolina).

RESULTS

Habitat

Carr Creek and Barker Creek are both 3rd order streams similar in watershed size, elevation and slope (Table 2). From habitat measurements taken during the study, Barker Creek had a greater proportion of riffles (72.3%) and a smaller proportion of runs (17.4%) and pools (10.3%), than Carr Creek (56.2% riffles, 28.8% runs, and 15.0% pools). The mean maximum pool depth was similar in Carr Creek and Barker Creek (0.60 m and 0.66 m respectively).

Environmental Variables

The variation in discharge throughout the study was similar in Carr and Barker creeks (Figure 4). Five distinct storms occurred during sampling intervals 3, 4 and 5. The most important difference between sites was in temperature regime (Table 3). The mean temperatures recorded were warmer in Carr Creek than in Barker Creek during the summer months (sampling intervals 1 and 6). Temperature varied on a daily basis to a greater extent in Carr Creek than in Barker throughout the year. Maximum daily temperature recorded in the early summer (June-August 2003) was on average 5.3 degrees warmer in Carr Creek than in Barker Creek.

Table 2. Comparison of Barker Creek and Carr Creek watersheds, Trinity County, California, from topographic maps and summer habitat typing. Watershed metrics provided describe basin conditions above study reaches.

Characteristic	Barker Creek	Carr Creek
Stream order	3	3
Drainage area (km^2)	13.4	16.1
Mean slope in study reach (%)	2	2
Elevation (m)	800 - 920	830 - 940
Mean wetted width (m)	3.7	3.6
Area in pools (%)	10.3	15.0
Mean maximum pool depth (m)	0.66	0.60
Area in riffles (%)	72.3	56.2
Mean riffle depth (m)	0.18	0.15
Area in runs (%)	17.4	28.8
Mean run depth (m)	0.20	0.18
Number of units	60	69
Pool:Riffle Ratio	0.14	0.27

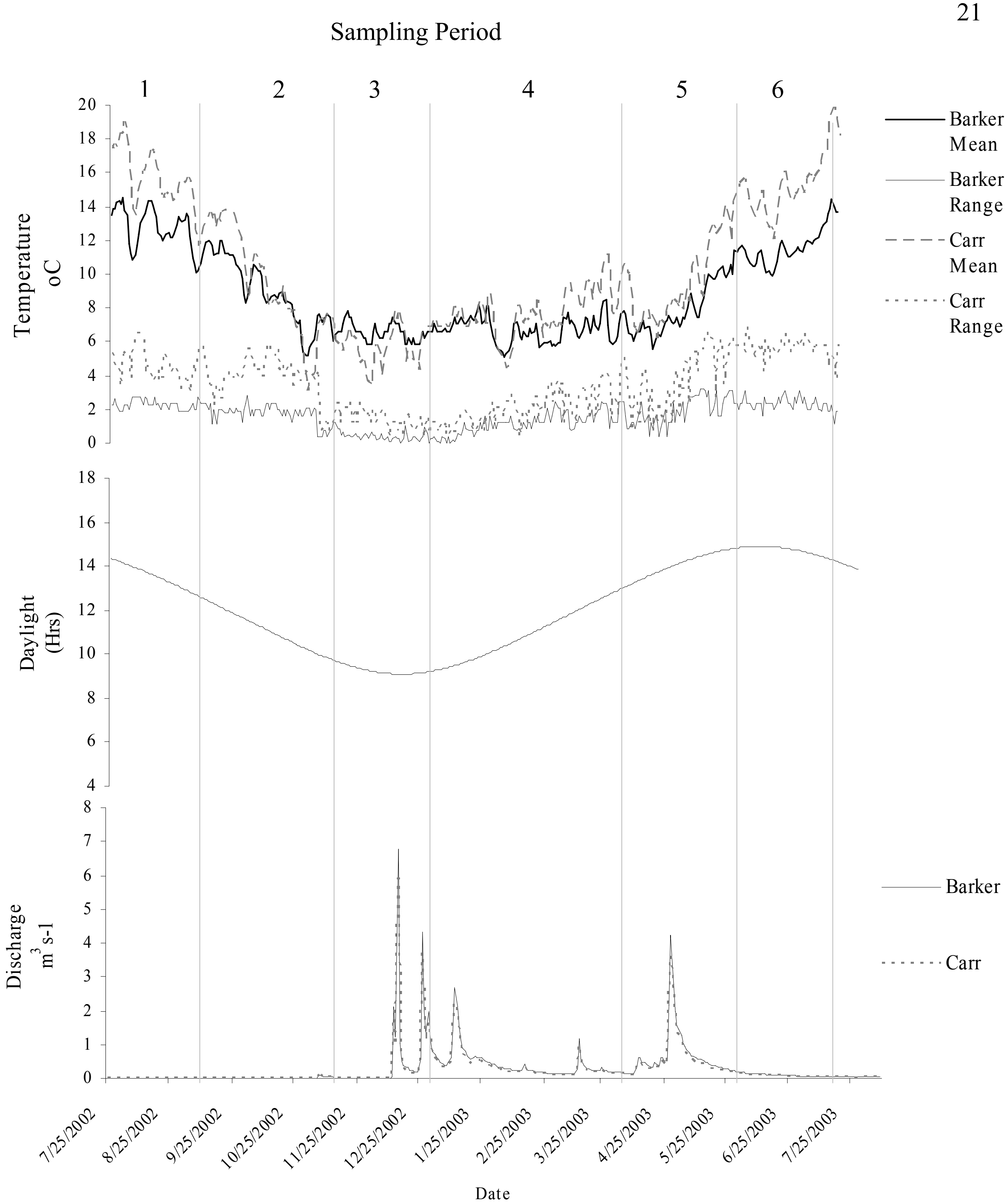

Figure 4. Mean daily temperature, daily range in temperature, photoperiod, and estimated mean daily discharge measured in Barker and Carr creeks, Trinity County, California during 2002-2003. Vertical lines indicate sampling periods.

Table 3. Summary statistics of environmental variables included in models of Barker and Carr creeks, Trinity County, California. Interval periods are: 1 = July – September 2002, 2 = September – November 2002, 3 = November 2002 – January 2003, 4 = January – April 2003, 5 = April – June 2003 and 6 = June – August 2003.

	Barker Creek					
Interval	1	2	3	4	5	6
Days/ interval	51	55	64	83	54	65
Mean temperature ^{o}C	12.3	8.4	6.6	6.7	7.9	12
Degree days	627	1088	1512	2179	2599	3379
Mean daily range in temperature ^{o}C	2.2	1.7	0.4	1.2	2	2.2
Mean daily maximum temperature ^{o}C	13.4	8.9	6.7	7.3	9.2	13.2
Mean hours daylight	13.2	10.9	9.3	10.8	14	14.6
Mean discharge (m^3/s)	0.01	0.02	0.63	0.4	0.68	0.07
Standard deviation discharge (m^3/s)	0.00	0.02	1.12	0.39	0.71	0.04

	Carr Creek					
Interval	1	2	3	4	5	6
Days/ interval	59	49	63	84	51	66
Mean temperature ^{o}C	14.7	7.9	6	7.8	9.2	15.7
Degree days	868	1264	1638	2294	2752	3802
Mean daily range in temperature ^{o}C	4.3	3.8	1.3	2.3	3.5	5.4
Mean daily maximum temperature ^{o}C	16.8	9.9	4.9	7.6	11.3	18.5
Mean hours daylight	13.1	10.7	9.3	11.2	14	14.6
Mean discharge (m^3/s)	0.01	0.014	0.54	0.23	0.58	0.06
Standard deviation discharge (m^3/s)	0.00	0.01	0.98	0.16	0.62	0.03

Steelhead Abundance

Density of juvenile steelhead trout varied among habitat types in both Barker and Carr creeks (Table 4). In Barker Creek, the highest density observed throughout the study in run habitats (0.75 fish/m^2) was recorded in July 2002. Steelhead were generally observed at higher densities in run habitats than in pools or riffles in Barker Creek. However during the November sampling period, pools had a higher density of steelhead (0.49 fish/m^2) than runs (0.27 fish/m^2) or riffles (0.21 fish/m^2). In Carr Creek, the highest density of juvenile steelhead in was recorded in pool habitats (1.12fish/m^2) in August 2003. There was no clear pattern in steelhead density among the habitat units throughout the study in Carr Creek.

In Barker Creek, one sampling unit 4 feet long was considered complex and excluded from the population estimate during each sampling period. At the beginning of the study, the estimated total number of juvenile steelhead in sampled study reaches was higher in Barker Creek (962) than in Carr Creek (840). In 2002, however, cohort populations were similar in the two streams (730 and 767, respectively). Abundance in Barker Creek was similar at the next sampling event in September, but declined in Carr Creek (Figure 5). At the end of the study, the estimated population of the 2002 cohort was 105 in Carr Creek and 128 in Barker Creek.

Patterns of Growth

Mean length of 2002 cohort steelhead increased throughout the study period in both Carr and Barker creeks (Table 5). In Barker Creek, steelhead increased in fork length from 51.8 to 106.0 mm during the study. Absolute growth in Barker Creek was least (9.3 mm) between the July and September 2002 and greatest (24.1 mm) between April and June 2003.

Table 4. Density (number/m^2) of steelhead trout (all ages) in runs, pools and riffles in Barker and Carr creeks, Trinity County, California during 2002 and 2003.

Barker Creek

Sampling Period	Runs	Pools	Riffles
Jul-02	0.75	0.56	0.48
Sep-02	0.75	0.61	0.27
Nov-02	0.27	0.48	0.21
Apr-03	0.09	0.06	0.04
Jun-03	0.12	0.11	0.12
Aug-03	0.35	0.31	0.17

Carr Creek

Sampling Period	Runs	Pools	Riffles
Jul-02	0.50	0.52	0.36
Sep-02	0.22	0.39	0.16
Nov-02	0.16	0.14	0.13
Apr-03	0.04	0.03	0.05
Jun-03	0.09	0.07	0.11
Aug-03	0.55	1.12	0.39

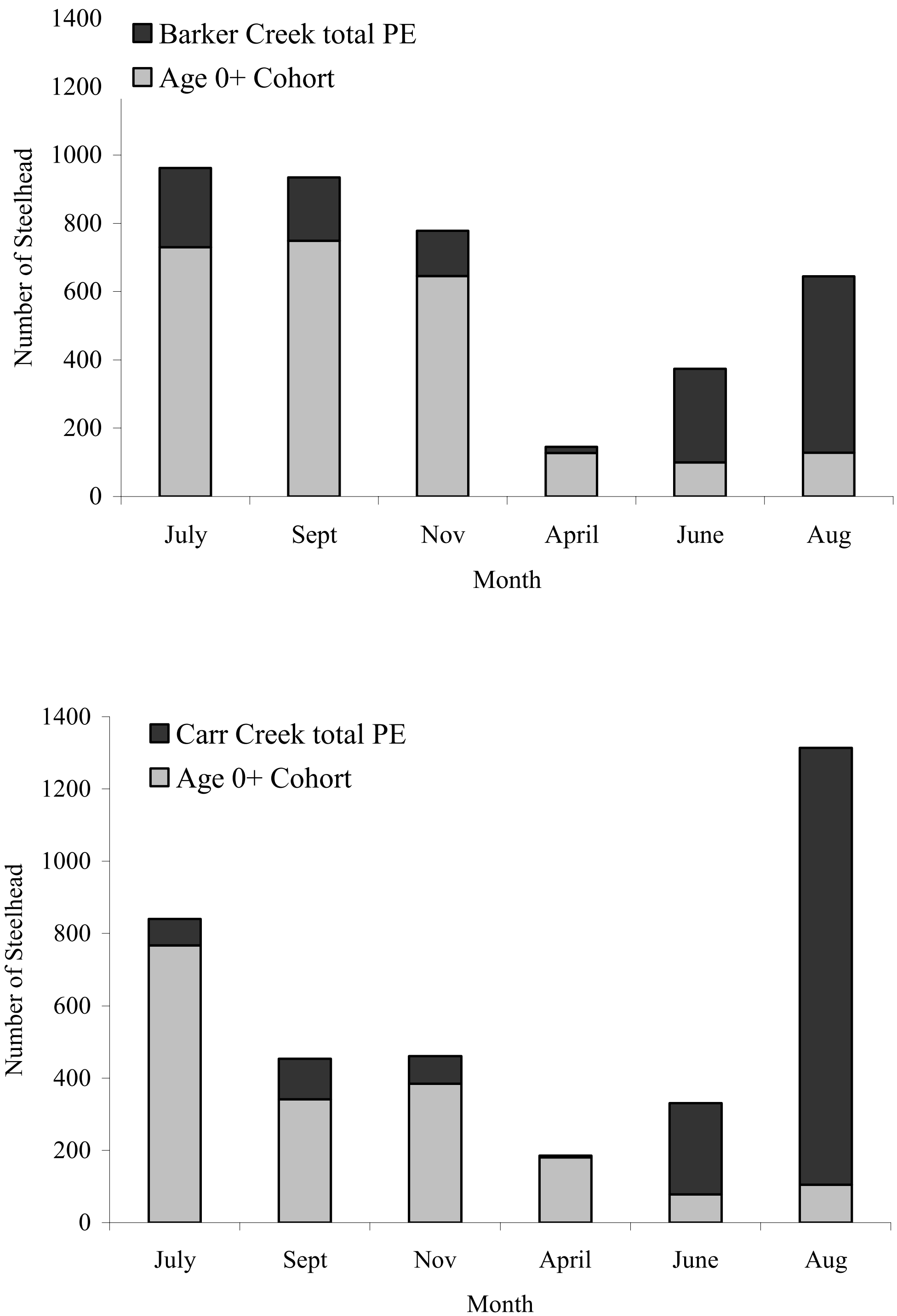

Figure 5. Population estimates for the 2002 cohort and all other age classes of steelhead trout population estimates in Barker and Carr creeks, Trinity County, California 2002-2003.

Table 5. Mean length (mm) of 2002 cohort steelhead selected for lipid analysis and all other 2002 cohort steelhead measured in Barker and Carr creeks, Trinity County, California, during 2002-2003. P-values are results of a T-test to compare steelhead size in the two categories.

	Lipid samples			All remaining steelhead			
Date	n	Mean (mm)	σ^2	n	Mean (mm)	σ^2	P-value
Barker Creek							
Aug 1, 2002	12	50.4	61.2	109	51.8	59.7	0.553
Sept 21, 2002	13	58.8	29.6	155	61.1	38.5	0.212
Nov 15, 2002	10	62.8	73.7	103	62.1	55.2	0.776
Jan 17, 2003[a]	5	63.7	9.4				
Apr 11, 2003	8	73.1	156.1	46	70.8	94.1	0.490
Jun 3, 2003	8	104.4	545.4	31	94.9	303.7	0.211
Aug 6, 2003	6	106.8	147.4	24	106.0	214.7	0.904
Carr Creek							
Jul 30, 2002	13	60.8	56.6	149	64.4	72.6	0.148
Sept 27, 2002	12	66.8	36.8	69	66.4	47.4	0.871
Nov 16, 2002	11	72.5	54.3	49	72.2	98.5	0.915
Jan 17, 2003[a]	7	63.6	5.9				
Apr 12, 2003	14	83.8	165.1	42	84.8	241.1	0.821
Jun 1, 2003	6	101.7	151.5	20	105.1	299.6	0.600
Aug 7, 2003	6	101.7	27.5	19	120.1	299.0	< 0.001*

[a] All steelhead collected during the January sampling period were used for lipid analysis.

Post comparison of means in Barker Creek revealed no significant increase in length between the September and November sampling periods, but increases were significant between all other sampling periods (Table 6). Year 2002 cohort steelhead were consistently longer in Carr Creek than in Barker Creek, but not significantly so (ANOVA df = 11, p-value = 0.52). In Carr Creek, steelhead increased in fork length from 64.4 mm in July 2002 to 120.1 mm in August 2003. Absolute growth in Carr Creek was least (2.0 mm) between the July and September 2002 and greatest (20.3 mm) between April and June 2003. Post comparison of means in Carr Creek revealed that there was no significant increase in length between July 2002 and September 2002 or between June 2003 and August 2003 (Table 6).

Mean weight of 2002 cohort steelhead increased throughout the study period in both Carr and Barker creeks (Table 7). In Barker Creek, steelhead increased in weight from 1.70 to 15.50 g during the study. Absolute growth in weight in Barker Creek was also least (0.20 g) between September and November 2002 and greatest (6.76 g) between April and June 2003. The weight of 2002 cohort steelhead differed among sampling periods in Barker Creek (df = 5, p=0.001) and post comparison of means revealed that there was no significant increase in weight between the September 2002 to November 2002 sampling interval (Table 6). Mean weight of year 2002 cohort steelhead was consistently greater in Carr Creek than in Barker Creek, but not significantly so (ANOVA df = 11, p = 0.54). In Carr Creek, steelhead increased in weight from 3.29 g in July 2002 to 20.80 g in August 2003. Absolute growth in Carr Creek was least (0.08 g) between the July and September 2002 and greatest (6.65 g) between April and June 2003. The weight of 2002 cohort 0+ steelhead differed among sampling periods in Carr Creek (df=5, p=0.001) and post comparison of means revealed

Table 6. Results of Student Newman-Keuls multiple comparison test performed on log transformed fork length (FL) and weight (WT) for 2002 cohort steelhead in Barker and Carr creeks, Trinity County, California during 2002-2003. Horizontal bars indicate groups with no significant difference.

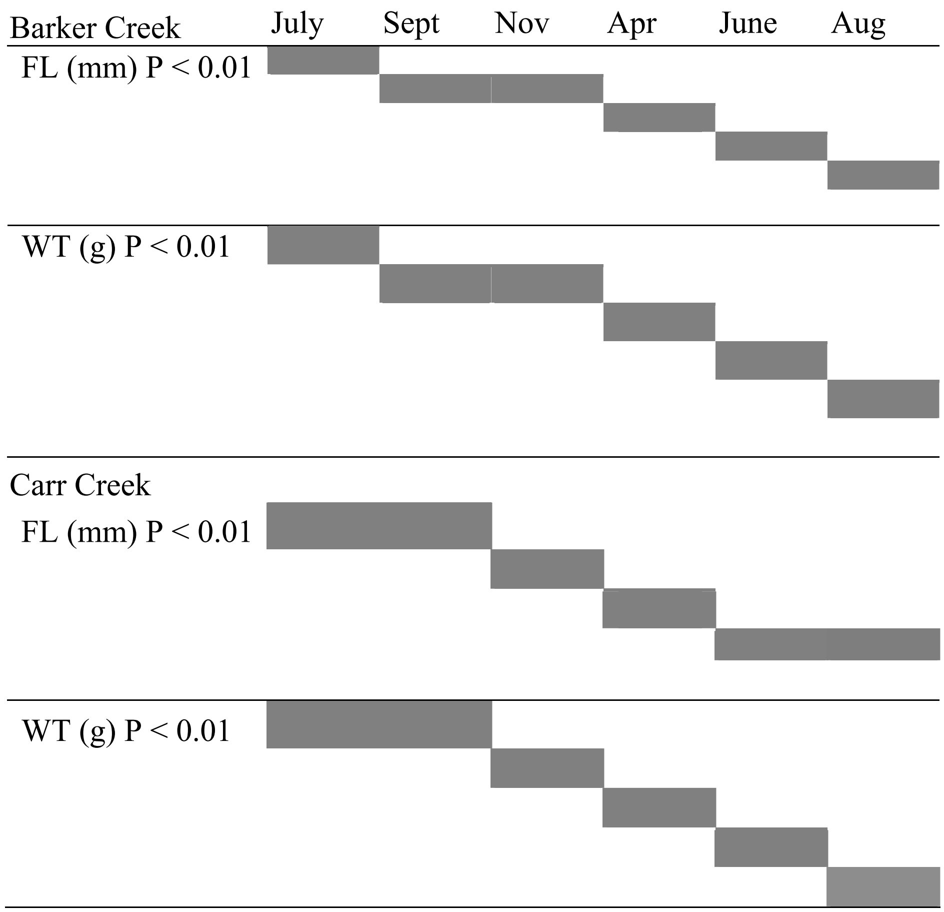

Table 7. Mean wet weight (g) of 2002 cohort steelhead selected for lipid analysis and all other 2002 cohort steelhead measured in Barker and Carr creeks, Trinity County, California during 2002-2003. P-values are results of t-test to compare steelhead size in the two categories.

	Lipid samples			All remaining fish measured			
Date	N	Mean Wt (g)	σ^2	n	Mean Wt (g)	σ^2	P-value
Barker Creek							
Aug 1, 2002	12	1.52	0.44	109	1.70	0.57	0.436
Sept 21, 2002	13	2.13	0.34	155	2.50	0.56	0.083
Nov 15, 2002	10	2.74	1.12	103	2.70	0.89	0.907
Jan 17, 2003[1]	7	3.22	1.21				
Apr 11, 2003	8	5.28	7.76	46	4.96	4.83	0.337
Jun 3, 2003	8	15.84	100.91	31	11.72	48.51	0.182
Aug 6, 2003	6	15.50	31.24	24	15.35	50.19	0.963
Carr Creek							
Jul 30, 2002	13	2.66	0.96	149	3.29	1.52	0.074
Sept 27, 2002	12	3.26	0.85	69	3.37	1.20	0.739
Nov 16, 2002	11	4.07	1.80	49	4.38	3.25	0.598
Jan 17, 2003[1]	7	3.10	0.99				
Apr 12, 2003	14	7.69	9.12	42	8.96	27.85	0.274
Jun 1, 2003	6	12.55	19.23	20	15.61	86.16	0.340
Aug 7, 2003	6	12.19	3.68	19	20.80	74.22	0.001*

[1] All steelhead collected during the January sampling period were used for lipid analysis.

that there was no significant increase in weight between the July 2002 to September 2002 sampling interval (Table 6).

Following an F-test for equality of sample variances, the appropriate t-test (assuming equal variance or assuming unequal variance) was used to compare the length (Table 5) and weight (Table 7) of 2002 cohort lipid steelhead to the rest of 2002 cohort measured steelhead for each sampling period in each stream. Length and weight measurements of steelhead collected for lipid analysis were significantly different from the measured steelhead in Carr Creek during August 2003. No significant differences occurred during the remaining sampling periods in Carr Creek. In Barker Creek, length and weight of steelhead collected for lipid analysis were not significantly different than the measured steelhead during any of the sampling periods.

Whole body lipid content of 2002 cohort steelhead increased throughout the study in both creeks (Figure 6). In Barker Creek, lipid content increased from a mean of 28 mg/fish in July 2002 to 751 mg/fish in August 2003. In Carr Creek, lipid content increased from a mean of 132 mg/fish in July 2002 to 852 mg/fish in August 2003. The lipid content of 2002 cohort steelhead in Barker Creek increased during the first sampling interval from 28 mg/fish in July 2002 to 47 mg/fish in September 2002. In contrast, lipid content in Carr Creek remained relatively steady during the first sampling interval. Mean lipid content remained steady from September 2002 to January 2003 in both creeks, and then increased through the rest of the study. The period of greatest increase in whole body lipid content occurred during the April 2003 to June 2003 for both Barker Creek (632 mg/fish increase) and Carr Creek (432 mg/fish increase).

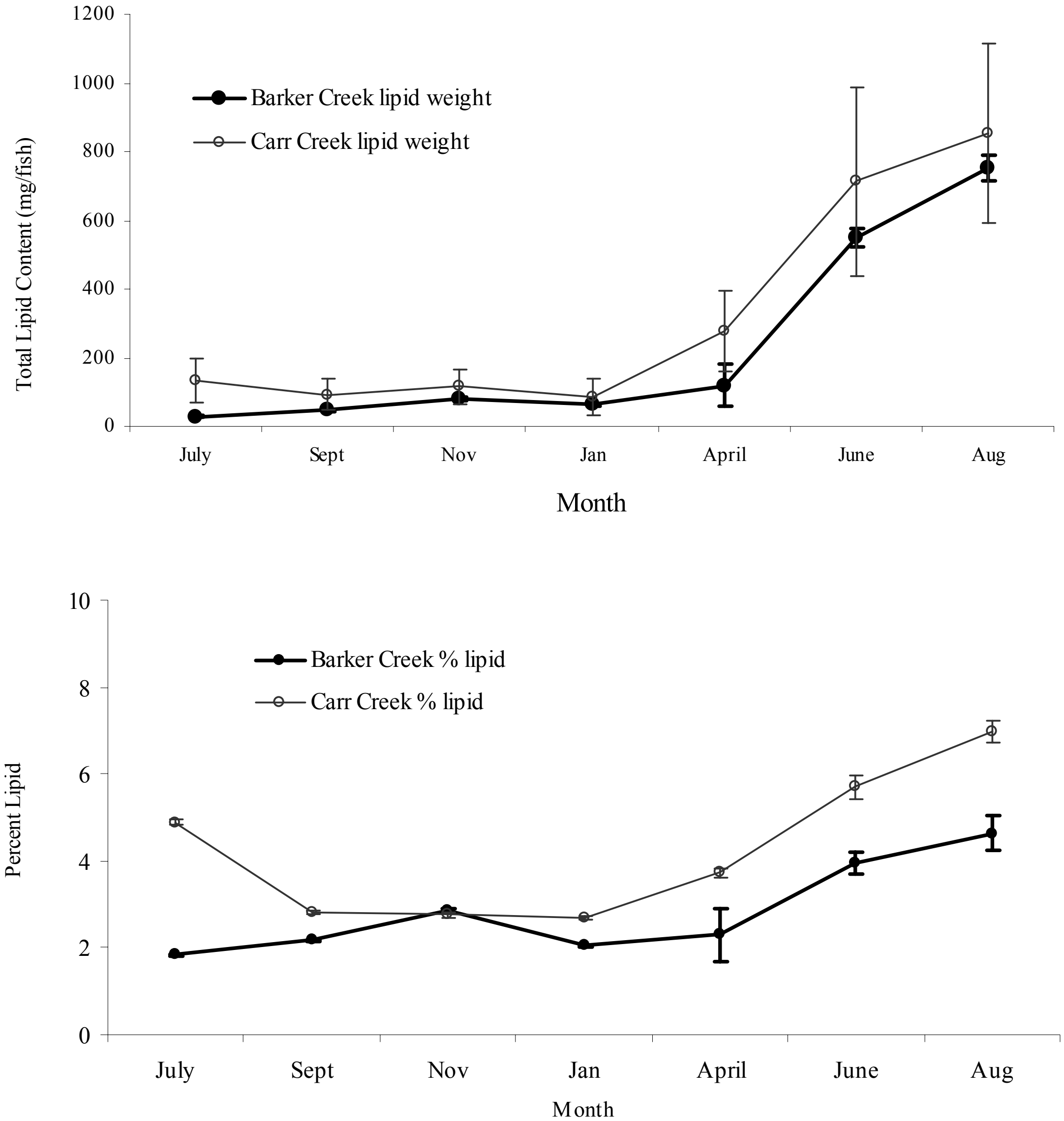

Figure 6. Whole body lipid content (mg/fish) and percentage lipids for 2002 cohort steelhead in Barker and Carr creeks, Trinity County, California during 2002-2003. Error bars depict the 95 percent confidence intervals on estimated means.

Percentage lipid increased overall throughout the study in both creeks (Figure 6). In Barker Creek, percentage lipid increased from 1.84% in July 2002 to 4.63% in August 2003. In Carr Creek, percentage lipid increased from 4.87% in July 2002 to 6.98% in August 2003. During the first sampling period, mean percentage lipids increased from 1.84% to 2.17% in Barker Creek, while mean percentage lipids decreased from 4.87% to 2.82% in Carr Creek. In Barker Creek, lipids increased from September 2002 to November 2002, and then decreased from November 2002 to January 2003. In Carr Creek, lipids remained steady from September 2002 to January 2003. From April 2003 to August 2003, percentage lipids increased in both streams. Percentage lipid was higher in Carr Creek than in Barker Creek during most sampling periods.

Relative Growth Rates

The general pattern of relative growth rates for 2002 cohort steelhead was similar in the two streams throughout the study, but differences did occur (Figure 7). During the July to September sampling interval in Barker Creek, relative growth in weight and lipids increased at the second highest rates observed during the study. Lipid weight decreased in Carr Creek during the July to September interval without relative growth in length or weight. Lipids increased during the next sampling interval in both streams. An early winter decline in lipids was observed during the November to January interval in both Barker and Carr creeks. April through June was a period of high relative growth in length, weight and lipid in both streams. During the April 2003 to June 2003 sampling interval, the lipid relative growth rate for Barker Creek (6.7%/day) was over twice that of Carr Creek (3.0%/day).

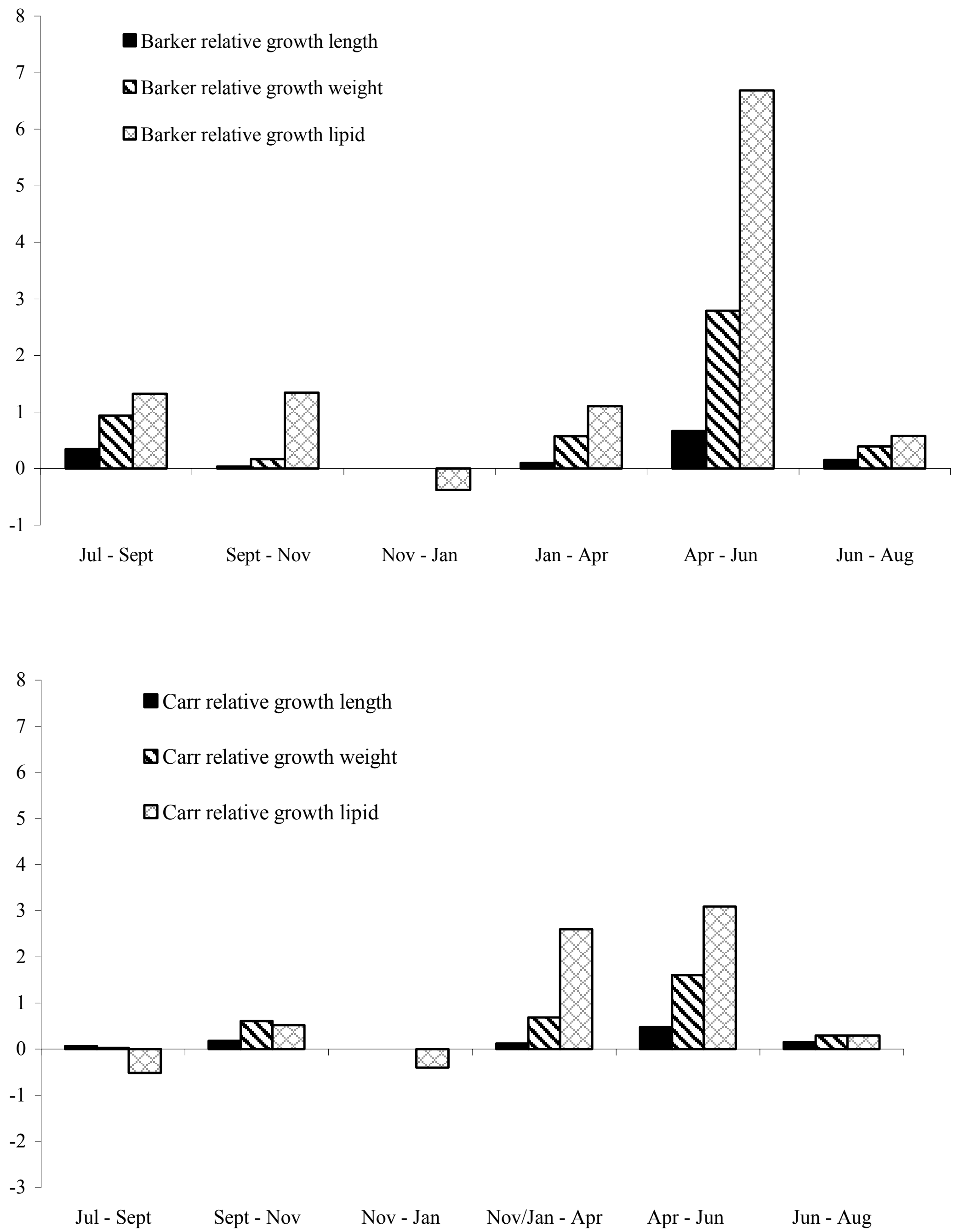

Figure 7. Relative growth calculations for length, weight and lipid content in 2002 cohort steelhead in Barker and Carr creeks, Trinity County, California during 2002-2003.

Production

Total production during the study was higher in Carr Creek (63.2 kg/ha) than in Barker Creek (55.0 kg/ha) (Table 8). During the July to September interval, production in Barker Creek was ten times higher than in Carr Creek. Production was lowest in Barker Creek during the September to November interval. Production was lowest in Carr Creek during the July to September interval. The April to June interval was the period of highest productivity for 2002 cohort steelhead in both streams.

Relations to Environmental Conditions

January sampling data were included in this analysis to examine early winter impacts on lipid reserves. The five 2002 cohort steelhead collected from Barker Creek in January had a mean of 2.05 percent lipid (Figure 6). The seven 2002 cohort lipid steelhead collected from Carr Creek in January had a mean of 2.70 percent lipid. These steelhead were included in general linear models examining lipid content relations to environmental variables.

As is typical of the Pacific Northwest region, Carr and Barker creeks underwent significant seasonal changes in flow and temperature. Water temperatures and temperature variation were highest during summer and lowest during winter. Discharge was highest during winter with concurrent increases in variability. As a result, predictor variables in many models were correlated in Barker Creek (Appendix A) and Carr Creek (Appendix B). Of the models without significant multicollinearity, variation in total lipid content was best modeled as a positive relationship for both mean discharge and day length in Barker Creek (R^2 = 0.595, Table 9) and as a positive relationship for both mean discharge and range in daily temperature in Carr Creek (R^2 = 0.697).

Table 8. Mean biomass per area sampled and production estimates during the study for 2002 cohort of steelhead in Barker and Carr creeks, Trinity County, California, during 2002-2003.

	Barker Creek		Carr Creek	
Sampling Interval	Mean biomass/area (kg/ha)	Production (kg/ha)	Mean biomass/area (kg/ha)	Production (kg/ha)
Jul – Sept	6.6	5.3	9.0	0.5
Sept - Nov	7.0	1.4	5.1	5.0
Nov – Apr	3.9	8.9	4.0	17.4
Apr – Jun	2.9	22.4	3.4	24.4
Jun – Aug	5.5	17.0	5.3	16.0
Total Production (kg/ha)		55.0		63.2

Table 9. Model results of relationships between lipid weight and environmental variables in Barker and Carr creeks, Trinity County, California during 2002-2003. For selected models, the influence of independent variables on lipid content (+) (-), R-square (R^2), AIC, change in AIC (Δ_i), and relative Akaike weights (w_i) are shown.

Stream	R^2	p-value	(Δ_i)	AIC	w_i
Barker Creek					
MQ (+), HR (+)	0.595	0.0001		-28.94	0.9369
MQ (+), RANG (+)	0.551	0.0001	5.40	-23.53	0.0628
MQ (+), MT (+)	0.441	0.0001	11.36	-12.18	0.0002
HR (+)	0.248	0.0002	13.39	1.22	2.83E-07
MQ (+)	0.193	0.0011	3.70	4.91	4.46E-08
RANG (+)	0.054	0.0978	8.26	13.17	7.17E-10
MT (-)	0.001	0.8639	2.85	16.02	1.73E-10
Carr Creek					
MQ (+), RANG (+)	0.697	0.0001		-59.00	0.9999
MQ (+), HR (+)	0.579	0.0001	18.33	-40.67	0.0001
MQ (+), MT (+)	0.438	0.0001	16.22	-24.45	3.15E-08
HR (+)	0.254	0.0001	13.83	-10.63	3.14E-11
MQ (+)	0.172	0.0015	5.85	-4.78	1.69E-12
RANG (+)	0.049	0.1000	7.75	2.97	3.5E-14
MT (+)	0.025	0.2460	1.42	4.39	1.72E-14

Condition Factor

Condition of steelhead trout varied between streams, but also exhibited a common seasonal pattern of biological interest. Maximum condition of steelhead was recorded in both streams in November at the beginning of the winter period. In Barker Creek, condition increased from summer through fall. After November, it declined through spring and summer. In Carr Creek, condition recorded in both summer sampling periods was only slightly less than in November, while being low in spring and fall.

Length and weight relationships of steelhead trout were not isometric (slope = 3) in the two streams on all sampling dates (Table 10). In Barker Creek, the slope of the length weight relation differed from 3 during the July and November sampling events. In Carr Creek, the slope differed from 3 during the July sampling event. ANCOVA analysis did not provide a common slope for 2002 cohort steelhead between streams during the July sampling period. And therefore, condition factor was not compared between streams for this time period.

Table 10. Sample size (N), slope, condition factors, and adjusted R^2 (Adj. R^2) of the fitted linear regression of $\log_e(W)$ versus $\log_e(L)$ for 2002 cohort of steelhead in Barker and Carr creeks, Trinity County, California during 2002 and 2003.

	Barker Creek				Carr Creek			
Month	N	Slope	Condition Factor	Adj. R^2	N	Slope	Condition Factor	Adj. R^2
July	121	3.10[a]	0.524	0.98	162	2.83[1]	2.416	0.94
Sept	168	3	1.407	0.92	81	3	0.883	0.96
Nov	112	2.82[a]	2.262	0.95	60	3	2.965	0.96
Apr	54	3	1.060	0.92	56	3	1.007	0.95
Jun	19	3	1.037	0.95	20	3	1.397	0.96
Aug	30	3	0.570	0.97	30	3	2.167	0.97

[a] Slopes were significantly different from 3 using a t-test, and no common slope was achieved for the two streams in one season using ANCOVA.

DISCUSSION

Patterns of growth in fish are influenced by the interplay of overlapping environmental conditions, which vary seasonally. The growth strategies employed with available resources and limitations, in combination with behavioral tactics, have strong implications for survival. In this study, selection of two watersheds similar in environmental setting, but with different temperature regimes, allowed for a description of observed growth strategies in response to different thermal patterns. In addition, changes in photoperiod and stream flow were investigated to examine which environmental condition influences growth patterns and, in particular, lipid stores for young of the year steelhead trout throughout the year. Both similarities and differences in growth patterns and population characteristics were observed between the two streams.

Water temperature has a great effect on poikilothermic organisms. Higher water temperatures increase rates of development from egg to fry and elevate metabolic activity, increasing rates at which consumed food is converted to somatic or energetic growth. When temperatures are within the range of physiological tolerance and an ample food supply is available, greater size can be achieved. The 2002 cohort of steelhead in Carr Creek were longer, heavier and had larger lipid reserves than their Barker Creek counterparts at the start of the first sampling period. Higher mean temperatures and a greater range in daily temperature during early development of the Carr Creek 2002 cohort may have resulted in the greater size and lipid stores by the start of the first summer sampling period.

Throughout their first summer, however, it does appear that environmental conditions were not favorable for growth for Carr Creek steelhead, as evidenced by the significant use of lipid reserves and very limited somatic growth during summer months. In addition, the population decline in Carr Creek during summer months, as mortality or emigration, was the greatest observed throughout the study (Forseth et al. 1999). Production estimates during the first sampling interval in Carr Creek were the lowest observed throughout the study. These observations suggest that summertime conditions are taxing for young of the year steelhead. Biomass during that interval was the highest observed during the study. Zorn and Muhfer (2007) observed that biomass density of brook and brown trout within a year class to have a negative "density dependent" effect on growth of those species.

In contrast, Barker Creek steelhead trout exhibited summer growth in length and weight during their first summer. This somatic growth during the July- August sampling period occurred at the expense of lipid reserves, consistent with the findings of Post and Parkinson (2001). Production estimates were ten times higher in Barker Creek than in Carr Creek during this time period. Barker Creek steelhead started out much smaller and with lower lipid content than the Carr Creek steelhead, emphasizing the importance of the first summer growing season in Barker Creek.

Lipid anabolism continued in Carr Creek throughout the fall, while there was a slight increase in lipid content in Barker Creek steelhead. Acclimatization to declining water temperatures can be energetically demanding (Cunjak et al. 1987). The rate of water temperature decline was more substantial in Carr Creek. If food supplies were limited, lipid reserves may have been utilized to meet the increased energy demand to adjust to declining water temperatures. yet percent lipid in Carr still remained higher than in Barker Creek However, ample food supplies may offset increased energy demands to adjust to cooler water temperatures. Collecting information on food supply was beyond the scope of this study and so the reason for lipid declines is unknown.

Neither population demonstrated the fall period of growth observed by Reeves (1979). However, Reeves described rain events as the trigger for fall growth, and there were no significant rain events prior to the November sample period in this study. Steelhead from both streams entered winter with similar lipid stores.

The factors that limit over winter survival have been studied for a number fish species. Early winter energy depletions observed by Cunjak et al. (1987) in brook trout populations were attributed to acclimatization to cooling water temperatures and energy intake insufficient to meet metabolic activity. This may have been the cause of declines in lipid reserves for Barker Creek during the early winter period from November to January

In areas with sustained harsh winter conditions, the accumulation of energy stores is essential to sustain individuals though periods of starvation. Many authors have reported increased over winter survival with increased fish length (Thompson et al. 1991, Hunt 1969, Oliver et al. 1979) because the smaller fish use energy reserves at a faster rate than larger fish (Miranda and Hubbard 1994). Cunjak et al. (1987) suggested that metabolic deficiencies are a result of an inability to assimilate food rather than prey availability during low water temperatures. However his studies were conducted in a region with prolonged minimum winter temperatures of 0.1 to 1.5 ^{o}C. In this study, winter water temperatures rarely dipped below 4 ^{o}C, and were usually near 6 ^{o}C. Warmer water temperatures increase standard metabolic rates. Limited food availability during winter combined with increased sustained metabolic costs at warmer temperatures may present physiological challenges to steelhead trout, particularly to the larger individuals (Connolly and Peterson 2003).

Beckman et al. (2000) found that average body lipid levels increased in February – March in Yakima River juvenile Chinook salmon at some sites. An effort was made in my study to sample each creek earlier in the spring, however high flows prevented capturing enough steelhead trout for an adequate sample. From January to April, lipid content of steelhead trout in Carr Creek increased by an average of 1 percent, and in Barker Creek lipid content increased to a lesser extent (0.2 percent). Other researchers have found increased lipid content during late winter/early spring when temperatures are still low (Cunjak et al. 1987), and have attributed these anabolic processes to changing photoperiod (Beckman et al. 2000). The results from Barker Creek in this study agree with those findings,, the top model shows a positive relationship between hours of daylight and lipid content.

This study identified early spring as a period of rapid anabolism as reflected in all types of growth, with preference to somatic growth. This is similar to the research of Berg and Bremset (1998), who found increases in percentage body lipid from April to June in populations of Atlantic salmon and brown trout. Throughout the study, the 2002 cohort in Carr Creek had generally faster growth rates than Barker Creek, and lipid content in Carr Creek steelhead trout was overall higher than that of Barker Creek. This is consistent with the work of Post and Parkinson (2001) who proposed that rainbow trout of the same size tend to have higher lipid content in aquatic systems that support faster growth rates.

Model results for both Carr and Barker creeks in this study show a positive relationship between mean discharge and lipid content in both streams in top models. This was not what I expected. I thought that greater discharge in winter months would tax young steelhead because of the energy expended to maintain their position and feed at high water levels. These model results appear to be a result of the April to June 2003 interval that had the highest increase in lipid content observed throughout the study and also highest mean flow. Perhaps high flow and flood events provided a greater food supply for young of the year steelhead by dislodging macroinvertebrates from instream substrate or riparian habitats (White and Harvey 2007).

Condition factor indices have been widely used as an index of the health and robustness of fish with the assumption that increases in weight are reflective of increases in fat tissue. Some researchers have found relatively high correlations between condition factor and percent fat (Herbinger and Friars 1991). This would support the steady increases in both Fulton's condition factor and percentage lipid that was observed in Carr Creek. However, other researchers have found low correlations between Fulton's condition factor and percentage fat (Simpson et al. 1992). In Barker Creek, increases were not consistent between percentage lipid and condition factor. The reason for this is unknown,, however, the weak correlation of water weight of fish to fat weight (Sutton et al. 2000) could contribute to these findings.

Some researchers consider production rate to be a powerful indicator of a species ecological success (Le Cren 1969, O'Connor and Power 1976).   Production rates are influenced by water quality of the system, and are the combined result of a population's recruitment, growth, total biomass and mortality. Production rates in this study loosely followed relative growth rates for weight, with population size driving the differences in the discrete increment summation production calculations. The productive April to June interval in Barker Creek was influenced largely by growth, while in Carr Creek, high productivity calculations were influenced by greater biomass due to the larger size of the steelhead.

Carr and Barker creeks produced a similar number of fish at the end of the study. However, Carr Creek fish were longer, heavier and with greater lipid reserves than their Barker Creek counterparts, indicating a generally heartier cohort. Condition factor and production metrics support this claim as well. Model results show that diel temperature fluctuations were positively related to lipid stores, consistent with Spigerelli et al. (1982). Diel fluctuations were greatest during summer. From field observations, I attribute these fluctuations in Carr Creek to low flows and limited riparian cover. Although temperature fluctuations appear to benefit steelhead overall during the study period, there was evidence of stress during the first summer for young of the year fish. Continued increases in temperature may have a negative impact on steelhead.

This study provided data that can be useful in understanding survival of steelhead in the region by identifying periods of anabolism and catabolism in wild populations of juvenile steelhead over the course of one year. A multi-year project would reveal variability in physical factors over time and would yield greater insights into growth patterns and their drivers, as would identification of growth patterns in individual steelhead. Additional studies that include measurements of available food supply will be able to further narrow the causes of lipid anabolism and catabolism. Further research should include these elements.

LITERATURE CITED

Association of Official Analytical Chemists. 1975. Official methods of analysis. 12th edition. Association of Official Analytical Chemists, Washington DC.

Allen, M. A. 1986. Population dynamics of juvenile steelhead trout in relation to density and habitat characteristics. Master's Thesis, Department of Fisheries, Humboldt State University, Arcata California.

Beckman, B. R., D. A. Larsen, C. Sharpe, B. Lee-Pawlak, C. B. Schreck, and W. W. Dickhoff. 2000. Physiological status of naturally reared juvenile spring Chinook salmon in the Yakima River: Seasonal dynamics and changes associated with smolting. Transactions of the American Fisheries Society 129:727-753.

Berg, O. K., E. Thronaes, and G. Bremset. 2000. Seasonal cycle of body composition and energy of brown trout (*Salmo trutta*) in a temperate zone lake. Ecology of Freshwater Fish 9:163-169.

Berg, O. K and G. Bremset. 1998. Seasonal changes in the body composition of young riverine Atlantic salmon and brown trout. Journal of Fish Biology 52:1272-1288.

Bisson, P.A., J.L. Nielsen, R.A. Palmason, and L.E. Grove. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. Pages 62-73 *in* N.B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland.

Burke, M. G., M. R. Kirk, N. A. MacBeth, D. J. Bevan, and R. D. Moccia. 2005. Influence of photoperiod and feed delivery on growth and survival of first-feeding Arctic char. North American Journal of Aquaculture 67:344-350.

Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Second Edition. Springer, New York, New York.

Connolly, P. J., and J. H. Peterson. 2003. Bigger is not always better for overwintering young-of-the-year steelhead. Transactions of the American Fisheries Society, 132:262-274.

Cunjak, R.A., R.A. Curry, and G. Power. 1987. Seasonal energy budget of brook trout in streams: Implications of a possible deficit in early winter. Transactions of the American Fisheries Society 116:817-828.

Denton, J. E. and M. K. Yousef. 1976. Body composition and organ weights of rainbow trout, *Salmo gairderi*. Journal of Fish Biology 8:489-499.

DeVries, D. R. and R. V. Frie. 1996. Determination of age and growth. B. Murphy and D. Willis, editors. Fisheries techniques. Second Edition. American Fisheries Society, Bethesda, Maryland.

Forseth, T., T.F. Naesje, B. Jonsson and K. Haraker. 1999. Juvenile migration in brown trout: a consequence of energetic state. Journal of Animal Ecology 68:783-793.

Forsman, A. and L.E. Lindell. 1991. Tradeoff between growth and energy storage in male *Vipera berus* (L.) under different prey densities. Functional Ecology 5:717-723.

Groot, C., L. Margolis, and W.C. Clarke. 1995. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver, British Columbia, Canada.

Herbinger, C. M. and G. W. Friars. 1991. Correlation between condition factor and total lipid content in Atlantic salmon, *Salmo salar* L parr. Aquaculture and Fisheries Management 22:527-529.

Hirsch, R. M. 1982. A Comparison of four streamflow record extension techniques. Water Resources Research 18:1081-1088.

Hunt, R. L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. Journal of the Fisheries Research Board of Canada 26:1473-1483.

Kuehl, R. O. 2000. Design of experiments: statistical principles of research design and analysis. Second Edition. Duxbury Press, Pacific Grove, California.

Larsen, D.A., B. R. Beckman, and W. W. Dickhoff. 2001. The effect of low temperature and fasting during the winter on growth and smoltification of Coho salmon. North American Journal of Aquaculture 63: 1-10.

Le Cren, E. D. 1969. Estimates of fish populations and production in small streams in England. Pages 269-280 *in* T.G. Northcote, editor. Symposium on salmon and trout in streams. H.R. MaxMillan Lectures in Fisheries, University of British Columbia, Vancouver, British Columbia, Canada.

Miranda, L.E. and W. D. Hubbard. 1994. Length dependent winter survival and lipid composition of Age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Transactions of the American Fisheries Society 123:80-87.

Mohr, M. S. and D. G. Hankin. 2005. Two-phase survey designs for estimation of fish abundance in small streams. Technical Memorandum, National Oceanic Atmospheric Administration Fisheries, Southwest Fisheries Science Center, Santa Cruz, California. Unpublished.

O'Connor, J. F. and G. Power. 1976. Production by brook trout (*Salvelinus fontinalis*) in four streams in the Matamek watershed, Quebec. Journal of the Fisheries Research Board of Canada 33:6-18.

Oliver, J. D., G. F. Holeton, and K. E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Transactions of the American Fisheries Society 108:130-136.

Post, J. R. and E. A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology 82:1040-1051.

Rand, P. S., B. F. Lantry, R. O'Gorman, R. W. Owens, and D. J. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978-1990: Implications for salmonine energetics. Transactions of the American Fisheries Society 123:519-534.

Reeves, G. H. 1979. Population dynamics of juvenile steelhead trout in relation to density and habitat characteristics. Master's Thesis, Department of Fisheries, Humboldt State University, Arcata California.

Rennie, M. D., N. C. Collins, B. J. Shuter, J. W. Rajotte, and P. Couture. 2005. A comparison of methods for estimating activity costs of wild fish populations: more active fish observed to grow slower. Canadian Journal of Fisheries and Aquatic Science 62: 767-780.

Rikardsen, A. H. and J. M. Elliott. 2000. Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in north Norway. Journal of Fish Biology 56:328-346.

Simpson, A. L., N. B. Metcalfe, and J. E. Thorpe. 1992. A simple non-destructive biometric method for estimating fat levels in Atlantic salmon, *Salmo salar* L. parr. Aquaculture and Fisheries Management 23:23-29.

Spigarelli, S. A., M. M. Thommes, and W. Prepejchal. 1982. Feeding, growth, and fat deposition by brown trout in constant and fluctuating temperatures. Transactions of the American Fisheries Society 111:199-209.

Sutton, S. G., T. P. Bult, and R. L. Haedrich. 2000. Relationships among fat weight, body weight, water weight and condition factors in wild Atlantic salmon parr. Transactions of the American Fisheries Society 129:527-538.

Thompson, J. M., E. P. Bergersen, C A Carlson, L.R. Kaeding. 1991. Role of size condition and lipid content in the overwinter survival of age-0 Colorado squawfish. Transactions of the American Fisheries Society 120:346-353.

Warren, C. E. and P. Doudoroff. 1971. Biology and water pollution control. W. B. Saunders Co., Philadelphia, Pennsylvania.

White, J. L. and B. C. Harvey. 2007. Winter feeding success of stream trout under different streamflow and turbidity conditions. Transactions of the American Fisheries Society 136:1187-1192.

Wootton, R. J. 1984. Introduction: strategies and tactics in fish reproduction. In: G. W. Potts and R. J. Wootton, editors. Fish reproduction: strategies and tactics. Academic Press, London, United Kingdom.

Appendix A. Pearson Correlation Coefficients examining correlation between environmental predictor variables in general linear model analysis in Barker Creek, Trinity County, California 2002-2003. Relationships with a coefficient less than 0.75 (shown in bold) were considered adequately free of multicollinearity to be used in modeling. Parameter abbreviations are listed in Table 1.

Barker Creek

	MT	RANG	HR	MQ
MT	1	**-0.7114**	**0.7231**	-0.7738
RANG	**0.7114**	1	0.8391	**-0.5806**
HR	**0.7231**	0.8391	1	**-0.2599**
MQ	-0.7738	**-0.5806**	**-0.2599**	1

Appendix B. Pearson Correlation Coefficients examining correlation between environmental predictor variables in general linear model analysis in Carr Creek, Trinity County, California 2002-2003. Relationships with a coefficient less than 0.75 (shown in bold) were considered adequately free of multicollinearity to be used in modeling. Parameter abbreviations are listed in Table 1.

Carr Creek

	MT	RANG	HR	MQ
MT	1	0.8195	0.8625	**-0.6073**
RANG	0.8195	1	0.8049	**-0.7042**
HR	0.8625	0.8049	1	**-0.2668**
MQ	**-0.6073**	**-0.7042**	**-0.2668**	1