SECONDARY PRODUCTION OF *PARALEPTOPHLEBIA* (EPHEMEROPTERA) WITHIN THREE NORTHERN CALIFORNIA COASTAL STREAMS

by

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A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

Of the Requirements for the Degree

Masters of Science

In Natural Resources: Freshwater Fisheries

November, 2006

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06-FI-609-12/06

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ABSTRACT

Secondary production of *Paraleptophlebia* (Ephemeroptera) within three northern California coastal streams

Sarah Beesley

Annual production was estimated for the mayfly genus *Paraleptophlebia* occupying riffle habitats of three coastal streams within the Prairie Creek watershed, California. Monthly invertebrate collections yielded 4,579 *Paraleptophlebia* nymphs: 1,786 from Prairie Creek, 1,738 from Boyes Creek and 1,055 from Streelow Creek. *Paraleptophlebia* populations in the three streams were presumed univoltine based on monthly size frequency distributions. Emergence appeared to occur from spring through fall with early instars present from late summer through spring. Models relating ln total length to ln dry mass and ln head width to ln dry mass were developed from fresh Prairie Creek *Paraleptophlebia* nymphs to estimate dry mass of preserved nymphs. Annual production estimates were 89.7 mg•m^{-2}•yr^{-1} in Prairie Creek, 69.9 mg•m^{-2}•yr^{-1} in Boyes Creek and 74.0 mg•m^{-2}•yr^{-1} in Streelow Creek. Annual production to biomass ratios were 8.56 in Prairie Creek, 11.39 in Boyes Creek and 5.89 in Streelow Creek. Water temperature accumulation was monitored to assess whether differences in thermal regime existed among the three streams. Annual degree day totals were very similar among the streams with values from 3,447 in Streelow Creek, 3,473 in Prairie Creek, and 3,486 in Boyes Creek.

ACKNOWLEDGMENTS

I want to thank the National Marine Fisheries Service for providing funding to conduct this study and the California Cooperative Fisheries Research Unit at Humboldt State University for providing equipment and support staff. I would also like to thank my major professor: Dr. Walt Duffy and my committee: Dr. Ken Cummins and Dr. Mike Camaan for all their efforts and especially for their patience. Very special thanks go to Bethany Matousek for all the hard work she did in the field and behind the microscope! "Miss" Bethany always went the extra mile for me and her spirit, thoughtfulness and innovation were critical to completing this study. Thanks also go to Karen Lamoncha for all her incredible work sorting and identifying invertebrates and for trooping around the streams, tackling old growth and chasing invertebrates. My gratitude also goes to Beverly Bulaon and Sarah Kleinschmidt for all their help in the laboratory and to all the other folks who helped sort invertebrates. I would also like to thank Dana McCanne for all his support and for the sweet size frequency plots he provided! Special thanks also go to Dr. David Hankin for spending the time to review a draft of this study and for providing much needed moral support. My co-workers and boss at Yurok Tribal Fisheries deserve my gratitude for allowing me time to complete this study. Finally, I want to thank my family, Rocco and my friends for putting up with me and helping me through this crazy adventure.

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INTRODUCTION

Mayflies of the genus *Paraleptophlebia* (Lestage) are widely distributed throughout lotic environments and are responsible for transforming primary producers and detrital energy sources into animal tissue (Gilpin and Brusven 1970, Edmunds et al. 1976, Shapas and Hilsenhoff 1976). Edmunds and others (1976) list approximately 35 individual *Paraleptophlebia* species in North and Central America. Allen and Edmunds (1956) reported the presence of ten species in Oregon. Day (1956) described more than ten species in California. He reported nymphs were distributed throughout California but were especially abundant in coastal redwood dominated streams.

Paraleptophlebia nymphs have slender, streamlined bodies that move by undulation and are considered awkward swimmers (Needham et al. 1935, Edmunds et al. 1976). Nymphs are common in low order alluvial streams, often colonizing coarse gravel substrates or leaf accumulations in both erosional and depositional habitats (Needham et al. 1935, Lehmkuhl and Anderson 1971, Edmunds et al. 1976). Mattingly (1987) studied resource utilization by *P. gregalis* and *P. temporalis* in both a laboratory setting and in Berry Creek, a second order stream located in Benton County, Oregon. She observed densities in riffle habitats of Berry Creek in excess of 100 individuals per square meter with less than half that number in depositional habitats. Gilpin and Brusven (1970) found *Paraleptophlebia* nymphs of the St. Maries River, Idaho, to inhabit rock surfaces in detritus rich cobble riffles of moderate to slow velocities. Leonard and Leonard (1962) studying mayflies in Michigan streams reported *Paraleptophlebia* colonized gravel substrates in streams of almost any size but were not common in areas deeper than two feet.

Paraleptophlebia species are described as facultative gathering collectors feeding primarily on detritus and diatoms (Gilpin and Brusven 1970, Shapas and Hilsenhoff 1976, Smock et al. 1985, Rader and Ward 1989). Mattingly (1987) found *Paraleptophlebia* nymphs were morphologically adapted to feed on a wide range of food types and sizes including periphyton, fine and coarse particulate organic matter, and alder leaves (*Alnus oregona*). She concluded *Paraleptophlebia* were capable of inhabiting many different types of habitat and tolerating a wide range of environmental conditions. Chapman and Demory (1963) studied food habits of several aquatic invertebrate species including *Paraleptophlebia* in two Oregon Coast Range streams. Nymphs were found in several different habitat types in locations where algal growth or detritus accumulations were relatively high. They reported nymphs were negatively phototropic, spending daylight hours under gravel substrates consuming available detritus and migrating to the top of these substrates at night. They also observed nymphs shifted from a diet dominated by leaf debris in the fall to a diet dominated by algae in early spring prior to tree leaf out.

Mature nymphs can range from 6 – 10 mm in total body length (Coleman and Hynes 1970, Edmunds et al. 1976, Welton et al. 1982). Leonard and Leonard (1962) reported body lengths for mature nymphs of *Paraleptophlebia debilis*, *P. adoptiva*, and *P.*

mollis from 7 – 9 mm. Lehmkuhl and Anderson (1971) studied the biology and taxonomy of west Oregon *Paraleptophlebia* species in the foothills of the Coast Range and on the east side of the Cascade Range. They observed mature body lengths from 6 – 8 mm for nymphs of *P. debilis*, *P. mollis* and *P. temporalis* and 5 mm for nymphs of *P. moerens*.

Emergence of nymphs living north of 30º latitude was reported to begin in spring and extend through late fall for some species (Leonard and Leonard 1962, Corkum 1978). Water temperature and stream flow are reported to influence timing of emergence (Edmunds et al. 1976, Corkum 1978, Harper et al. 1995). Lehmkuhl and Anderson (1971) observed adults of *P. temporalis* and *P. gregalis* from April to June and from June to November for *P. debilis* and *P. bicornuta* in a western Oregon stream. Gilpin and Brusven (1970) reported that emergence for several *Paraleptophlebia* species occurred in August through late October. Markarian (1979) studied the relationship between insect growth and water temperature in a small Pennsylvania stream. He observed an extended emergence pattern for *P. assimilis* with mature nymphs observed from April through June. Coleman and Hynes (1970) observed adults of *P. mollis* from May through August in the Speed River in southern Ontario.

Mating takes place soon after subimagos complete their final molt. Males initiate the event by congregating above or near to the stream in the late afternoon to early evening (Leonard and Leonard 1962, Lehmkuhl and Anderson 1971, Edmunds et al.

1976). Males repeatedly fly a select distance upwards and then drop or float down almost to the ground or surface of the water. Females join the flight and mating takes place on the wing with males grasping the females as they float down through the male swarm (Leonard and Leonard 1962, Lehmkuhl and Anderson 1971, Edmunds et al. 1976). Females begin depositing eggs shortly after being released by the males. The general method for egg laying consists of females repeatedly dipping their abdomen into the stream and releasing select numbers of eggs until all are deposited (Leonard and Leonard 1962, Lehmkuhl and Anderson 1971, Edmunds et al. 1976). Leonard and Leonard (1962) observed females of *P. debilis* extruding eggs in masses and dropping them several feet into the stream. Death generally occurs shortly after mating and egg deposition for most mayflies (Leonard and Leonard 1962, Lehmkuhl and Anderson 1971, Edmunds et al. 1976).

Timing of egg hatching is thought to depend on stream flow and water temperature (Edmunds et al. 1976). Lehmkuhl and Anderson (1971) found most of the western Oregon species over wintered in the egg stage. Chapman and Demory (1963) suggested that *Parapleptophlebia* eggs continuously hatched over most of the year based on their observations of early instars at each sampling date. After hatching, nymphs are reported to grow rapidly during fall and spring with negligible growth occurring in winter (Coleman and Hynes 1970, Lehmkuhl and Anderson 1971, Kovalak 1978, Markarian 1979). Corkum (1978) studied nymphal development of the univoltine species *P.*

adoptiva and *P. mollis* from the Credit River in Ontario, Canada. She first observed early instars in August and September and reported nymphs grew rapidly during fall (early instars) and spring (late instars), and slowly (*P. adoptiva*) or not at all (*P. mollis*) during winter.

Northern *Paraleptophlebia* species (north of 30º latitude) are widely reported as univoltine (Coleman and Hynes 1970, Gilpin and Brusven 1970, Lehmkuhl and Anderson 1971, Corkum 1978, Markarian 1979, Welton et al. 1982, Harper et al. 1995, Savage 1986, Rader and Ward 1989). However, the number of instars completed prior to reaching sexual maturity is flexible in most mayflies and is strongly influenced by environmental conditions (Clifford 1970, Rader and Ward 1989, Benke 1993). This plasticity often results in asynchronous cohort development making individual cohorts difficult to discern due to extended periods of emergence and egg hatching (Benke and Jacobi 1986). Several authors report a high degree of cohort asynchrony for *Paraleptophlebia* species in the northern United States (Leonard and Leonard 1962, Lehmkuhl and Anderson 1971, Corkum 1978).

The extent to which aquatic invertebrates influence energy transfer in an ecosystem is controlled in part by the magnitude of their production (Huryn and Wallace 2000). Net production, that production occurring above respiration and excretion costs, is the elaboration of biomass by a population, per unit area, per unit time (Edmondson and Winberg 1971, Benke 1984). By integrating quantitative measures of population density, individual growth rate, reproduction, survivorship, and development time, production studies can provide critical insight into the flow of energy produced from individual populations or entire communities (Benke et al. 1984, Benke et al. 1985, Benke and Wallace 1980, Benke 1993). Production studies can also detail shifts in the energetic expressions of populations exposed to different environmental conditions (Benke 1993, Krueger and Waters 1983, Lugthart and Wallace 1992, Cole et al. 1991).

Production methods rely heavily on the ability to approximate true growth and survivorship of a population over its life cycle (Benke 1984). Approximating these curves for populations developing in a relatively synchronous pulse is generally straightforward and standard cohort methods may be applied to estimate production (Benke 1984, Benke 1993). However, accurately approximating growth and survivorship for populations displaying asynchronous development is complicated given the difficulty of discerning individual cohorts (Benke 1984, Benke 1993).

The size-frequency (SF) method (Hynes 1961, Hynes and Coleman 1968, Hamilton 1969, Benke 1979, Hynes 1980) is ideal for such populations because it allows production estimation without approximating true growth and survivorship. Instead, a mean size-frequency distribution calculated from samples collected over a year is used to approximate the average survivorship of a hypothetical average cohort (Hamilton 1969, Benke and Waide 1977, Benke 1979, Menzie 1980, Benke 1984). For these purposes an average cohort represents the approximate number of individuals in a given population to reach a given size class over a year (Hamilton 1969, Benke and Waide 1977, Benke 1984). The SF method also allows production estimation for groups of coexisting species with similar growth characteristics (Waters and Crawford 1973, Waters 1977, Benke and Wallace 1980, Benke et al. 1984, Benke et al. 1985, Benke and Jacobi 1986, Morin and Dumont 1994).

In this study, annual production was estimated for the mayfly genus *Paraleptophlebia* occupying riffle habitats in three coastal streams located in the Prairie Creek watershed, California. The streams were selected based on differences that existed in timing and magnitude of watershed disturbance. Here disturbance referred to impacts associated with timber harvest and road networks. The objective was to determine whether differences in life history patterns and annual production existed among three populations occupying streams of varied habitat quality (i.e. relatively undisturbed, recently disturbed and recovering from disturbance). Other parameters examined were annual production to biomass ratios and water temperature accumulation within the three streams.

STUDY SITE

The Prairie Creek watershed, located in the northern Coast Range of California, covers approximately 100 km^2 and ranges in elevation from 15 – 380 meters. A majority of this coastal watershed is underlain by weakly consolidated shallow marine and alluvial sediments known as the Prairie Creek Formation (Cashman et al. 1995). Sediments of the Prairie Creek Formation were derived from the ancestral Klamath River and estuary (Cashman et al. 1995). Close proximity to the Pacific Ocean results in relatively moderate and constant air temperatures with cool summers and wet winters. Average annual precipitation ranges from 135 – 200 cm, falling almost exclusively as rain from November through March (Janda et al. 1975). A total of 165.6 cm of precipitation was recorded in upper Prairie Creek during water year 1999.

Most of the Prairie Creek watershed is contained in Redwood National and California State Parks. The watershed supports old growth coast redwoods (*Sequoia sempervirens*), Sitka spruce (*Picea sitchensis*), and Douglas fir (*Pseudotsuga menziesii*). Under-story vegetation includes black and red huckleberry (*Vacinium ovatum* and *V. parvifolium*, respectively), red alder (*Alnus rubra*), big leaf maple (*Acer macrophyllum*), salmonberry (*Rubus spectabilis*), and ferns (*Polystichum sp.*). Prairie Creek and its tributaries are inhabited by coastal cutthroat trout (*Onchorynchus clarki clarki*), steelhead trout (*O. mykiss*), chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*). Coho salmon are listed as “threatened” under the federal Endangered Species Act. Additional non-salmonid fish species include threespine stickleback (*Gasterosteus aculeatus*), prickly sculpin (*Cottus asper*), coastrange sculpin (*C. aleuticus*), and multiple lamprey species including Pacific lamprey (*Lampetra tridentata*) and Pacific brook lamprey (*L. pacifica*).

Single study reaches were defined in upper Prairie Creek, Boyes Creek, and Streelow Creek (Figure 1, Table 1). The Prairie Creek study reach extended upstream from the confluence of Brown's Creek approximately 6 km to the confluence of Ten Taypo Creek (Figure 1) and encompassed 15.6 km^2 of the watershed (Table 1). Upper Prairie Creek was considered nearly pristine because riparian vegetation was dominated by old growth conifers. The Newton B. Drury highway parallels upper Prairie Creek and once served as a section of U.S. Highway 101 into the late 1980's when a bypass was constructed to direct commercial traffic away from Prairie Creek Redwoods State Park (Redwood National Park 1986). Dominant habitat types classified in the study reach during fall 1998 were low gradient riffles, lateral scour pools, and glides. A stream gage upstream of Brown's Creek was operated by Redwood National Park during water year 1999 (Figure 1). Mean daily discharge ranged from 7.06 $m^3 \bullet s^{-1}$ on 21 November 1998 to 0.05 $m^3 \bullet s^{-1}$ on 8 January 1999 (Figure 2). Bankfull discharge at this gage was estimated at 5.6 $m^3 \bullet s^{-1}$ (personal communication, R. Klein 1999. Redwood National Park, 1655 Heindon Road, Arcata, CA 95521).

Boyes Creek drains to Prairie Creek from the east approximately 2.7 km downstream of the Prairie Creek study reach (Figure 1). The Boyes Creek reach extended from the mouth upstream approximately 2 km to the confluence with South Fork Boyes Creek (Figure 1). Low gradient riffles dominated the habitat in the Boyes

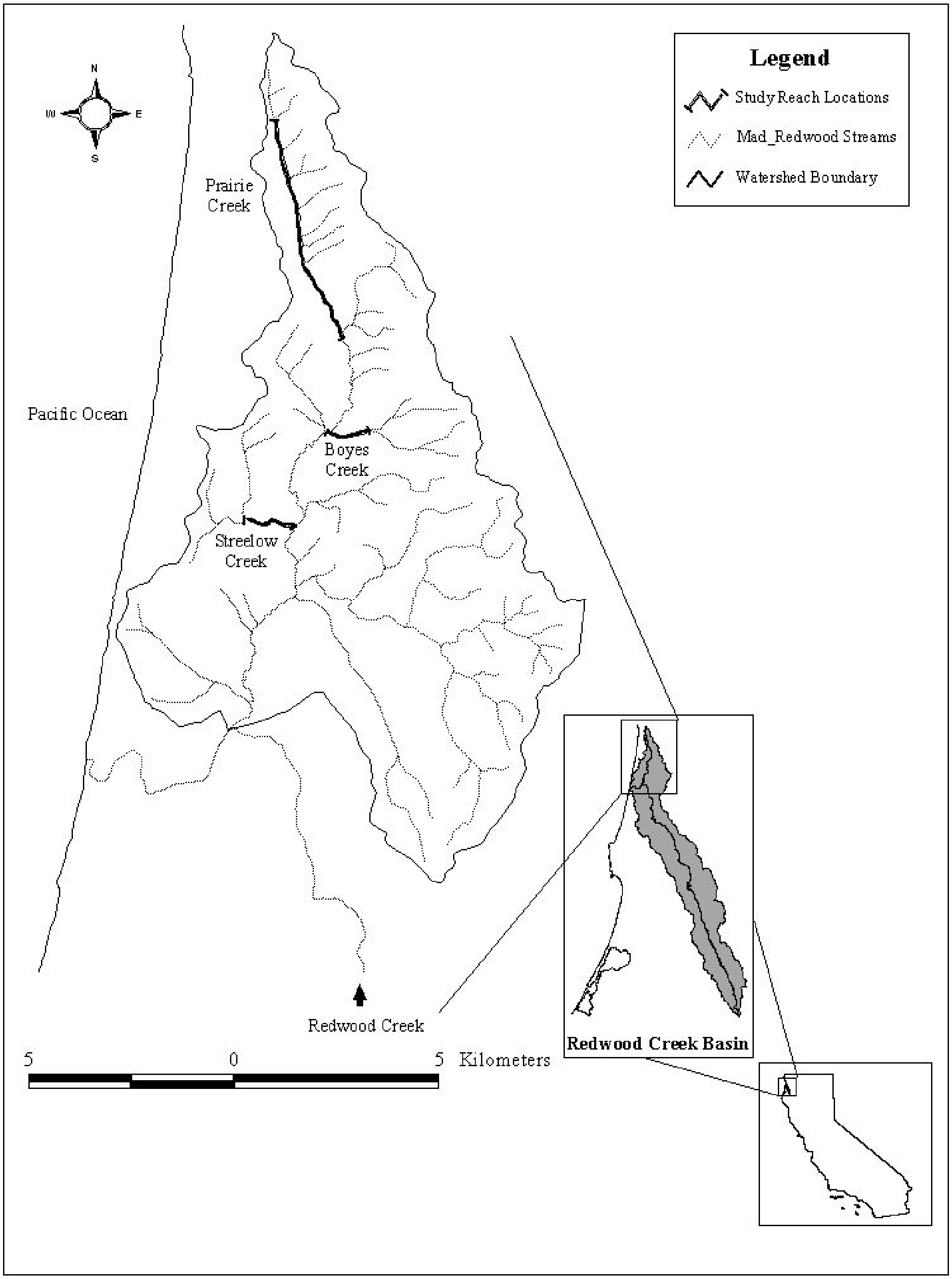

Figure 1. Map of the Prairie Creek watershed depicting locations of study reaches established in Prairie Creek, Boyes Creek and Streelow Creek, California.

Table 1. Physical parameters for three coastal stream reaches located in the Prairie Creek watershed, Humboldt County, California.

Parameter	Prairie Creek	Boyes Creek	Streelow Creek
Drainage area (km^2)	15.65[a]	5.40	7.04
Elevation range (m)	15 - 380	49 - 551	30 - 227
Study reach length (km)	6	2	2
Length of habitat survey[b] (m)	1362.8	2248.8	2214.4
Total riffles surveyed (No.)	152	122	28
Mean riffle area (m^2)	41.1	19.2	32.0
Percent total riffle area (%)	24.3	38.1	7.7
Mean percent embeddedness[c] (%)	26 - 50	51 - 75	51 - 75
Mean diameter of riffle substrate[d] (mm)	61.0	57.8	22.7
Average annual discharge[e] ($m^3 \bullet s^{-1}$)	0.48	0.17	0.22

[a] Drainage area upstream of study reach start

[b] Habitat survey conducted October 1998 by California Cooperative Fisheries Research Unit, Humboldt State University, Arcata, California.

[c] Qualitative measure of the percent of pool tail substrates that are embedded or surrounded by fine sediments.

[d] Derived from Wolman pebble count data collected May 1999.

[e] Stream gage was located in upper Prairie Creek (drainage area at gage 15.65 km^2). Average annual discharge for Boyes Creek and Streelow Creek were derived from the relationship of Prairie Creek average annual discharge to drainage area.

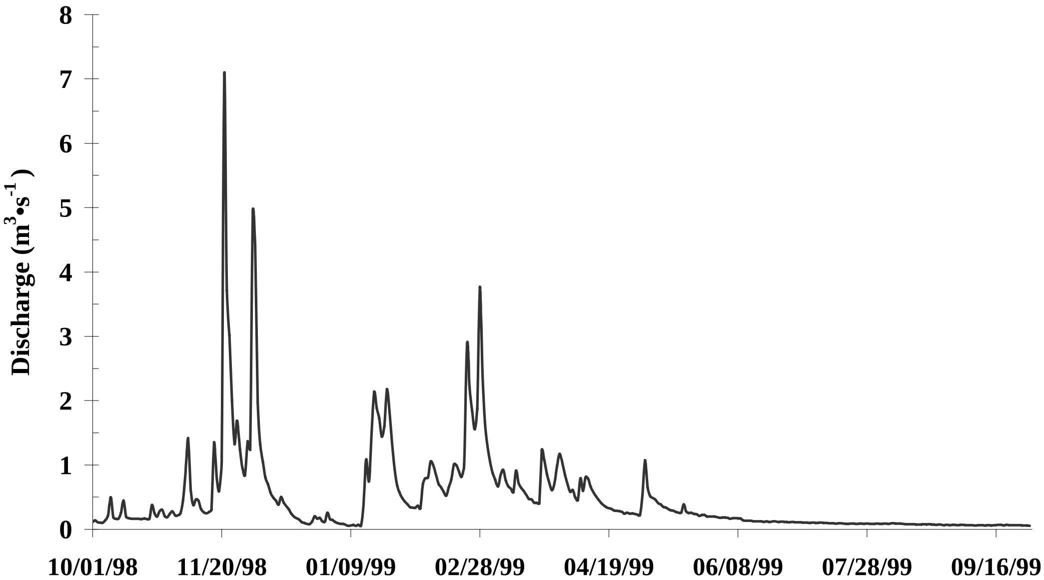

Figure 2. Mean daily discharge recorded for water year 1999 in upper Prairie Creek, Humboldt County, California (drainage area at gage was 15.65 km^2).

Creek study reach during fall 1998. Riparian forests located along the study reach consisted primarily of old growth conifers with dense under-story vegetation. Boyes Creek was considered recently disturbed. Timber in the headwaters of Boyes Creek was harvested in the mid 1970's and in 1984 when construction of the U.S. Highway 101 bypass began (Redwood National Park 1986). Hillslope and road failures associated with the bypass began in 1989 and have since delivered several hundred tons of fine sediments to Boyes Creek. The bypass crosses five major streams including May Creek, Boyes Creek and Brown's Creek, all tributaries to Prairie Creek. These drainages continue to experience elevated sediment delivery and alterations in their hydrologic conductivity resulting from this bypass.

MATERIALS AND METHODS

Benthic macroinvertebrates were collected monthly from riffle habitats located in the three study reaches from October 1998 through September 1999. Every month, six riffle habitats were randomly selected for each reach using the stream habitat classification data collected during fall 1998 by the California Cooperative Fisheries Research Unit, Humboldt State University, Arcata, California. To calculate invertebrate densities and estimate mean individual biomass per unit area, riffles were sampled using a Surber sampler (net mesh size 350 *u*m) that delineated a 0.093 square meter sample area. A single Surber sample was obtained from each selected riffle. The sample location within a given riffle was selected from an area in the thalweg that appeared to represent average substrate, flow and depth conditions in that riffle.

Individual samples were rinsed from the Surber net into a sieve (mesh size 212 *u*m). To reduce sorting time and maintain specimen quality, samples containing large portions of sand and gravel were transferred to a plastic container where organic material was separated from the substrate using a super-saturated solution of sugar and water (Anderson 1959, Benke et al. 1984). Elutriation of a given sample was repeated until no invertebrates were observed in the solution or substrate. The sample was rinsed with water and placed in a zipper top bag containing 70 percent ethanol. All samples were labeled with the stream name, a unique habitat unit number and date of collection. In the laboratory, invertebrates were sorted and all *Paraleptophlebia* nymphs were placed in separate vials for length determinations. Due to difficulties distinguishing nymphs of

Paraleptophlebia species at early instars, all analyses were conducted at the genus level (Coleman and Hynes 1970, Edmunds et al. 1976, Benke and Jacobi 1986).

Total length (TL), measured from the anterior of the labrum to the posterior of the last abdominal segment, and head capsule width (HW), the widest distance across the eyes, were measured (nearest 0.01 mm) for all nymphs (Figure 3). Body lengths were measured using computer imaging software (Image-Pro Plus version 4.1 for Windows) and a zoom lens (Navitar TV Zoom 7000) attached to an adjustable mechanical arm. When aquatic invertebrates are preserved in ethanol they lose a substantial portion of their dry mass (DM) through leaching (Howmiller 1972, Benke et al. 1999). Therefore, a body length to DM relationship was developed from fresh *Paraleptophlebia* nymphs to estimate DM of preserved nymphs.

Live *Paraleptophlebia* nymphs were collected from cobble surfaces and detritus accumulations in riffle habitats in the Prairie Creek reach on 16 May 2002. Individuals were placed into Beem capsules with water and transported on ice to the laboratory. Total length and head width (nearest 0.01 mm) were measured for all *Paraleptophlebia* nymphs using the previously mentioned imaging software. Nymphs were individually dried at 60°C for 24 hours and allowed to cool in a desiccator for 24 hours (Benke et al. 1984, Benke et al. 1999, Johnston and Cunjak 1999). Invertebrates were weighed individually using a Metler M3 balance. Prior to weighing invertebrates, the balance weigh chamber was filled with small packets of desiccant, and the balance was

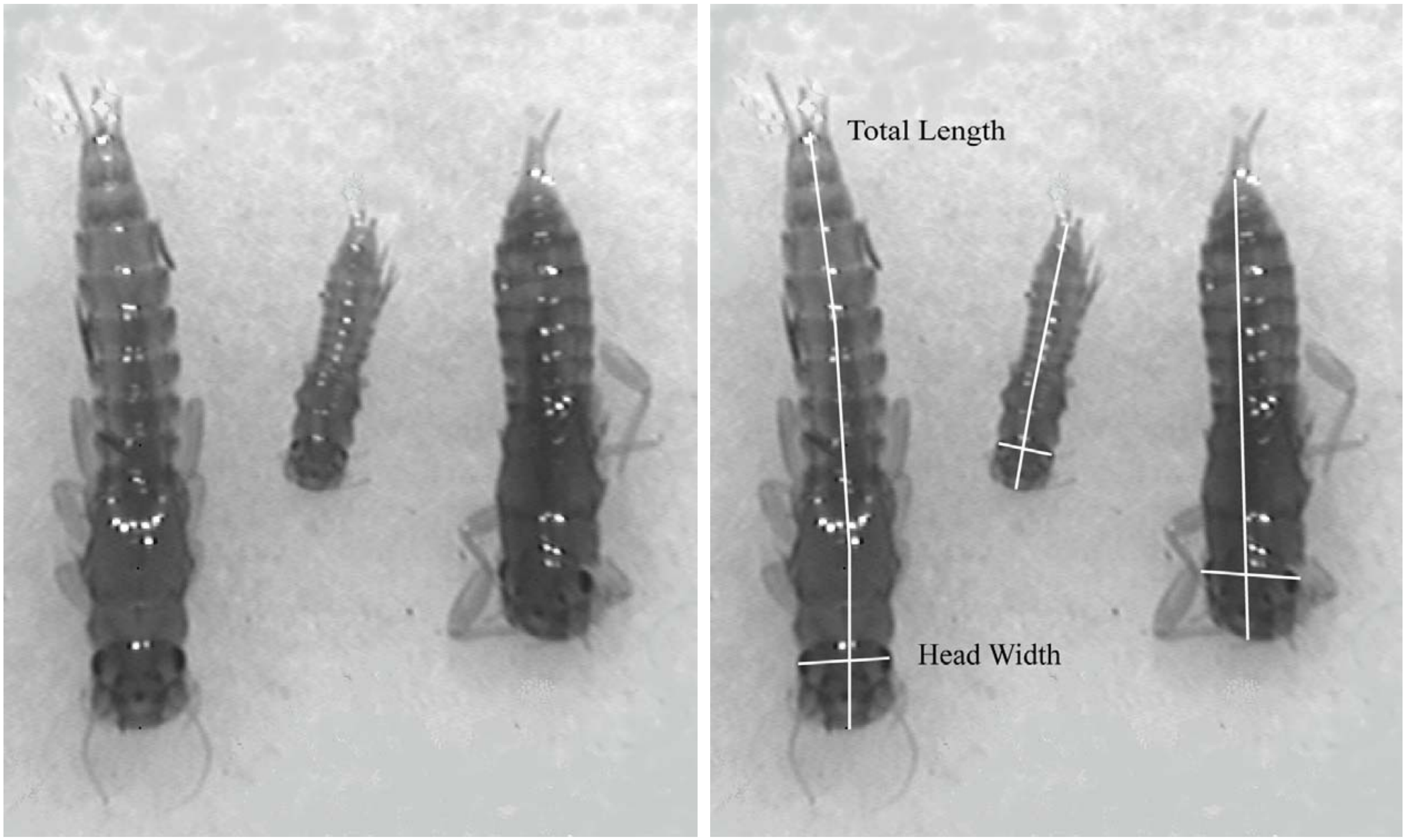

Figure 3. Photographs of *Paraleptophlebia* nymphs collected in upper Prairie Creek, Humboldt County, California. The image on the right depicts total length and head width measures obtained from the photograph using Image-Pro Plus version 4.1 for Windows.

The weigh pan was cleaned prior to weighing each new individual. Mean individual weight was calculated from five measurements of DM (nearest 0.001 mg).

Regression analysis was used to determine the line of best fit relating measured linear dimensions (TL and HW) and mean individual DM. The model best describing insect DM from body length data is often a power function of the form:

$$DM = a \bullet L^{b} \quad (1)$$

for which a ln – ln transformation generates a straight line relation:

$$\ln DM = \ln a + b \bullet L \quad (2)$$

where DM is presented in mg, L is any linear dimension in mm, and ln a and b are intercept and slope terms respectively (Rogers et al. 1976, Humpesch 1979, Smock 1980, Benke et al. 1999, Johnston and Cunjak 1999). The body dimension best accounting for the total variation in mean individual DM was used to estimate individual DM for all preserved *Paraleptophlebia* nymphs.

The size-frequency (SF) method (Hynes 1961, Hynes and Coleman 1968, Hamilton 1969, Benke 1979, Hynes 1980) was used to estimate annual production for each population of *Paraleptophlebia*. The mean number of individuals reaching a given size class over a year provided the basis for calculating production using the SF method. Mean annual density for a given size class was assumed to approximate the survivorship of an average cohort (Hamilton 1969, Benke and Waide 1977, Benke 1979, Menzie 1980). Production of a given average cohort was calculated as the net change in mean annual density and mean individual DM between size classes. The number of size classes present in a given population was assumed equal to the number of cohorts present during one year (Benke and Wallace 1980). Therefore, average cohort production was multiplied by the number of size classes (*K*) and summed to yield annual production. If development time differed greatly from a year, annual production estimates would have been corrected for the population's actual cohort production interval (CPI), the mean number of days required by an invertebrate population to complete their aquatic stage (Benke 1979, Menzie 1980, Benke 1984).

The annual production calculation using the SF method may also be expressed as:

$$P = \frac{365}{CPI} \bullet \sum_{i=1}^{K} K\overline{W_i}\Delta N_i \tag{3}$$

where P is annual production ($g{\bullet}m^{-2}{\bullet}yr^{-1}$), CPI is in days, *i* is an individual size class, *K* is the number of size classes, and $\overline{W_i}$ is the mean individual DM (g) for individuals in a given size class, and ΔN_i is the change in mean annual invertebrate density ($N{\bullet}m^{-2}$) from *i* to *i*+1.

Nymphs collected over the year were grouped into 1 mm size classes based on TL measurements. SF distributions for each stream were developed using S-Plus 2000 for Windows. Distributions were used to estimate voltinism and CPI for each *Paraleptophlebia* population (Prairie, Boyes and Streelow Creeks). Mean annual density for a given size class ($\overline{N_i}$) was obtained by calculating the sample period means, summing them over the sampling period, and dividing the sum by the total number of sampling dates (n = 11). Mean annual densities were extrapolated to totals per square meter of riffle habitat for production analyses. Mean individual DM for nymphs within a given size class ($\overline{W_i}$) was calculated for each stream individually from DM values estimated using the Prairie Creek length to mass model. Mean DM values were also calculated from the combined estimated DM values from all three streams. Mean DM values were also calculated using DM values estimated from published length to mass models for *Paraleptophlebia* genera (Benke et al. 1999, Johnston and Cujak 1999).

A critical statistic for understanding invertebrate production is the rate of biomass turnover or the production to biomass ratio (Waters 1969, Smock 1980, Benke 1984, Hauer and Benke 1987, Waters 1987, Benke 1993). Annual production to biomass was calculated for each population using the equation:

$$\frac{P}{\overline{\overline{B}}} = \frac{P}{\sum_{i=1}^{K} \overline{B}} \tag{4}$$

where P is annual production ($g \bullet m^{-2} \bullet yr^{-1}$), and $\overline{B}$ is the sum of the mean biomass values over the *K* size classes.

Stream temperature strongly influences growth and development of aquatic invertebrates (Edmunds et al. 1976, Corkum 1978, Markarian 1979, Harper et al. 1995). Markarian (1979) reported that growth of *P. assimilis* in Schalls Run, a small stream in Pennsylvania, was directly proportional to the total number of degree days (above 2.5 ºC) experienced. Therefore, mean daily water temperatures were monitored from 18 October 1998 through 17 October 1999 using continuously recording optic thermisters.

Thermisters were placed in the water column of select riffle habitats located in all three study reaches. Degree days were calculated for each stream by summing mean daily water temperatures above 0 ºC over the sampling period to document thermal conditions in all three streams (Wigglesworth 1972).

RESULTS

A total of 196 samples were collected over the sampling period (October 1998 – September 1999): 64 samples from Boyes Creek and 66 samples each from Prairie Creek and Streelow Creek. Samples yielded 4,579 *Paraleptophlebia* nymphs: 1,786 from Prairie Creek, 1,738 from Boyes Creek and 1,055 from Streelow Creek. Mean daily flow for dates when Prairie Creek was sampled ranged from 1.34 $m^3 \cdot s^{-1}$ on 17 November 1998 and 25 January 1999 to 0.06 $m^3 \cdot s^{-1}$ on 21 September 1999 (Figure 4). Flows influenced timing of collections through most of the winter. High flows in all streams prevented sampling during the month of February (Figure 4).

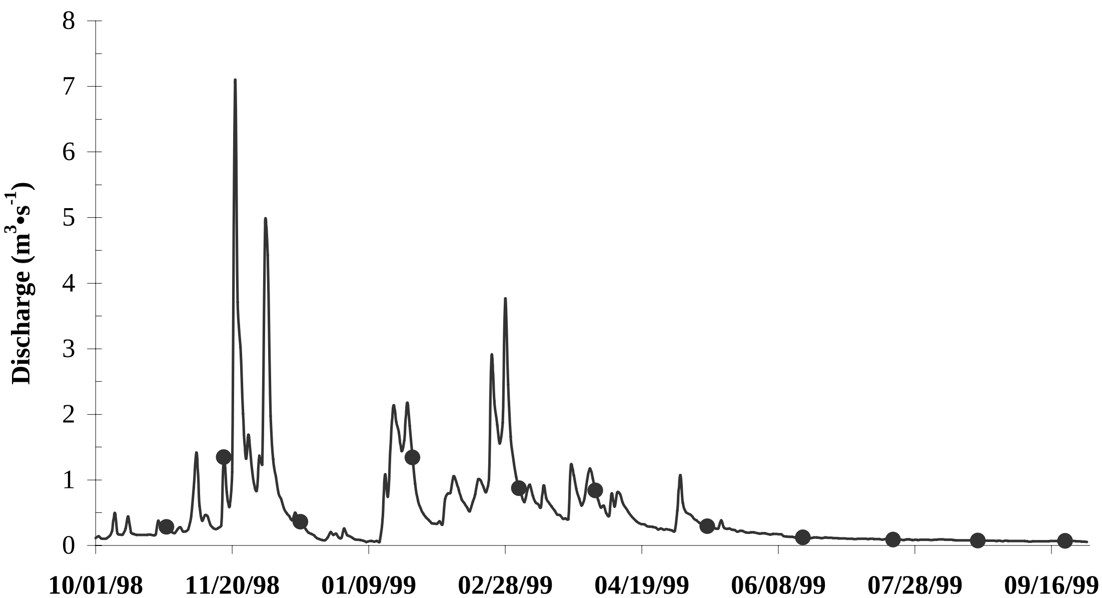

Figure 4. Mean daily discharge recorded for water year 1999 in upper Prairie Creek, Humboldt County, California (drainage area at gage was 15.65 km^2). Invertebrate sampling dates are indicated by the black dots.

A total of 28 live *Paraleptophlebia* nymphs were collected for length to mass determination. Nymphs ranged in size from 2.11 – 6.32 mm TL (mean = 4.26 mm, S.D. = 1.083) (Figure 5) with head widths ranging from 0.46 – 1.21 mm (mean = 0.81, S.D. = 0.165). Mean individual DM values ranged from 0.031 – 0.772 mg (Figure 5). The fitted parameter constants (ln a and b) and their associated standard errors were obtained by least-squares regression (lm procedure, S-Plus 2000 for Windows) relating both ln TL to ln DM and ln HW to ln DM (Table 2).

Prairie Creek model constants differed slightly than published coefficient values for *Paraleptophlebia* species (Table 2) (Benke et al. 1999, Johnston and Cujak 1999). Differences in intercept and slope terms for the same taxa may have resulted from the small sample size and limited size range of nymphs used to develop the models. For nymphs collected in Prairie Creek riffles, ln TL best accounted for the total variation in mean individual ln DM. This model was used to estimate DM of preserved *Paraleptophlebia* nymphs collected in all three streams (Figure 5).

Size of *Paraleptophlebia* nymphs collected over the sampling period ranged from 0.72 – 6.22 mm TL in Prairie Creek, 0.72 – 6.05 mm TL in Boyes Creek and 0.71 – 6.36 mm TL in Streelow Creek. Head widths for these same individuals ranged from 0.23 – 1.17 mm in Prairie Creek, 0.18 – 0.84 mm in Boyes Creek and 0.19 – 0.89 mm in Streelow Creek. A large variation in individual size was observed on every sampling date in all streams (Figure 6). In general, mean individual size was greatest from April

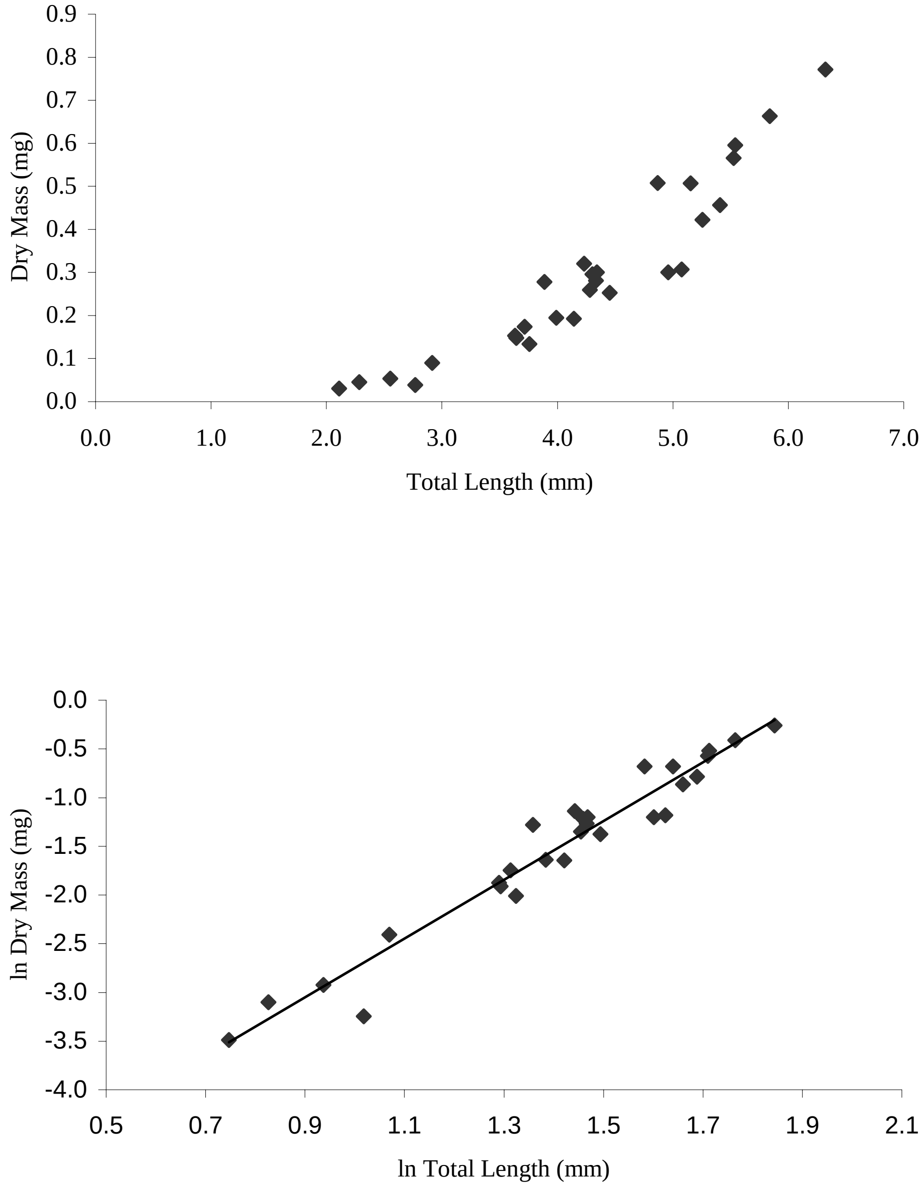

Figure 5. Dry mass plotted against total length (top) and ln dry mass plotted against ln total length (bottom) for *Paraleptophlebia* nymphs collected in riffle habitats of upper Praire Creek, Humboldt County, California. The solid line depicts the fitted regression model.

Table 2. Summary of linear regression for models relating ln body length (total length (TL) and head width (HW) in mm) to ln dry mass (DM in mg) for *Paraleptophlebia* nymphs collected in upper Prairie Creek, Humboldt County, California and published length to mass model parameters for *Paraleptophlebia*.

a	ln a	+/- 1 SE	b	+/- 1 SE	Body Length	R^2	n	Size Range (mm)	Location	Reference
0.003[a]	-5.764	0.1982	3.016	0.138	TL	0.95	28	2.11 - 6.32	California	This Study
0.540[a]	-0.615	0.0787	3.912	0.256	HW	0.90	28	0.46 - 1.21	California	This Study
0.006		0.0005	2.624	0.189	TL	0.88	55	1.0 - 7.8	Virginia	Benke et al. 1999
0.526		0.2777	3.038	0.558	HW	0.76	55	0.4 - 1.7	Virginia	Benke et al. 1999
0.009		NA	2.510	NA	TL	0.96	50	1.8 - 7.1	Canada	Johnston and Cunjak 1999
0.622		NA	3.230	NA	HW	0.92	50	0.40 - 1.2	Canada	Johnston and Cunjak 1999

[a]The value represents the exponent of the natural log of a.

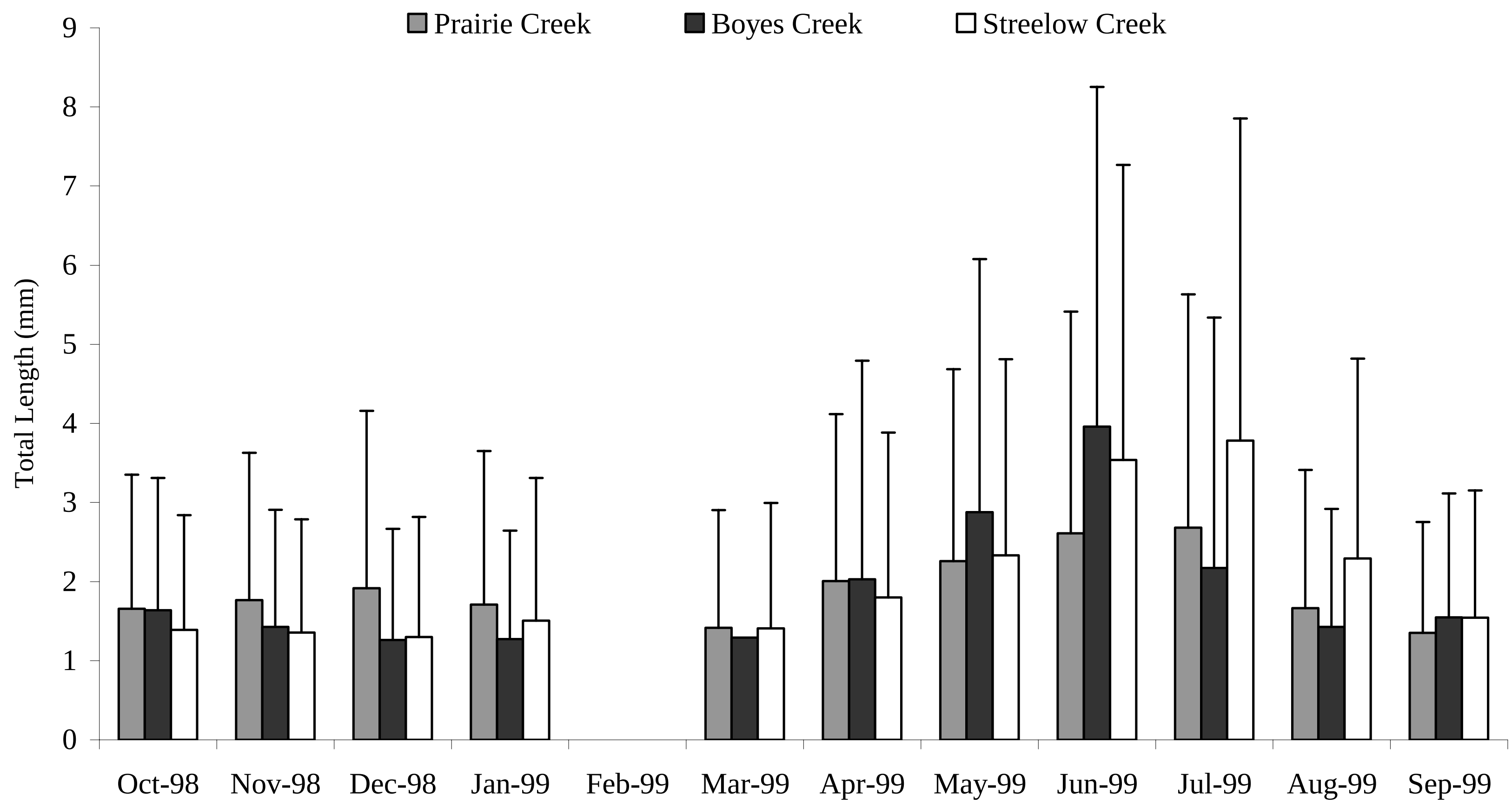

Figure 6. Mean size of *Paraleptophlebia* nymphs from monthly samples collected in riffle habitats of three coastal streams draining the Prairie Creek watershed, Humboldt County, California. Lines depict the + 95 percent confidence intervals on estimated means.

through July with peaks observed in June and July in all streams (Figure 6). For all other months, mean individual size was from 1 – 2 mm TL in all three streams (Figure 6).

Large bodied nymphs (TL >5mm) were present in Prairie Creek from March through August with a peak observed in July (Figure 7). The Prairie Creek population displayed the least degree of cohort or generational synchrony among the streams (Figure 7). The two tributary populations appeared to have slightly shorter periods when larger bodied individuals were present than observed in Prairie Creek (Figure 7). Larger nymphs were generally present from April through July in Boyes Creek with a peak observed in June (Figure 7). In Streelow Creek, larger nymphs were present in May through August with the peak occurring in July (Figure 7).

Very few nymphs within the first size class (0 – 1 mm TL) were collected relative to numbers collected within the second size class (1 – 2 mm TL) in all streams (Table 3). Individuals within the first size class were present in Prairie Creek from October through April and in September (Figure 7). Individuals within the first size class were present in Boyes Creek from August through November with a peak observed in January (Figure 7). In Streelow Creek the smallest nymphs were present in October through December, March through May and in September (Figure 7). The peak for small bodied nymphs occurred in December in Streelow Creek (Figure 7).

From the monthly size-frequency distributions it was assumed that all three *Paraleptophlebia* populations were univoltine or produced only one asynchronous

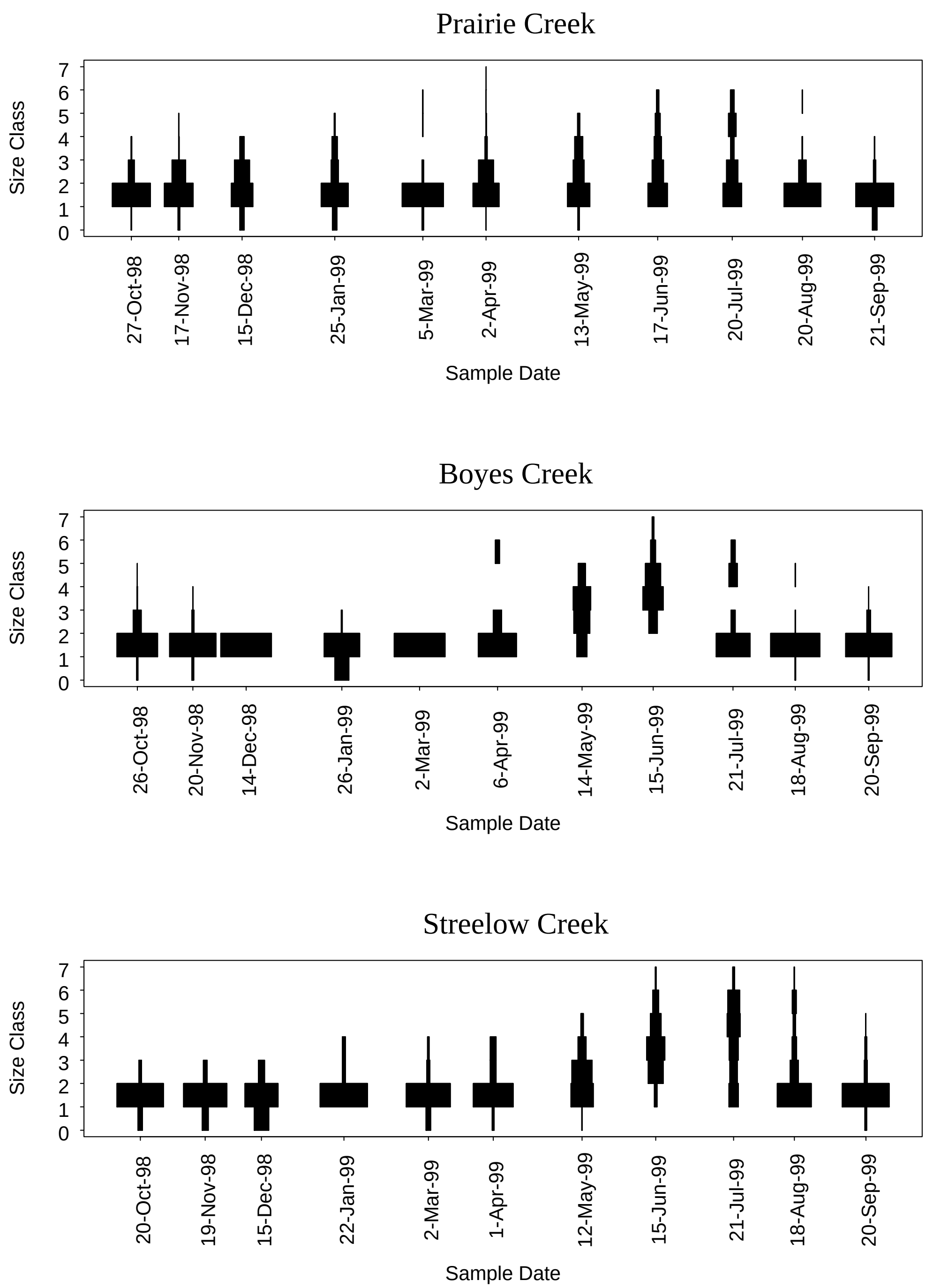

Figure 7. Monthly frequency distributions for *Paraleptophlebia* nymphs in riffle habitats of three coastal streams draining the Prairie Creek watershed, Humboldt County, California. Width of each band represents percentage of total nymphs collected in a select size class.

Table 3. Number of Paraleptophlebia nymphs within 1 mm size classes based on total length data from monthly samples collected in three coastal streams draining the Prairie Creek watershed, Humboldt County, California.

Size Class (*i*)	Prairie Creek Frequency	Boyes Creek Frequency	Streelow Creek Frequency
0 to 1	56	49	42
1 to 2	1257	1450	630
2 to 3	319	181	155
3 to 4	84	33	108
4 to 5	48	19	65
5 to 6	21	5	48
6 to 7	1	1	7
Total	1786	1738	1055

generation per year. Mating was assumed to occur in late spring and extend through summer with maximum emergence occurring in June and July (Figure 7). Egg hatching may have occurred in the fall with nymphs growing slowly over the winter or hatching could have occurred slowly over the winter (Figure 7). Estimating exact CPI values for the three populations from the field samples was not possible given the high degree of cohort asynchrony displayed by each population. Therefore, a CPI of 365 days or one year was assumed for all three *Paraleptophlebia* populations.

Paraleptophlebia densities were generally greatest during fall and least in winter in all three streams (Figure 8). Prairie Creek densities were fairly consistent over the year

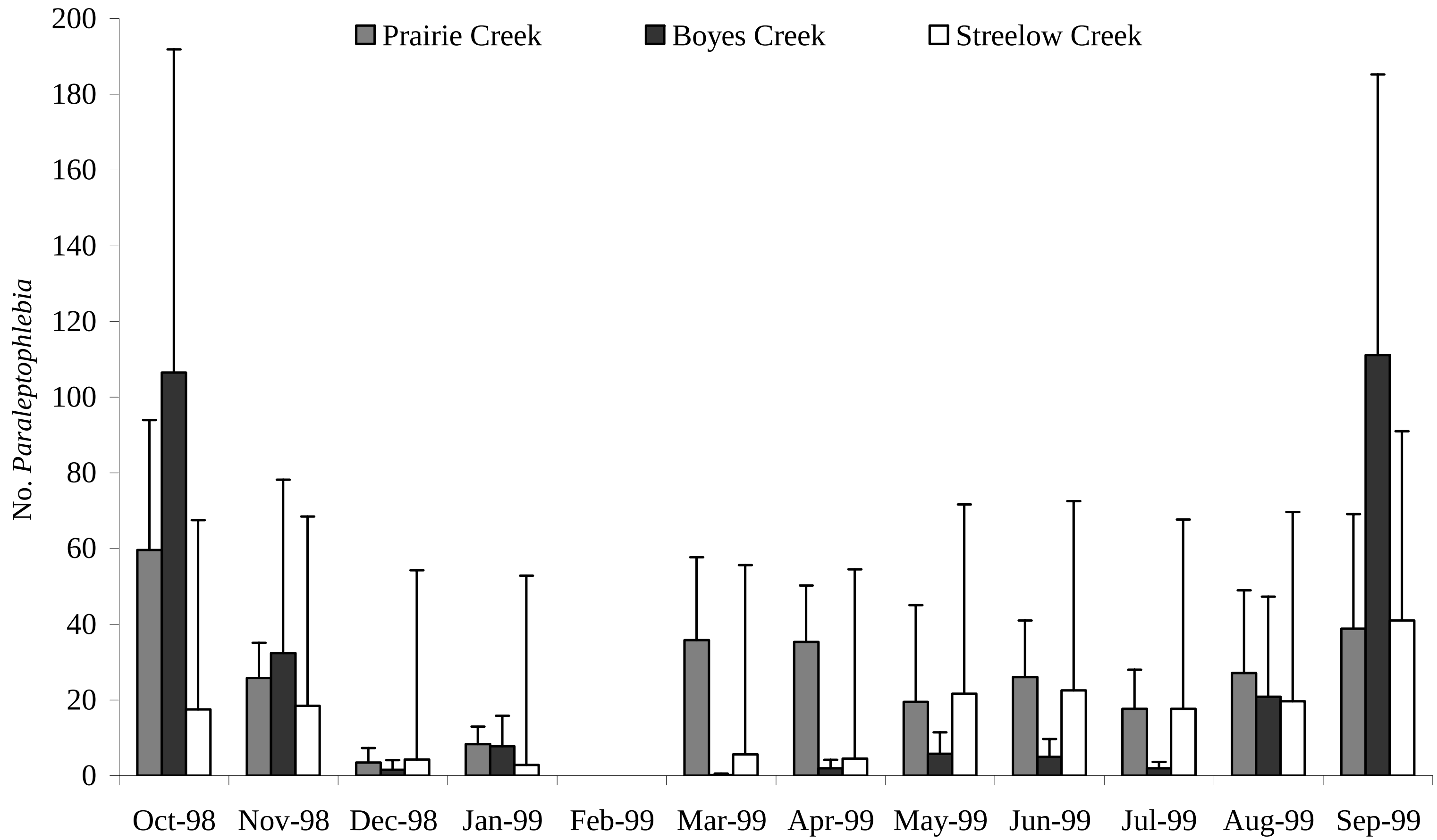

Figure 8. Mean number of *Paraleptophlebia* nymphs from monthly samples collected in riffle habitats of three coastal streams draining the Prairie Creek watershed, Humboldt County, California. Lines depict the + 95 percent confidence intervals on estimated means.

with the highest densities observed in October and the lowest in December and January (Figure 8). Densities in Boyes Creek were very low from December through July with intermediate densities observed in November and August (Figure 8). Densities observed in Boyes Creek during October and September were the highest observed among the three streams. Streelow Creek densities were lowest from December through April, slightly higher from May through November with a peak observed in September (Figure 8). Sample densities were highly variable on all sample dates in each stream (Figure 8).

Mean monthly and mean annual densities varied among size classes and by stream (Table 4). Mean annual densities in all streams were lowest within the first and last size class and greatest within the second size class (Table 4). However, the mean annual density estimated for the second size class in Streelow Creek was considerably lower than values estimated for the other two streams (Table 4). No substantial differences in mean individual DM values for *Paraleptophlebia* within a given size class were observed among the three streams (Table 5). Therefore, values obtained from combining the data were used in production calculations. Differences did exist in mean individual DM values when published length to mass models were used to estimate DM (Table 5). The model presented by Benke et al. (1999) resulted in slightly higher estimates of mean individual DM for the first five size classes and lower DM estimates for the last two size classes (Table 5). The model presented by Johnston and Cunjak (1999) produced larger estimates of mean individual DM for each size class relative to those obtained using the Prairie Creek model (Table 5).

Table 4. Monthly densities (no.•m^{-2}) of *Papraleptophlebia* nymphs collected from riffle habitats of three coastal streams draining the Prairie Creek watershed, Humboldt County, California.

Prairie Creek

Size Class	27-Oct-98	17-Nov-98	15-Dec-98	25-Jan-99	5-Mar-99	2-Apr-99	13-May-99	17-Jun-99	20-Jul-99	20-Aug-99	21-Sep-99
0 to 1	53.82	64.59	21.53	53.82	86.11	21.53	43.06	0.00	0.00	0.00	258.34
1 to 2	3240.04	1065.66	107.64	322.93	2120.56	1324.00	624.33	721.21	473.63	1431.65	2099.03
2 to 3	495.16	505.92	75.35	86.11	75.35	764.26	301.40	419.81	290.64	290.64	129.17
3 to 4	64.59	21.53	21.53	64.59	0.00	107.64	226.05	269.11	86.11	21.53	21.53
4 to 5	0.00	10.76	0.00	10.76	21.53	32.29	64.59	182.99	193.76	0.00	0.00
5 to 6	0.00	0.00	0.00	0.00	10.76	21.53	0.00	86.11	96.88	10.76	0.00
6 to 7	0.00	0.00	0.00	0.00	0.00	10.76	0.00	0.00	0.00	0.00	0.00
Totals	3853.61	1668.46	226.05	538.21	2314.32	2282.02	1259.42	1679.22	1141.01	1754.57	2508.07

Boyes Creek

Size Class	26-Oct-98	20-Nov-98	14-Dec-98	26-Jan-99	2-Mar-99	6-Apr-99	14-May-99	15-Jun-99	21-Jul-99	18-Aug-99	20-Sep-99
0 to 1	182.99	64.59	0.00	139.94	0.00	0.00	0.00	0.00	0.00	21.53	118.41
1 to 2	5489.77	1593.11	86.11	355.22	10.76	96.88	75.35	0.00	86.11	1302.48	6512.38
2 to 3	1108.72	75.35	0.00	10.76	0.00	21.53	118.41	53.82	10.76	10.76	538.21
3 to 4	75.35	10.76	0.00	0.00	0.00	0.00	129.17	129.17	0.00	0.00	10.76
4 to 5	21.53	0.00	0.00	0.00	0.00	0.00	53.82	96.88	21.53	10.76	0.00
5 to 6	0.00	0.00	0.00	0.00	0.00	10.76	0.00	32.29	10.76	0.00	0.00
6 to 7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.76	0.00	0.00	0.00
Totals	6878.36	1743.81	86.11	505.92	10.76	129.17	376.75	322.93	129.17	1345.53	7179.76

Streelow Creek

Size Class	20-Oct-98	19-Nov-98	15-Dec-98	22-Jan-99	2-Mar-99	1-Apr-99	12-May-99	15-Jun-99	21-Jul-99	18-Aug-99	20-Sep-99
0 to 1	96.88	139.94	75.35	0.00	32.29	10.76	10.76	0.00	0.00	0.00	86.11
1 to 2	979.55	968.78	172.23	161.46	301.40	215.29	581.27	75.35	204.52	807.32	2314.32
2 to 3	53.82	86.11	32.29	10.76	21.53	32.29	527.45	409.04	161.46	193.76	139.94
3 to 4	0.00	0.00	0.00	10.76	10.76	32.29	215.29	495.16	193.76	107.64	96.88
4 to 5	0.00	0.00	0.00	0.00	0.00	0.00	64.59	290.64	279.87	53.82	10.76
5 to 6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	161.46	258.34	96.88	0.00
6 to 7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	21.53	43.06	10.76	0.00
Totals	1130.25	1194.83	279.87	182.99	365.98	290.64	1399.35	1453.18	1141.01	1270.18	2648.01

Table 5. Mean annual dry mass values for *Paraleptophlebia* nymphs collected in riffle habitats of three coastal streams draining the Prairie Creek watershed, Humboldt County, California.

Size Class (*i*)	Prairie Creek Mean Dry Mass (mg)	Boyes Creek Mean Dry Mass (mg)	Streelow Creek Mean Dry Mass (mg)	Published[a] Combined Mean Dry Mass (mg)	Published[b] Combined Mean Dry Mass (mg)
0 to 1	0.0025	0.0025	0.0025	0.0050	0.0078
1 to 2	0.0108	0.0108	0.0101	0.0174	0.0256
2 to 3	0.0442	0.0416	0.0479	0.0607	0.0844
3 to 4	0.1291	0.1342	0.1324	0.1566	0.2094
4 to 5	0.2876	0.2729	0.2915	0.3097	0.4021
5 to 6	0.5157	0.4810	0.5324	0.5230	0.6640
6 to 7	0.7798	0.7154	0.7687	0.7265	0.9096

[a]Published source was Benke et al. 1999

[b]Published source was Johnston and Cunjak 1999

Annual production calculations for the three *Paraleptophlebia* populations are presented in SF tables according to Benke (1984). Negative biomass and production values calculated for the first size class were excluded from production calculations following Benke and Wallace (1980). Annual production estimates were 89.7 mg•m^{-2}•yr^{-1} in Prairie Creek (Table 6), 69.9 mg•m^{-2}•yr^{-1} in Boyes Creek (Table 7) and 74.0 mg•m^{-2}•yr^{-1} in Streelow Creek (Table 8). Mean annual density and mean standing stock biomass values in Prairie Creek were relatively high for all size classes present (Table 6). Therefore, production contributions from each average cohort were relatively large resulting in the highest annual production estimate among the three populations.

Although mean annual density summed over all size classes was relatively high in Boyes Creek, low densities in all the larger size classes resulted in low production contributions and the lowest estimate of mean annual standing stock biomass and annual production (Table 7). Although mean annual densities were lowest in Streelow Creek, a relatively large number of individuals were greater than five mm TL (Table 8). Therefore, large production contributions were generated for the last two size classes and resulted in the second highest estimate of annual production.

Mean annual standing stock biomass was greatest in Streelow Creek at 12.6 mg•m^{-2} with Prairie Creek a close second at 10.5 mg•m^{-2}. Mean annual standing stock biomass was considerably lower in Boyes Creek at 6.1 mg•m^{-2}. Annual production to biomass values were 8.56 in Prairie Creek, 11.39 in Boyes Creek and 5.89 in Streelow Creek (Table 9). The relatively high annual production estimate and the moderate

Table 6. Size frequency table generated from monthly collections (October 1998 – September 1999) of *Paraleptophlebia* nymphs in riffle habitats of Prairie Creek, Humboldt County, California.

Total Length (mm)	Annual Mean Density ($No.•m^{-2}$)	Mean Individual Biomass (mg)	Annual Mean Standing Stock ($mg•m^{-2}$)	Number Lost ($No.•m^{-2}$)	Individual Biomass at Loss (mg)	Biomass Loss ($mg•m^{-2}$)	Correction Factor x7
0-1	9.13	0.00	0.02				
				-195.88	0.01	-1.29	-9.03
1-2	205.01	0.01	2.19				
				152.98	0.03	4.21	29.45
2-3	52.03	0.04	2.31				
				38.33	0.09	3.37	23.58
3-4	13.70	0.13	1.80				
				5.87	0.21	1.23	8.61
4-5	7.83	0.29	2.25				
				4.40	0.41	1.79	12.51
5-6	3.42	0.52	1.80				
				3.26	0.64	2.10	14.71
6-7	0.16	0.76	0.12				
				0.16	0.76	0.12	0.87
Totals	291.29		10.49				89.72

Table 7. Size frequency table generated from monthly collections (October 1998 – September 1999) of *Paraleptophlebia* nymphs in riffle habitats of Boyes Creek, Humboldt County, California.

Total Length (mm)	Annual Mean Density (No.•m^{-2})	Mean Individual Biomass (mg)	Annual Mean Standing Stock (mg•m^{-2})	Number Lost (No.•m^{-2})	Individual Biomass at Loss (mg)	Biomass Loss (mg•m^{-2})	Correction Factor x7
0-1	8.38	0.00	0.02				
				-233.19	0.01	-1.54	-10.75
1-2	241.58	0.01	2.58				
				211.83	0.03	5.83	40.78
2-3	29.75	0.04	1.32				
				23.68	0.09	2.08	14.57
3-4	6.07	0.13	0.80				
				2.81	0.21	0.59	4.11
4-5	3.26	0.29	0.94				
				2.61	0.41	1.06	7.41
5-6	0.65	0.52	0.34				
				0.49	0.64	0.32	2.21
6-7	0.16	0.76	0.12				
				0.16	0.76	0.12	0.87
Totals	289.85		6.12				69.95

Table 8. Size frequency table generated from monthly collections (October 1998 – September 1999) of *Paraleptophlebia* nymphs in riffle habitats of Streelow Creek, Humboldt County, California.

Total Length (mm)	Annual Mean Density ($No.\bullet m^{-2}$)	Mean Individual Biomass (mg)	Annual Mean Standing Stock ($mg\bullet m^{-2}$)	Number Lost ($No.\bullet m^{-2}$)	Individual Biomass at Loss (mg)	Biomass Loss ($mg\bullet m^{-2}$)	Correction Factor x7
0-1	6.85	0.00	0.02				
				-95.90	0.01	-0.63	-4.42
1-2	102.75	0.01	1.10				
				77.47	0.03	2.13	14.91
2-3	25.28	0.04	1.12				
				7.67	0.09	0.67	4.72
3-4	17.61	0.13	2.31				
				7.01	0.21	1.47	10.28
4-5	10.60	0.29	3.05				
				2.77	0.41	1.13	7.88
5-6	7.83	0.52	4.10				
				6.69	0.64	4.31	30.15
6-7	1.14	0.76	0.87				
				1.14	0.76	0.87	6.11
Totals	172.07		12.57				74.04

Table 9. Mean annual density (N), mean annual biomass (B), mean annual production (P) and annual production to biomass values for *Paraleptophlebia* nymphs collected in riffle habitats of three coastal streams draining the Prairie Creek watershed, Humboldt County, California.

Study Reach	N ($No.•m^{-2}$)	B ($mg•m^{-2}$)	P ($mg•m^{-2}•yr^{-1}$)	Annual P/B
Prairie Creek	291.3	10.5	89.7	8.56
Boyes Creek	289.9	6.1	69.9	11.43
Streelow Creek	172.1	12.6	74.0	5.89

estimate of mean annual standing stock biomass resulted in a moderate production to biomass ratio in Prairie Creek. The production to biomass ratio estimated for Boyes Creek was fairly high due to low mean annual standing stock biomass and the large number of small bodied nymphs collected over the year. Conversely, the low production to biomass ratio estimated in Streelow Creek was due to the relatively high mean annual standing stock biomass.

Mean daily water temperatures and seasonal temperature fluctuations were very similar among the three streams over the sampling period (Figure 9). Prairie Creek displayed the widest range in mean daily water temperature with 3.6 ºC recorded on 23 December and 13.6 ºC on 28 August. Minimum daily means were 5.1 ºC on 24 December in Boyes Creek and 4.7 ºC on 23 December in Streelow Creek (Figure 9). Maximum daily means were 12.6 ºC in Boyes Creek and 12.7 ºC in Streelow Creek on 30

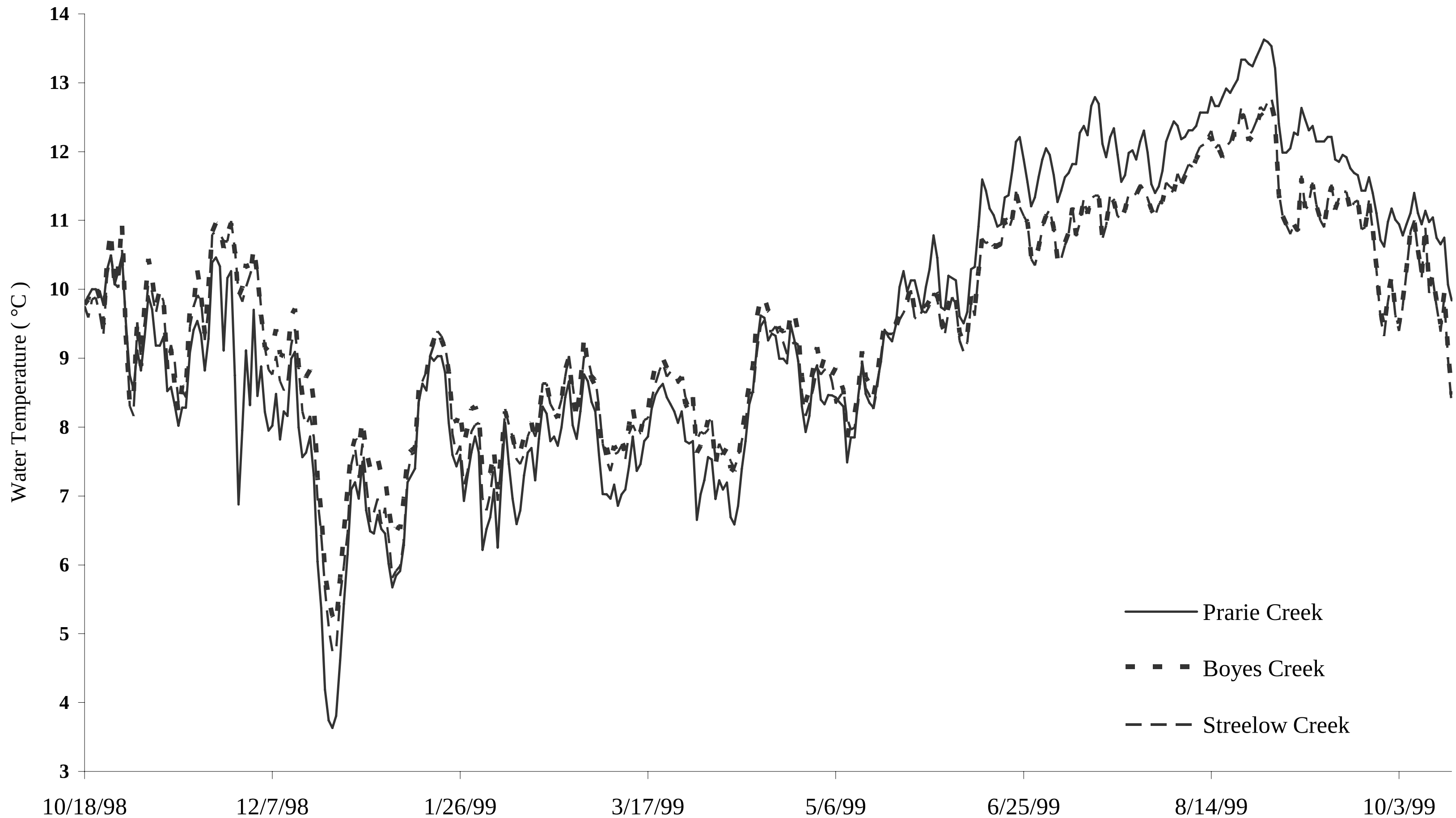

Figure 9. Mean daily water temperatures for the period 18 October 1998 to 17 October 1999 in riffle habitats of three coastal streams draining the Prairie Creek watershed, Humboldt County, California.

August (Figure 9). Annual degree day values were 3,473 for Prairie Creek, 3,486 for Boyes Creek and 3,447 for Streelow Creek (Table 10). Although annual water temperature accumulation was very similar among the streams, slight differences were observed in monthly temperature accumulations (Table 10, Figure 10). Prairie Creek appeared to accumulate fewer degree days during winter months and more in the summer months relative to the tributary streams (Table 10, Figure 10).

Table 10. Water temperature accumulation presented in degree days for the period 18 October 1998 to 17 October 1999 in riffle habitats of three coastal streams draining the Prairie Creek watershed, Humboldt County, California.

Accumulation Interval		n	Prairie Creek	Boyes Creek	Streelow Creek
18-Oct-98	30-Nov-98	44	411	433	428
1-Dec-98	31-Dec-98	31	220	254	244
1-Jan-99	31-Jan-99	31	229	247	236
1-Feb-99	28-Feb-99	28	211	226	224
1-Mar-99	31-Mar-99	31	240	256	255
1-Apr-99	30-Apr-99	30	247	260	255
1-May-99	31-May-99	31	279	282	278
1-Jun-99	30-Jun-99	30	327	310	309
1-Jul-99	31-Jul-99	31	371	344	344
1-Aug-99	31-Aug-99	31	397	373	375
1-Sep-99	17-Oct-99	47	540	500	498
Totals			3473	3486	3447

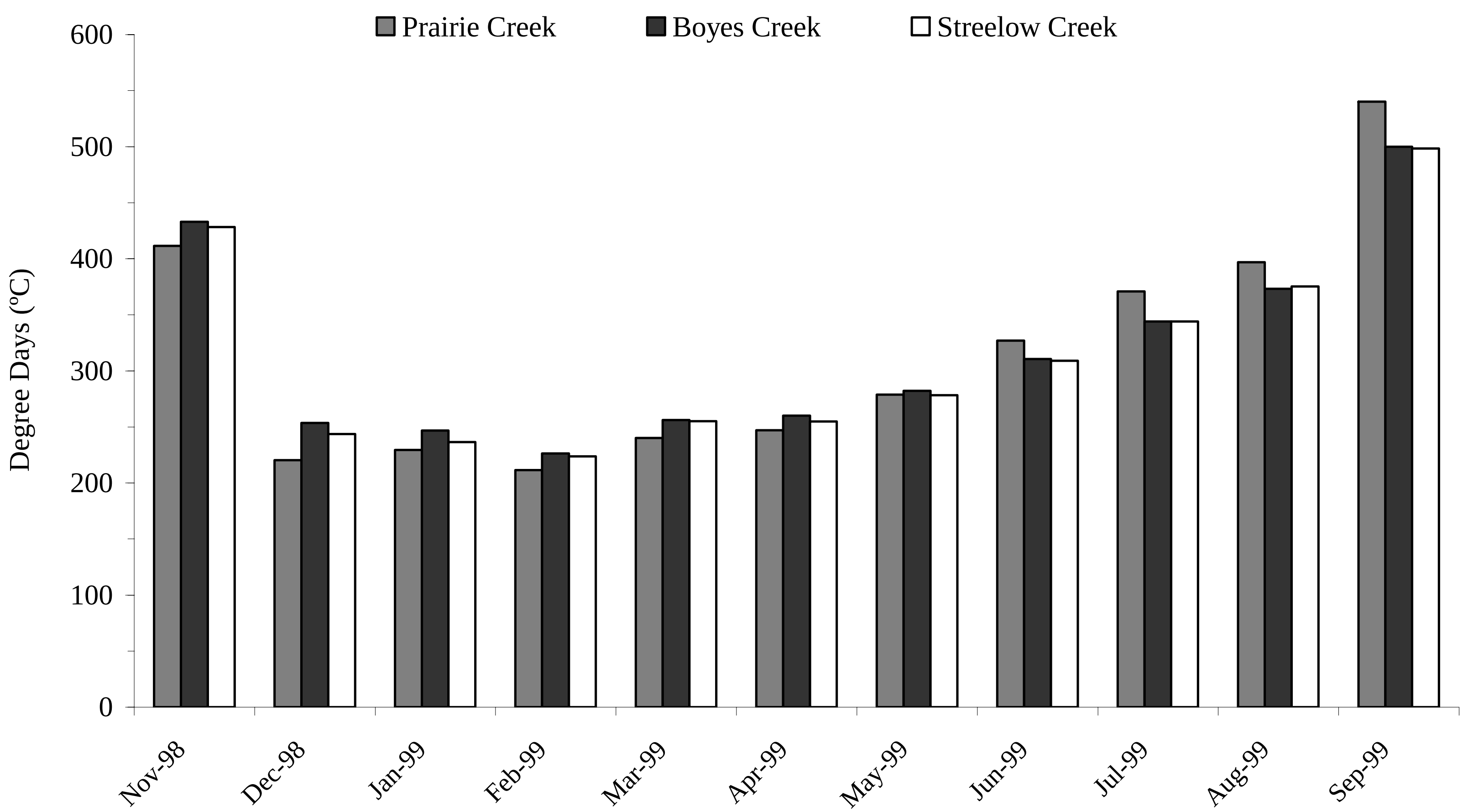

Figure 10. Water temperature accumulation presented in degree days for the period 18 October 1998 to 17 October 1999 in riffle habitats of three coastal streams draining the Prairie Creek watershed, Humboldt County, California.

DISCUSSION

The SF method was originally developed to estimate entire fauna production and over the years was modified to also provide reasonably good results when applied to individual species, groups of coexisting species with similar growth characteristics and to populations displaying asynchronous development (Hynes 1961, Hynes and Coleman 1968, Hamilton 1969, Benke 1979, Benke and Wallace 1980, Benke 1984, Benke et al. 1984, Benke et al. 1985, Benke 1993, Morin and Dumont 1994). The versatility of this method resides in the ability to estimate production from an average size frequency distribution calculated from field samples collected over a year instead of approximations of true growth and survival curves (Hynes 1961, Hynes and Coleman 1968, Hamilton 1969, Benke 1979, Benke 1984). Therefore, the SF method was ideal for use in my study given the inability to separate species and the apparent asynchronous development of *Paraleptophlebia* in all three streams.

However, accuracy and precision of the SF method have always been questioned and few have attempted to identify and quantify all sources of error associated with production estimation (Benke 1984, Benke 1993). Although Krueger and Martin (1980) developed a method for calculating confidence intervals on SF production estimates, Hynes (1980) and Benke (1984) cautioned other sources of error inherent to the methodology remained unaccounted for. Other disadvantages of the SF method are the numerous assumptions that are often difficult or impossible to meet (Benke 1993). For example, when estimating production from a specific habitat it is generally assumed that immigration of invertebrates approximates emigration (Benke 1984, Huryn and Wallace 2000). However, movement of aquatic invertebrates from one habitat type to another as specific developmental stages are reached is fairly common (Hall et al. 1980, Minshall 1984). There is no way to know the significance of immigration and emigration without sampling the range of habitats available (Huryn and Wallace 2000).

Another difficult assumption is that individuals in the average cohort of interest spend equal amounts of time in each of the size classes present. Benke (1984) suggested the assumption of linear growth was likely never met. However, failure to account for non-linear growth when using the SF method was reported not likely to lead to large errors in production estimates (Hamiltion 1969, Benke and Waide 1977). Accurately determining CPI from field samples collected over a year is critical when estimating production using the SF method (Waters 1979, Benke 1984). This often proves difficult given the various sampling issues associated with quantifying aquatic invertebrate population parameters in complex lotic environments (Egglishaw 1964, Benke 1984, Minshall 1984). Sampling issues that often confound CPI and production estimation include under-sampling both the smallest and the largest individuals in the population of interest (Benke and Wallace 1980, Waters and Crawford 1973, Benke 1984, Huryn and Wallace 2000). Benke (1993) suggested that an independent estimate of a population's CPI may be required when using the SF method.

Monthly sampling over the year was assumed adequate for estimating annual production for each *Paraleptophlebia* population using the SF method (Benke 1984, Lugthart and Wallace 1992). However, the sample design employed during my study likely limited the ability to accurately estimate invertebrate densities. Sample densities were highly variable in all three streams on nearly every sampling occasion (Figure 8, Table 4). This was probably the result of obtaining only one sample within a given riffle. This method relied on the assumption that variation within a single sample, with respect to the parameter of interest (i.e. invertebrate density), was representative of the true variation within the sampling universe (i.e. the riffle habitat). This was a poor assumption given the complex nature of lotic habitats and the resulting heterogeneous distribution of invertebrates (Egglishaw 1964, Benke 1984, Minshall 1984). Collecting multiple samples within a given riffle would have allowed assessment of within habitat unit variation and possibly improved the accuracy of population parameter estimates.

Timing and magnitude of flow events occurring in the Prairie Creek watershed directly affected sampling efforts from November through April (Figure 4). It was unclear how flow regimes affected invertebrate abundance, biomass and the ability to sample invertebrate populations in these drainages. Peak flow events likely caused invertebrates to burrow deeper into channel substrates or migrate to edge water habitats to avoid high water velocities. The relatively large magnitude flow event in November and peak flow events in early December and February may in part explain the low numbers collected over winter (Figures 4, 8). Again, collecting multiple samples per riffle and collecting from different areas within a select riffle may have improved population parameter estimates.

Prairie Creek has been the focus of many terrestrial and aquatic research and monitoring programs due to the old growth forests that persist in the watershed. In the early 1980's, studies were initiated to assess impacts to aquatic ecosystems associated with construction of the U.S. Highway 101 bypass (Redwood National Park 1986). Aquatic invertebrate data was collected prior to highway construction from fall 1980 through summer 1981 with invertebrate sampling stations located throughout Prairie Creek and in several tributaries. *Paraleptophlebia* nymphs were present at several of the Prairie Creek locations and in a majority of the tributaries (Redwood National Park 1986). The Redwood National Park study allowed me to compare density patterns observed in Prairie Creek and Boyes Creek in 1998 – 1999 with those observed nearly twenty years prior. Unfortunately, no aquatic invertebrate sample locations were established in Streelow Creek during the 1980 – 1981 study.

In 1980 – 1981, density patterns of *Paraleptophlebia* at a site in Prairie Creek located upstream of Boyes Creek were very similar to those observed in Prairie Creek during my study. Nymphs were reported most abundant in June, August and October with the peak occurring in August (Redwood National Park 1986). Nymphs were reported least abundant during winter and spring at this site (Redwood National Park 1986). In 1980 – 1981, *Paraleptophlebia* nymphs were also observed at Prairie Creek sites located downstream of Boyes Creek and in the vicinity of May Creek. However, nymphs were less frequent and the data was more variable (Redwood National Park 1986). Strange (1989) reported consistently collecting *Paraleptophlebia* over the year in Prairie Creek with low numbers observed in July 1986 and peak numbers in October 1986.

Redwood National Park (1986) reported moderately high numbers of *Paraleptophlebia* nymphs in Boyes Creek during 1980 – 1981 and *Paraleptophlebia* was described as a dominant collector. Nymphs were reported most abundant in September, December and June and least abundant in January, March and October (Redwood National Park 1986). In my study, densities in Boyes Creek were consistently low over the year and were only high during October (1998) and September (1999) (Figure 8). The differences observed in these two studies may in part be due to varied sampling techniques or the result of unknown sampling errors. It may also be that alteration of hydrologic conductivity and increased sediment delivery associated with the U.S. Highway 101 bypass has affected life history patterns of *Paraleptophlebia* in Boyes Creek.

Unfortunately, none of these past studies provided body length or biomass data for *Paraleptophlebia* nymphs collected in the watershed. In this study, no individuals greater than 7 mm TL and relatively few individuals from 6 – 7 mm TL were collected over the sampling interval (Tables 3, 4). Edmunds and others (1976) reported nymphs in the genus *Paraleptophlebia* tended to migrate to slower velocity habitats such as runs or glides in the last stages of maturity. Lehmkuhl and Anderson (1971) found *P. temporalis* nymphs hatching in riffles migrated to slower velocity habitats as they matured. They reported mature body lengths for many Oregon coastal *Paraleptophlebia* species from 6 to nearly 8 mm TL. The minimal number of nymphs 6 – 7 mm TL collected in my study may have resulted from late instar emigration to other habitat types. Alternatively, species inhabiting streams of northcoast California may not attain terminal sizes greater than 7 mm TL.

Under-sampling nymphs from 0 – 1 mm TL in all three streams occurred for several reasons including: the short amount of time mayfly nymphs spend as early instars, failure of the sampler to retain early instars and exclusion of these individuals due to difficulties separating them to genus. Under-sampling early instars resulted in negative production estimates for the first size class of *Paraleptophlebia* in all three streams (Tables 6, 7, 8). These negative terms were omitted in the production summations based on the assumption that biomass contributed from the smallest size class was negligible (Benke and Wallace 1980, Benke 1984). Waters and Crawford (1973) extrapolated density estimates for size classes yielding negative production using the catch curve method. Employing several production estimators, they compared production estimates obtained using extrapolated density values versus estimates obtained using the original data. Production estimates that did not account for production of under-sampled size classes were on average ten to twenty percent less than estimates incorporating extrapolated density values.

Assuming a single generation of *Paraleptophlebia* was produced per year in the three streams seemed reasonable based on the SF distributions and knowledge of the life history strategy common to the genus (Coleman and Hynes 1970, Gilpin and Brusven 1970, Lehmkuhl and Anderson 1971, Edmunds et al. 1976, Rader and Ward 1989). Jacobi and Benke (1991) reported extended emergence and delayed egg hatching often resulted in a single generation of adults producing several cohorts in a given year. They suggested the "successive cohorts" did not necessarily represent multiple generations. Corkum (1978) found some *P. mollis* individuals passed winter as relatively large bodied nymphs, while the majority of nymphs could still be classified as early instars as late as April. She concluded this wide range in individual size at any one time resulted from extended emergence and delayed egg hatching. Waters and Crawford (1973) reported nymphs of a relatively synchronous mayfly population (*Ephemerella subvaria*), displayed a wide size range during a single year.

The heterogeneous size distributions observed in this study may have in part resulted from the presence of multiple *Paraleptophlebia* species within all or some of the streams. Coleman and Hynes (1970) reported even closely related species such as *P. moerens* and *P. mollis* exhibited very different growth and life history patterns. Many studies conducted in the Prairie Creek watershed reported collecting *Paraleptophlebia* but did not provide species information (Harrington 1983, Redwood National Park 1986). In this study, several of the largest individuals (> 5 mm) from each stream were identified as *P. temporalis* using the key to mature nymphs presented in Lehmkuhl and Anderson

(1971). Unfortunately, most western *Paraleptophlebia* species can only be reliably separated by identification of adult males (personal communication, K. Cummins 2006. Humboldt State University, Arcata, CA 95521). Strange (1989) reported the presence of *P. bicornuta*. *Paraleptophlebia bicornuta* are distinctive due to the tusks located on their mandibles. Lehmkuhl and Anderson (1971) occasionally observed *P. bicornuta* in western Oregon streams in areas of low velocity. To the best of my knowledge, this species was not observed in any of the samples collected for this study.

The large variability in individual size observed in all three streams made determining exact CPI values from the monthly SF distributions very difficult (Figure 7). It was likely that actual CPI values for *Parapleptophlebia* were slightly less than 365 days in all three streams. Benke (1984) reported production estimates for univoltine species not incorporating a more accurate CPI value did not generally result in large differences. Overestimating the CPI by a month or less would have resulted in a slight underestimate of production (Benke 1984). More accurate CPI estimates may have been obtained by increasing the number of samples collected per site or by collecting independent samples during periods of rapid temperature accumulation or rapid growth (Thorup 1963, Brittain 1976).

Differences in annual production among the three streams seemed minimal especially without knowledge of the variability of these estimates (Table 9). Although differences appeared minimal, the pattern of production magnitude fit the pattern of perceived disturbance among the streams. Prairie Creek was considered the least disturbed of the three streams and annual production was highest. Boyes Creek was considered the most recently disturbed stream and annual production was the lowest. Streelow Creek was considered in a state of recovery from disturbance and annual production was moderate relative to the other streams. Huryn and Wallace (2000) suggested physical disturbance could greatly affect survival, growth and biomass of stream invertebrates. Invertebrate biomass is often lower in streams experiencing frequent or continuous physical disturbance relative to more stable streams (Rader and Ward 1989, Huryn and Wallace 2000). The timing and magnitude of disturbance may have played a major role in determining *Paraleptophlebia* production in Boyes Creek given the relatively low mean annual standing stock biomass calculated for a majority of the size classes present (Table 7).

Comparing annual production estimates from my study to other published estimates was difficult given variations in environmental conditions and the numerous assumptions and unknown sources of error involved in production estimation (Benke 1984). Rader and Ward (1989) studied the influence of river impoundments on mayfly diets, life history and production in the upper Colorado River. They used the SF method to estimate annual production for *P. heteronea* at a free flowing site located upstream of a reservoir and at a site located downstream of the impoundment. Production values were 0.51 g DM•m^{-2}•yr^{-1} at the upper site and 4.25 g DM•m^{-2}•yr^{-1} at the lower site. Annual production estimates for *Paraleptophlebia* in the California coastal streams of this study were considerably lower than values reported by Rader and Ward (1989).

Lugthart and Wallace (1992) reported estimates of annual habitat-weighted production for *Paraleptophlebia* in headwater streams of the southern Appalachian Mountains. Production for *Paraleptophlebia* in one headwater stream was 0.25 g ash free dry mass (AFDM)$\cdot m^{-2} \cdot yr^{-1}$ the first year and 0.10 g AFDM$\cdot m^{-2} \cdot yr^{-1}$ the second. To document the effects on aquatic invertebrate and larval salamander populations, one of the first order streams was treated with insecticide. Production for *Paraleptophlebia* in the treated stream was 0.10 g AFDM$\cdot m^{-2} \cdot yr^{-1}$ in the year prior to insecticide application and not measurable in the year following treatment. Regardless of differences in methodology, annual production estimates from the California coastal streams of this study were also extremely low relative to values reported by Lugthart and Wallace (1992) for untreated headwater streams.

Production magnitude depends heavily on growth rate and standing stock biomass, therefore, possible explanations for low annual production include factors that limit one or both of these parameters (Benke 1984, Benke 1993, Huyrn and Wallace 2000). Limitations to growth may include low temperatures, poor food quality and inadequate food quantity, while factors such as emigration, predation and habitat disturbance can greatly affect biomass (Huryn and Wallace 2000). The low annual production estimates reported for *Paraleptophlebia* in this study likely resulted from a combination of factors. This study only accounted for production occurring in riffle habitats and therefore represented only a portion of the total production for this genus. Emigration of late instars to slower velocity habitats likely had a greater affect on production estimation than was anticipated. Annual production estimates are greatly improved when the spatial distribution of aquatic invertebrates within and among the range of habitats available is taken into account (Resh 1977, Benke et al. 1984, Smock et al. 1985, Lugthart and Wallace 1992). Sampling all areas within a given habitat and sampling the range of available habitats would have allowed assessment of production within and among habitats and likely improved our understanding of life history and production dynamics associated with this genus.

Annual production to mean standing stock biomass (P/$\overline{B}$) approximates cohort P/$\overline{B}$ for populations with a CPI of 365 days (Waters 1987). Therefore, P/$\overline{B}$ reported in this study should represent cohort P/$\overline{B}$ for all three populations. Cohort P/$\overline{B}$ values generally range from 2 – 8 with values near 5 being typical for many aquatic invertebrate species (Waters 1969, Benke 1984, Waters 1987). While the P/$\overline{B}$ estimates for Prairie Creek and Streelow Creek agreed with this reported range, the estimate for Boyes Creek seemed relatively high (Table 9). This high estimate may be the result of overestimating the CPI, slower growth of Boyes Creek nymphs or from a substantial loss of individuals through emigration or mortality (Waters 1987). Given the difficulties estimating CPI for the three *Paraleptophlebia* populations, P/$\overline{B}$ estimates may more closely represent annual P/$\overline{B}$. Annual P/$\overline{B}$ estimates vary greatly among aquatic invertebrate populations depending on biological interactions and environmental conditions (Benke 1984). Smock and others (1985) reported a CPI of 9 months and an annual P/$\overline{B}$ of 9.2 for *P. volitans* in a South Carolina blackwater stream. Rader and Ward (1989) reported a CPI of 12 months for *P. heteronea* and annual P/$\bar{B}$ values from 2.6 upstream of the impoundment to 3.3 downstream of the dam.

Unfortunately, my study did not address any environmental factors other than water temperature. Therefore, I can only speculate on causes for the differences in production parameters observed among the streams. Similarities in thermal regimes (Figure 9, 10), average size of surface substrates (Table 1) and riparian composition were strongest in the Prairie Creek and Boyes Creek study reaches. Patterns of standing stock biomass over the size classes present were very similar in Prairie Creek and Boyes Creek (Table 6, 8). However, standing stock biomass was much lower at nearly every size class in Boyes Creek and loss or mortality between size classes was greatest in Boyes Creek (Table 8). The major difference among these two study reaches was the timing and magnitude of disturbance occurring in the headwaters of these streams. Alterations in hydrologic conductivity, riparian canopy structure and sediment delivery associated with timber harvest activities and the construction and presence of the highway bypass likely negatively affected growth and biomass in Boyes Creek.

Based on physical habitat data and observations made over the sampling period, Streelow Creek seemed fairly unique when compared with the other two streams. The perceived differences of this reach included riparian structure and composition, average size of surface substrates (Table 1) and the relatively fine-grained nature of the adjacent floodplains. Patterns in standing stock biomass observed in Streelow Creek were very different relative to patterns observed in Prairie Creek and Boyes Creek (Table 7).

Standing stock biomass values for the last four size classes were substantially higher and losses between size classes were low in Streelow Creek relative to the other streams (Table 8). Reasons for the high mean annual standing stock biomass and the relatively high production estimated for *Paraleptophlebia* in Streelow Creek were unclear. I think the main reasons were that sediment delivery and transport rates were fairly stable and that late instar emigration occurred to a lesser degree in Streelow Creek.

Recommendations for future research efforts include conducting community based production estimates within these same stream reaches. Community invertebrate production estimates would improve our understanding of aquatic invertebrate production dynamics in California coastal streams and provide better insight into how environmental disturbance magnitude and frequency affect these populations. Conducting production studies on individual species or communities living under different habitat conditions or watershed disturbance regimes further our understanding of population response to various environmental pressures (Elliott 1981, Benke 1993, Huryn and Wallace 2000). Integrating these types of production studies with comprehensive biological and physical monitoring programs could provide critical insights into the factors most affecting life history and production of aquatic invertebrates. Ultimately, aquatic invertebrate production may prove a powerful indicator for assessing alterations in stream function resulting from land management practices and/or watershed rehabilitation efforts (Odum 1985, Wallace and Gurtz 1986).

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