DIET AND PREY CONSUMPTION OF JUVENILE COHO SALMON (*ONCORHYNCHUS KISUTCH*) IN THREE NORTHERN CALIFORNIA STREAMS

by

Eric J. Gonzales

A Thesis
Presented to
The Faculty of Humboldt State University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science
In Natural Resource Management: Fisheries

December 2006

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Eric J. Gonzales

Approved by the Master's Thesis Committee:

Walter Duffy 10/23/06
Walter G. Duffy, Co-Major Professor Date

Margaret A Wilzbach 10/24/06
Margaret A. Wilzbach, Committee Member Date

Terry D Roelofs 25 Oct. 06
Terry D. Roelofs, Committee Member Date

Bret C Harvey 27 Oct 06
Bret C. Harvey, Committee Member Date

Gary L. Hendrickson 31·X·06
Coordinator, Natural Resources Graduate Program Date

06-FI-605-10/19

Natural Resources Graduate Program Number

Chris A. Hopper, Interim Dean for Research and Graduate Studies Date

ABSTRACT

Diet and prey consumption of juvenile coho salmon (*Oncorhynchus kisutch*) were studied in three northern California streams. Diet and abundance (to estimate density and survival) of juvenile coho salmon was assessed in July and October 2002 and March 2003. A bioenergetic model developed for juvenile coho salmon was used to estimate prey consumption and prey conversion efficiency. Density estimates varied among creeks and seasons and ranged from 1.45 coho salmon · m^{-2} in July 2002 to 0.070 coho salmon · m^{-2} in March 2003. Peak standing stock biomass varied among streams and seasons. Peak biomass estimates raged from 23,339 g · ha^{-1} in July to 8,578 g · ha^{-1} in October 2002. No increase in standing stock biomass was observed in the stream with the highest density of coho salmon. Standing stock biomass increased in the low to moderate coho salmon density streams during July through October 2002. Minimum survival estimates varied among streams and seasons and ranged from 9-75%. July to October specific growth rates were highest in streams with the lowest densities. October 2002 to March 2003 minimum survival estimates were highest in streams in which mean weight of juvenile coho salmon was highest in October 2002. Diet of juvenile coho salmon varied among sampling periods and among streams. Terrestrial insects contributed significantly to the diet of juvenile coho salmon in all three streams, making up 25 to 50% of the biomass consumed for all three sampling periods. Amphipods were a significant portion of the biomass consumed in only one of the streams. Seasonal estimates of prey conversion efficiency ranged from 23% during April to July 2002 to 8%

during July to October 2002. Prey consumption by each of the juvenile coho salmon populations was highest in the July 2002 and lowest in March 2003. Prey consumption for the population of juvenile coho salmon in the high-density stream was as high or higher than in streams having lower density, even when standing stock biomass was lower. Results from this study suggest that differences between summer and fall rearing potential arising from variation and availability of prey for juvenile coho salmon bearing streams are likely secondary in importance to the amount of available winter habitat in regulating smolt production.

ACKNOWLEDGEMENTS

This thesis would have not been possible without the support of numerous individuals and agencies. First I would like to acknowledge The National Marine Fisheries Service for funding this study and the California Cooperative Research Unit for providing me with an opportunity. Kay Brisby took care of me and my fellow Unit graduate students. My major Advisor Dr. Walt Duffy provided mentorship that provoked an open thinking environment of ideas and data interpretation. Dr. Peggy Wilzbach willingly gave thorough review and detailed constructive criticism throughout the project. Dr. Ken Cummins shared his invertebrate biomass regressions and expert advice on processing fish diet samples. Doctors Bret Harvey and Terry Roelofs critically reviewed this thesis. Dr. Dave Hankin taught me sampling theory and how to think about survey design.

All of the staff at the California Cooperative Research Unit assisted with collection of field data including, Donald Baldwin, Mike Mettee, Mike Carney, Aaron Bleisner, Mourad Gabriel, Greta Wengert, Anstey Hinkson, and Russ Carpenter. Special thanks to Mariah Talbot and Brent Redd who were dedicated bug sorters.

I thank the Humboldt State Fisheries graduate students for all their inspiration and support throughout my tenure at the university. Mathew Krachey helped me to figure out clever ways to sort invertebrate data. Ben Ransom provided a map of the study area and shared his excellent field data collection capabilities. Jennifer Feola, Sharon Frazey, Michele Wheeler, and Bethany Reisberger all provided much needed support. Kasey

Bleisner helped me with the diet collection tray. Samantha Hadden, Osvaldo Hernandez, and John Matousek helped me with invertebrate identification.

Extra special thanks to Melissa Mata for helping with just about every aspect of this project including data entry, field collection of samples, and invertebrate sorting. I would also like to thank her for dealing with my constant grumbling, bellyaching, and endless fish discussions throughout. Her encouragement throughout this time will not be forgotten.

Last but not least I would like to thank my family for their constant love and support. Extra special thanks to my father for never giving up on me, even at times when I gave up on myself.

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INTRODUCTION

Declines in abundance of coho salmon (*Oncorhynchus kitsch*) throughout the Pacific Northwest (Nehlsen et al. 1991, Brown et al. 1994) have led to the identification of critical freshwater habitat requirement for the species (Sandercock 1991). The amount of summer and winter habitat (Nickleson et al. 1992, Quinn and Peterson 1996, Solazzie et al. 2000), stream temperature and discharge (Shirvell 1994, Giannico and Healy 1998, Giannico and Hinch 2003), and intra and interspecific interactions (Fausch 1984, Fausch 1993, Harvey and Nakamoto 1996) are among the factors that have been shown to affect growth and survival of juvenile coho salmon in freshwater. Mortality in freshwater can be substantial (Sandercock 1991, Bradford 1995, Solazzie et al. 2000) and has been documented to decrease with increased juvenile size prior to increased winter discharge (Bradford 1995, Brakensiek 2002). Additionally, prey availability and quality would likely affect growth and survival of juvenile coho salmon throughout their freshwater life history (Nielsen 1992).

In freshwater juvenile coho salmon are visual feeders that rarely feed on non-moving food or off of stream bottoms (Sandercock 1991). The diet of juvenile coho salmon in streams is more closely associated with drifting invertebrates than benthic macroinvertebrates (Johnson and Ringler 1980, Hetrick et al. 1998), and is comprised of similar proportions of taxa from aquatic and terrestrial origins (Hetrick et al. 1998, Wipfli 1997, Allan et al. 2003). The types and abundance of aquatic and terrestrial macroinvertebrates found in the diet of juvenile coho salmon can be quite variable and are often related to the amount and types of stream riparian cover (Sandercock 1991, Wipfli 1997, Allan et al. 2003).

Aquatic macroinvertebrate communities in lotic environments are closely associated with riparian vegetation (Cummins et al. 1989), and have been shown to exhibit various responses to disturbance that either directly or indirectly alter riparian zones and or watersheds (Karr and Chu 1999). Disturbance may affect aquatic invertebrate communities in many ways. Removal of riparian vegetation results in increased autochthonous production as is evident by shifts in functional feeding group abundance of stream macroinvertebrates (Cummins 1974). Pollution, and increased sedimentation may also change macroinvertebrate community structure from one dominated by Ephemeroptera (mayfly), Plecoptera (stonefly), and Trichopera (caddisfly) (EPT) structure too one dominated by only one or two tolerant taxa (e.g. some diptera) (Karr and Chu 1999). In streams, the primary food sources for fish are aquatic and terrestrial insect communities associated with riparian zones.

Disturbance can have an effect on energy sources available for juvenile stream salmonids (Wipfli 1997, Hetrick et al. 1998, Perry et al. 2003). Disturbance can lead to substantial variation among streams in the contribution of primary energy sources to higher trophic levels, even among streams of similar size and structure (Perry et al. 2003). The authors also suggested that disturbance is an important mechanism regulating energy flow from primary energy sources to higher trophic levels.

Studies relating temperature, diet quality and ration size to growth of fish consist largely of laboratory experiments. These experiments have clearly documented the effect of diet quality and temperature and their constraints on growth and maximum daily ration on fish (Koueta et al. 2002, Deng et al. 2002, Morris et al. 2003). Despite the high degree of variability in caloric content among prey taxa (Cummins and Wuycheck 1971, Driver et al. 1974, Griffiths 1997), studies exploring the effects of diet quality and temperature on wild stream fish are lacking.

Although information exists regarding disturbance and resultant diet of stream fish (Edwards and Huryn 1996,Wipfli 1997, Hetrick et al. 1998,), little is known about how differences of diet quality relate to wild fish populations. In this study I estimated growth and survival of three populations of juvenile coho salmon in the Prairie Creek watershed, Redwood National and State Parks, California. My assessment considered water temperature, diet quality and density of coho salmon in each stream. A bioenergetic model developed for juvenile coho salmon (Hanson et al. 1997, Willey 2004) was used to estimate consumption and prey conversion efficiency.

The three streams studied; Prairie, Boyes, and Streelow creeks have all experienced varying amounts of disturbance (e.g. relatively undisturbed, recovering from disturbance and recently disturbed) and thus may be considered to vary in habitat quality (Sparkman 2003). My specific objectives were to: 1) characterize the diet of juvenile coho salmon in all three streams, and 2) seasonally estimate prey consumption and prey conversion efficiency by individual coho salmon and populations occupying all three streams using a bioenergetic model.

STUDY AREA

The three study sites are located within the Prairie Creek watershed, which lies within Redwood National and State Parks, Humboldt County, California (Figure 1). Prairie Creek drains into Redwood Creek, which drains into the Pacific Ocean near Orick, California. Weather in the region is mild, with wet winters and relatively dry summers. Maximum air temperature in August averages 21.0 ^{o}C, while the average minimum air temperature in January is 2.7 ^{o}C. Mean annual precipitation is 170.8 cm, occurring primarily from October through March.

The Prairie Creek watershed is forested with redwood (*Sequoia sempervirens*), sitka spruce (*Picea sitchensis*), and Douglas fir (*Pseudotsuga menziesii*). Under-story vegetation includes black huckleberry (*Vaccinium ovatum*), red huckleberry (*Vaccinium parvifolium*), and ferns (*Polystichum sp.*). Riparian vegetation is primarily composed of red alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), and salmonberry, (*Rubus spectabilis*). Fish species within the watershed include coho salmon, Chinook salmon (*Oncorhynchus tshawytscha*), steelhead trout (*O. mykiss*), coastal cutthroat trout (*O. clarki clarki*), threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), coastrange sculpin (*C. aleuticus*), Pacific lamprey (*Lampetra tridentata*), and Pacific brook lamprey (*L. pacifica*).

Prairie Creek is a 22.5 km long, third order stream that drains an area of 77.5 km^2. Hill slope gradients range from 40 - 70%. The section of Prairie Creek chosen for study began at the Brown’s Creek confluence and extended upstream for 6.3 km.

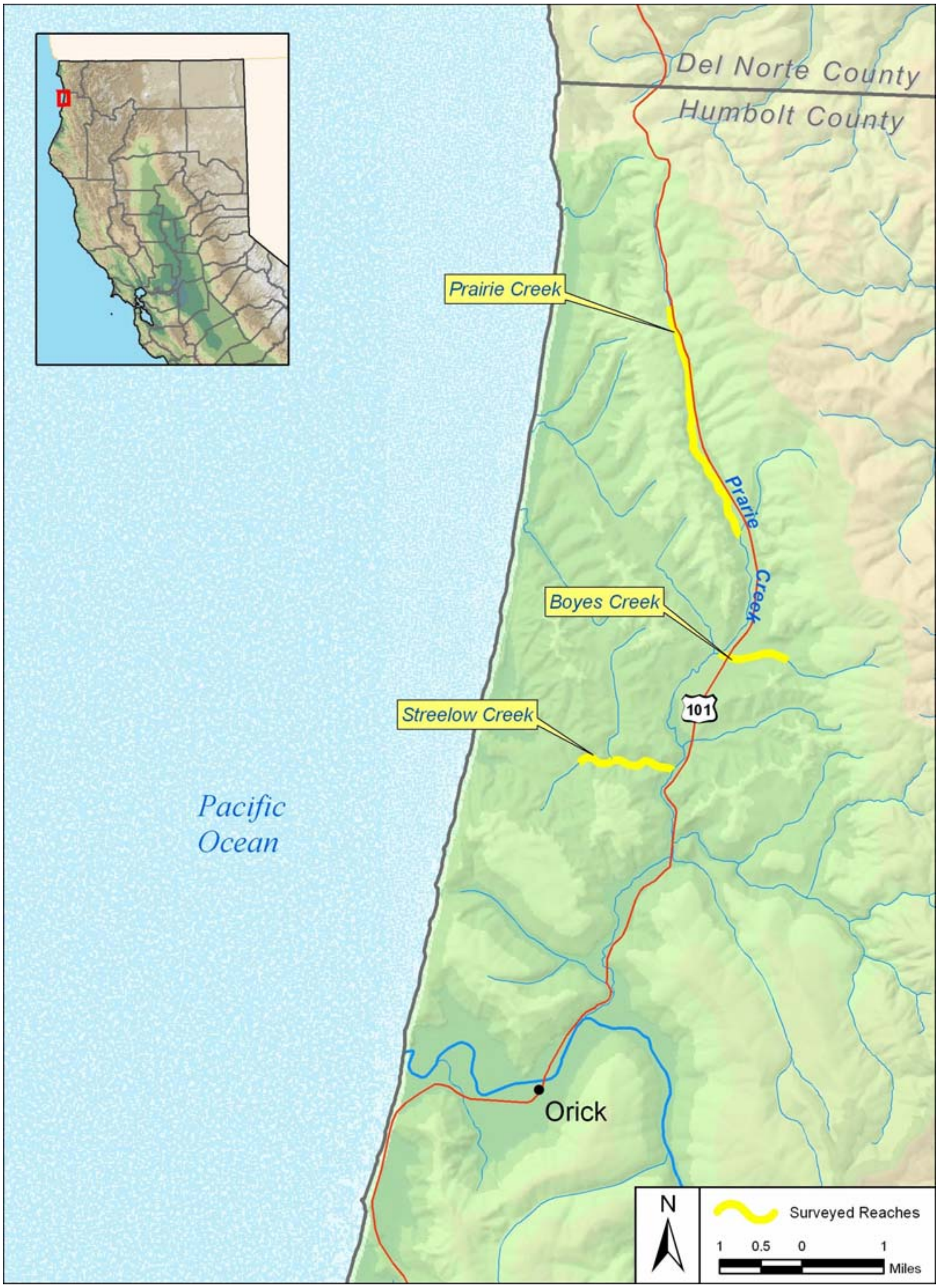

Figure 1. Map of Prairie Creek watershed, Humboldt County, California. Study stream reaches are highlighted.

Drainage above the study reach was 10 km^2 with an October through March base discharge of 0.56 $m^{-3} \bullet s^{-1}$ and a bank full discharge of 5.6 $m^{-3} \bullet s^{-1}$. The study reach was undisturbed and characterized by stands of old-growth redwood, and sitka spruce. Stream substrate within the study reach consists of well-sorted cobbles and gravels. The reach is low gradient (<2%) and has substantial amounts of large woody debris.

The section of Streelow Creek chosen for study extended from the Prairie Creek confluence upstream 2.2 km. Streelow Creek is a third order, low gradient stream (<2%) draining a 5.7 km^2 watershed. Mean annual discharge is 0.25 $m^{-3} \bullet s^{-1}$. Streelow Creek was logged from the 1950's to the 1960's for old growth lumber and is considered to be recovering from that disturbance. The watershed is forested with secondary growth redwood and red alder. Substrate within the study reach consists of cobbles mixed with sands.

The section of Boyes Creek chosen for study extends from the Prairie Creek confluence upstream 2.3 km. Boyes Creek is a third order stream, with a moderate channel gradient (>2%) draining a 4.4 km^2 watershed. Within the study reach the gradient is low (<2%). Mean annual discharge is 0.19 $m^{-3} \bullet s^{-1}$. Boyes Creek experienced the introduction of several hundred tons of sediment due to road construction failure in 1989 and is considered to be recently disturbed. The watershed contains some old growth redwood but is dominated by secondary growth species including red alder, western hemlock, and big leaf maple. Substrate within the study reach consists of cobbles mixed with large amounts of fine sediments and silts.

MATERIALS AND METHODS

Physical Characteristics

Physical data gathered included water temperature and the distribution of habitat units. Water temperature was recorded within each study reach from April 2002 through March 2003 using data loggers (HOBO Inc., Pocasse, MA) set to record at 1.5 hr intervals. Average daily water temperature (˚C) was calculated for each stream along with annual degree-days (Merritt and Cummins 1996) for comparative purposes.

Habitat was inventoried in July 2002, using a hierarchical approach similar to that described by Hawkin et al. (1993). Individual habitat units in each study reach were classified as either pools, deep pools (maximum depth $\geq$1.1m), runs, riffles or complex (units that could not be sampled effectively due to heavy large woody debris loading and excessive undercut banks). Small habitat units with prominent geomorphic breaks that had a length to average wetted width ratio less than one were included in the next upstream unit (Brakensiek 2002). Maximum depth, mean width, and length were recorded for each habitat unit.

Density and Survival

Abundance of juvenile coho salmon in each of the three streams was estimated at the reach scale and for individual experimental habitat units so as to estimate density and survival. Abundance estimates were derived from sampling during three periods; July and October 2002 and March 2003. Because Prairie Creek is larger than Boyes and

Streelow creeks, methods used to estimate abundance there differed from the other two streams.

Abundance was estimated in Prairie Creek using a two-phase sampling scheme. In this two-phase sampling scheme, 50% of the pool and run habitat units were selected for sampling using a quasi-systematic approach that is approximately equivalent to a simple random sample, guaranteeing that units are selected from the full spectrum of upstream and downstream locations within the study reach. Habitat units identified as first phase sample units (50%) were sampled by single pass direct diver observation. Those identified as second phase units (25% of first phase units) were sampled using the first and three additional diver observation passes, if $\leq$ 20 coho salmon were observed during the first pass observation. If > 20 coho salmon were observed during the first pass diver observation, second phase units were sampled using 2-3 pass electrofishing. Before electrofishing, each habitat unit sampled was isolated with block-nets on the upstream and downstream ends, with care taken to minimize disturbance. Two passes were considered sufficient if the number of juvenile coho salmon captured on the second pass was < 25% of the number captured on the first pass. If the number of juvenile coho salmon captured in the second pass was $\geq$ 25% of the number captured on the first pass, a third pass was conducted. Abundance estimates were calculated from this two-phase sampling scheme using bounded counts or jackknife depletion estimators for estimates of unit abundance (Hankin and Mohr, in preparation).

Abundance in Boyes and Streelow creeks was estimated using 2-3 pass electrofishing of a systematic random sample of habitat units within each stream reach

(Hankin 1984). I selected 25% of pool and run habitat units for sampling in each stream using randomization procedures suggested by Hankin (1984). Electrofishing was then conducted as described for Prairie Creek.

Reach scale abundance estimates for all three streams were derived from abundance in pool and run habitats using correction estimators for the total surface area of each habitat available in a stream. Complex habitat units, deep pools, and riffles were excluded from sampling (Hankin and Mohr, in preparation).

Only experimental habitat units were sampled in March 2003. In each stream, I randomly selected four runs and four pools from the July 2002 random samples (24 total samples) and designated them experimental habitat units. Abundance of juvenile coho salmon in experimental habitat units was estimated using 2-3 pass depletion electrofishing using methods identical to methods for estimating reach scale abundance in Boyes and Streelow creeks during July and October 2002.

Abundance within habitat units was estimated using a robust jackknife estimator, ($\hat{Y}$) (Pollock and Otto 1983):

$$\hat{Y} = \sum_{i=1}^{r-1} c_i + rc_r .$$

where, c_i denotes the number of fish captured on pass *i* and *r* denotes the number of passes. In contrast to the usual maximum likelihood estimator of unit abundance (Seber 1982) the jackknife estimator will not fail and will not produce improbable values for low number of passes and poor capture probabilities (Hankin and Mohr, in preparation).

Density (D) was estimated for reach scale abundance (pools and runs combined) and experimental habitat units as:

$$D = \frac{\hat{Y}_i}{m_i^2}$$

Where, $\hat{Y}_i$ is abundance in stream or experimental unit *i* and m_i^2 is the surface area (m^2) of stream or experimental unit *i*.

Survival estimates for juvenile coho salmon were calculated as:

$$S_{t+1} = \frac{N_{t+1}}{N_t}$$

where S_{t+1} = survival at time (t + 1), N is the abundance estimate and t is the sampling period or time. Survival was estimated for stream reaches and individual experimental habitat units.

Size and Growth

Size of juvenile coho salmon was measured in each stream on each sampling date so that growth could be calculated. An initial size for juvenile coho salmon from populations in each stream was estimated from fry captured in downstream migrant traps operated at the downstream end of each study site on April 12, 2002. This date corresponded with the first day that substantial numbers of coho salmon fry were captured in all downstream migrant traps (W. Duffy, U. S. Geological Survey, California Cooperative Fish Research Unit, unpublished data). Wet mass of coho salmon fry did not differ among streams (one-way anova ($F_{2,30} = 0.4621$, $P = 0.634$) on April 12, 2002.

Therefore, the grand mean mass (mean = 0.432 g, n = 33, SE = 0.009) was used as the initial mass for all three streams and the grand mean fork length (mean FL = 38 mm, n= 33, SE = 0.25) was as the initial length.

Size of all juvenile coho salmon captured in experimental habitat units on all subsequent sampling periods was measured. To better characterize size of fish in each stream, size data were also measured from additional habitat units during reach scale abundance estimates in July and October 2002. Fish were anesthetized using MS-222. Wet mass was measured (0.01 g) using a portable electronic balance and fork length (mm) was measured with a metric measuring board.

Juvenile coho salmon captured in experimental habitat units were tagged with Passive Integrated Transponder (PIT) tags to allow for measuring growth of individuals. Ten juvenile coho salmon, or fewer if < 10 were captured, were tagged in each experimental habitat unit during July and October, 2002.

Size data were used to estimate specific growth rates and absolute growth in both length (AG_{LT}) and mass (AG_{WT}). Specific growth rate (G) was calculated as:

$$G = (\frac{\log_e y_2 - \log_e y_1}{t_2 - t_1}) * 100$$

where, y_1 and y_2 are mean wet mass at time t_1 and t_2 (Busacker et al. 1990). Absolute growth was calculated as:

$$AG_{LT} = FL_{t2} - FL_{t1}$$

where, FL_{t1} and FL_{t2} are fork lengths at time 1 and 2 respectively. Absolute growth in mass was calculated similarly by substituting wet mass for length. These three growth rate measures were calculated from data on all fish weighed and measured in each stream during each sampling period.

Scales were collected from larger juvenile coho salmon on each sampling date to assess the proportion of each population made up of age 1+ and age 2+ fish. Only nine age 2+ juvenile coho salmon were identified out of 2,800 fish. Age 2+ coho salmon were recorded only during July 2002 when they represented 1.39%, 0.35% and 0.82% of the fish collected in Boyes, Prairie and Streelow creeks, respectively. Since the proportion of fish that were age 2+ was so small, they were not considered separately in any further analysis.

Diet Analysis

To characterize the diet of juvenile coho salmon, I collected stomach samples from fish in experimental habitat units of each stream during each sampling period. Stomach samples were collected from the first 10 juvenile coho salmon captured from the first pass of depletion electrofishing in each experimental habitat unit between 1000 to 1600 hrs. If < 10 juvenile coho salmon were captured during the first pass, stomach samples were taken from fish captured on subsequent passes until ten stomach samples, if available, were collected. Pulsed gastric lavage was used to flush stomach contents onto a measuring board fitted with a Nytex (250μm aperture) netting receptacle (Foster 1977). Stomach samples were placed into Whirl-Pak sample bags and preserved in 80% ethanol.

Stomach contents were sorted, identified to family or the lowest practical level of taxonomic resolution and measured to the nearest 0.5 mm. Biomass (dry mass, mg) for all taxa except oligochaetes was estimated by measuring the total length of prey and converting length to dry mass using ordinal level length-mass relationships (Benke 1999, Sabo 2002). The head and thorax were assumed to represent 1/3 of the total length of partially digested prey (K. Cummins, 2004, U. S. Geological Survey, California Cooperative Fish Research Unit, Personal Communication).

A wet length-dry mass relationship was developed for oligochaetes. Total length and width (nearest 0.5mm) of preserved specimens was measured, and their volume was calculated using the formula for a cylinder. Three pre-measured preserved specimens were placed in pre-weighed aluminum foil pans and dried in an oven at 60^{o}C for 24hrs. Wet volume of the three specimens was then divided by dry mass to obtain density. Average density (0.37 mg · mm^{-3}) was estimated and multiplied by volume to obtain individual oligocheate biomass (Bowen 1996). Using this method, dry mass of oligocheates varied little among individuals (Table 1).

Stomach fullness was estimated as dry mass of stomach content (mg) per wet mass of individual fish (g). Diet was described using mean percent by stomach content biomass (Bowen 1996) for pools and runs combined during each sampling period for each stream.

Bioenergetic Modeling

Consumption was estimated using a bioenergetic model developed for juvenile coho salmon (Hanson et al. 1997, Wiley 2004). Data required to estimate consumption

Table 1. Length, volume, dry mass and density of oligocheates used to estimate dry mass. Dry mass was estimated as DM = (3.14 · radius2) · length · average density (Bowen 1996).

Sample	Length (mm)	Volume (mm^3)	Dry mass (mg)	Density ($mg \cdot mm^{-3}$)	Estimated dry mass using average density (mg)
1	27	21.195	6.7	0.32	7.8
2	20	15.700	7.5	0.48	5.8
3	21	16.485	5.0	0.30	6.1
Average	23	17.793	6.4	0.37	6.6

included: site specific water temperature, proportion of each prey in the diet, energy density of prey, and an initial and final wet mass. Water temperature used in the model was the temperature recorded during this study. Proportions of prey in the diet were derived from stomach analyses, while prey energy density was derived from the literature (Brocksen et al. 1968, Cummins and Wuycheck 1971). A complete description of the juvenile coho salmon bioenergetics model formulation and equation structure may be found in Willey (2004). Hanson et al. (1997) provide a general overview of bioenergetics modeling. Physiological parameter values used in the juvenile coho salmon bioenergetic model are from Willey (2004) and are listed in Table 2.

Stream specific simulations were set up by inputting average daily temperature starting on April 12, 2002 and ending on the last sampling day for each stream in March 2003. Proportions of prey in the diet estimated in March 2003 were assumed to represent juvenile coho salmon diet for the simulation periods of April 12 through May 31, 2002

Table 2. Physiological processes and parameters used in the juvenile coho salmon bioenergetic model (modified from Wiley 2004).

Equation/Parameter	Value	Description	Source
$C = C_{\max} \cdot p \cdot f(T)_C$		Specific consumption rate (g / g/d)	
a_C	0.303	Intercept of the allometric mass function.	Hanson et al. (1997)
b_C	-0.275	Slope of the allometric mass function.	Hanson et al. (1997)
CQ	5	The lower water temperature at which consumption is a small fraction ($CK1$) of the maximum consumption rate.	Hanson et al. (1997)
CTO	15	The water temperature corresponding to .98 of the maximum consumption rate.	Hanson et al. (1997)
CTM	18	The water temperature (> CTO) at which dependence is still .98 of maximum consumption rate.	Hanson et al. (1997)
CTL	26	The water temperature at which dependence is some reduced fraction (CK4) of the maximum consumption rate.	Hanson et al. (1997)
$CK1$	0.42	A small fraction of maximum consumption rate.	Wiley (2004)
$CK4$	0.03	A small fraction of maximum consumption rate.	Wiley (2004)
$R = a_R W^{a_R} \cdot f(T)_R \cdot ACT$		Specific respiration rate (g/ g/d)	
a_R	0.0046	Intercept of the allometric mass function.	White and Li (1985)
b_R	-0.217	Slope of the allometric mass function.	Hanson et al. (1997)
RQ	2.1	Approximation of Q_{10}.	Wiley (2004)
RTO	18	Optimum temperature for respiration (where respiration is highest).	Brett (1952)
RTM	26	Maximum (lethal) water temperature.	Brett (1952)
ACT	2	Activity multiplier.	Kitchell et al. (1977)

Continued

Table 2. Physiological processes and parameters used in the juvenile coho salmon bioenergetic model (modified from Wiley 2004) (continued).

Equation/Parameter		Description	Source
SDA	0.172	Specific dynamic action	Hanson et al. (1997)
$F = a_F T^{a_F} \cdot e^{(G_F \cdot p)} \cdot C$		Egestion rate dependent on mass, temperature and ration.	
a_F	0.212	The intercept of the proportion of consumed energy egested versus water temperature and ration.	Hanson et al. (1997)
b_F	-0.522	The coefficient of water temperature dependence of egestion.	Wiley (2004)
G_F	0.631	The coefficient for feeding level dependence of egestion.	Hanson et al. (1997)
$U = a_U T^{a_U} \cdot e^{(G_U \cdot p)} \cdot C - F$		Excretion rate dependent on mass, temperature and ration.	
a_U	0.0214	The intercept of the proportion of consumed energy excreted versus water temperature and ration.	Wiley (2004)
b_U	0.380	The coefficient of water temperature dependence of excretion.	Wiley (2004)
G_U	-0.299	The coefficient for feeding level dependence of excretion.	Hanson et al. (1997)
$ED = \alpha + \beta W$		Predator energy density (J / g / d).	
α	4111	The intercept of the allometric mass function (J /g).	Wiley (2004)
β	155	The slope of the allometric mass function.	Wiley (2004)
Mass cutoff	10	Mass (g) at which energy density equations switches from alpha and beta 1 to alpha and beta 2.	
$\alpha 2$	7602		Hanson et al. (1997)
$\beta 2$	0.5266		Hanson et al. (1997)

and December 1, 2002 through the last sampling date of each stream in March 2003. Proportions of prey in the diet estimated in July 2002 were assumed to represent juvenile coho salmon diet for the simulation periods of June 1 through August 31, 2002. Proportions of prey in the diet estimated in October 2002 were assumed to represent juvenile coho salmon diet for the simulation periods of September 1 through November 30, 2002. Prey energy density was held constant throughout the study period. All simulations were run using the “fit-to-end-weight” option between sampling dates (Hanson et al. 1997).

A sensitivity analysis of deviations in model estimates of consumption to changes in physiological and user inputs was assessed following Kitchell et al. (1977) as:

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

where, $S_x(p)$ is model sensitivity to changes of output parameter x resulting from changes to input parameter p. Individual parameters were increased or decreased by 10% of the nominal value used in the model (Beauchamp et al. 1989).

Average daily individual consumption and specific consumption rate ($g \cdot g^{-1} \cdot d^{-1}$) were estimated from bioenergetics model forecasts of consumption during three periods; April 12 – July 2002, July – October 2002 and October 2002 – March 2003. The model was run using the “fit to end weight” option, with the grand mean wet mass of coho salmon fry in all three streams on April 12, 2002 used as the initial weight and weights from individual streams used to parameterize the model in July and October 2002 and March 2003.

Total consumption was estimated for PIT-tagged fish by fitting the model to the initial and final wet mass of each PIT-tagged fish for both July to October 2002 and October 2002 to March 2003 tag groups. Conversion efficiency (CE) was estimated for each individual stream and PIT Tagged fish as:

$$CE = \frac{G}{C} * 100$$

where, G is energy allocated to growth and C is model estimated consumption. CE represents the percentage of model estimated consumption left over after all other daily metabolic needs have been met, which varies with diet quality, temperature, and fish size.

Population level consumption and biomass were estimated using inputs on abundance and survival estimates for each stream. Simulations were run by fitting the model to the initial and final wet mass estimated for each stream by date, starting on the last day each stream was sampled in July (initial) and October 2002 (final), and October 2002 (initial) and March 2003 (final). Model estimates of prey consumption and biomass for each population throughout the periods were expressed by g (wet mass)/ hectare for comparative purposes.

Statistical Analysis

Analyses were carried out to test for statistical differences in response variables among streams and seasons. Arcsine transformations were used to normalize density and stomach fullness data before applying the ANOVA (Kuehl 2000). A log transformation was applied to size data before applying the ANOVA. A three factor fixed effects ANOVA model was used to test for differences in density, size, and stomach fullness among streams, seasons and habitat types. If interactions between variables were detected a one-way ANOVA was used to test for differences among streams. If interactions were not detected only the results from the main effects variables were presented.

A two factor fixed effects ANOVA was used to test for differences in survival between streams, and habitat units. A one-way ANOVA was used to test for differences between survival estimates for the July to October 2002 and October 2002 to March 2003 periods. Arcsine transformations were used to normalize the survival data before applying the ANOVA (Kuehl 2000).

A one-way ANOVA was used to test for differences among streams in mean mass and length of PIT tagged fish during both July and October 2002 sampling periods. Differences among streams and between habitats, for specific growth rate, absolute growth, and conversion efficiency of PIT tagged fish were also tested with a one-way ANOVA. A two sample t-test was used to test for differences in specific growth rate, absolute growth and conversion efficiency between the July to October 2002 and October 2002 to March 2003 periods. Arcsine transformations were used to normalize conversion efficiency data before applying the ANOVA or two sample t-test (Kuehl 2000). Alpha was set at 0.05 for all tests.

RESULTS

Physical Characteristics

Daily average water temperature during the study was most variable in Boyes Creek (Figure 2). In Prairie and Streelow creeks average daily temperature ranged from 6.9 to 12.7 °C and 6.4 to 12.3 °C, respectively. Average daily temperature in Boyes Creek was highest in summer (14.3 °C) and lowest in winter (6.3 °C) among all three streams. Calculated degree-days were greatest in Boyes Creek (3,561), intermediate in Prairie Creek (3,427) and least in Streelow Creek (3,363).

A total of 802 habitat units were mapped, of which 383 were in Prairie Creek, 235 in Boyes Creek and 184 in Streelow Creek (Table 3). In Prairie Creek, pool habitats made up 27% of the habitat area followed by runs and riffles, which made up 23% and 25% of the habitat area. Conversely, riffle habitats comprised about half the habitat area and length in Boyes Creek, followed by pools and runs. In Streelow Creek, pool habitats comprised about one third of the total habitat area, followed by runs and riffles. Linear measures of habitat showed less variation than surface area measures did. Complex and deep pool habitats comprised a minor proportion of habitat in all three streams and there were no deep pools in Boyes Creek.

Density and Survival

Density of juvenile coho salmon was greatest during July and declined each sampling period after that. Density differed among seasons ($F_{2, 54} = 113$, $P = < 0.001$), but not

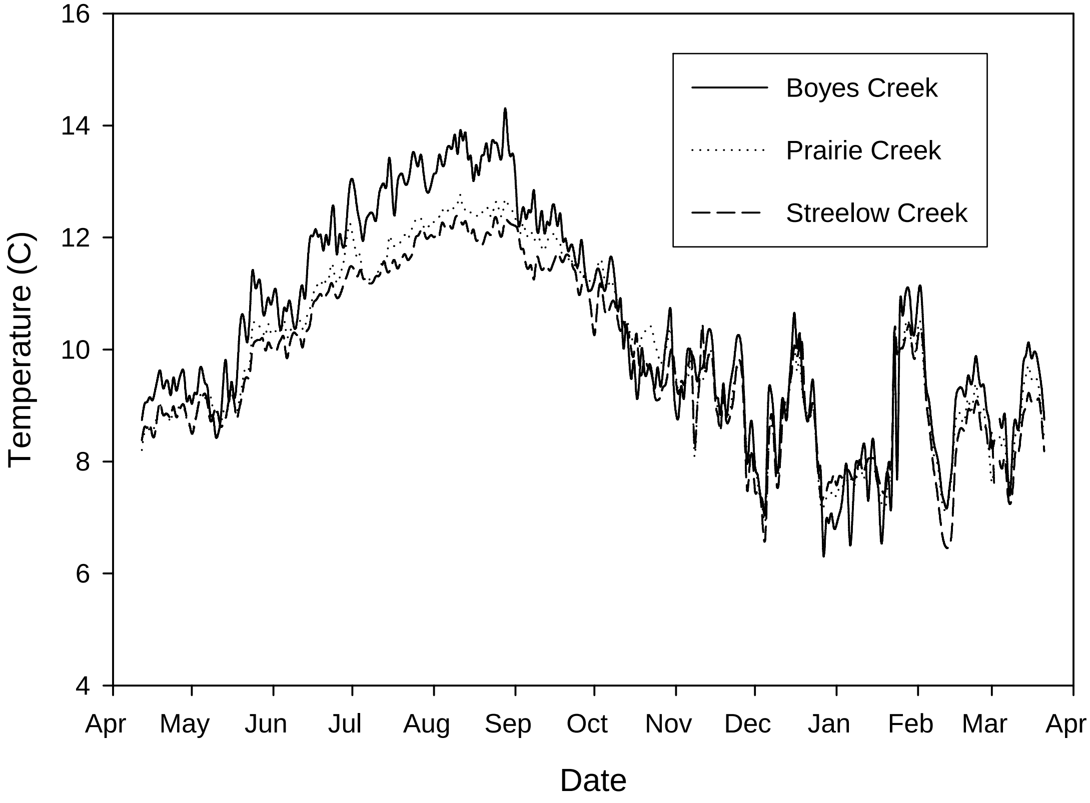

Figure 2. Average daily temperature in all three streams during April 2002 – April 2003.

Table 3. Number of habitat units, area (m^2), percentage area, length (km), and percent length of habitat units by type sampled in 2002 and 2003.

Habitat	n	Area (m^2)	Area (%)	Length (km)	Length (%)
Boyes Creek					
Run	57	1126	20	0.49	22
Pool	62	1537	27	0.53	24
Riffle	95	2628	46	1.09	48
Deep pool	0	0	0	0.00	0
Complex	21	402	7	0.15	6
Total	235	5693	100	2.26	100
Prairie Creek					
Run	113	6275	23	1.64	26
Pool	93	9317	35	1.85	29
Riffle	135	6790	25	2.00	31
Deep pool	12	1902	7	0.29	5
Complex	30	2490	9	0.57	9
Total	383	26774	100	6.35	100
Streelow Creek					
Run	52	2650	32	0.73	34
Pool	58	3024	36	0.70	32
Riffle	57	1589	19	0.54	24
Deep pool	6	491	6	0.09	4
Complex	11	531	6	0.13	6
Total	184	8285	100	2.19	100

among streams ($F_{2, 54} = 2.45$, $P = 0.095$), nor between pool and run habitats ($F_{1, 54} = 0.227$, $P = 0.635$). Although significant differences were not found among streams, densities were highest in Boyes Creek at the reach and habitat unit level in July and October 2002 (Table 4).

Season patterns in population (standing stock) biomass ($g \bullet ha^{-1}$) varied somewhat among streams. In Prairie and Streelow creeks, population biomass increased from July through October 2002, then declined through March 2003 (Figure 3). In Boyes Creek, population biomass declined between July and October 2002, then declined more rapidly through March 2003 than it did in Prairie and Streelow creeks. Peak biomass estimates in Prairie and Streelow Creeks in October 2002 were 8,578 and 15,042 $g \bullet ha^{-1}$, respectively. In Boyes Creek peak biomass was estimated in July 2002 and was 23,339 $g \bullet ha^{-1}$.

Survival decreased with time, but did not appear to exhibit any other patterns. Survival was greater during the July – October 2002 period than during the October 2002 – March 2003 period (Table 6; $F_{1,44} = 31.765$, $P < 0.001$). Survival did not differ among streams ($F_{2,40} = 0.108$, $P = 0.898$), between habitat types ($F_{1,40} = 1.150$, $P = 0.289$), nor between stream reaches and experimental habitat types ($F_{2,40} = 0.97830$, $P = 0.388$). Differences in survival between pool and run habitats showed no consistent pattern, nor did differences between stream reaches and experimental habitats (Table 5).

Table 4. Estimated mean density (no • m^{-2}) of coho salmon in stream reaches and experimental habitat units during each sampling period. Standard errors of means are shown in parentheses.

		Density/Reach			Density/Experimental Habitat		
Stream	Habitat	July 02	Oct. 02	March 03	July 02	Oct. 02	March 03
Boyes Creek							
	Run	1.50	0.94		1.68 (0.43)	0.63 (0.26)	0.08 (0.05)
	Pool	1.40	1.02		1.13 (0.24)	0.99 (0.13)	0.13 (0.04)
	Combined	1.45	0.99	0.09	1.41 (0.25)	0.81 (0.15)	0.11 (0.03)
Prairie Creek							
	Run	0.62	0.43		1.11 (0.25)	0.84 (0.22)	0.05 (0.03)
	Pool	0.82	0.44		0.76 (0.10)	0.45 (0.04)	0.08 (0.02)
	Combined	0.74	0.43	0.07	0.93 (0.14)	0.65 (0.13)	0.07 (0.02)
Streelow Creek							
	Run	0.79	0.52		0.88 (0.05)	0.51 (0.11)	0.07 (0.04)
	Pool	0.75	0.56		0.78 (0.14)	0.58 (0.12)	0.19 (0.05)
	Combined	0.77	0.54	0.11	0.83 (0.07)	0.55 (0.08)	0.13 (0.04)

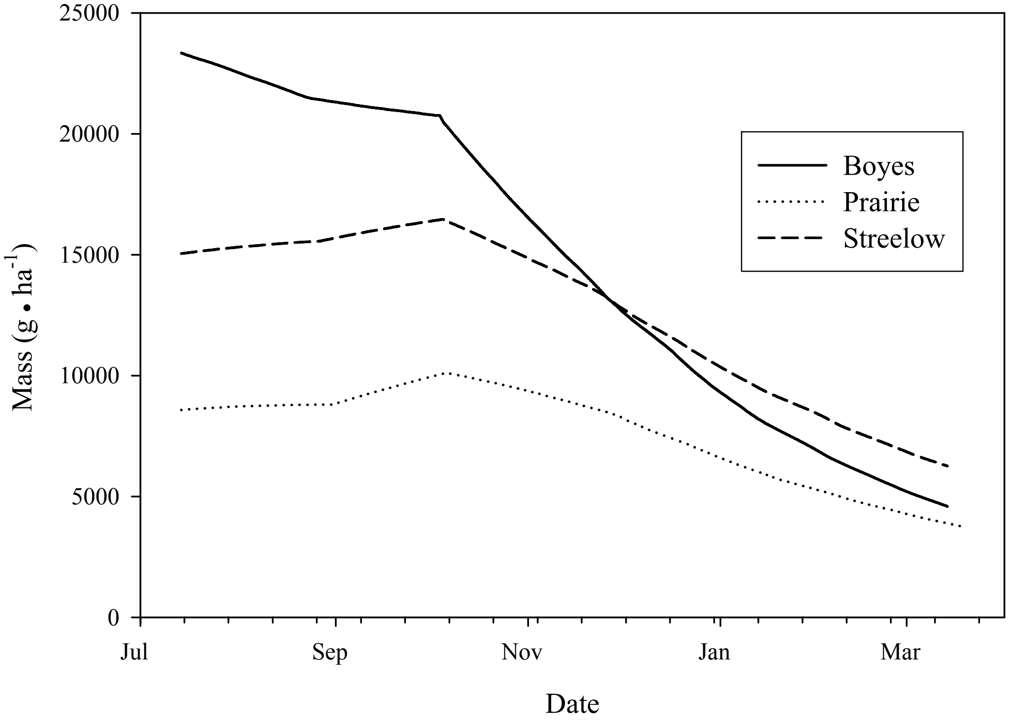

Figure 3. Model predicted daily standing stock biomass of juvenile coho salmon in the Boyes, Prairie and Streelow creeks, Humboldt County California during 2002 and 2003.

Table 5. Mean percentage survival of juvenile coho salmon in pool and run habitats from study reaches and experimental habitat units of all three streams. Standard errors are presented in parentheses. Survival listed under October is for the period July – October 2002 while that listed under March is for the period October 2002 – March 2003.

	Boyes Cr.				Prairie Cr.				Streelow Cr.			
	Reach		Experimental		Reach		Experimental		Reach		Experimental	
	Oct.	March	Oct.	March	Oct.	March	Oct	March	Oct	March	Oct.	March
Runs	72	-	40.6 (14.0)	29.4 (23.7)	53	-	79.2 (13.9)	8.4 (4.5)	74	-	57.0 (9.0)	19.4 (10.4)
Pools	63	-	84.9 (7.5	13.5 (3.0)	69	-	60.8 (4.2)	18.3 (5.2)	66	-	73.4 (4.2)	45.6 (19.9)
Combined	68	9	62.8 (11.1)	22.6 (12.3)	58	17	70.0 (7.6)	14.0 (3.7)	70	20	65.2 (5.6)	32.5 (11.5)

Size and Growth

Size of juvenile coho salmon varied among dates, streams, and between habitat types. Interactions between date, stream and habitat type dictated the use of one-way ANOVA to analyze size differences among streams. Among streams, fork length ($F_{2, 2990}$ = 89.835, $P < 0.001$) and mass ($F_{2, 2990}$ = 99.154, $P < 0.001$) were greater in Streelow Creek than in the other two streams for all three dates (Table 6). Among dates, fork length ($F_{2, 2990}$ = 624.601, $P < 0.001$) and mass ($F_{2, 2990}$ = 562.853, $P < 0.001$) became greater on each subsequent date and all dates differed. Among habitats, fork length ($F_{1, 2991}$ = 35.259, $P < 0.001$) and mass ($F_{1, 2991}$ = 34.894, $P < 0.001$) of juvenile coho salmon was greater in pools than in runs (Appendix A).

Analysis of the size of fish PIT tagged in experimental habitat units was limited to fish tagged in July and recaptured in October 2002 because of low recapture rates in March 2003. Neither the mass of fish PIT tagged in July ($F_{2, 53}$ = 2.51, $P = 0.090$) nor the mass of PIT tagged fish recaptured in October ($F_{2, 53}$ = 1.64, $P = 0.203$) differed among streams (Table 6). Similarly, the fork length of fish PIT tagged in July ($F_{2, 53}$ = 2.61, $P = 0.0822$) and PIT tagged fish recaptured in October ($F_{2, 53}$ = 2.51, $P = 0.090$) did not differ among streams. Between pools and runs, fork length of fish PIT tagged in July ($F_{1, 54}$ = 1.37, $P = 0.246$) and recaptured in October ($F_{1, 54}$ = 2.06, $P = 0.132$) did not differ. Similarly, mass of PIT tagged fish in July ($F_{1, 54}$ = 1.19, $P = 0.279$) and recaptured in October ($F_{1, 54}$ = 2.33, $P = 0.132$) was not different between pools and runs.

Table 6. Sample size, mean wet mass and mean fork length of juvenile coho salmon from study reaches of all three streams and for fish PIT tagged in experimental habitat units. Standard errors of means are presented in parentheses.

	Stream Reaches			Experimental Habitats		
	n	Mean Wt. (g)	Mean FL (mm)	n	Mean Wt. (g)	Mean FL (mm)
Boyes Creek						
July 02	288	1.61 (0.06)	50.5 (0.51)	16	3.92 (0.35)	68.3 (1.9)
Oct. 02	361	2.12 (0.06)	56.4 (0.48)	16	4.38 (0.37)	71.9 (1.9)
March 03[1]	48	5.29 (0.34)	75.1 (1.68)	2	5.48	76.5
Prairie Creek						
July 02	569	1.61 (0.04)	50.4 (0.37)	24	3.23 (0.12)	64.5 (0.7)
Oct. 02	759	2.38 (0.05)	57.4 (0.35)	24	4.68 (0.26)	73.0 (1.2)
March 03[1]	91	5.15 (0.23)	75.6 (1.16)	4	8.07 (0.75)	87.0 (3.4)
Streelow Creek						
July 02	364	1.94 (0.05)	53.2 (0.41)	16	3.94 (0.43)	68.6 (2.0)
Oct. 02	402	3.26 (0.09)	63.9 (0.51)	16	5.24 (0.46)	71.9 (2.0)
March 03[1]	111	6.21 (0.26)	80.1 (1.14)	6	6.86 (0.94)	84.2 (3.9)

[1] Size recorded in March 2003 was recorded from fish tagged in October 2002.

Specific growth rates varied among seasons and streams. Specific growth rates were greatest during the period April to July 2002 (Table 7). In Prairie and Streelow creeks specific growth was lowest during October 2002 to March 2003. Specific growth rates were greatest in Streelow Creek during the first two sampling periods, but greatest in Boyes Creek during October 2002 to March 2003. Lowest specific growth rates were found in Boyes Creek during July to October 2002.

Specific growth rates of fish PIT tagged in experimental habitat units varied among creeks. Specific growth rates of PIT tagged fish were greater in Prairie and Streelow creeks than in Boyes Creek ($F_{2, 65} = 7.61$, $P = < 0.001$) (Table 8). Specific growth rates of PIT tagged fish were not significantly different ($F_{1, 66} = 1.19$, $P = 0.280$) between runs and pools. Between the two seasons compared, specific growth rates were not significantly higher during from October 2002 to March 2003 than during July to October 2002 (two sample t-test, $t_{66} = -0.8452$, $P = 0.401$).

The timing of absolute growth differed from that of specific growth. Qualitatively, the greatest absolute growth in mass and length was found during October 2002 to March 2003, the exception being absolute growth in fork length in Prairie Creek (Table 7). Absolute growth in length and weight also was lowest during July to October 2002, with the single exception again being absolute growth in mass in Prairie Creek during this period.

Table 7. Mean specific growth rate (SGR, $g \cdot g^{-1} \cdot d^{-1}$) and absolute growth in mass (AG_{WT}, g) and fork length (AG_{LT}, mm) for juvenile coho salmon captured in stream study reaches and for those PIT tagged and recaptured in experimental habitat units. Standard errors of means are presented in parentheses.

	Boyes Creek			Prairie Creek			Streelow Creek		
	July 2002	Oct. 2002	March 2003[1]	July 2002	Oct. 2002	March 2003[1]	July 2002	Oct. 2002	March 2003[1]
Stream Reaches									
n	288	361	48	569	759	91	364	402	111
SGR	1.33	0.33	0.57	1.43	0.45	0.43	1.55	0.62	0.35
AG_{WT}	1.18	0.51	3.16	1.18	0.77	2.63	1.51	1.32	2.66
AG_{LT}	12.9	5.8	18.8	12.8	7.0	18.1	15.5	10.7	15.5
Experimental Habitats									
n		16	2		24	4		16	6
SGR		0.12	0.36		0.38	0.40		0.36	0.33
		(0.02)			(0.02)	(0.06)		(0.02)	(0.04)
AG_{WT}		0.46	2.43		1.45	3.73		1.31	2.67
		(0.19)			(0.18)	(0.56)		(0.21)	(0.28)
AG_{LT}		3.6	12.0		8.5	17.0		7.2	13.7
		(0.8)	(0.4)		(0.8)	(2.9)		(1.1)	(1.3)

[1] Growth rates from experimental habitats reported for October were taken from fish tagged in July, those reported for March were taken from fish tagged in October.

Absolute growth in length of PIT tagged fish was greater in October 2002 to March 2003 than during July to October 2002 (two sample t-test, $t_{66} = -5.6275$, $P = < 0.001$). Absolute growth in weight of PIT tagged fish was also greater in October 2002 to March 2003 than during July to October 2002 (two sample t-test, $t_{66} = -21.7416$, $P = < 0.001$) (Table 7). Absolute growth of PIT tagged fish in length ($F_{2, 65} = 6.60$, $P = 0.002$) and weight ($F_{2, 65} = 5.49$, $P = 0.003$) was greater in Prairie Creek than in other streams. Absolute growth of PIT tagged fish was higher in pools (average $AG_{LT} = 9.48$mm, average $AG_{WT} = 1.78$ g) than runs (average $AG_{LT} = 1.78$ mm, average $AG_{WT} = 1.02$ g) for both length ($F_{2, 65} = 4.78$, $P = < 0.001$) and weight ($F_{2, 65} = 7.61$, $P = < 0.022$).

Diet Analysis

Prey of juvenile coho salmon included 14 categories at the order or higher level of taxonomic resolution for non-insect taxa. Remaining taxa were categorized as “other”. Other taxa made up < 7.5% of juvenile coho salmon diet by biomass for each sampling period. Appendix B lists all taxa identified in stomach samples of juvenile coho.

Diet of juvenile coho salmon varied among streams and seasons (Table 8). Three to four taxa typically made up >50% of the biomass consumed for any one sampling period. Biomass of Diptera in the diet increased in all three streams between July and October, then decreased in March 2003. Biomass of Diptera in the diet was highest in Boyes Creek on all three sampling dates. Amphipods made up a substantial proportion of the biomass consumed by juvenile coho salmon in Streelow Creek on all three sampling dates, but never contributed more than 6% to the diet of fish in Boyes and Prairie creeks.

Table 8. Mean percentage biomass of juvenile coho coho salmon diet collected in July and October 2002, and March 2003 from the three northern California streams. L, A, and P denote larval, adult, and pupal life stages.

	Boyes Creek			Prairie Creek			Streelow Creek		
Taxa	July 02	Oct 02	Mar 03	July 02	Oct 02	Mar 03	July 02	Oct 02	Mar 03
Amphipoda	0	0	6.01	1.33	0.93	2.21	23.24	17.19	23.74
Aranea	6.45	3.61	7.28	9.83	4.52	1.5	8.89	5.01	5.75
Coleoptera (L+A)	12.41	9.01	18.48	13.13	2.89	8.31	3.56	8.74	9.4
Collembolla	0.57	0.98	0.46	1.12	11.78	1.89	0.82	0.7	0.4
Diplopoda	3.75	3.88	2.26	0.54	3.69	1.73	4.93	7.47	0.03
Diptera (L+A+P)	32.37	47.34	13.63	16.67	24.21	8.26	18.78	23.93	9.51
Ephemeroptera (L+A+P)	5.46	7.53	5.96	12.85	7.92	11.54	2.03	4.63	3.26
Homoptera (L+A)	0.63	3.07	1.33	0.7	1.78	0.93	0.76	2.27	0.53
Hymenoptera	1.39	2.76	0.39	4.26	0.84	0.27	0.64	4.36	0.87
Isopoda	2.3	0	2.07	4.61	0	1.35	4.53	1.41	4.47
Lepidoptera (L+A)	4.21	2.49	1.24	2.16	5.73	1.33	3.04	4.61	1.78
Oligochaeta	19.72	2.98	20.89	13.09	6.35	24.6	16.61	10.38	18.5
Plecoptera (L+A)	2.02	1.09	6	2.89	4.56	9.29	4.59	2.47	8.74
Trichoptera (L+A+P)	5.89	10.32	6.63	11.2	18.39	23.94	5.6	4.96	9.5
Other	2.83	4.94	7.37	5.62	6.41	2.85	1.98	1.87	3.52
	100	100	100	100	100	100	100	100	100
Sample Size	54	55	29	61	76	46	55	81	39

Trichoptera contributed to the diet of juvenile coho salmon in all three streams on all sampling dates. Fish in Prairie Creek consumed more Trichoptera than fish in other streams on all sampling dates. Oligochaetes also contributed substantially to the biomass consumed, particularly in July 2002 and March 2003.

Stomach fullness differed among streams, ($F_{2, 47} = 10.73$, $P = < 0.0001$) and sampling dates ($F_{2, 47} = 11.51$, $P = < 0.0001$) (Figure 4). However, no difference in stomach fullness was found between runs and pools ($F_{1, 47} = 0.075$, $P = 0.784$). Stomach fullness was lowest for all three streams in October 2002 and highest in Streelow Creek for all three seasons.

Bioenergetic Modeling

Parameters used in the juvenile coho salmon bioenergetic model were relatively insensitive to perturbations of the nominal values used (Table 9). Ten percent changes in all model parameters resulted in estimates of consumption changing less than $\pm$ 10%. The intercept of the respiration equation (a_R), and the optimum temperature for respiration (RTO) were the most sensitive model parameters resulting in 9.0 and 9.2% deviations in consumption, respectively. Q_{10} (RQ) and the activity multiplier (ACT) were also sensitive parameters. The input parameter of prey energy density resulted in 4.6 and 4.5% changes in estimated consumption.

Specific consumption rate was predicted to be highest in spring, decreasing through summer and fall for Prairie and Streelow creeks. The lowest specific consumption rate throughout the study period (average = $0.040\ g \bullet g^{-1} \bullet d^{-1}$) was predicted

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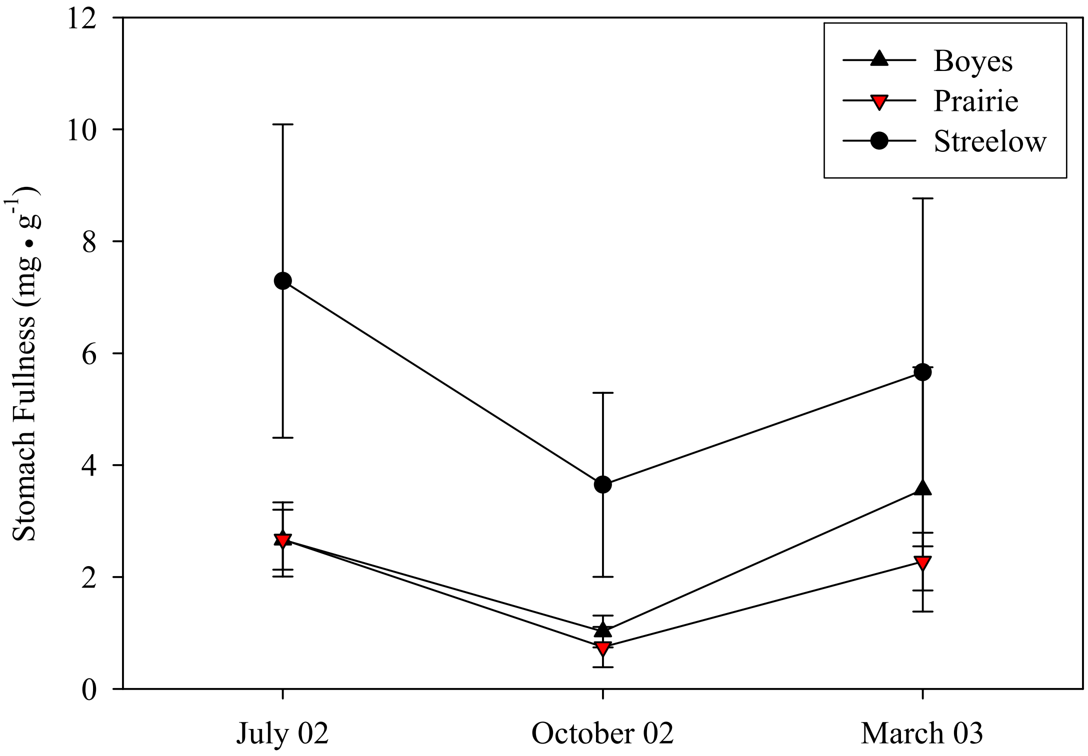

Figure 4. Mean stomach fullness averaged over all stomach samples collected from each stream by sampling date. Error bars represent 95% confidence intervals.

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Table 9. Sensitivity analysis of juvenile coho salmon bioenergetic model estimates of consumption (g). Data are the proportional change from nominal values (Table 2) after a perturbation of ± 10%. A sensitivity of ± 1.0 indicates that a change of parameter by 10% causes a resultant 10% change in estimated consumption (Kitchell et al.1977).

	Proportional change in model output with a ± 10% change in nominal value	
	Consumption (g)	
Parameter	+ 10% of nominal value	- 10% of nominal value
a_C	0.01	0.02
b_C	0.21	-0.18
CQ	0.01	0.01
CTO	0.01	0.01
CTM	0.01	0.01
CTL	0.01	0.01
$CK1$	0.01	0.01
$CK4$	0.01	0.01
a_R	0.60	-0.90
b_R	-0.27	0.29
RQ	-0.42	0.46
RTO	-0.87	0.92
RTM	0.09	-0.06
ACT	0.69	-0.43
SDA	0.22	-0.21
a_F	0.09	-0.07
b_F	-0.08	0.11
G_F	0.02	0.00
a_U	0.06	-0.06
b_U	0.06	-0.05
G_U	0.00	0.00

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for Prairie Creek. Boyes and Streelow creeks were predicted to have the highest specific consumption rates throughout the study period (average = 0.044 and 0.043 g $\bullet$g^{-1}$\bullet$ d^{-1}). Predicted specific consumption rates were highest in Streelow Creek during spring. They were highest in Boyes Creek in fall and winter (Figure 5).

Prey consumed by individual juvenile coho salmon, were predicted to increase throughout the study period in all three streams. The model predicted a slight decrease in consumption in all three streams in mid-July (Figure 6). for Prairie Creek. Individual prey consumption throughout the study period was predicted to be highest in Streelow Creek (average = 0.111 g $\bullet$ d^{-1}) lowest in Prairie Creek (average = 0.085 g $\bullet$ d^{-1}) and intermediate in Boyes Creek (average = 0.092 g $\bullet$ d^{-1}).

Average prey conversion efficiency varied seasonally and among streams (Figure 7). Prey conversion efficiency was highest for April to July 2002, lowest in July to October 2002 and intermediate in October 2002 to March 2003. The exception was Streelow Creek, where prey conversion efficiency was highest for April to July 2002, then declined through the remaining two sampling periods. Among streams, average prey conversion efficiency was highest in Streelow Creek for April to July 2002 (23.0 %) and July to October 2002 (15.1 %). During October 2002 to March 2003, prey conversion efficiency was highest in Boyes Creek (15.4 %). Prey conversion efficiency was intermediate in Prairie Creek for all three sampling periods.

Prey conversion efficiency by PIT tagged juvenile coho salmon in experimental habitat units varied among streams (Table 10). Prey conversion efficiency was greater in

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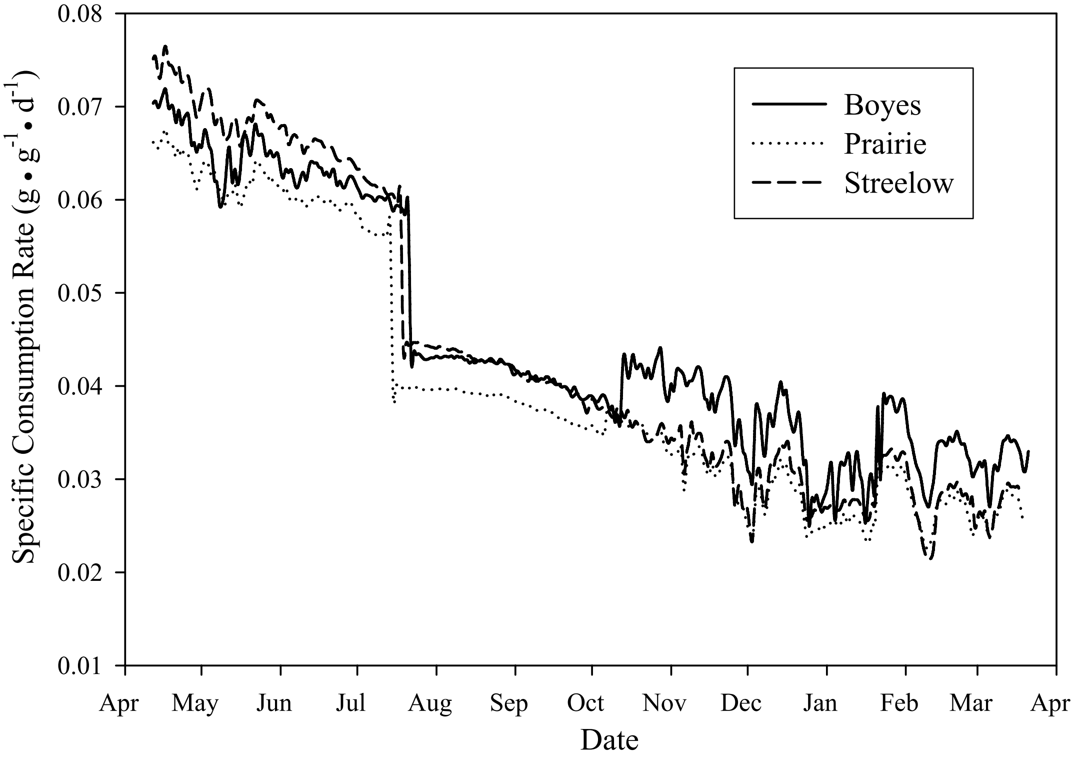

Figure 5. Specific consumption rate for juvenile coho salmon predicted by the bioenergetic model. Expressed as ($g \bullet g^{-1} \bullet d^{-1}$) throughout the study period for the three northern California streams.

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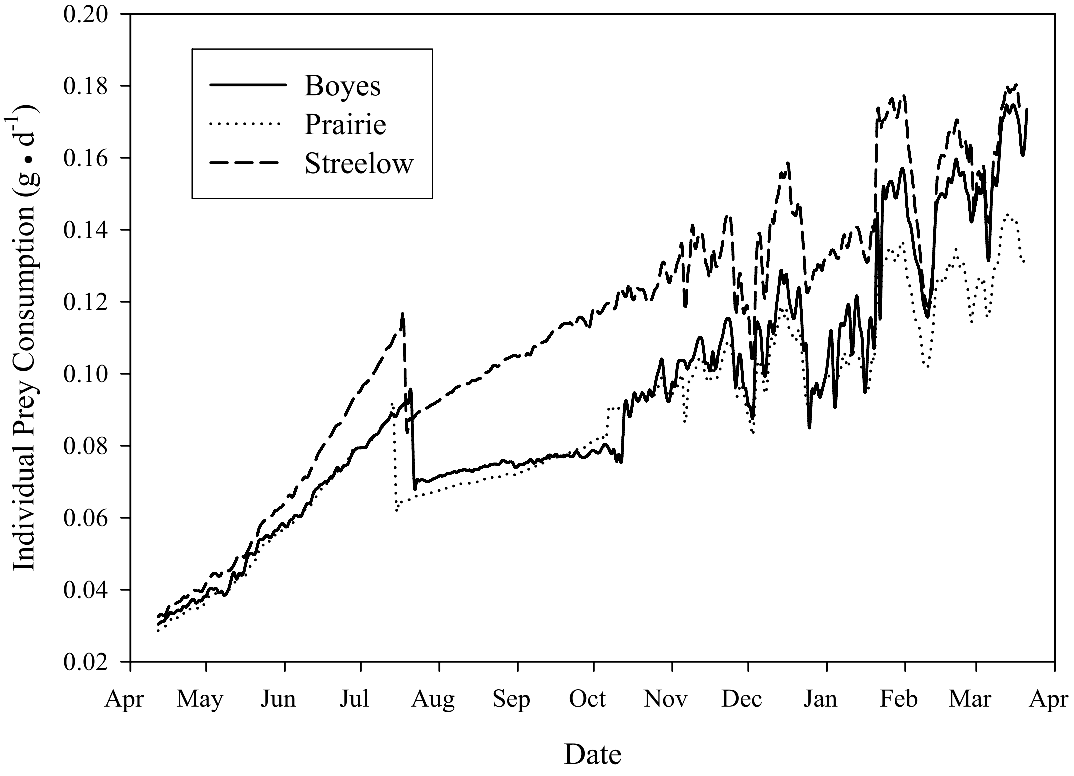

Figure 6. Model estimated daily average juvenile coho salmon prey consumption expressed as (g • d^{-1}) wet mass.

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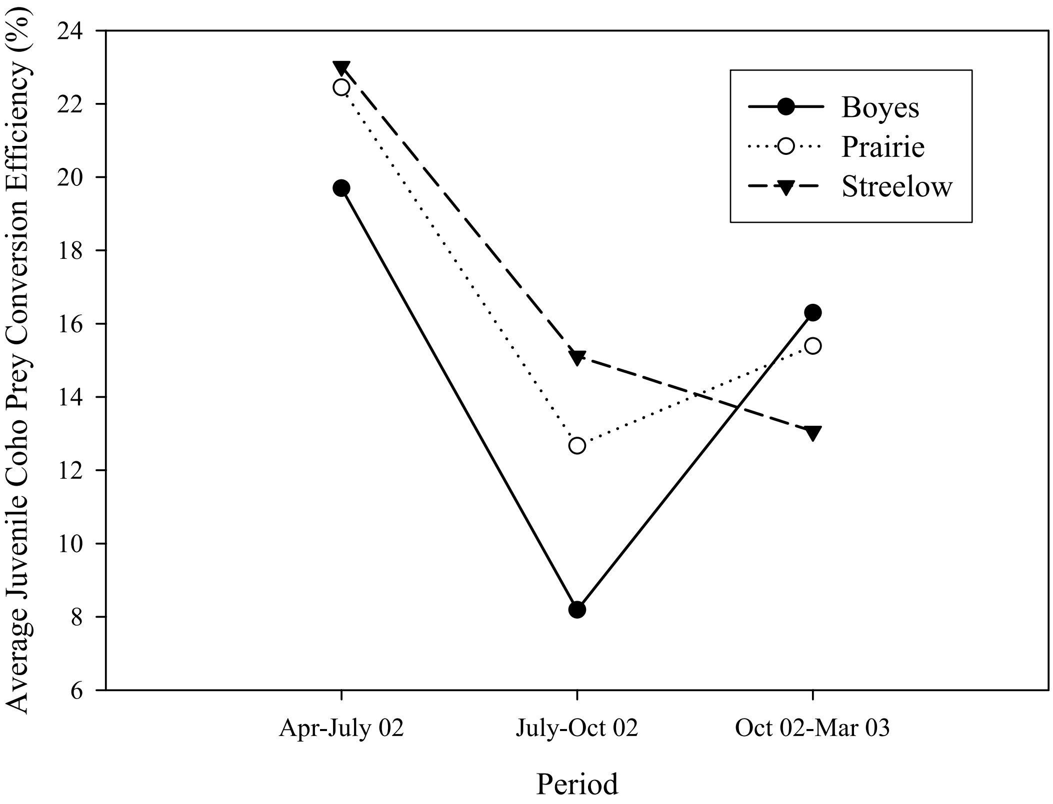

Figure 7. Average individual juvenile coho salmon prey conversion efficiency predicted by the bioenergetic model. Calculated for April – July 2002, July – October 2002, and October 2002 – March 2003.

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Table 10. Mean conversion efficiency, associated standard errors and sample sizes of PIT tagged fish in the three northern California streams.

	July – October 2002			October 2002 – March 2003		
	n	Mean CE	S.E.	n	Mean CE	S.E.
Boyes	16	3.6	1.4	2	12.1	na
Prairie	24	12.1	1.3	4	14.1	1.5
Streelow	16	10.2	1.1	6	11.1	0.9

Prairie and Streelow creeks than in Boyes Creek ($F_{2,65} = 10.972$, $P = < 0.001$). Prey conversion efficiency by individual PIT tagged fish ranged from -3.9% in Boyes Creek to 20.2% in Prairie Creek.

Conversion efficiency of PIT tagged fish did not differ between July to October 2002 and October 2002 to March 2003 (two sample t-test, $t_{66} = -1.603$, $P = 0.1137$). Qualitatively, conversion efficiency was higher for October 2002 to March 2003 (average = 12.26 %) than the July to October 2002 period (average = 9.10 %). Mean prey conversion efficiency during October 2002 to March 2003 varied less among streams but was still highest in Prairie Creek, while it was slightly lower in Streelow and Boyes creeks (Table 10).

Total daily prey consumed by juvenile coho salmon populations also varied among streams. Daily population prey consumption was estimated to be greatest in July 2002, ranging from 1007 $g \bullet ha^{-1} \bullet d^{-1}$ in Boyes Creek to 433 $g \bullet ha^{-1} \bullet d^{-1}$ in Prairie Creek (Figure 8). Daily population prey consumption rates then declined through March 2003 in two streams to amounts ranging from 96 $g \bullet ha^{-1} \bullet d^{-1}$ in Prairie Creek to 177 $g \bullet ha^{-1} \bullet d^{-1}$

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in Streelow Creek. In Boyes Creek, daily population prey consumption was predicted to increase slightly in October 2002. Overall, daily population prey consumed was greatest in Boyes Creek (average = 572 $g \bullet ha^{-1} \bullet d^{-1}$) intermediate in Streelow Creek (average = 449 $g \bullet ha^{-1} \bullet d^{-1}$), and lowest in Prairie Creek (average = 274 $g \bullet ha^{-1} \bullet d^{-1}$).

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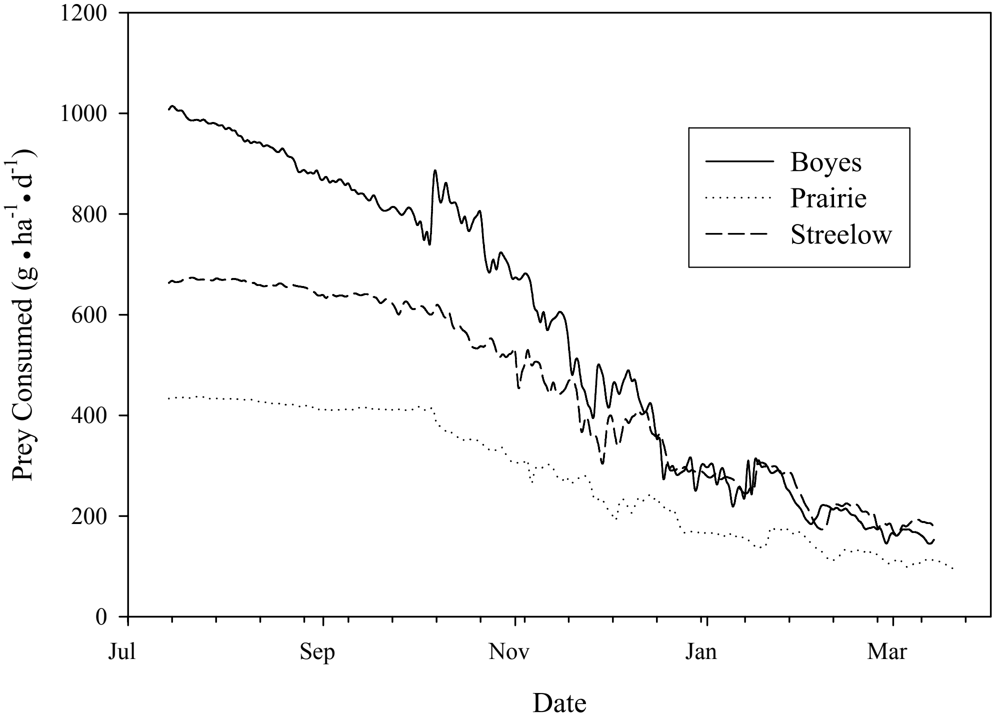

Figure 8. Estimated daily prey consumption by juvenile coho salmon populations in the three northern California streams.

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DISCUSSION

Habitat quality differed among the three study streams and was reflected through rearing potential of juvenile coho salmon. Differences in habitat quality were evident through the summer and fall, and less so between fall and spring. Higher and more variable stream temperatures in Boyes Creek were likely an artifact of shallower pools and a high proportion of shallow low-gradient riffle habitat (Table 3). Additionally, the higher densities observed in pools and runs in Boyes Creek reflects the lack of preferred juvenile coho habitat (pools and runs) in that stream.

I found that juvenile coho salmon abundance and density were almost twice that previously reported for Prairie Creek (Brakensiek 2002), while minimum survival estimates for July to October 2002 and October 2002 to March 2003 were lower than those previously reported. However, estimates of juvenile coho salmon density in all three streams I studied are well within the range of those reported by other authors (Dolloff 1987, Thedenga et al. 1989, Nielsen 1992) as were estimates of survival (Solazzi et al. 2000, Bell 2001, Johnson et al. 2005) for Pacific Northwest streams. Estimated juvenile coho salmon density in July 2002 was 0.74 fish • m^{-2} in Prairie Creek and 0.77 fish • m^{-2} in Streelow Creek. These densities are similar to that suggested to be full rearing capacity for juvenile coho salmon of 0.70 coho salmon fish • m^{-2} in pools of Oregon streams (Rodgers 2000, Nickleson et al. 1992).

Estimated coho salmon density in Boyes Creek (1.45 fish • m^{-2}) was twice that suggested to be at full rearing capacity for pools in Oregon streams (Rodgers 2000, Nickleson et al. 1992).

Although density did not vary statistically among streams, density was highest in Boyes Creek and similar in Prairie and Streelow creeks at the reach and habitat unit levels in July and October 2002. In March 2003 reach and habitat unit density was similar among streams, although slightly higher in Streelow Creek, but notably lower as compared to July and October 2002 estimates. Within streams reach and habitat unit densities were similar for all three seasons sampled. Habitat units sampled to estimate density and abundance in March 2003 represented only a small fraction of habitat units sampled in July and October 2002. This smaller sample may have resulted in underestimation or overestimation of juvenile coho salmon in either or all three streams. This is especially true for Prairie Creek, where in March 2003 only 7% of habitat units sampled in July and October 2002 were sampled. Additionally, average pool and run surface area was greater in all three streams in March 2003 than during other sampling periods, which could also have resulted in underestimation of juvenile coho salmon present during that period (Rodgers et al. 1992).

Size of juvenile coho salmon occupying all three streams was significantly different for all three factors tested. Fish in Streelow Creek were the larger than in other streams on all three sampling dates. Fish in Prairie and Boyes creeks were about the same size in July 2002. In October 2002 juvenile coho salmon were larger in Prairie Creek than in Boyes Creek however they were smaller in March 2003. Seasonal

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variation in rearing potential between Prairie and Boyes creeks could have resulted in variation of size rankings observed during the study period. Additionally, the low number of fish measured in March 2003 may have not been of sufficient sample size to accurately estimate the mean length and mass of fish in each stream during that period.

Growth of juvenile coho salmon was highly variable among streams and seasons. Among streams, I found significant differences in specific growth rates and absolute growth in terms of length and mass of PIT tagged fish. Estimates of growth of PIT tagged fish did not follow those observed for all fish weighed and measured in each population. The inability to tag smaller fish, which made up the majority of the fish measured in each stream in July 2002, likely influenced this result. Overall, growth rates in Streelow Creek were highest in April to July and July to October 2002, while they were highest in Boyes Creek for October 2002 to March 2003. The influence of increasing fish size on specific growth rates (Weatherley and Gill 1995) likely resulted in the reduced specific growth rate observed in Streelow Creek for October 2002 to March 2003. It is also possible that larger juvenile coho salmon in Streelow Creek reached a size threshold for smoltification, which influenced their out migration timing, thus influencing growth rates observed for October 2002 to March 2003 in that stream (Irvin and Ward 1989, Bell 2001).

Variation in growth observed among the three populations could have been influenced by many factors. In Streelow Creek, the riparian zone is dominated by alder, which may partially explain the higher growth rates in April to July 2002 and July to October 2002 relative to Prairie and Boyes creeks. Alder dominated stream riparian

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zones may favor increased instream production and the transport of invertebrates relative to those dominated by conifers (Wipfli 1997, Allan et al. 2003, Wipfli et al. 2004). Streams having riparian zones dominated by alder have been predicted to be capable of supporting more fish biomass than streams with little or no red alder (Wipfli et al. 2004).

Reductions in growth rate observed for juvenile coho salmon in Boyes Creek relative to Prairie and Streelow creeks for July to October 2002 could be partially explained as density dependent growth (Roni and Quinn 2001). In this study only density of juvenile coho salmon was documented. Steelhead trout (*Oncorhynchus mykiss*) density has been shown to affect juvenile coho salmon growth (Harvey and Nakamoto 1996). Presumably similar effects on juvenile coho salmon growth can be expected from Coastal cutthroat trout (*Oncorhynchus sp. clarki clarki*). Steelhead and cutthroat trout densities were highest in Boyes and Streelow creeks.

Lower density and moderate to low growth rates observed for juvenile coho salmon in Prairie Creek relative to Boyes and Streelow creeks makes explanation of growth rates as density dependent difficult. The section of Prairie Creek studied runs through old growth redwood that has a minimal amount of light penetration throughout the day. Growth rates of coastal cutthroat trout and steelhead trout have been documented to be higher in open canopy sections than in closed canopy sections of coastal streams in the Pacific Northwest (Wilzbach et al. 2005). Presumably similar affects could be expected for juvenile coho salmon. Reduced primary productivity and hence secondary production due to reduced light penetration, may have affected growth of juvenile coho salmon in Prairie Creek.

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Overwinter and smolt to adult survival are thought to be largely influenced by size (Quinn and Peterson 1996, Brakensiek 2002). Qualitatively, results from this study support size dependent overwinter survival for juvenile coho salmon. The highest October 2002 to March 2003 juvenile coho salmon survival rates were in Streelow and Prairie creeks. These populations both had the highest mean mass and length in October 2002. Additionally, Rodgers et al. (1992) found that capture probability is inversely related to habitat unit surface area. Thus, abundance estimates in both Prairie and Streelow creeks may have had a higher negative bias for the March 2003 sampling period than the estimate for Boyes Creek, which had the smallest habitat units of all three streams. It is plausible then that survival was higher in Prairie and Streelow creeks than values reported here.

Overall diet composition of juvenile coho salmon in all three streams was similar to that reported by other studies (Nielsen 1992, Hetrick et al. 1998, Allan et al. 2003). The exception being that in this study oligochaetes made up more than 10% of the overall biomass ingested for all three streams. In Pudding Creek, California oligochaetes made up as much as 90% of the diet of juvenile coho salmon and up to 30% of the drifting biomass sampled during the winter in 1990-91 (Pert 1993). When oligochaetes were found to be a significant proportion of the diet they only made up a small proportion of the drift (Pert 1993). Availability of oligochaetes as prey could influence the behavioral means of prey procurement for juvenile coho salmon, which are thought to be predominately drift feeders (Sandercock 1991). I found that oligochaetes ranked second in Boyes Creek and third in both Prairie and Streelow creeks in terms of total biomass

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ingested. It is likely that juvenile coho salmon employed a search feeding means of prey procurement when feeding on oligochaetes, especially in July and October 2002, when lower water velocities would have made entrainment of oligochaetes into the water column unlikely. Employment of search type means of prey procurement is contrary to the commonly held belief that juvenile coho salmon feed primarily on drifting prey in suspension or floating on top of the water column, and rarely on non-moving food or off the bottom of streams (Sandercock 1991).

Terrestrial insects represented from 25 – 50% of the biomass ingested by coho salmon in all streams and seasons. These findings are similar to results found by others (Wipfli 1997, Hetrick et al. 1998, Allan et al. 2003). Amphipods made up 17 – 23% of the biomass ingested by Streelow Creek juvenile coho salmon, but were only found occasionally in the diet of juvenile coho salmon in Prairie and Boyes creeks. Diptera made up the largest proportion of diet in Boyes Creek, while Ephemeroptera, Plectoptera and Trichoptera (EPT) taxa contributed 24 – 44% to the diet in Prairie Creek in all three seasons.

Stomach fullness was highest in Streelow Creek and lowest in Prairie Creek for all three sampling periods. Estimates of stomach fullness were similar to those reported for juvenile coho salmon in winter by Pert (1993). The significantly higher stomach fullness observed during this study for juvenile coho salmon in Streelow Creek indicates that juvenile coho salmon growth may be related to stomach fullness, which may be related to prey availability (Nielsen 1992).

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Diet influenced modeled prey energy density. Modeled prey energy density of in Prairie Creek of approximately 4000 – 4600 j • g^{-1} wet mass for all three seasons was the result of greater EPT and springtail taxa in the diet there than in the other streams. Modeled prey energy density was similar in Boyes and Streelow creeks (3600 – 4000 j • g^{-1}). A diverse mixture of EPT, and terrestrial taxa should be an ideal diet for juvenile coho salmon and other stream salmonids.

Prey energy density can influence predictions from bioenergetics modeling. The mean prey energy density values I used in the bioenergetics model were higher than those used by some authors using bioenergetics models for stream salmonids (Van Winkle et al. 1998, Railsback and Rose 1999, Railsback and Harvey 2002), but similar to values used by Nislow et al. (2000). Values used in this study ranging from 3600 – 4600 j • g^{-1} wet mass. These are likely closer to the actual value of prey energy density for stream salmonids have been previously used. The modeled value of around 2500 j • g^{-1} wet mass (Van Winkle et al. 1998, Railsback and Rose 1999, Railsback and Harvey 2002), is similar to the overall aquatic invertebrate mean of 2600 j • g^{-1} wet mass reported by Cummins and Wuycheck (1971). That estimate however includes lower energy density taxa not commonly consumed by stream salmonids. The diet of juvenile salmonids usually contains a substantial proportion of terrestrial insect taxa (Wipfli 1997, Hetrick et al. 1998, Allan et al. 2004). Terrestrial insect taxa are generally higher in energy density than aquatic insect taxa (Cummins and Wuycheck 1971). High energy density of

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stomach contents has been reported for juvenile coho salmon whose diet composition had a significant terrestrial insect component (Nielsen 1992).

The rapid decline in model estimated specific consumption rate in July for all three streams is an artifact of model structure when fitting the model to initial and final mass between April and July 2002. The uncertainty in using the mean mass of fry on April 12, 2002 as the starting mass and date for simulations may have influenced this decline. Additionally, the bioenergetic model developed for juvenile coho salmon used in this study may need refinement for fish < 2 g because of uncertainties of the model in predicting growth of small fish (Willey 2004). Despite this, model estimates of prey conversion efficiency were consistent with those reported by other authors for juvenile salmon (Brett et al. 1969, Beauchamp et al. 1989).

Estimates of daily specific consumption rates were well within the range of those reported for juvenile coho salmon in summer by Nielsen (1992). Estimates of daily specific consumption rates during winter were lower in both Prairie and Streelow creeks than Nielsen's (1992) summer estimates. The relative similarity of model estimated daily specific consumption rates in Boyes and Streelow creeks during the July to October 2002 period is largely an effect of increased temperature in Boyes Creek (Figure 3). Prey energy density was similar in these streams. Lower daily specific consumption rates for Prairie Creek throughout the study period, relative to Boyes and Streelow creeks, are the result higher prey energy density used in the model and a moderate to low thermal regime. Model results suggest that although juvenile coho salmon in Prairie Creek did not grow as fast or as large, those in Streelow Creek, they did not have to eat as much

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prey relative to their body size as juvenile coho salmon in both Boyes and Streelow creeks.

Model estimated conversion efficiencies were highest for April to July 2002, decreasing for July to October 2002, and increasing or decreasing slightly (Streelow Creek) for October 2002 to March 2003 for all three streams (Figure 11). For the most part estimates of conversion efficiency for each population mimicked those of specific growth rates. This is a result of the models formulation based on empirical evidence that the specific metabolic rate of fish decreases its magnitude with increasing mass (Elliot 1976, Brett 1995, Bohlin et al. 1994).

Reductions in growth for July to October 2002 indicates a limiting prey supply relative to stream temperatures and coho salmon densities for that period. When fed an unlimited ration, juvenile coho salmon growth was highest at 15°C in laboratory settings (Edsall et al. 1999). Average daily stream temperatures during the study period never reached 15°C at any of the study sites. Seasonal declines in drift abundance in summer (Waters 1972, Bachman 1984) combined with increased temperature, likely caused observed reductions in growth rate and conversion efficiency for July to October 2002.

The difference among streams in prey conversion efficiency by PIT tagged fish during July to October 2002 indicates that larger juvenile coho salmon in Boyes Creek were unable to successfully feed at a rate that would satisfy daily metabolic needs while providing enough excess energy for growth. Model estimates of prey conversion efficiency were driven by inputs of prey energy density, thermal regimes for that period, and beginning and ending mass. Lowered prey energy density, a higher thermal regime,

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and small initial and final mass in Boyes Creek resulted in the lowest estimates of prey conversion efficiency among PIT tagged fish in all three streams. Most recaptured juvenile coho salmon in Boyes Creek showed little weight gain, although a few individual fish had substantial gains in weight and five individuals lost weight. Only one PIT tagged juvenile coho salmon in both Prairie and Streelow creeks lost mass during July to October 2002 while the majority showed sizable weight gains. Results from this analysis indicate that no size advantage exists for juvenile coho salmon rearing in Boyes Creek for July to October 2002. It is also possible to infer that because of increased temperature and higher coho densities in Boyes Creek, competition for food between juvenile coho salmon was higher than in Prairie and Streelow creeks. Additional support for this finding was observed when reductions in density during October 2002 to March 2003 corresponded with increases in conversion efficiency and growth rates for PIT tagged fish in Boyes Creek.

Standing stock biomass increased between July and October 2002 and then declined at a slower rate in Prairie and Streelow creeks relative to Boyes Creek. The decline is an artifact of how the Fish Bionergetics 3.0 model treats mortality. This model applies an average daily instantaneous mortality rate calculated from initial and final observations making user inputs of abundance from the starting to the ending date a linear interpolation between dates (Hanson et al. 1997). It is likely that biomass in Prairie and Streelow creeks would have continued to increase until the first major winter storm of the water year, after which a significant decline would be expected. In Prairie and Streelow creeks, biomass eventually declined to about 73% of the observed peak in

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October. In Boyes Creek, standing stock biomass never increased beyond the initial value observed in July 2002. Biomass in Boyes Creek eventually declined to about 81% of the initial value observed in July 2002. Peak October 2002 estimates in Prairie and Streelow creeks were similar to values reported for Godwood Creek, a tributary to Prairie Creek (Burns 1971). Peak July 2002 estimates in Boyes Creek were similar to those reported for Prairie Creek (Burns 1971). It is likely that both Prairie and Streelow creeks could have supported more juvenile coho salmon biomass given the high estimate by Burns (1971) in Prairie Creek and the increase of biomass observed for the July to October 2002 period. The reduction in all three streams to similar amounts of standing stock biomass by March 2003 supports assertions made by Solazzie et al. (2000) that winter habitat limits smolt production of juvenile salmonids in Pacific Northwest streams.

Daily prey consumption by the juvenile coho salmon population and their efficiency in converting that consumption to body tissue may provide important information on populations. Daily prey consumption by the juvenile coho salmon population in Boyes Creek was higher than in other streams from July to December 2002. It remained equal to that in Streelow Creek through April 2003, even after standing stock biomass in Boyes Creek declined. The higher loss of biomass consumed by juvenile coho salmon in Boyes Creek throughout the simulation period indicates that this type of analysis may be useful for studying source sink dynamics of juvenile coho salmon populations. Source populations are likely to have higher population conversion efficiencies, while sink populations would have lower population conversion efficiencies (Cooper and Mangel 1999).

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Differences in prey energy density and temperature among streams can translate into increased growth, which may be magnified at the population level. Slight variability in observed growth between fish of different populations of similar abundance can translate into notable increased rates of population biomass production. The high variability in energy density between taxa commonly eaten by stream fish (Cummins and Wuycheck 1971, Higgs et al. 1995) supports maintenance of biotic diversity of aquatic and terrestrial invertebrates associated with riparian zones to maintain the health and stability of stream fish populations (Higgs et al. 1995). Reductions in species richness associated with human induced disturbance (Cummins 1974, Karr and Chu 1999) could result in tolerant taxa of a low energy density (e.g. some aquatic diptera) (Cummins and Wuycheck 1971, Higgs et al. 1995). Bound by temperature, stream macroconsumer growth and survival (excluding predation) rates are controlled by food quantity and quality (Cummins 1974). Combined with increased stream temperature, a condition associated with removal of streamside riparian vegetation (Chamberlin et al. 1991, Keith et al. 1998), lowered prey energy density can result in negative affects on stream fish populations. Water temperature was never more than 3 ^{o}C warmer in Boyes Creek than Prairie or Streelow creeks during this study. However, specific consumption rates and daily prey consumption, even when standing stock biomass was lower, were as high or higher in that stream than in the others.

It is difficult to attribute observed increases in growth and survival to prey energy density and thermal regimes alone. Juvenile coho salmon density likely had a direct effect on the population dynamics observed in Boyes Creek, suggesting that summer and

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fall density appears to be a misleading indicator of habitat quality. Digestibility of juvenile coho salmon prey also varies and prey digestibility can increase or decrease gastric evacuation (Higgs et al. 1995). In this study waste was modeled as a constant that varied with temperature regardless of prey type. Although not reported here, I collected information on prey availability in the three streams and found it was highest in Streelow Creek. Prey availability has also been correlated to increased growth rates of juvenile coho salmon (Koski et al. 1984, Nielsen 1992).

Food quantity has been thoroughly investigated for juvenile salmonids (Elliot 1973, Nielsen 1992, Hetrick et al. 1998) and has been shown to directly influence growth of juvenile coho salmon (Koski et al. 1984, Nielsen 1992). Food quality however, is commonly modeled for juvenile salmonids (Sweka and Hartman 2001, Railsback and Harvey 2002, Hughes et al. 2003), but seldom estimated from diet or prey availability samples. Prey quality is a basic building block upon which all of the previous models rely regardless of their application. Further attention should focus on the role that prey quality has on stream fish populations. A thorough understanding of prey quality from an energy density and digestibility standpoint would serve to benefit advancements in ecological modeling of stream fish.

Similar studies should focus on a thorough description of juvenile coho salmon diet by sampling every 300 degree-days (Merritt and Cummins 1996), throughout early summer to fall. During this time, accurate estimates of abundance (Rodgers et al. 1992), survival, and growth are relatively easy to obtain. Additionally calorific determination of diet components would provide valuable data on a parameter that is commonly modeled

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for stream fish. Lastly prey availability should be documented so that relative effects of temperature, prey energy density, and prey availability on growth can be assessed. Increased model performance can be expected by reducing the length of the simulation interval (Rice and Cochran 1984, Beauchamp et al. 1989), and by frequently measuring variables used to drive model outputs (e.g. growth, diet, prey availability, and temperature).

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Appendix A. Mean wet mass, fork length associated standard errors and sample size for juvenile coho salmon salmon measured in experimental habitat units during each sampling period.

	n	Mean Wt (g)	S.E.	Mean FL (mm)	S.E.
Boyes					
Run					
July 02	143	1.49	0.19	49.45	1.68
Oct. 02	77	1.96	0.19	55.77	1.90
March 03	8	3.77	1.68	67.13	4.44
Pool					
July 02	140	1.71	0.19	51.93	1.78
Oct. 02	121	2.25	0.26	57.66	1.97
March 03	23	4.59	1.79	72.09	4.47
Prairie					
Run					
July 02	213	1.59	0.12	50.44	1.15
Oct. 02	205	2.32	0.2	56.87	1.27
March 03	7	3.62	1.17	64.25	4.47
Pool					
July 02	289	1.65	0.14	50.55	1.15
Oct. 02	231	2.71	0.29	58.49	1.27
March 03	49	5.29	0.65	75.72	4.63
Streelow					
Run					
July 02	209	2.09	0.23	54.07	1.57
Oct. 02	134	3.2	0.28	63.78	1.69
March 03	28	5.6	1.95	75.72	4.55
Pool					
July 02	157	2.16	0.18	55.47	1.46
Oct. 02	141	3.18	0.2	64.15	1.65
March 03	32	6.71	1.14	81.24	4.39

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Appendix B. List of taxa identified in juvenile coho salmon diet samples from the three northern California streams. (L), (P), and (A) denote larval, pupal and adult life stages.

Aquatic Prey

- Acari
- Amphipoda
  - Gammeridae
- Coleoptera
  - Chrysomelidae(A)
  - Chrysomelidae(L)
  - Curculionidae(L)
  - Curculionidae(A)
  - Dytiscidae(A)
  - Dytiscidae(L)
  - Elmidae(A)
  - Elmidae(L)
  - Georyssidae(L)
  - Haliplidae(L)
  - Hydraenidae(L)
  - Hydrophilidae(A)
  - Hydrophilidae(L)
  - Melryidae(A)
  - Psephenidae(L)
  - Salpingidae(L)
  - Staphylinidae(A)
- Diptera
  - Canacidae(A)
  - Ceratopogonidae(A)
  - Ceratopogonidae(L)
  - Chaoboridae(A)
  - Chironomidae(A)
  - Chironomidae(L)
  - Chironomidae(P)
  - Dixidae(A)
  - Dixidae(L)
  - Dixidae(P)
  - Dolichopodidae(A)
  - Empididae(A)
  - Empididae(L)
  - Ephydriidae(A)
  - Ephydriidae(L)
  - Pelecohynchidae(L)
  - Muscidae(A)
  - Phoridae(A)
  - Psychodidae(A)

Diptera (Continued)

  - Psychodidae(L)
  - Ptychopteridae(L)
  - Scizomyidae(A)
  - Simulidae(L)
  - Stratyiomyidae(L)
  - Tabanidae(L)
  - Thaumaleidae(A)
  - Tipulidae(A)
  - Tipulidae(L)
  - Tipulidae(P)
- Ephemeroptera
  - Ameletidae(L)
  - Baetidae(A)
  - Baetidae(L)
  - Heptageniidae(L)
  - Leptophlebiidae(L)
- Hemiptera
  - Gerridae(L)
  - Pleidae(L)
- Hemiptera (A)
- Megaloptera
  - Sialidae(L)
- Neuroptera
  - Sisyridae(A)
- Plecoptera
  - Chloroperlidae(L)
  - Leuctridae(A)
  - Leuctridae(L)
  - Nemouridae(A)
  - Nemouridae(L)
  - Peltoperlidae(L)
  - Perlidae(A)
  - Perlidae(L)
  - Perlodidae(L)
  - Pteronarcyidae(L)
- Salmon Eggs
- Trichoptera
  - Brachycentridae(L)
  - Calamoceratidae(L)
  - Glossosomatidae(A)
  - Hydropsychidae(L)

Trichoptera (Continued)

  - Hydroptilidae(L)
  - Lepidostomatidae(L)
  - Limnephilidae(A)
  - Limnephilidae(L)
  - Philopotamidae(L)
  - Rhyacophillidae(L)
  - Sericostomatidae(A)
  - Uenoidae(L)
- Unknown(L)
- Turbellaria

Terrestrial Prey

- Aranea
- Chilopoda
- Collembolla
- Diplopoda
- Gastropoda
  - Pleuroceridae
- Hirundinea
- Homoptera
  - Aphidae(A)
  - Aphidae(L)
  - Cicadelidae(A)
- Hymenoptera (A)
  - Formicidae(A)
  - Formicidae(L)
- Isopoda
- Lepidoptera
  - Cosmopterigidae(L)
  - Cossidae(L)
  - Noctuidae(L)
  - Pyralidae(A)
  - Pyralidae(L)
  - Pyralidae(P)
- Nematoda
- Nematomorpha
- Oligochaeta
  - Lumbricidae
- Orthoptera
  - Tettigonidae(L)
- Thysanoptera

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