

Winter Food Habits of Coastal Juvenile Steelhead and Coho Salmon in
Pudding Creek, Northern California

By

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Abstract

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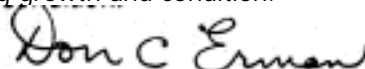
Master of Science in Wildland Resource Science

University of California at Berkeley

Professor Don C. Erman, Chair

Diets of juvenile coho salmon and steelhead and the composition and density of drift were examined from November 1990 to April 1991 in the coastal stream Pudding Creek, California. Coho salmon were present only in the upper site and steelhead were found in both sites. Antecedent Precipitation Index (API) was used as a surrogate for discharge. Stream temperatures ranged from 5 to 10°C, except during a cold snap in December, when temperatures dropped to 2°C. Drift density was low except during the onset of storms after an extended period of low flow. Diet composition was highly variable. Diet diversity increased for steelhead at both sites and decreased for coho salmon during periods of high flow. Coho salmon diets were less diverse and had a larger component of terrestrial invertebrates than steelhead. Drift density, API, and water temperature combined were good predictors of steelhead stomach fullness; whereas, coho salmon stomach fullness was generally low and not predictable with any of the variables measured. Fish condition and growth increased for both species by the end of the study. Flooding appears to allow juvenile salmonids access to a wider range of food resources. In Pudding Creek and possibly other coastal streams, winter floods may be important for food supply and sustaining growth and condition.

Chair of the Thesis Committee:



Professor Don C. Erman, Chair

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The objectives of this study were to determine winter food sources, availability, and preferences for coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) in Pudding Creek, California. The majority of research on overwintering strategies of salmonids on the West Coast has been done in cooler, northern climates studying primarily the role of habitat and secondarily, if at all, the role of food availability and diet. Refuge from high flows, high sediment loads, and freezing temperatures can be essential for overwintering fish (Mundie and Traber 1983, Dolloff 1987, Hartman and Brown 1987). However, in California coastal streams where freezing temperatures are rarely reached, climate was milder, and instream cover can be abundant, habitat availability may not play as critical a role as food.

Pudding Creek was an ideal coastal stream to study the role of food availability to overwintering salmonids because of its geographic location and abundance of instream cover. The natural range of coho salmon is from Point Hope Alaska to the northern edge of Monterey Bay; steelhead are native from the Kuskokwin River Alaska south to northwestern Mexico. In California, steelhead are native to coastal streams from the Ventura River north to the Klamath River (Moyle 1976). Pudding Creek, Mendocino County, is in the southern range of coho salmon and the mid-northern range of the natural distribution of steelhead trout.

Salmonid production is often limited by habitat diversity or food availability in summer and by shelter in winter (Everest et al. 1987). Simply, production is the total elaboration of biomass over time. Current literature indicates habitat complexity frequently determines fish abundance and survival while food availability influences fish condition and growth. Typically only one factor is limiting. For example, food availability during the summer is generally thought to limit smolt production. During

winter, harsh physical conditions such as storms and freezing cause high mortality independent of fish density or condition (Mundie 1969).

Winter survival is primarily determined by habitat availability (Mundie and Traber 1983; Dolloff 1987; Hartman and Brown 1987). Pools with cover are preferred wintering area for juvenile salmonids (Bustard and Narver 1975, Tschaplinski and Hartman 1983, Heifetz et al. 1986). Small tributaries and adjacent floodplains are thought to provide an important refuge for overwintering salmon and trout during high flow conditions (Skeesick 1970). In early winter studies, juvenile coho salmon occupied the same pool habitat as steelhead (Hartman 1965). Low population numbers, low aggressiveness, and different microhabitat preferences within the pool were thought to be responsible for this coexistence (Hartman 1965). Recent research has shown that juvenile steelhead and coho salmon partition winter habitat on a microhabitat (within pool) scale (Hartman and Brown 1987).

Maintenance of biomass during the winter will be dependent on food availability, if habitat is not limiting. Early winter energy depletion may limit the extent to which salmonids can endure unusually long winters or adverse environmental conditions (Cunjak and Power 1987). Reimers (1957) suggested that high mortalities of rainbow trout in late winter occurred because fish were already so weakened that increasing water temperature worsened the situation by accelerating their metabolic demands. Any disturbance, whether natural or human-made, which is detrimental to water quality and stream invertebrate populations will be quickly reflected in the fish populations as well (Lemly 1982). For example, Allen (1951) found severe floods in New Zealand caused a reduction in the bottom fauna that limited the trout stock to a lower biomass and production.

Food sources for juvenile steelhead and coho salmon consist of drift and benthic macroinvertebrates. Drift can be composed of benthos, emerging invertebrates, and terrestrial invertebrates. The importance of drift or benthos to salmonids is highly

variable and can be influenced by the stream, the fish species, and the invertebrate population (Waters 1969).

Juvenile salmonids use winter and summer food resources differently. During summer months or under conditions of high densities juvenile steelhead and coho salmon are able to coexist in streams by partitioning food and space resources. Juvenile coho salmon prefer pool habitat with available cover from undercut banks and submerged roots (Nickelson and Reisenbichler 1977). They feed primarily on drifting invertebrates (Mundie 1969). Juvenile steelhead, on the other hand, inhabit riffles (Shapovalov and Taft 1954) and feed primarily on benthos (Allee 1974) supplemented by drift. How food resources are partitioned between these two species during winter conditions is not clear.

Winter food sources are highly variable. During winter immature aquatic insects are in greatest abundance (Maciolek and Needham 1952). However, juvenile salmonids may switch to food which temporarily becomes available. For example, pink salmon eggs were selected by coho salmon when they became available in September (Koski and Kirchhofer 1982). Unpredictable food sources, such as salmonid eggs or invertebrates temporarily available in flooded vegetation, may provide critical energy allowing fish to maintain body size.

Issues concerning steelhead and coho salmon have been extensively studied from northern California to British Columbia. However, studies looking at overwintering survival are predominantly limited to cooler or northern climates such as British Columbia (Tschaplinski and Hartman 1983, Brown and Hartman 1988), Alaska (Heifetz et al. 1986, Dolloff 1987), Washington (Cederholm and Scarlett 1982, Peterson 1982a, Peterson 1982b), Oregon (Skeesick 1970), or Sierran streams (Maciolek and Needham 1952). California coastal streams provide a warmer over-wintering environment and are not subject to freezing over as are many northwest streams.

In warm temperatures, fish-food needs are high and the availability of food is crucial (Cederholm and Martin 1983). The slightly higher stream temperatures in coastal California streams have the potential to make food availability during the winter vital to over-wintering survival. The potentially increased metabolic rate of juveniles during an established non-growth period makes the availability of food resources critical. Frequently, it is assumed that low water temperatures, harsh physical conditions, and low food availability lead to little or no feeding by juvenile salmonids, which in turn translates to low growth rates. However, this theory has not been adequately addressed in coastal California streams. At the time of this study (December 1990 to April 1991), California was in its fifth year of drought. Stream flows were low with more variable water temperatures than normally expected.

Food availability and sources during the summer has been thoroughly studied, however, information addressing winter food sources is sparse. The importance of winter food availability and abundance for overwintering survival and condition of juvenile salmonids is not clearly understood in mild climates. The paucity of winter food studies, especially in milder climates, points to the need for further work in this area.

The objectives of this study were:

- 1) to describe diet, preferences, and availability of food to juvenile steelhead and coho salmon during winter conditions.
- 2) to determine if fish are feeding opportunistically or selectively.
- 3) to assess condition of fish during winter. Is food supply adequate to maintain fish biomass?
- 4) to determine if there is evidence for competition between steelhead and coho salmon for food resources.

STUDY AREA

Pudding Creek is a low gradient, coastal stream in northern California (Figure 1). The mouth of Pudding Creek is located on the northern edge of Fort Bragg, Mendocino County, California. It is a second order stream approximately 22.4 km in length. Elevations range from sea level at the mouth to 244 m at the headwaters. However, 70% of the stream is below 73 m in elevation. The area is subject to mild temperatures with an average rainfall of 85 cm per year.

A weir, owned by Georgia Pacific Lumber Co., has been in place at the mouth of the stream since the early 1950's. The weir does not act as a barrier to fish migration when it is properly operated and maintained. Water impounded behind the weir is used by Georgia Pacific at the local lumber mill. The lower 2.5 km of Pudding Creek is uncharacteristically wide and deep with slow moving waters. Above this point the stream is typical of many coastal streams with an abundance of woody debris, instream cover, and pool habitat.

Approximately 70% of Pudding Creek is adjacent to a railroad track (in the lower section) or a dirt road (the upper section). The road is within 18-350 m of the creek for over 50% of the length of the creek. Two sample reaches (named "Site 3" and "Site 4") of approximately 400 m each were selected in the upper section. Both reaches have streamside buffers of at least 100 m between the stream and the road. Site 3 was approximately 8.3 km and Site 4 was approximately 11.5 km from the mouth of the stream. Lower sections of Pudding Creek were not included in the study because they were either inaccessible (private land holdings), influenced by the estuary, or too deep to sample with techniques used in the study.

Steelhead are found in both sites 3 and 4; whereas, coho salmon are found only in Site 4. Site 3 has less instream cover and large woody debris than Site 4 which may explain the absence of coho salmon.

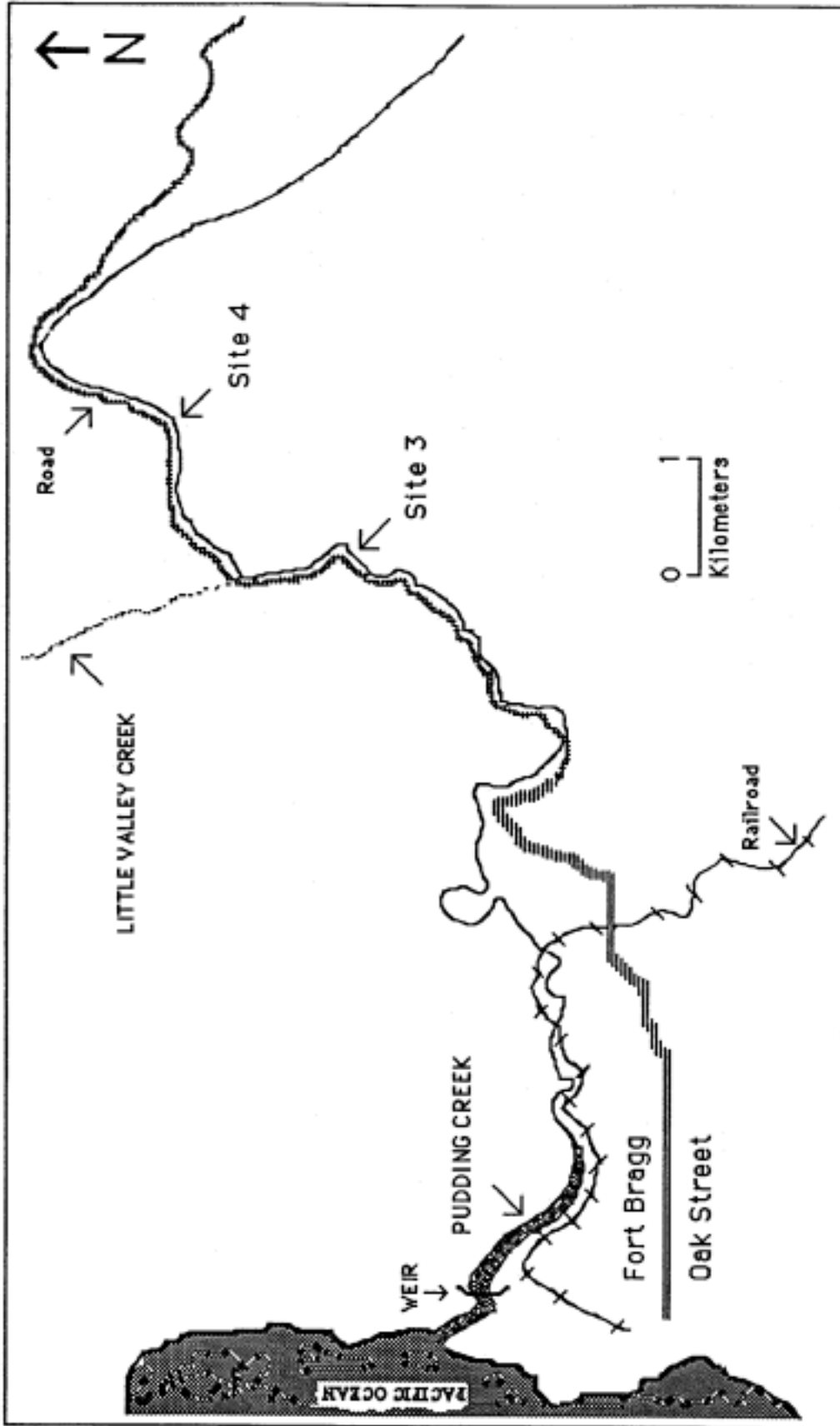


Figure 1. Pudding Creek study area indicating location of sample sites.

MATERIALS AND METHODS

Sampling Scheme

Previous studies have indicated juvenile salmonids shift from using both pool and riffle habitat to predominantly deeper water depths, as found in pool habitat, during winter conditions in small streams (Hartman 1965, Bustard and Narver 1975, Bisson and Nielsen 1983, Murphy et al. 1984a). These findings are similar to fish distribution data for Pudding Creek. Therefore, riffles were not sampled on a routine basis. Riffles were periodically electrofished to determine if juvenile salmonids were residing in the riffles. Sampling started in late November 1990 and ended in mid-April 1991. Approximately every two weeks, one randomly selected sampling unit (pool habitat type) from each of two study reaches was chosen and each pool habitat type was sampled in one day. A total of nine paired dates (or 18 sample dates) were sampled. The pools were assigned numbers and selected at random, without replacement. I choose a two-week sampling period to estimate the high variability in discharge and temperature during winter months.

Physical Data Collection

Habitat Measurements

The two reaches were initially classified to habitat according to Bisson (1982) during fall base flows. For simplicity, similar habitat types were grouped together into two broad categories of pool or riffle. Parameters such as length, width, average depth, and maximum depth were collected in each habitat unit.

Stream gradient, depth, instream cover, and overhanging vegetation were measured for each sampled unit during winter base flows. Instream cover is provided by

woody debris, substrate, water depth, undercut banks, and riparian vegetation. The stream channel was defined as the area inundated during bankfull discharge and bounded by low banks (Swanson et al. 1984). The flood plain was the flat area adjoining the river channel constructed in the current climate and overflowed at times of high discharge (Dunne and Leopold 1978). A series of transect lines, perpendicular to the thalweg, were established to measure the depth within the stream channel.

The first transect line was randomly selected and the remaining transect lines were spaced at 5 m intervals within the sampling unit. Stream width (wetted perimeter) was measured along each transect. Water depths were determined at 1 m intervals along the transect line.

Gradient was measured for each habitat unit using a hand level and a stadia rod. Surface area was calculated by multiplying length by average width. These measures were collected at average winter base-flows for all the sample units over a short time.

Cover habitat from rootwads, small woody debris (less than 10 cm in diameter and less than 1 m in length), large woody debris (greater than 10 cm in diameter at one end and greater than 1 m in length), terrestrial vegetation, bank undercuts, rock undercuts, and turbulence were estimated using a stadia rod. The boundaries of the cover object were measured to calculate total and percent cover provided for the entire sampling unit.

Average values of width, length, surface area, depth, and maximum depth for all sampled habitat units were tested for significant differences between sites 3 and 4 with a Mann-Whitney U test ($\alpha=0.05$; Zar 1984).

Rainfall, Discharge, and API

A rain gauge was maintained by the USDA Forest Service Pacific Southwest Research Unit near the mouth of Pudding Creek. Total rainfall, for a 24-hour period, was recorded every morning at 8 am.

Stream discharge measurements were first collected on February 16, 1990 and every proceeding sample date were it was physically feasible to cross the stream channel. A stream cross section in a reasonably straight section of the sampling unit was selected on each sample date, after the fish had been electrofished. The stream cross section was divided into 0.30 m sections and the distance from an initial point on the shore to the center of each partial section was measured. Within each partial section the velocity and water depth were measured with a pygmy flow meter and stadia rod, respectively (Dunne and Leopold 1978). A discharge gauging station was not present in the area of the study site. Antecedent Precipitation Index (API) was used as a surrogate for discharge. API relates directly to moisture deficiency of the watershed basin and links annual rainfall and runoff values (Viessman et al. 1977). Daily API, representative of a 24-hour period, was calculated from daily rainfall by multiplying the previous daily API by 0.9 and then adding the daily rainfall. For a given date, the total rainfall recorded represented the rainfall from the preceding date. Therefore, the Antecedent Precipitation Index (API) value calculated on the following day (called lag API) best represented the API for a given sample date. Lag API was used for all analyses.

Simple linear regression (Zar 1984) was used to test the relationship between lag API and manually collected stream discharge measurements.

Temperature

Continuous air and water temperature records were collected beginning December 12, 1990 with an Onset data logger calibrated at 0.1° C. The data logger was located at the bottom of the Site 4 reach with a probe in the air, in a riffle, and in an adjacent pool (0.24 m deep). The average temperature was collected every 30 minutes. Manual temperature readings were collected, with a pocket thermometer calibrated at 0.1° C, prior to continuous recording and at the time of sampling as a check against the temperature data logger. The Onset data logger thermistors are more accurate than

manual thermometers (Rodney Nakamoto, U. S. Forest Service fisheries biologist, personal communication). After checking the continuous temperature records for large discrepancies from the manually collected temperature readings, I used data from the Onset logger.

Simple linear regression equations were developed between data logger temperature records and manually measured air and water temperatures at Sites 3 and 4. The Onset data logger temperature readings were adjusted, using the simple linear regression equations, to reflect temperature differences between the sample sites and the data logger site and used for all further analyses. Due to equipment failures, continuous temperature records are missing from February 23, 1991 to March 16, 1991. Mean daily temperature readings for air and water cover the time period from 1400 hours on one day to 1400 hours the next. This time span was chosen because stomach samples were collected usually by 1400 hours on a sample date.

Biological Data Collection

Fish Population Abundance and Biomass

Pools were electrofished with a three-pass removal-depletion method (Zippin 1958) to estimate fish population size. Block nets were placed at both ends of the sampling unit and the unit was measured to the nearest meter. A Smith-Root, Inc. Type XII backpack shocker was used.

I anesthetized fish with 2-phenoxyethanol, measured standard lengths (nearest mm), and wet mass. Initially, wet mass was estimated by volumetric water displacement (nearest ± 0.5 ml). After the fourth sample date, fish mass was measured with an Ohaus electronic balance (precision ± 0.1 g). The relationship between volumetric and weighed wet mass was determined with a least squares regression. Volumetric estimates were converted to wet mass from the developed equation (Wet mass = $0.28508 + 0.98495(\text{volume})$; $R^2 = 0.995$).

I used a modular statistical program, Pop/Pro, to calculate population abundance and biomass, by age class (Kwak 1992). I used length-frequency distributions to determine age classes of adult, juvenile, and young-of-the-year (YOY). During periods of extreme high flow, population abundance was not estimated. Fish densities were calculated as the population abundance divided by the surface area of the habitat unit. Associated standard deviations were similarly calculated. Steelhead larger than 115 mm were considered to be one year or older. Older fish were infrequently encountered and not representative of the juvenile population. The older age class was excluded from all further analysis except fish density.

An unpaired two-sample t-test was used to compare length and mass between allopatric (Site 3) and sympatric steelhead (Site 4) on a given sample date. The null hypothesis was that the allopatric steelhead lengths and mass were the same as sympatric steelhead lengths and mass ($\alpha=0.05$). For each species in Sites 3 and 4, length and mass for juveniles were plotted over time. A simple linear regression was used to test the null hypothesis that the slope of line was equal to zero (H_0 : slope = 0, $\alpha=0.05$). A positive trend, over time, would indicate an increase in length or mass.

Fish Condition and Growth Rate

Instantaneous growth rate (G) was determined from the difference between the natural logarithms of mass over the time interval (Busacker et al. 1990) as follows:

$$G = \frac{(\log_e M_2 - \log_e M_1)}{(t_2 - t_1)}$$

where M_1 is the initial mass, M_2 is the final mass, t_1 is the initial time, and t_2 is the final time.

Relative condition factor (Kn) was calculated as follows:

$$Kn = \frac{W}{aL^b}$$

where W is wet mass of individual, L is length of individual, and a and b are the constants from a least squares regression equation for log transformed mass and length of individuals (Anderson and Gutreuter 1983). Constants a and b were derived for each species by combining all length and mass data for the study period.

The Kruskal-Wallis test (Zar 1984) was used to detect differences for growth rates and relative condition factor, between dates, for each species, in both sites. The Wilcoxon-Rank sum test was used as multiple comparison procedure when significant differences were found with the Kruskal-Wallis test. Simple correlation between species was used to detect similar trends in growth or condition over time. Lag API,

water temperature, average daily drift, and mean stomach fullness were used in multiple regressions to explain trends in fish condition and growth.

Stomach Contents

Stomach contents were collected from as many fish as possible during electrofishing. Stomach contents were evacuated by filling a blunt hypodermic syringe (needle size = 18) with stream water, placing the tip of the syringe far inside the mouth of the fish, and flushing out the stomach contents with the water pressure generated by depressing the syringe (Meehan and Miller 1978). A total of 60 cc or 3 syringes of stream water were used to flush the stomach contents from the foregut. This procedure is non-lethal. Stomach content samples were preserved in 80% ethyl alcohol. To standardize diet variation in feeding habits, I collected stomach contents at approximately the same time of day (mid-morning to early-afternoon). Immediately after each electrofishing pass, the stomach contents were collected to stop any further digestion.

In the laboratory, organisms were sorted from debris using Rose Bengal stain and a dissecting microscope. Organisms were identified to order and when possible or appropriate to family or genus. Identification at higher taxonomic levels (order or family) and data on prey size have provided significant insight into the trophic ecology of fish (Bowen 1983).

Forty-six invertebrate taxonomic categories were identified to order and family in the drift and stomach samples (Appendix I). For ease of data manipulation and calculation, the invertebrate data were summarized into the following 10 categories:

Category 1 - Ephemeroptera: nymphs of Baetidae, Caenidae, Ephemerellidae, Heptageniidae, Leptophlebiidae, Siphonuridae, Tricorythidae.

Category 2 - Plecoptera: nymphs of Capniidae, Chloroperlidae, Leuctridae, Nemouridae, Perlidae, Perlodidae, Pteronarcidae, Taeniopterygidae.

Category 3 - Trichoptera: larvae and pupae of Brachycentridae, Calamoceratidae, Glossosomatidae, Hydropsychidae, Hydroptilidae, Lepidostomatidae, Leptoceridae, Limnephilidae, Philopotamidae, Polycentropodidae, Rhyacophilidae.

Category 4 - Winged terrestrial adults: Anoplura, Coleoptera, Dermaptera, Diptera, Hymenoptera, Isoptera, Lepidoptera, Psocoptera, Thysanoptera.

Category 5 -Winged aquatic adults: Coleoptera, Diptera, Ephemeroptera, Neuroptera, Odonata, Plecoptera, Trichoptera.

Category 6 - Aquatic Diptera: larvae and pupae of Chironomidae

Category 7 - Annelida

Category 8 - Miscellaneous aquatic invertebrates: immature and adult Amphipoda, Cladocera, Coelenterata, Collembola, Copepoda, Gastropoda, Hemiptera (Gelastocoridae, Reduviidae, Veliidae), Hydracarina, Isopoda, Nematoda, Ostracoda, Tardigradi.

Category 9 - Miscellaneous terrestrial invertebrates: immature and adult Arachnida, Chilopoda, Coleoptera, Diptera, Hemiptera (Anthocoridae, Berytidae, Lygaeidae, Tingidae), Homoptera (Aleyrodoidea, Aphidoidea, Cicadoidea, Cercopidae, Coccoidea, Fulgoroidea), Mallophaga, Siphonaptera, Unidentifiable objects.

Category 10 -Aquatic Diptera (excluding Chironomidae) and Coleoptera larvae and pupae.

The ten categories were based first on aquatic or terrestrial origin, and then on other characteristics such as relative abundance, size and shape, and behavioral patterns. Most food items were intact and could readily be identified making it straightforward to categorize adults into aquatic or terrestrial. Ephemeroptera, Plecoptera, and Trichoptera were kept in separate categories because of their relative abundance and to facilitate comparisons to other studies. Annelids (earthworms) were

kept separate because of their large size and ephemeral, yet significant, contribution to drift. Chironomidae were categorized separately from other aquatic Diptera because they appeared more frequently and in greater numbers than all other Diptera. Other aquatic Diptera (excluding Chironomidae) were predominately Simuliids, and aquatic Coleoptera larvae were predominately elmids; because they were commonly found in the benthos, present in intermediate abundance, and similar in size and shape they were lumped together. The final two categories were "catchalls" for miscellaneous contributions from terrestrial and aquatic sources.

Invertebrate volumes were estimated using length-volume and width-volume regressions (Dolloff 1983). Body width and length were measured to the nearest 0.1 mm using an ocular micrometer for a subsample of individual invertebrates from each taxon. Estimates of food item volume were computed from length-width regressions, after assigning a spheroidal or cylindrical shape to the individual taxon (Table 2). Partial invertebrate volumes were estimated by measuring width and using the relationship established from width-volume regression of whole invertebrate items. Unidentifiable food items were considered to be the missing part of partial items. The sum of the whole and partial invertebrate volumes were considered an estimate of the total volume of food in a stomach. Invertebrate volumes (ml) were converted to dry mass as $1 \text{ mm}^3 = 0.1 \text{ mg}$ (Bowen 1983).

Stomach fullness was calculated as dry mass of gut content (mg)/ wet mass of individual fish (grams). A few fish were observed to opportunistically feed on invertebrates kicked up in the sampling unit while making electrofishing passes. Fish feeding on recently dislodged invertebrates would result in higher stomach volumes in the second and third passes. The Mann-Whitney U test was used to test for significant differences in stomach fullness between electrofishing passes. If significant differences were detected, only fish from the first pass were used in further analysis.

Allopatric and sympatric steelhead mean stomach fullness were tested for site and date effects with a two-factor unbalanced Model II ANOVA ($\alpha=0.05$). If no significant differences were detected between mean stomach fullness of allopatric (Site 3) and sympatric steelhead (Site 4), then the values were lumped and tested for date effect with an one-factor Model II ANOVA. A Fisher's Protected Least Significant Difference test was used for multiple comparison's ($\alpha=0.05$).

I used the Kruskal-Wallis test (Zar 1984) to detect significant differences in stomach fullness (mg/g) for each species between sample dates. The null hypothesis was that the mean stomach fullness was the same for each sample date ($\alpha=0.05$). When significant differences were detected, the Wilcoxon-Rank Sum test was used for multiple comparisons (Zar 1984). I used multiple regressions to test the ability of measured biotic and abiotic parameters (water temperature, lag API, and average daily drift) to predict stomach fullness of juvenile steelhead and coho salmon.

Table 1. Formulas used to calculate volume of organisms collected in drift and stomach samples from Pudding Creek, California, 1990-1991.

Shape	Formula	Organism
Sphere	$P \left\{ \frac{4}{3} \left(\frac{\text{length} + \text{width}}{4} \right)^3 \right\}$	Cladocera Hydracarina Mollusca Ostracoda
Cylinder	$P \left\{ \text{length} \left(\frac{\text{depth} + \text{width}}{4} \right)^2 \right\}$	Amphipoda Annelida Araneida Chelonethida Chiiopoda Coelenterata Coleoptera Collembola Copepoda Diptera Ephemeroptera Hemiptera Homoptera Hymenoptera Isopoda Isoptera Lepidoptera Nematoda Nematomorpha Neuroptera Odonata Plecoptera Psocoptera Siphonaptera Thysanoptera Trichoptera

Food Availability

Food availability and sources were measured by estimating water column drift. The contribution of benthic invertebrates to the diet of juveniles was not measured. Sampling benthic invertebrates before sampling the fish populations would have biased the diet of the fish, since fish could have fed opportunistically on dislodged invertebrates. If benthic samples had been collected after electrofishing the habitat, the bottom of the pool would have been disturbed and undoubtedly changed the composition of the benthos. For the above reasons, benthic samples were not collected.

Invertebrate drift was measured with two adjacent 36 cm x 36 cm x 100 cm long conical drift nets from November 30, 1990 to February, 1991 and three adjacent 30 cm x 30 cm x 61 cm long conical drift nets after February, 1991. Mesh size was 125 μ m for the 36 cm x 36 cm drift nets and 264 μ m for the 30 cm x 30 cm drift nets. The drift net mesh size may have underrepresented the small organisms (Cladocera, Ostracoda, Hydracarina, and Copepoda); however values were all relative if qualitative. Drift samples were collected daily at: pre-dawn, mid-day, and post-dusk for 15 minutes to 2 hours depending on the flow conditions and drifting detritus in the stream. For each sampling period two or three drift nets were placed adjacent to each other and perpendicular to the main flow of water (Allan and Russek 1985). The bottom lip of the net was 1.5 cm above the substrate to prevent non-drifting invertebrates from crawling into the net. To avoid the influence of electrofishing on drift (Elliott and Bagenal 1972, Bisson 1976) I collected drift above the sampling unit well out of the field of the electricity. Drift nets were placed above the sampling unit, personnel worked downstream of the nets to avoid possible initiation of drift from local disturbance of the stream channel. Invertebrate samples were preserved in 80% ETOH.

Drift density (number of invertebrates per unit volume of water) was determined by measuring water discharge through the drift net. Volume was calculated

from average velocity, length of exposure, and exposed cross-sectional area of the net. Water velocity was collected at the mouth of the net at the beginning of each sampling period, or if the flow was changing rapidly the average of the velocity at the beginning and end of each sampling period. Drift density was expressed as (mg/m³) and number (#/m³) for each prey category. Average daily drift was computed as the mean of all samples collected in a sample day.

Variability of food availability was tested for site and time effects with a two factor unbalanced Model II ANOVA ($\alpha=0.05$). If no significant differences were detected, between Site 3 and Site 4 mean daily drift, then the values were pooled and tested for date effects using a one-factor Model II ANOVA ($\alpha=0.05$). Multiple comparisons were made using Fisher's Protected Least Significant Difference Test ($\alpha=0.05$).

Diet Preference Analysis

Diet was described by percent by number and percent by volume (Bowen 1983).

Diet breadth was measured using a Shannon index

$$H' = - \sum p_j \log_e p_j$$

where p_j is the proportion of individuals found in the i th species (Magurran 1988). The maximum value obtained by H' is $\log r$, where r = number of invertebrate categories. Variance of H' was calculated as

$$s^2 (H') = \frac{\sum P_i (\log_e P_i)^2 - \sum (P_i \log_e P_i)^2}{N} + \frac{S-1}{2N^2}$$

where S = total number of species and N = total number of individuals.

Diet preference was evaluated with a linear index of electivity (Strauss 1979) within sites and between sample dates over the sampling period for all species. The index uses the unweighted difference in proportions:

$$L = r_i - P_i$$

where r_i = relative abundance of the prey item i in the gut and p_i = relative abundance of the prey item i in the drift. The index has a range of values from -1 to +1, with negative values indicating avoidance, zero indicating random selection, and positive values indicating selection. Variance was calculated as:

$$s^2 (L) = \frac{r_i(1-r_i)}{n_r} + \frac{p_i(1-p_i)}{n_p}$$

where n_r = number of stomach samples and n_p is the number of drift samples.

Statistically significant differences were detected with a t-test.

Diet overlap was determined with Horn's overlap index (Horn 1966) between steelhead and coho salmon and between drift density and fish species for each sample date over the sampling period. Horn's index was chosen because it uses proportions (mass) and appears to have the least bias under changing numbers of resources, sample size, and resource evenness (see Krebs, 1989 for review). The Horn index gives values from 0 (no overlap) to 1 (complete overlap), overlap is considered biologically significant when the value exceeds 0.60 (Zaret and Rand 1971). It was calculated from relative proportions:

$$R_o = \left(\frac{2 \sum_{i=1}^n (p_{xi} \cdot p_{yi})}{\sum_{i=1}^n (p_{xi})^2 + \sum_{i=1}^n (p_{yi})^2} \right)$$

where p_{xi} is the proportion of food category i in the diet of species x and p_{yi} is the proportion of food category i in the diet of species y .

RESULTS

Physical Data

Habitat Measurements

The upper site (Site 4) was composed of 84.4% pools and 15.6% riffles by surface area and 81.2% pools and 18.8% riffles by length. Site 4 was 396 m long and had thirty-four pools and fifteen riffles (Figure 2). The lower site (Site 3) was composed of 86.1 % pools and 13.9% riffles by surface area and 79.1 % pools and 20.9% riffles by length. Site 3 was 440 m long and had eighteen pools and six riffles. In Pudding Creek the riffles tend to be short, steep, and shallow (< 0.1 m). Stream gradient was equal to or less than 1 % at both sites.

There was no significant difference between sites 3 and 4 in average width, average depth, and maximum depth of habitat units ($p > 0.26$). The average depth of habitat units was 0.28 m in Site 3 and 0.30 m in Site 4. The average maximum depth of habitat units was 0.64 m in Site 3 and 0.65 m in Site 4. The average width of habitat units was 4.21 m in Site 3 and 3.84 m in Site 4. The average length of habitat units in Site 3 (19.6 m) was significantly larger ($p = 0.005$) than the average length of habitat units in Site 4 (9.2 m).

Rainfall, Discharge, and API

The Lag Antecedent Precipitation Index increased in direct proportion to measured discharge ($R^2 = 0.604$, $P = 0.05$, Figure 3). On March 3, 1991 discharge was measured at the peak flow; whereas, the API was reflective of the discharge for the 24-hour period. Removing the March 3, 1991, outlier from the regression improved the relationship ($R^2 = 0.834$, $P = 0.05$). Lag API was used as a surrogate for flow conditions in all subsequent analyses.

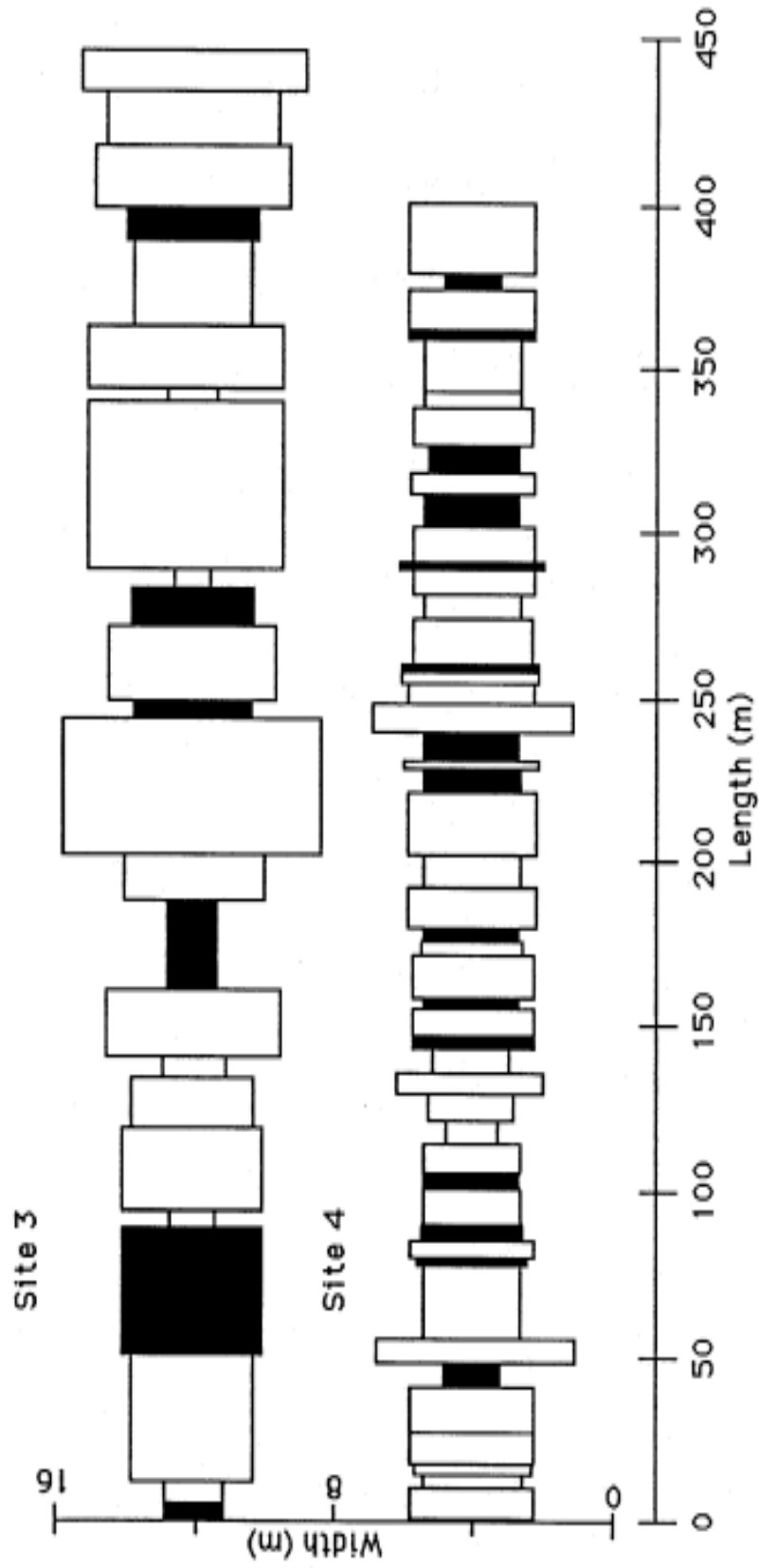


Figure 2. Ratio of pools to riffles in sites 3 and 4 in Pudding Creek, California. Shaded areas are riffles and unshaded areas are pools. Note that length (m) of each habitat unit is a different scale than the width.

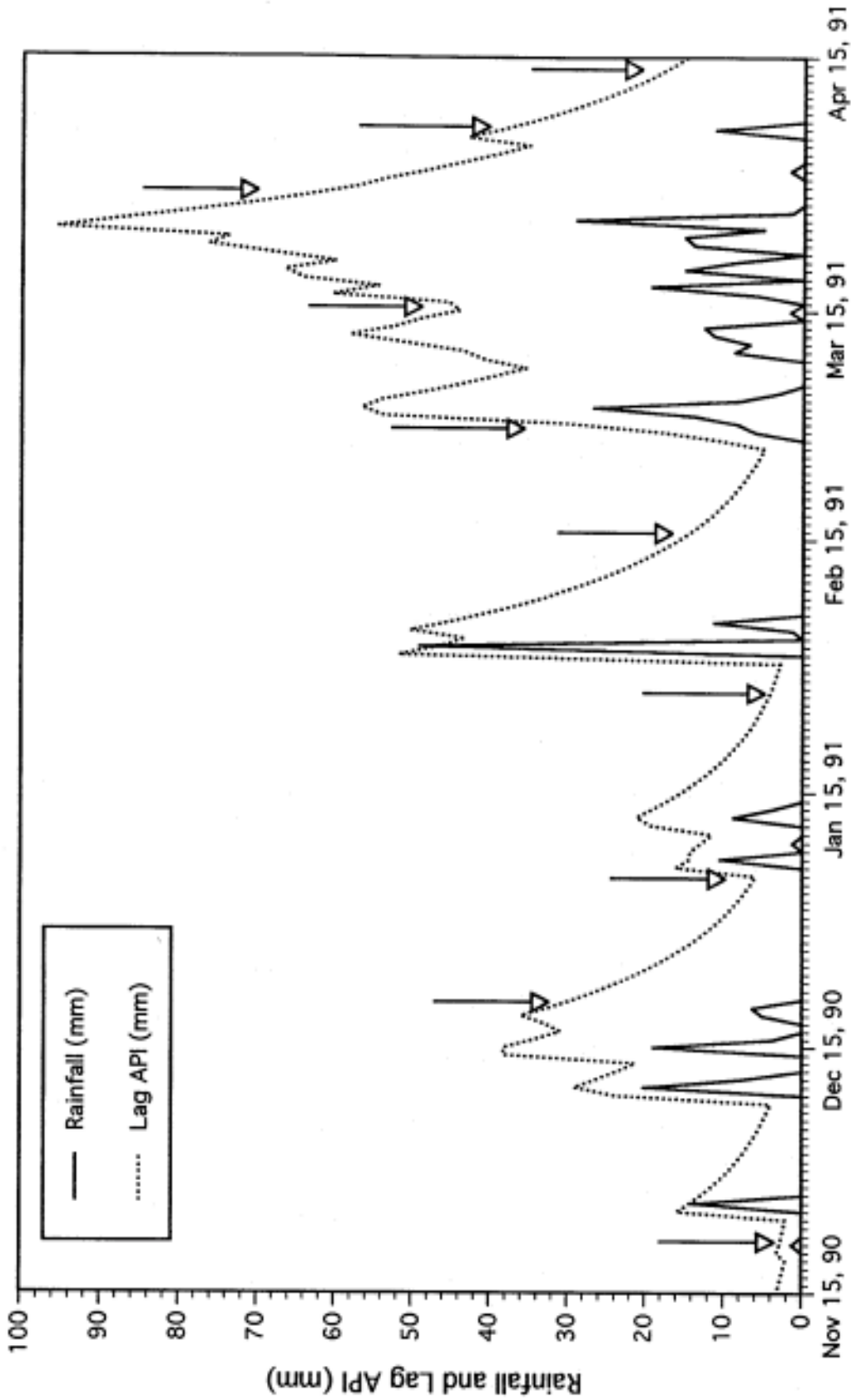


Figure 3. Rainfall (mm) and lag Antecedent Precipitation Index (API) are shown for study period. Arrows denote sample dates.

Temperature

Air and water temperature collected by manual and continuous records were essentially identical for site 4 (air $R^2 = 0.92$ and water $R^2 = 0.97$). Site 3 manual water temperature readings were also strongly related to the Onset data logger readings ($R^2 = 0.98$). However, the relationship between the Onset data logger air temperature readings and Site 3 air manual temperature readings were not as well correlated ($R^2 = 0.77$). This may be attributed to differences in riparian cover between the temperature site and Site 3. Data analysis will use primarily water temperature data, therefore, I used adjusted continuous temperature records for other analyses (Figure 4).

Biological Data

Population Characteristics and Estimates

Length and Mass

With one exception, there were no significant differences in length between sympatric (Site 4) and allopatric steelhead (Site 3), for all dates (Figure 5). Only on March 2, 1991, were lengths of sympatric steelhead significantly smaller than allopatric steelhead ($p=0.043$). Allopatric steelhead lengths ranged from 41 mm to 115 mm (Table 2). Sympatric steelhead lengths ranged from 40 mm to 113 mm. Coho salmon lengths ranged from 63 mm to 110 mm. Steelhead and coho salmon, in sites 3 and 4, significantly increased ($p<0.007$) in length over time (Figure 5).

There were no significant differences between sympatric (Site 4) and allopatric steelhead (Site 3) mass, for all dates. Allopatric steelhead mass ranged from 1.2 g to 25.6 g with the means ranging from 2.4 g to 8.5 g (Table 2). Sympatric steelhead mass ranged from 1.2 g to 17.5 g with the means ranging from 3.2 g to 7.3 g. Coho salmon mass, in Site 4, ranged from 6.2 g to 12.3 g with the mean ranging from 6.6 g to 12.6 g. Steelhead and coho salmon, in sites 3 and 4, significantly increased in mass over time ($p<0.02$).

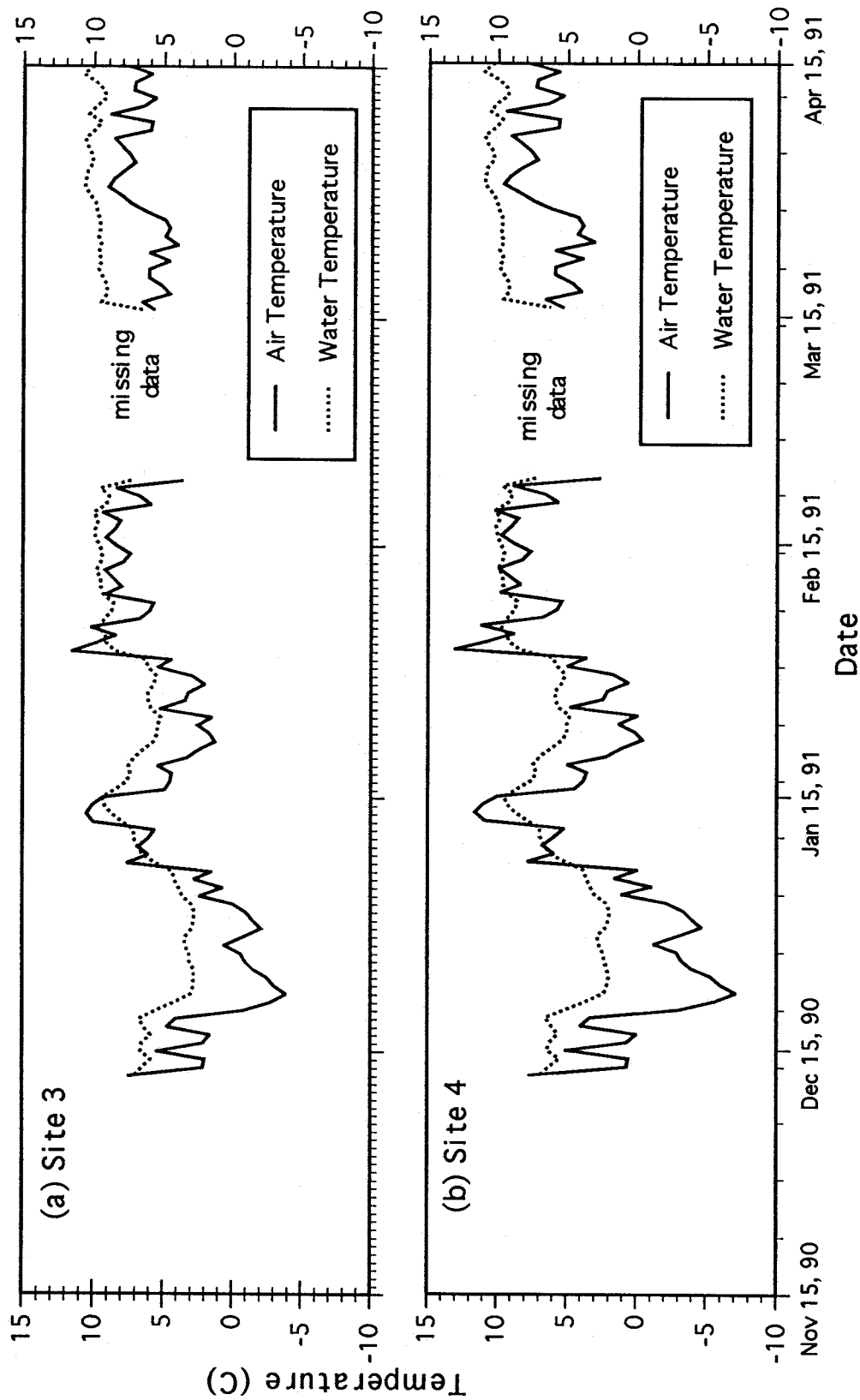


Figure 4. Mean daily air and water temperatures (C) at (a) Site 3 and (b) Site 4 on Pudding Creek from December 12, 1990 to April 15, 1991.

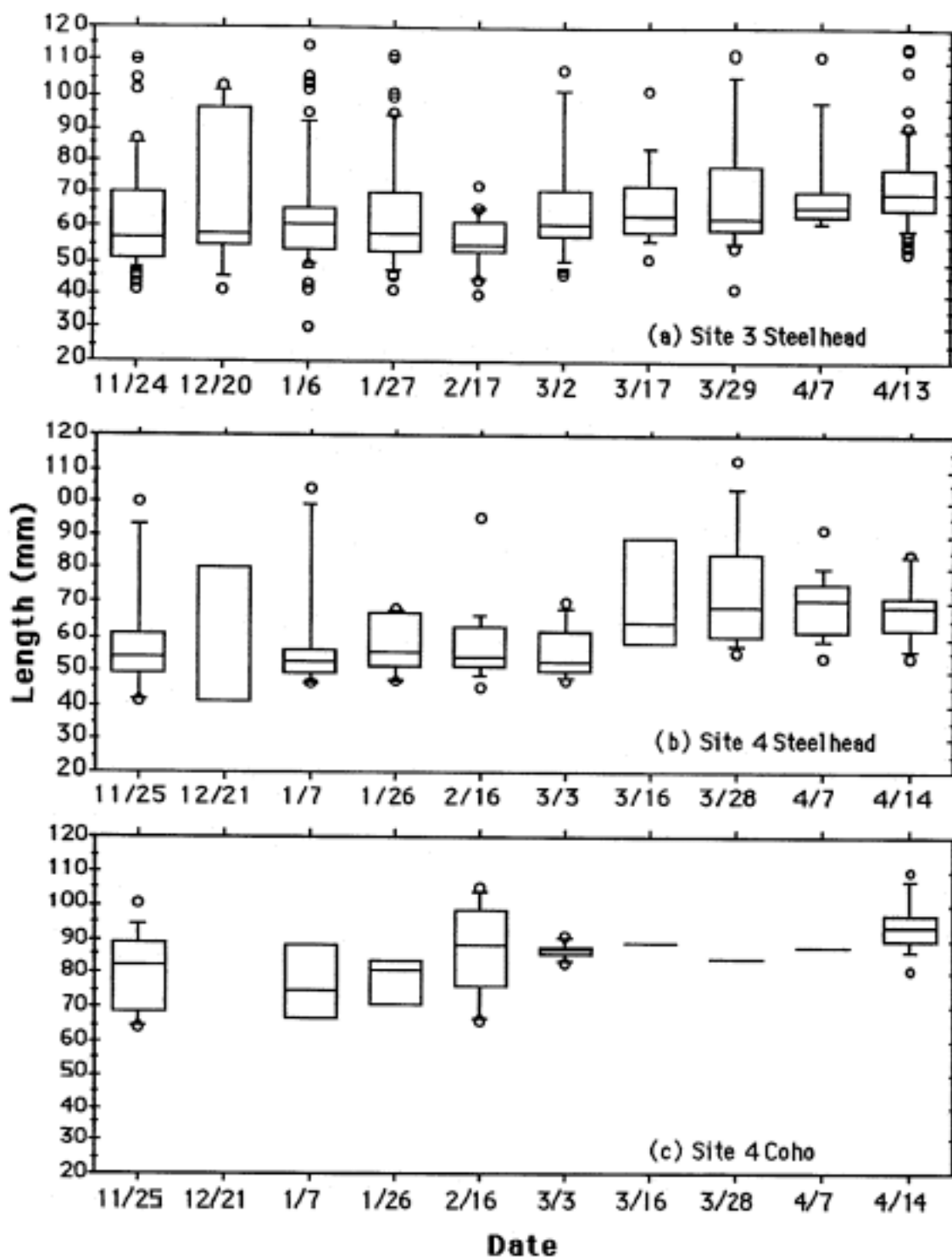


Figure 5. Boxplots of standard lengths (mm) for fish > 115 mm for all samples dates at each sample site (a) Site 3 steelhead, (b) Site 4 steelhead and (c) Site 4 coho salmon. Box represents interquartile range, line in the middle of the box is the median, bars represent the 95% range, and outliers are represented by circles.

Table 2. Species, site, sampling date, age number of fish sampled (n), mean standard length (mm) and standard deviation (SD), ranges of lengths, mean mass (g) and SD, for steelhead and coho salmon in Pudding Creek, California. NF = no fish captured.

Species	Site	Date	Age	n	Mean Length (mm)	Length SD	Length Range	n	Mean Mass (g)	Mass SD	Mass Range
Steelhead	3	Nov 24, 1990	0	47	62.5	17.1	41-111	47	4.7	4.1	1.3-18.2
		Dec 20, 1990	0	9	68.9	23.5	41-103	3	2.4	0.8	1.8-3.3
		Jan 6, 1991	0	64	64.0	16.4	41-115	20	4.6	4.1	1.8-16.2
		Jan 27, 1991	0	49	64.0	17.6	41-112	49	4.7	4.3	1.3-21.1
		Feb 17, 1991	0	16	55.8	8.2	40-72	16	3.0	1.1	1.2-5.3
		Mar 2, 1991	0	24	67.3	18.1	46-108	24	6.5	6.3	2.3-23.1
		Mar 17, 1991	0	15	66.8	13.0	51-102	15	5.7	3.6	3.0-17.1
		Mar 29, 1991	0	24	70.5	18.8	42-113	24	7.8	6.9	1.4-25.3
		Apr 7, 1991	0	10	72.5	15.6	62-112	10	8.5	6.8	3.8-25.6
		Apr 13, 1991	0	63	73.2	13.9	53-115	48	6.9	3.3	2.7-21.0
Steelhead	4	Nov 25, 1990	0	14	59.6	17.8	41-100	14	4.2	4.5	1.2-15.9
		Dec 21, 1990	0	3	58.0	30.3	40-93	3	4.2	5.1	1.2-10.0
		Jan 7, 1991	0	6	60.0	21.8	46-104	6	3.9	3.6	1.7-11.0
		Jan 26, 1991	0	9	58.1	8.9	47-68	9	3.2	1.6	1.7-5.2
		Feb 16, 1991	0	15	57.3	12.0	45-95	15	3.5	2.3	1.7-10.9
		Mar 3, 1991	0	12	55.8	7.9	47-70	12	3.4	1.4	1.7-5.9
		Mar 16, 1991	0	3	72.3	22.7	55-98	3	6.9	6.2	2.4-14.0
		Mar 28, 1991	0	10	74.4	18.4	55-113	10	7.3	4.8	3.4-17.5
		Apr 7, 1991	0	14	69.9	9.9	54-92	14	6.4	2.7	3.2-13.0
		Apr 14, 1991	0	13	68.2	9.5	54-85	13	5.6	2.2	3.2-10.5
Coho	4	Nov 25, 1990	0	11	78.9	12.2	64-100	11	7.2	2.9	4.3-13.9
		Dec 21, 1990	NF	0							
		Jan 7, 1991	0	3	77.0	15.1	63-93	3	6.6	2.4	4.9-9.3
		Jan 26, 1991	0	3	77.0	9.6	66-84	3	6.7	1.7	4.7-7.9
		Feb 16, 1991	0	8	87.0	14.1	66-105	8	9.8	2.2	6.1-13.3
		Mar 3, 1991	0	6	86.5	2.7	83-91	6	9.9	0.5	9.3-10.4
		Mar 16, 1991	0	2	89.0	5.7	85-93	2	11.4	2.4	9.7-13.1
		Mar 28, 1991	0	2	84.0	14.1	74-94	2	9.6	3.4	7.2-12.0
		Apr 7, 1991	0	2	87.5	12.0	79-96	2	10.7	3.2	8.4-12.9
		Apr 14, 1991	0	11	94.2	8.0	81-110	11	12.6	2.2	10.3-16.9

Abundance and Biomass

Steelhead biomass and densities were calculated with (Age = All) and without (Age = 0) fish greater than 115 mm (Table 2). Length frequency analysis indicated coho salmon were from one age class, therefore density and biomass estimates were made only for Age 0. Density and biomass estimates were not be made during high streamflow conditions. Overall, steelhead densities were higher in Site 3 than in Site 4 (Table 2). Site 3 steelhead densities for Age 0 ranged from 0.21 to 0.68 fish/m²; whereas, at Site 4, steelhead densities ranged from 0.21 to 0.39 fish/m². Coho salmon densities ranged from 0.00 to 0.21 fish/m². Combining steelhead and coho salmon densities in Site 4 resulted in values which were not significantly different (Wilcoxon Rank Sum, p=0.6) from the higher densities observed in Site 3.

Condition and Growth

Relative condition was highly variable for steelhead and coho salmon over the sample period (Figure 6a). Site 3 steelhead condition was correlated to Site 4 steelhead ($r=0.655$, $n=10$, $p=0.040$) and coho salmon ($r=0.692$, $n=9$, $p=0.039$); relative condition was also weakly correlated between site 4 steelhead and coho salmon ($r=0.62$, $n=9$, $p=0.076$). Condition decreased between December and January for all species and then gradually increased until the last two sample dates when there was a slight decrease. Site 4 steelhead exhibited the least variability and Site 4 coho salmon exhibited the highest variability in relative condition. Condition was only weakly correlated with stomach fullness for allopatric steelhead ($r=0.68$, $n=10$, $p=0.031$) and poorly for sympatric steelhead ($r=0.53$, $n=10$, $p=0.119$) and coho salmon ($r=0.54$, $n=9$, $p=0.132$). Whereas stream temperature was somewhat correlated with condition of sympatric steelhead ($r=0.83$, $n=10$, $p=0.003$) and sympatric coho salmon ($r=0.72$, $n=9$, $p=0.030$) but not for allopatric steelhead ($r=0.61$, $n=10$, $p=0.062$).

Table 3. Density and biomass with standard deviation (SD) for all fish and sites. Age of fish represents juveniles (0) or all ages (All). NF=no fish captured; -- storm dates; SS=small sample.

Species	Site	Date	Age	Density		Biomass			
				No./m ²	SD	g/m ²	SD		
Steelhead	3	Nov 24, 1990	All	0.44	0.03	2.21	0.38		
			0	0.44	0.03	1.35	0.16		
		Dec 20, 1990	0	0.60	0.35	1.30	0.81		
		Jan 6, 1997	All	0.68	0.02	3.56	0.62		
			0	0.66	0.03	2.87	0.62		
		Jan 27, 1991	All	0.40	0.01	2.32	0.26		
			0	0.39	0.02	1.81	0.26		
		Feb 17, 1991	0	0.21	0.02	0.58	0.09		
		Mar 2, 1991	0	--	--	-	-		
		Mar 17, 1991	0	-	---	---	-		
		Mar 29, 1991	0						
		Apr 7, 1991	0	--	--	--	-		
		Apr 13, 1991	All	0.29	0.04	2.96	0.67		
			0	0.23	0.03	1.58	0.20		
		Steelhead	4	Nov 25, 1990	All	0.26	0.01	1.51	0.56
	0			0.24	0.02	0.98	0.31		
Dec 21, 1990	0			0.22	0.04	0.93	0.41		
Jan 7, 1991	0			0.28	0.13	1.05	0.64		
Jan 26, 1991	All			0.24	0.02	1.08	0.39		
	0			0.22	0.02	0.66	0.14		
Feb 16, 1991	All			0.40	0.15	2.11	1.11		
	0			0.39	0.16	1.37	SS		
Mar 3, 1991	0			--	--	--	-		
Mar 16, 1991	0			--	--	--	-		
Mar 28, 1991	All								
	0								
Apr 7, 1991	0			--	--	--	--		
Apr 14, 1991	All			0.22	0.01	1.96	0.12		
	0			0.21	0.01	1.56	0.12		
Coho	4	Nov 25, 1990	0	0.21	0.04	1.40	0.32		
		Dec 21, 1990	NF						
		Jan 7, 1991	0	0.11	SS	0.67	SS		
		Jan 26, 1991	0	0.07	0.00	0.43	0.08		
		Feb 16, 1991	0	0.16	0.02	1.46	0.26		
		Mar 3, 1991	0	--	--	--	-		
		Mar 16, 1991	0	--	--	--	-		
		Mar 28, 1991	0	--	--	--	-		
		Apr 7, 1991	0	--	--	-	-		
		Apr 14, 1991	0	0.19	0.08	2.38	1.03		
		Coho & Steelhead (combined)	4	Nov 25, 1990	0	0.45	0.06	2.38	0.63
				Dec 21, 1990	0	0.22	0.04	0.93	0.41
				Jan 7, 1991	0	0.39	0.13	1.72	0.64
				Jan 26, 1991	0	0.29	0.02	1.09	0.22
				Feb 16, 1991	0	0.55	0.18	2.83	0.26
Mar 3, 1991	0			--	--	--	--		
Mar 16, 1991	0			--	--	--	--		
Mar 28, 1991	0			--	--	--	--		
Apr 7, 1991	0			--	--	--	--		
Apr 14, 1991	0			0.31	0.09	4.34	1.15		

Allopatric and sympatric steelhead had similar instantaneous growth rates (0.72 to 1.91) over the sample period (Figure 6b) but they were not significantly correlated ($r=0.390$, $n=9$, $p=0.298$). Coho salmon had significantly higher instantaneous growth rates (mean = 2.1) than the steelhead (means = 1.4) in both sites ($p<0.01$). Coho salmon instantaneous growth rates were not correlated with allopatric steelhead ($r=0.135$, $n=8$, $p=0.750$) or sympatric steelhead ($r=0.569$, $n=8$, $p=0.142$). Coho instantaneous growth rates had a generally upward trend over time (from 1.93 to 2.17); whereas steelhead in both sites exhibited upward instantaneous growth rates (0.72 to 1.82) from December to March and then a sharp decline in April. No single variable (lag API, drift density, water temperature, or stomach fullness) was strongly correlated with instantaneous growth rates of all fish species. However, mean stomach fullness was correlated to allopatric steelhead instantaneous growth rate ($r=0.755$, $n=9$, $p=0.019$) and weakly to coho growth rate ($r=0.597$, $n=8$, $p=0.118$). Lag API was weakly correlated to sympatric steelhead instantaneous growth rates ($r=0.62$, $n=9$, $p=0.075$).

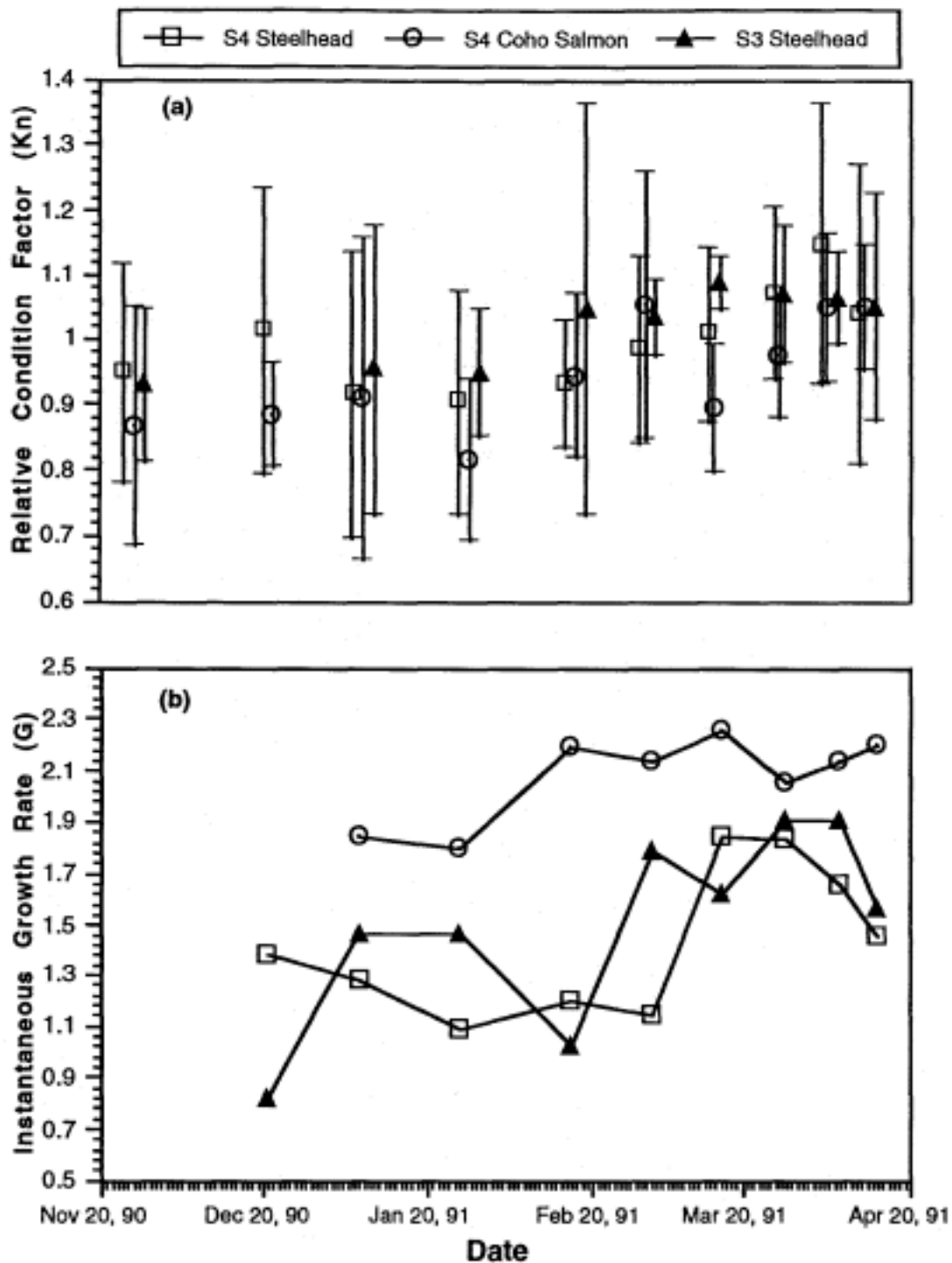


Figure 6. Mean relative condition factor (Kn) \pm one standard deviation (a) and instantaneous growth rate (G) based on mass (b), of juvenile steelhead and coho salmon in sites 3 (S3) and 4 (S4) in Pudding Creek, California from November 24, 1991 to April 14, 1991.

Food Availability

Average daily drift density (mg/m^3) was not significantly different between sites 3 and 4; however, drift increased over time ($p < 0.01$, Table 6). Site 4 had higher drift values than site 3 in 8 out of 10 sample dates (Figure 7).

Composition of drift was highly variable over time and did not exhibit any striking trends (Figure 8). Drift from both study sites was made up predominately of aquatic invertebrates, approximately 90% by mass or 95% by number (Tables 5 and 6). Periods of relatively high abundance of Ephemeroptera, Plecoptera, or Trichoptera larvae were generally followed by correspondingly high abundance of aquatic adults. Averaged over the study period, Trichoptera larvae was the predominant category in both sites 3 and 4, while the second most abundant category was miscellaneous aquatics in Site 3 and Ephemeroptera in Site 4. Terrestrial invertebrates contributed less than 11% by mass or 7% by number to the total drift over the study period. Chironomid and Plecoptera abundance's were fairly constant in Site 4 throughout the study period, while at Site 3 the values were slightly more variable during periods of high rainfall and increased water temperatures.

Invertebrate diversity, as measured by the Shannon index (H'), was not significantly different between sites 3 and 4 ($p = 0.77$; Tables 5 and 6). However Site 3 drift diversity was positively correlated ($r = 0.818$, $n = 8$, $p = 0.013$) and Site 4 was not correlated ($r = 0.399$, $n = 9$, $p = 0.287$) with lag API.

I pooled drift values for sites 3 and 4 and found that drift collected on December 20-21, 1990, (the first storm event of the season) was significantly higher than drift collected on March 16-17 and March 28-29, 1991 ($p < 0.05$). March 2-3, 1991, had significantly higher drift (pooled values for sites 3 and 4) than all other sample dates ($p < 0.05$), this sample date occurred during the first large storm event after a period of low-flow (Figure 3).

Major peaks in drift were associated with storm events and increased stream runoff. In both study sites, terrestrial 'adults had peak values which corresponded to high values of aquatic adults and increased rainfall. Miscellaneous terrestrials, larvae of Diptera (excluding Chironomidae) and Coleoptera, and Annelids were generally present in low percentages, with infrequent occurrences of relatively high values during storm events. The increased diversity of organisms in drift reflect evidence of "catastrophic" drift.

Table 4 . Average daily drift values and standard deviations (SD) for sites 3, 4, and combined values for both sites (both) are shown for each sample date. Significantly different dates ($p=0.05$) are shown as date code (DC).

Site	Date	DC	n	Average Daily Drift		Sig. Different Dates
				m /m ³	SD	
3	Nov 24, 1990	1	2	0.016	0.006	6
	Dec 20, 1990	2	4	0.288	0.137	6
	Jan 06, 1991	3	8	0.368	0.593	6
	Jan 27, 1991	4	6	0.164	0.184	6
	Feb 17, 1991	5	6	0.072	0.074	6
	Mar 02, 1991	6	9	1.204	0.938	1,2,3,4,5,7,8,10
	Mar 17, 1991	7	9	0.033	0.008	6
	Mar 29, 1991	8	9	0.085	0.047	6
	Apr 13, 1991	10	9	0.221	0.161	6
4	Nov 25, 1990	1	2	0.034	0.006	6
	Dec 21, 1990	2	6	0.762	0.679	6
	Jan 07, 1991	3	8	0.109	0.123	6
	Jan 26, 1991	4	6	0.233	0.264	6
	Feb 16, 1991	5	6	0.270	0.186	6
	Mar 03, 1991	6	6	2.321	1.929	1,2,3,4,5,7,8,10
	Mar 16, 1991	7	9	0.144	0.163	6
	Mar 28, 1991	8	9	0.098	0.048	6
	Apr 13, 1991	10	9	0.146	0.220	6
Both	Nov 25-26, 1990	1	4	0.025	0.012	6
	Dec 20-21, 1990	2	10	0.573	0.568	6, 7, 8
	Jan 6-7, 1991	3	16	0.239	0.435	6
	Jan 26-27, 1991	4	12	0.199	0.220	6
	Feb 16-17, 1991	5	12	0.171	0.170	6
	Mar 2-3, 1991	6	15	1.651	1.467	1,2,3,4,5,7,8,10
	Mar 16-i 7, 1991	7	18	0.088	0.125	2, 6
	Mar 28-29, 1991	8	18	0.091	0.046	2, 6
	Apr 13-14, 1991	10	18	0.183	0.191	6

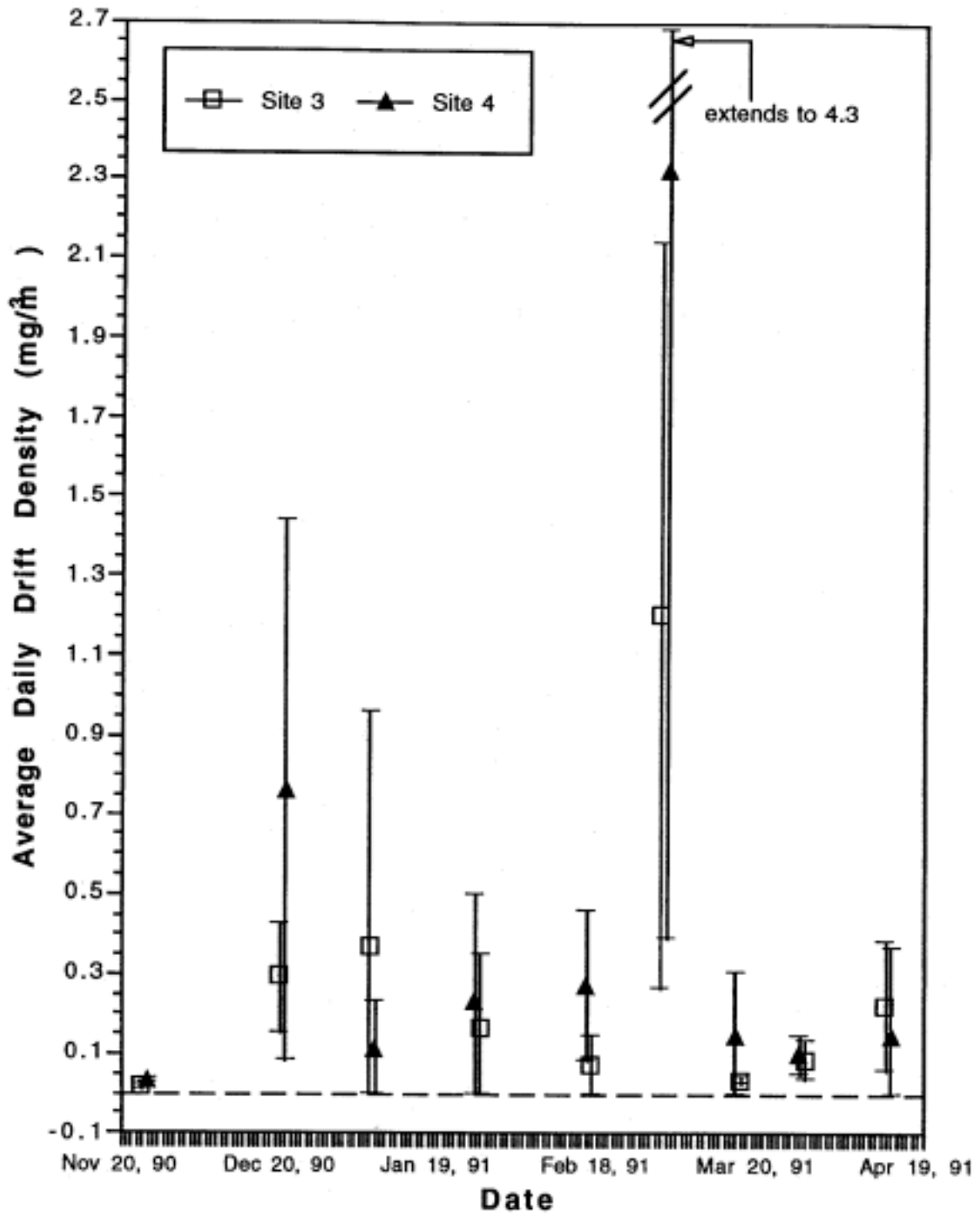


Figure 7. Food availability measured by average daily drift density (mg/m^3) \pm one standard deviation in sites 3 and 4 from November 24, 1990 to April 14, 1991. Dashed line indicates zero drift.

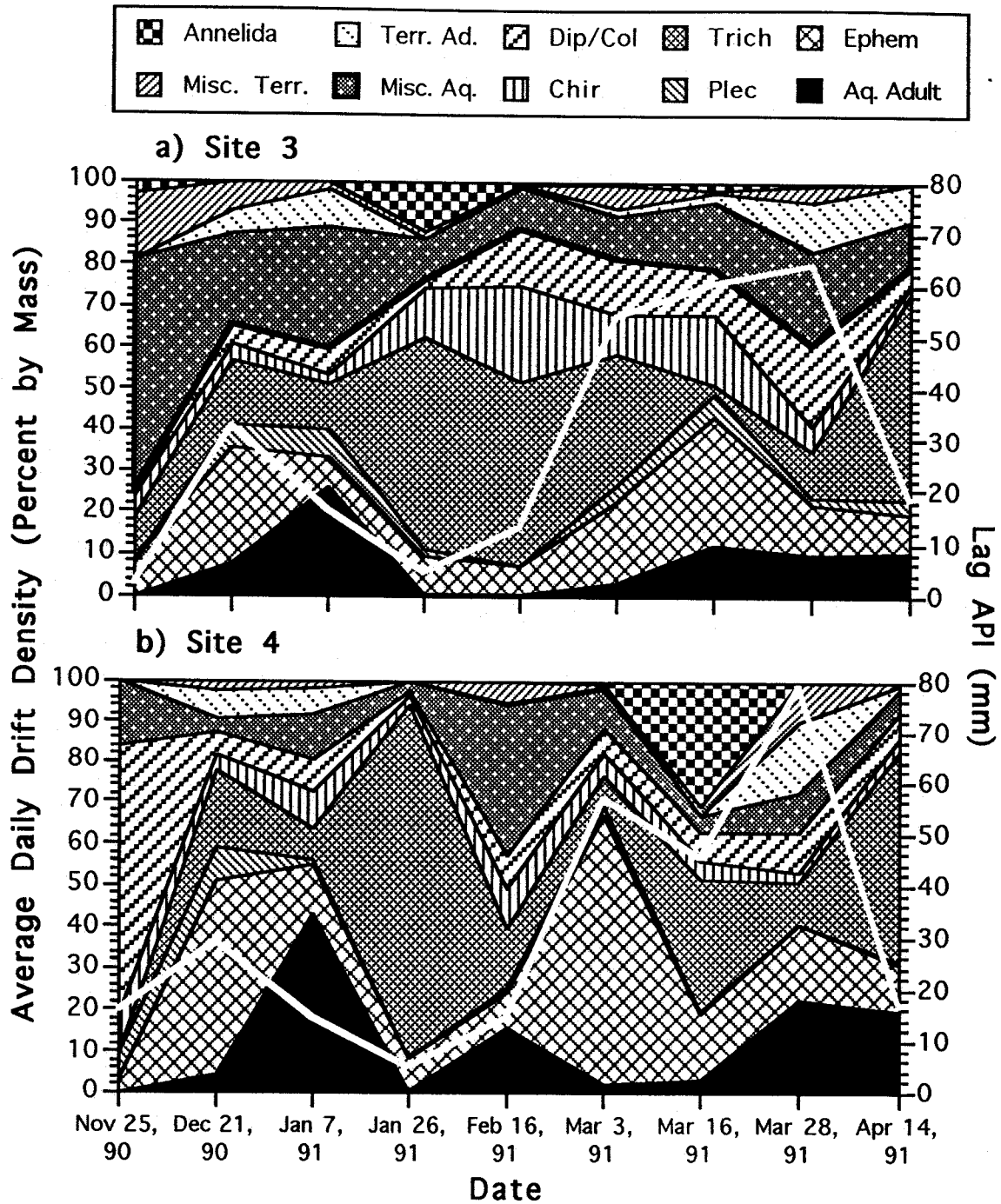


Figure 8. Invertebrate food categories, shown as % mass, measured in average daily drift density in sites 3 (a) and 4 (b) in Pudding Creek, California from Nov 24, 1990, to April 14, 1991. Solid white line indicates lag API (mm) for sample dates. Aq. Adults = Aquatic Adults, Ephem = Ephemeroptera, Plec = Plecoptera, Trich = Trichoptera, Chir = Chironomidae, Dip/Col = Diptera (other than Chironomidae) and Coleoptera, Misc. Aq. = Miscellaneous Aquatics, Terr. Ad. = Terrestrial Adults, Misc. Terr. = Miscellaneous Terrestrials, and Annelids.

Table 5. Composition of drift samples collected in Site 3 Pudding Creek, California for each sample date expressed as percent relative mass (%M) and percent by number (%N) of prey items. Number of samples, Shannon Index (H') and associated variance are also shown.

	November 24	December 20	January 8	January 27	February 17	March 2	March 17	March 29	April 13
Aquatic									
Adults		7.5 5.6	25.6 22.3	0.3 0.5	0.4 0.2	3.1 1.5	12.3 21.0	9.7 16.0	10.3 35.0
Ephemeroptera	8.2 2.6	28.1 15.6	7.9 1.3	9.0 17.2	6.8 21.1	19.3 23.1	31.0 17.3	12.0 10.1	9.5 13.7
Plecoptera		5.3 2.4	6.6 1.4	1.7 2.5	0.3 0.2	4.2 1.9	5.4 1.1	1.9 1.2	3.4 1.1
Trichoptera	10.4 0.5	15.9 1.2	11.1 0.8	51.5 2.6	44.7 0.7	32.1 1.8	2.7 2.7	11.0 1.8	50.3 2.5
Chironomidae	4.7 3.2	4.0 13.4	2.2 7.6	12.2 18.6	23.3 27.1	9.9 15.6	17.0 22.9	6.5 12.2	2.1 8.7
Dip/Coleop.	1.3 0.5	4.7 7.0	6.3 3.6	1.5 4.2	13.2 6.0	13.0 14.2	10.8 6.5	19.5 10.2	3.9 6.0
Misc. Other	56.8 92.0	21.8 48.5	29.5 51.4	10.2 51.1	10.2 42.5	10.3 37.6	16.5 20.3	22.8 34.3	11.0 23.3
Total	81.4 98.7	87.2 93.6	89.1 88.4	86.3 96.5	98.7 97.8	91.8 95.6	95.6 91.8	83.4 85.8	90.5 90.3
Terrestrial									
Adults	16.1 1.0	5.7 5.6	9.0 8.1	0.0 0.1	0.5 0.4	1.8 2.8	2.0 3.0	12.1 12.0	9.1 8.8
Misc. Terr.	2.5 0.3	7.1 0.4	1.8 2.9	1.4 1.5	0.3 0.6	5.6 0.8	0.5 0.8	3.8 1.7	0.4 0.9
Annelida		0.1 0.3	0.1 0.6	12.3 1.8	0.6 1.2	0.9 0.9	1.8 4.4	0.7 0.5	0.0 0.1
Total	18.6 1.3	12.8 6.4	10.9 11.6	13.7 3.5	1.3 2.2	8.3 4.4	4.3 8.2	16.6 14.2	9.5 9.7
No. of Samples	2	4	8	6	6	9	9	9	9
H'	0.39	1.60	1.49	1.45	1.38	1.66	1.90	1.86	1.76
Variance of H'	0.58	0.25	0.14	0.18	0.12	0.08	0.06	0.06	0.07

Table 6. Composition of drift samples collected in Site 4 Pudding Creek, California for each sample date expressed as percent relative mass (%M) and percent by number (%N) of prey items. Number of samples, Shannon index (H') and associated variance are also shown.

	November 25		December 21		January 7		January 26		February 16		March 3		March 16		March 28		April 14	
	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N
Aquatic																		
Adults			4.4	0.7	42.7	6.8	0.1	0.9	15.5	3.4	1.9	2.4	3.1	11.4	22.6	38.7	19.8	37.2
Ephemeroptera	3.3	8.7	46.4	54.3	12.4	14.9	8.0	27.5	8.8	14.9	64.9	40.8	15.9	23.8	17.9	10.8	11.5	12.0
Plecoptera	6.2	1.1	8.2	5.9	1.0	2.0	0.2	0.3	1.1	0.5	2.3	1.2	0.6	1.5	0.4	0.3	0.1	0.2
Trichoptera			18.7	2.4	7.1	3.6	85.9	2.7	13.9	2.5	7.6	2.0	32.0	4.2	9.8	2.1	51.3	2.4
Chironomidae	8.8	16.9	3.7	12.5	9.3	19.6	2.2	24.8	10.2	6.4	5.3	13.3	4.7	21.3	2.6	8.1	3.7	16.7
Dip./Coleop.	65.9	12.4	6.1	4.6	7.9	13.4	1.0	7.1	7.9	4.8	6.5	5.2	6.9	8.8	9.5	12.7	5.8	9.2
Misc. Other	15.9	60.9	3.3	18.6	11.7	36.5	2.5	34.7	36.9	66.6	9.8	28.6	3.8	23.1	9.9	23.2	5.6	17.8
Total	100.0	100.0	90.8	99.0	92.0	96.8	99.9	98.0	94.2	99.1	98.1	93.4	66.9	94.2	72.7	95.9	97.7	95.5
Terrestrial																		
Adults			6.8	0.6	6.2		0.0	0.5	0.3	0.6	0.7	0.4	0.1	1.0	17.5	1.9	1.5	3.1
Misc. Terr.			2.4	0.3	1.8				5.5	0.3	0.3	0.3	2.4	2.1	9.4	1.0	0.6	0.4
Annelida				0.1			0.1	1.5			0.9	5.9	30.7	2.8	0.4	1.2	0.1	1.0
Total	0.0	0.0	9.2	1.0	8.0		0.1	2.0	5.8	0.9	1.9	6.6	33.1	5.8	27.3	4.1	2.3	4.5
No. of Samples	2		6		8		6		6		6		9		9		9	
H'	1.22		1.39		1.75		1.50		1.16		1.57		1.89		1.68		1.72	
Variance of H'	0.42		0.17		0.08		0.10		0.23		0.14		0.06		0.08		0.07	

Feeding Habits

Stomach Analysis

There was no significant difference ($\alpha=0.05$, Mann-Whitney U test) in fish stomach fullness among the first, second, or third passes for either species on any dates where multiple electrofishing passes were done, with one exception when stomach fullness was significantly less in the second pass than in the first pass. Based on these findings I used stomach fullness estimates from all electrofishing passes.

There was no significant difference ($p=0.16$) in stomach fullness between allopatric and sympatric steelhead (i.e. site effects). Combined stomach fullness values of sympatric and allopatric steelhead showed percentage fullness increased significantly over time ($p=0.01$) and ranged from 0.00 to 2.41 mg/g (Figure 9). After the large storm event on March 2-3, 1991, pooled stomach fullness values of steelhead were significantly higher than values on all prior sample dates and the final sample dates, April 13-14, 1991 (Table 8). Pooled stomach fullness values for March 28-29, 1991, a period of high rainfall, were significantly higher than values on November 24-25, 1990, January 6-7, 1991, January 26-27, 1991 and February 16-17, 1991, all of which were periods of low streamflow.

Within a sample location and over time, there were significant differences between mean stomach fullness for allopatric steelhead (Rascal-Wallis, $p=0.0001$) and sympatric (Wallis-Wallis, $p=0.0001$) but not for coho salmon (Wallis-Wallis, $p=0.0545$). Mean stomach fullness was lowest (0.000-0.052 mg/g) and the percentage of empty stomachs was highest (63-100%) at the beginning of the study which was a period of low streamflows (Table 7).

Individually water temperature, lag API, and average daily drift were not intercorrelated ($r^2<0.12$) for sites 3 and 4, and they were not good predictors of stomach fullness ($r^2<0.5$). However, in multiple regressions the three parameters were effective predictors of stomach fullness for allopatric steelhead ($R^2=0.810$);

whereas, only lag API and water temperature were effective predictors of stomach fullness for sympatric steelhead ($R^2=0.655$) and lag API was the only parameter that moderately predicted stomach fullness for coho salmon ($R^2=0.329$). Lag API explained approximately 50% of the predicted stomach fullness of steelhead in both sites (Table 7).

Table 7. Results of stepwise multiple regression analysis of lag API, average daily drift density, and water temperature as predictors of mean stomach fullness. Variables are listed in order of importance. Not fitted indicates variables not included in the stepwise multiple regression.

Site	Species	Variable	Adjusted R ²	F	MS Error
3	Steelhead	Lag API	0.478	8.320*	0.589
		Average Daily Drift	0.748	12.863*	0.284
		Water Temperature	0.810	12.405*	0.214
4	Steelhead	Lag API	0.478	7.415*	0.201
		Water Temperature	0.670	8.116*	0.127
		Average Daily Drift	0.655	5.427	0.133
4	Coho salmon	Average Daily Drift	0.329	4.427*	0.040
		Water Temperature	0.285	2.394	0.043
		Lag API	Not fitted		

* indicated F values significant at 0.05 a level.

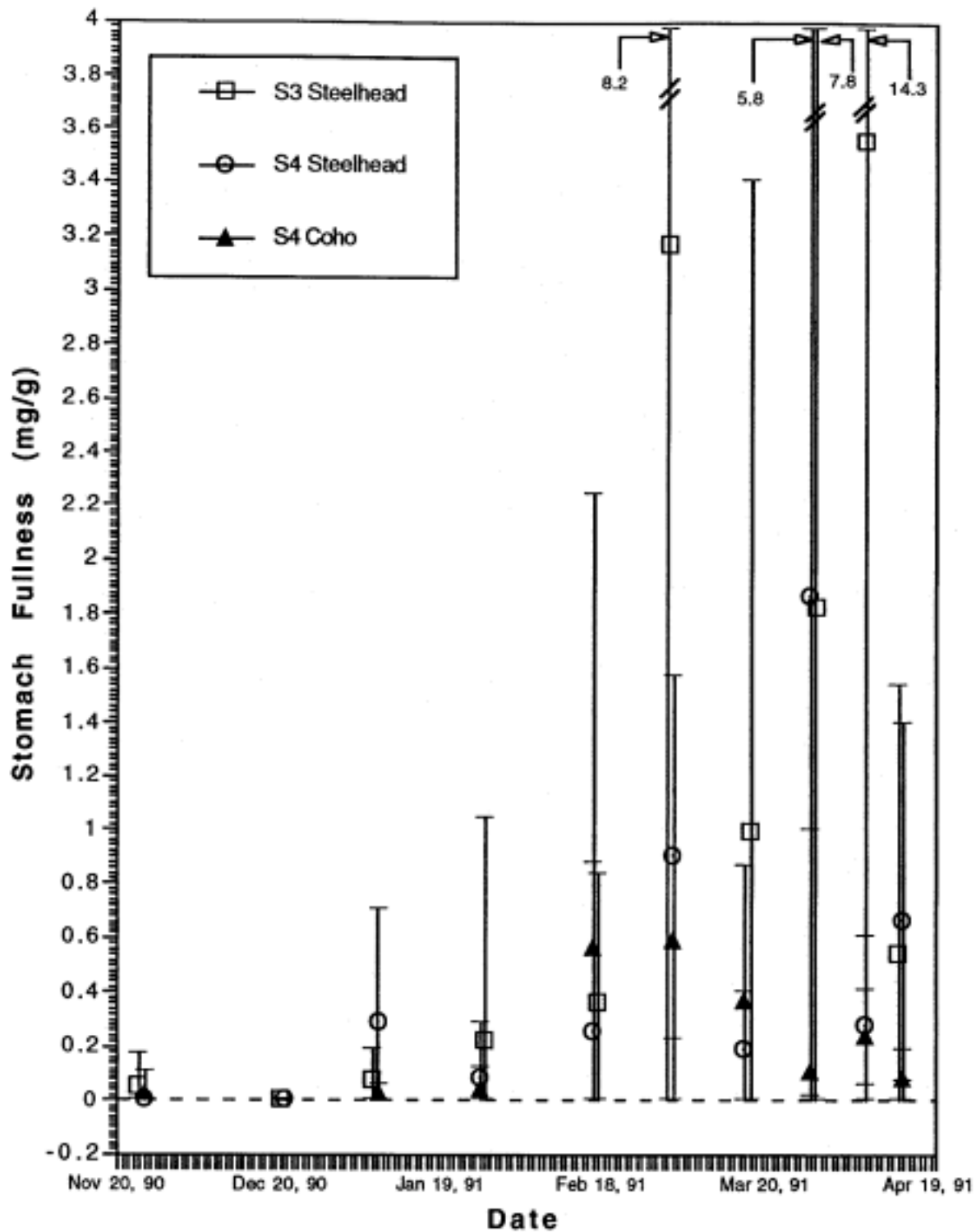


Figure 9. Steelhead and coho mean stomach fullness (mg/g) \pm one standard deviation in sites 3 (S3) and 4 (S4) in Pudding Creek, California from November 24, 1990 to April 14, 1991. Dashed line indicates zero stomach fullness.

Table 8. Mean mass of prey per gram of fish (mg/g) and associated standard deviation (SD) for steelhead and coho salmon in Pudding Creek, California. Significantly different dates ($p=0.05$) are shown as date code numbers (DC). Percent of empty stomachs are shown.

Site	Species	Date	DC	n	% Empty Stomachs	Mean Stomach Fullness		
						mg/g	SD	Sig. Different Dates
3	Steelhead	Nov 24, 90	1	16	50	0.052	0.122	2,4,5,6,7,8,9,10
		Dec 20, 90	2	9	89	0.001	0.000	1,3,4,5,6,7,8,9,10
		Jan 6, 91	3	15	47	0.072	0.117	2,5,6,7,8,10
		Jan 27, 91	4	48	19	0.226	0.819	1,2,5,6,7,8,9,10
		Feb 17, 91	5	16	13	0.361	0.472	1,2,3,4
		Mar 2, 91	6	24	13	3.168	4.996	1,2,3,4
		Mar 17, 91	7	15	0	0.996	2.408	1,2,3,4
		Mar 29, 91	8	24	4	1.831	5.989	1,2,3,4
		April 7, 91	9	10	0	3.558	10.789	1,2,4
		Apr 13, 91	10	47	9	0.546	0.994	1,2,3,4
4	Steelhead	Nov 25, 90	1	8	63	0.001	0.001	5,6,8,9,10
		Dec 21, 90	2	3	100	0.000	0.000	5,6,8,9,10
		Jan 7, 91	3	6	33	0.286	0.417	10
		Jan 26, 91	4	9	56	0.085	0.206	6, 8, 9,10
		Feb 16, 91	5	15	13	0.254	0.623	1 ,2,6,10
		Mar 3, 91	6	12	0	0.900	0.670	1, 2, 4, 5, 9,10
		Mar 16, 91	7	3	33	0.194	0.209	10
		Mar 28, 91	8	10	10	1.866	3.928	1 ,2,4
		April 7, 91	9	14	0	0.281	0.324	1,2,4,6,10
		Apr 14, 91	10	13	0	0.738	0.663	1,2,3,4,5,7,9
4	Coho	Nov 25, 90	1	8	63	0.027	0.077	
		Dec 21, 90	2	0	---	---	--	
		Jan 7, 91	3	3	0	0.024	0.038	
		Jan 26, 91	4	3	33	0.045	0.078	
		Feb 16, 91	5	8	13	0.563	1.562	
		Mar 3, 91	6	6	17	0.595	0.979	
		Mar 16, 91	7	2	0	0.372	0.496	
		Mar 28, 91	8	2	0	0.111	0.090	
		April 7, 91	9	2	0	0.163	0.048	
		Apr 14, 91	10	17	0	0.083	0.106	
3&4	Steelhead	Nov 24-25, 90	1	25	52	.033	.100	6,8
		Dec 20-21, 90	2	12	92	.001	.001	6
		Jan 6-7, 91	3	21	33	.133	.250	6,8
		Jan 26-27, 91	4	57	25	.204	.756	6,8
		Feb 16-17, 91	5	31	13	.309	.544	6,8
		Mar 2-3, 91	6	36	8	2.412	4.209	1,2,3,4,5,10
		Mar 16-17, 91	7	18	6	.862	2.208	
		Mar 28-29, 91	8	34	6	1.842	5.404	1, 3, 4, 5
		April 7, 91	9	24	0	1.646	6.952	
		Apr 13-14, 91	10	60	3	.587	.931	6

Diet Composition and Preference

Diet preference, as estimated by Strauss's L, was variable for all salmonid species over time (Figures 10-12). Aquatic invertebrates were the primary food source of sympatric steelhead and allopatric steelhead, the major food item frequently was Ephemeroptera nymphs (Tables 9 and 10). Ephemeroptera nymphs were the only food item preferred by one or more fish species on 8 out of 9 sample dates.

In general, coho salmon diets were less diverse and had a larger component of terrestrial invertebrates than steelhead (Table 11). Coho salmon diet diversity (H') was significantly lower than Site 3 steelhead (Mann-Whitney U, $p=0.02$) but not Site 4 steelhead diet diversity (Mann-Whitney U, $p=0.08$); there was no significant difference in diet diversity between site 3 and 4 steelhead (Mann-Whitney U, $p=0.77$). Coho salmon appear to switch between food items on different dates (Figure 13). Ephemeroptera nymphs were not consumed by coho salmon for the first three samples dates, yet then contributed over 80% by mass and 30% by number to the diet on three of the other sample dates. On 5 of the 8 sample dates, when Site 4 coho salmon exhibited a preference for Ephemeroptera nymphs then Site 4 steelhead exhibited avoidance, or vice versa.

During periods of high API (i.e. high stream flows) organisms that may not be available during low flows, such as earthworms (annelids) and terrestrial adults were the predominant food items of allopatric steelhead. There was no relationship between lag API and diet diversity of either steelhead or coho salmon ($r^2<0.1$). Annelids were significantly preferred, when they were available, by steelhead and coho salmon in both sites. Annelids were consumed infrequently yet could make up to 90% by mass of the diet when encountered. When present in the diet, earthworms represented a small proportion in terms of numbers (<5%) because of their relatively large size. Coho salmon diet diversity decreased on the two sample dates, March 3 and March 28, 1991 with the highest lag API and the highest stomach fullness values.

Miscellaneous terrestrials were preferred from November 1990 to January 1991 by steelhead or coho salmon and then appeared to be consumed in proportion to availability. Plecopteran nymphs were slightly preferred by all fish. Miscellaneous terrestrials were present in the coho salmon diet in 8 out of 9 sample dates. A higher proportion of coho salmon had similar food types than steelhead, although this may be an artifact of small sample size of coho salmon. On most sample dates, however, the contribution from terrestrials was less than 7%.

On December 20-21, 1990, stomachs of all species were either empty or had low volumes (0.001 mg/g), which may have been due to record cold temperatures rather than low food availability (average daily drift density), since on that date drift was higher than average for both sample sites and water temperatures were 2-4°C.

Relatively high consumption (12%) of aquatic adults corresponded to their peaks in drift for allopatric steelhead but not sympatric steelhead or coho salmon. Aquatic adults were consumed by sympatric steelhead infrequently except on two sample dates, which did not directly correspond to any peaks of aquatic adults in the drift.

Miscellaneous aquatics, larvae of Diptera (excluding Chironomidae) and Coleoptera, and Trichoptera larvae were consumed in relatively small proportions and in a random pattern by mass and by number. Trichoptera larvae were avoided ($p < 0.05$) by all fish species on 8 out of 9 sample dates. Site 3 steelhead significantly avoided ($p < 0.05$) miscellaneous aquatics on 3 of the 8 sample dates. Site 4 steelhead and coho salmon also avoided miscellaneous aquatics but the Strauss's L values were significant only on February 16, 1991.

Overlap values between all fish and drift densities were highly variable (Table 12). Comparison in diet overlap between species among and between sites did not yield any strong trends. Sympatric steelhead diets are as diverse as allopatric steelhead but did not appear to be as influenced by flow conditions.

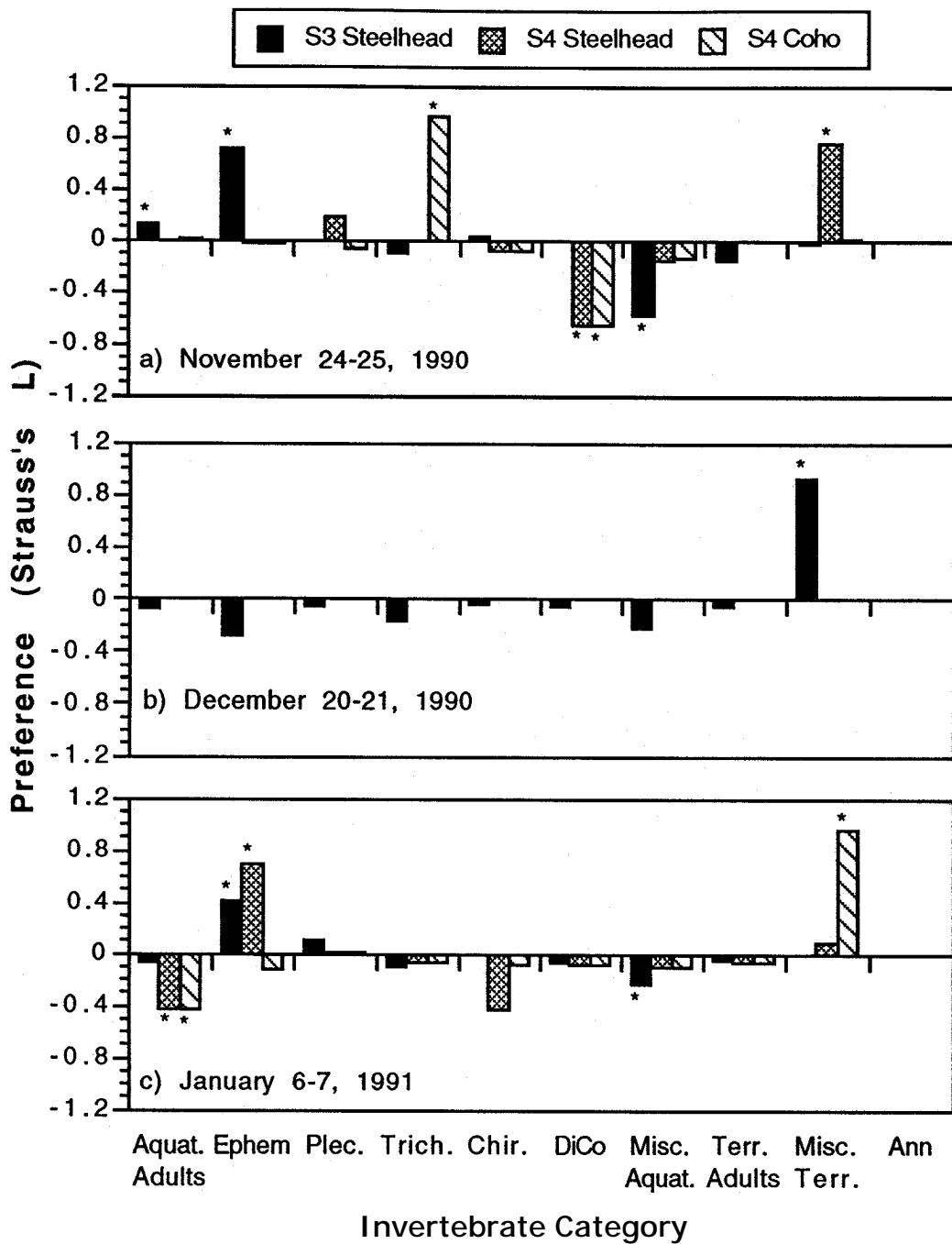


Figure 10. Diet preference (Strauss's L) of juvenile steelhead and coho salmon in sites 3 (S3) and 4 (S4) of 10 invertebrate categories for three sample dates a) November 24-25, 1990, b) December 20-21, 1990, and c) January 6-7, 1991. Significant values are indicated by * ($p > 0.1$). Aquat. Adults = Aquatic Adults, Ephem = Ephemeroptera, Plec = Plecoptera, Trich = Trichoptera, Chir = Chironomidae, DiCo = Diptera (other than Chironomidae) and Coleoptera, Misc. Aquat. = Miscellaneous Aquatics, Terr. Adults = Terrestrial Adults, Misc. Terr. = Miscellaneous Terrestrials, and Ann = Annelida.

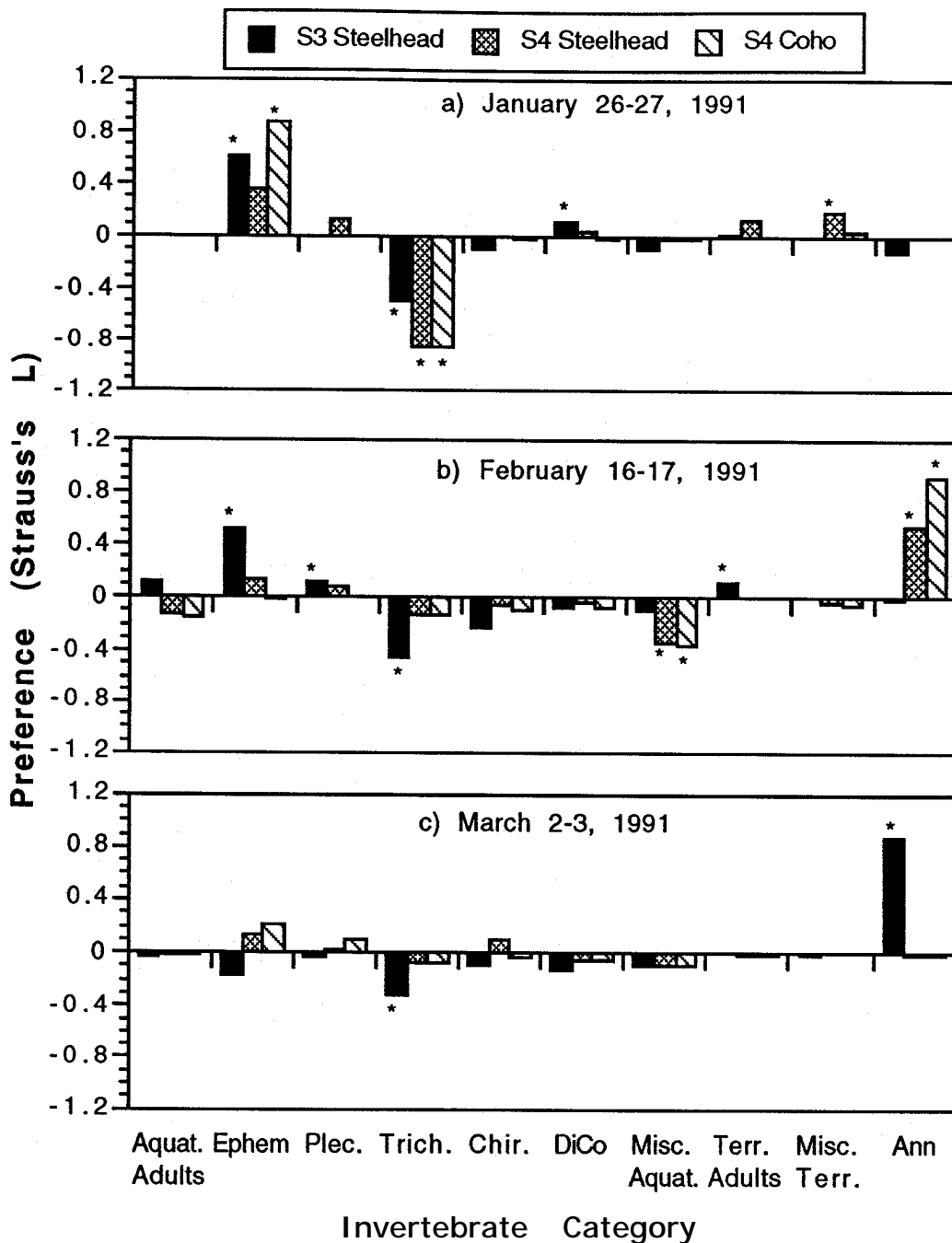


Figure 11. Diet preference (Strauss's L) of juvenile steelhead and coho salmon in sites 3 (S3) and 4 (S4) of 10 invertebrate categories for three sample dates a) January 26-27, 1991, b) February 16-17, 1991, and c) March 2-3, 1991. Significant values are indicated by * ($p > 0.1$). Aquat. Adults = Aquatic Adults, Ephem = Ephemeroptera, Plec = Plecoptera, Trich = Trichoptera, Chir = Chironomidae, DiCo = Diptera (other than Chironomidae) and Coleoptera, Misc. Aquat. = Miscellaneous Aquatics, Terr. Adults = Terrestrial Adults, Misc. Terr. = Miscellaneous Terrestrials, and Ann = Annelida.

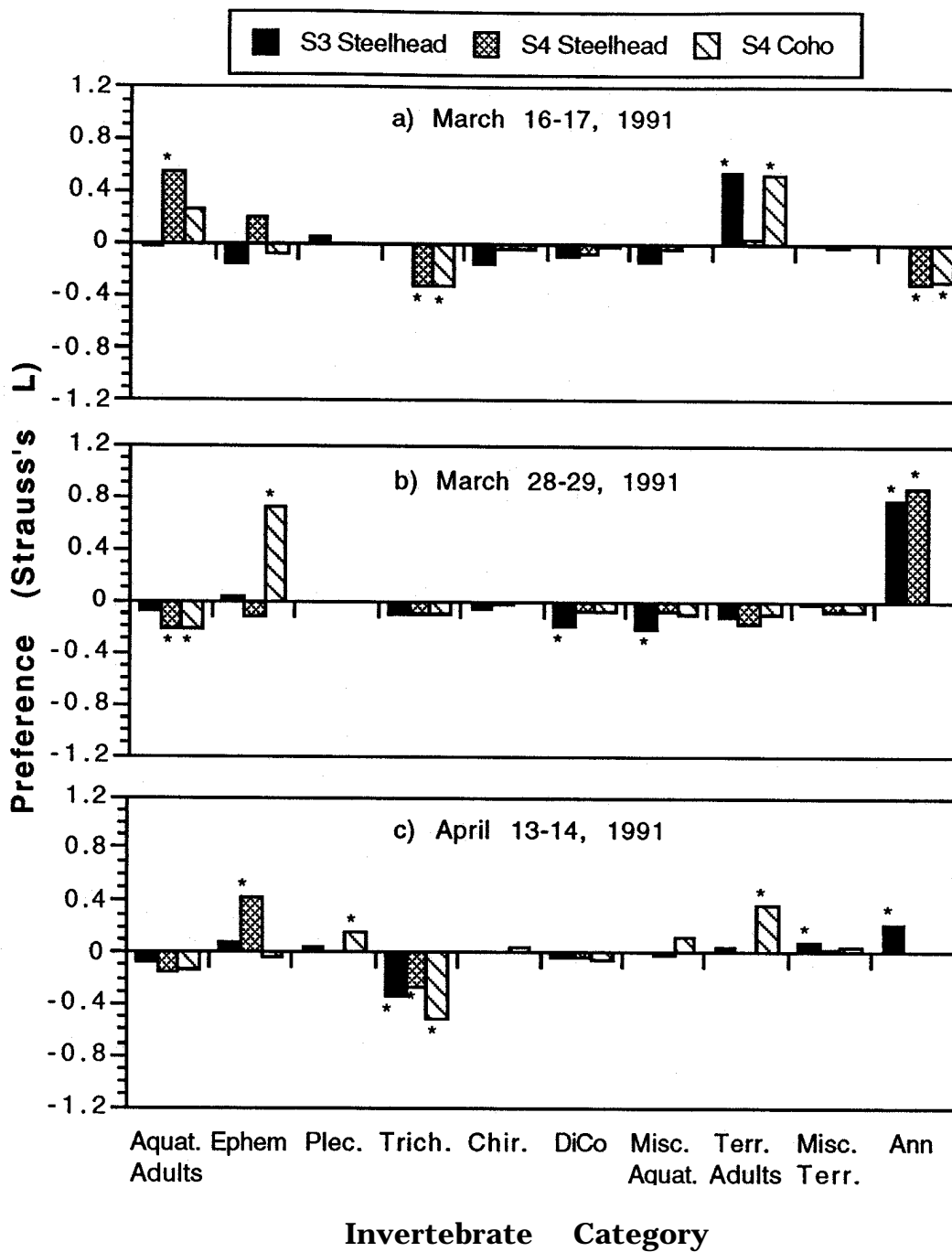


Figure 12. Diet preference (Strauss's L) of juvenile steelhead and coho salmon in sites 3 (S3) and 4 (S4) of 10 invertebrate categories for three sample dates a) March 16-17, 1991, b) March 28-29, 1991, and c) April 13, 1991. Significant values are indicated by * ($p > 0.1$). Aquat. Adults = Aquatic Adults, Ephem = Ephemeroptera, Plec = Plecoptera, Trich = Trichoptera, Chir = Chironomidae, DiCo = Diptera (other than Chironomidae) and Coleoptera, Misc. Aquat. = Miscellaneous Aquatics, Terr. Adults = Terrestrial Adults, Misc. Terr. = Miscellaneous Terrestrials, and Ann = Annelida.

Table 9. Diet composition of juvenile steelhead collected in Site 3 Pudding Creek, California for each sample date expressed as percent by relative mass (%M) and percent by number (%N) of prey items. Number of fish, % empty stomachs (% empty), Shannon index (H') and associated variance are also shown.

	November 24		December 20		January 6		January 27		February 17		March 2		March 17		March 29		April 7		April 13	
Aquatic	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N	%M	%N
Adults	12.3	26.4			19.5	40.7	1.3	2.9	11.0	1.1	0.3	3.3	9.4	8.0	0.7	4.3	0.1	2.0	2.8	11.5
Ephemeroptera	79.0	41.0			49.4	11.9	70.5	47.6	58.0	57.6	3.5	5.9	16.3	21.1	15.2	48.6	0.8			
Plecoptera	15.8	17.4	22.1																	
Trichoptera				1.8																
Chironomidae	12.7	15.1																		
	8.2	20.0			2.2	2.3	3.6	25.0	1.4	11.3	0.4	4.5	1.3	24.4	0.4	20.8	0.5			
Dip/Coleop.	38.0	3.5	28.1																	
Misc. Other																				
Total	99.5	87.4	0.0	0.0	6.3	13.4	0.4	1.4	0.1	2.1	0.3	1.1	2.1	17.1	0.5	10.5	0.1	7.1	9.7	6.9
	84.4	57.3	81.1		94.8	79.3	95.4	90.4	87.7	95.8	5.1	17.6	42.3	81.4	20.1	94.9	3.3			
Terrestrial																				
Adults					4.8	10.9	2.8	1.6	12.0	1.1	2.9	39.7	56.1	14.4	0.6	1.6	1.1	9.1	13.2	12.2
Misc. Terr.	0.5	12.6	100.0	100.0	0.4	9.8	1.8	8.0	0.3	3.1	3.1	40.7	0.5	3.6	1.2	1.8	2.1	3.4	8.6	5.8
Annelida											88.9	2.0	1.1	0.9	78.1	1.7	93.5	3.1	20.9	0.9
Total	0.5	12.6	100.0	100.0	5.2	20.7	4.6	9.6	12.3	4.2	94.9	82.4	57.7	18.9	79.9	5.1	96.7			
	15.6	42.7	18.9																	
Number of Fish	18		10		17		4	9	16		2	5	15		2	4	10	51		
% Empty	44.4		90.0		35.3		22.4		13.0		12.0		6.7		4.0		0.0	3.9		
H'	1.30		0.00		1.69		1.50		1.35		1.40		1.97		1.61		1.90	1.97		
Variance of H'	0.01		0.00		0.03		0.02		0.07		0.04		0.03		0.05		0.08	0.01		

Table 10. Diet composition of juvenile steelhead collected in Site 4 Pudding Creek, California for each sample date expressed as percent by relative mass (%M) and percent by number (%N) of prey items. Number of fish, % empty stomachs (% empty), Shannon index (H') and associated variance are also shown.

	November 25	December 21	January 7	January 26	February 16	March 3	March 16	March 28	April 7	April 14
Aquatic										
Adults			%M 0.2 %N 4.6	%M 1.7 %N 7.7	%M 21.8 %N 29.8	%M 0.2 %N 0.8	%M 58.1 %N 40.1	%M 1.9 %N 13.2	%M 13.6 %N 9.8	%M 4.8 %N 4.9
Ephemeroptera			%M 81.3 %N 52.9	%M 44.8 %N 16.5	%M 9.1 %N 5.4	%M 77.4 %N 45.6	%M 37.3 %N 45.9	%M 6.3 %N 26.4	%M 72.4 %N 39.0	%M 53.6 %N 43.4
Plecoptera	25.0	0.2	%M 1.9 %N 1.7	%M 13.8 %N 10.5	%M 0.1 %N 2.2	%M 4.1 %N 3.2	%M 0.4 %N 0.4	%M 0.2 %N 2.4	%M 4.2 %N 1.1	%M 1.5 %N 1.2
Trichoptera										
Chironomidae			%M 4.0 %N 10.9	%M 3.0 %N 10.6	%M 4.3 %N 26.0	%M 15.1 %N 46.5	%M 4.3 %N 15.1	%M 0.6 %N 20.2	%M 2.2 %N 21.5	%M 3.7 %N 23.3
DipJColeop.			%M 4.9 %N 6.6	%M 4.5 %N 8.6	%M 1.7 %N 1.7	%M 1.7 %N 1.7	%M 0.7 %N 7.5	%M 0.7 %N 7.5	%M 0.2 %N 2.5	%M 2.5 %N 11.3
Misc. Other			%M 1.5 %N 15.5	%M 2.5 %N 3.8	%M 3.8 %N 3.8	%M 0.3 %N 1.3	%M 1.1 %N 5.0	%M 1.1 %N 5.0	%M 0.1 %N 0.9	%M 3.2 %N 2.0
Total	25.0	0.2	88.8	66.7	44.0	99.8	95.4	11.1	93.8	94.1
		0.0	85.6	50.2	83.4	99.5	86.0	77.8	89.3	90.0
Terrestrial										
Adults										
Misc. Terr.	75.0	99.8								
Annelida										
Total	75.0	99.8	11.2	33.3	56.0	0.2	4.6	88.9	6.2	5.9
		0.0	14.4	49.8	16.6	0.5	14.0	22.2	10.7	10.0
Number of Fish	9	3	6	10	16	12	3	1	14	14
% Empty	55.6	100.0	33.3	50.0	12.5	0.0	33.3	9.1	0.0	0.0
H'	0.01	N/A	1.36	1.81	1.88	1.04	1.09	2.06	1.72	1.66
Variance of H'	0.01	N/A	0.12	0.02	0.04	0.07	0.13	0.04	0.05	0.07

Table 11. Diet composition of juvenile coho salmon collected in Site 4 Pudding Creek, California for each sample date expressed as percent by relative mass (%M) and percent by number (%N) of prey items. Number of fish, % empty stomachs (% empty), Shannon index (H) and associated variance are also shown.

	November 25	December 21	January 7	January 26	February 16	March 3	March 16	March 28	April 7	April 14
Aquatic										
Adults	%M 1.4 %N 33.2	%M %N	%M %N	%M %N	%M %N	%M %N	%M %N	%M %N	%M %N	%M %N
Ephemeroptera										
Plecoptera										
Trichoptera	96.4 33.2									
Chironomidae										
Diploleop.										
Misc. Other	0.9 33.2		1.4 10.9							
Total	98.6 99.5	0.0 0.0	1.4 10.9	95.6 32.6	9.4 93.2	99.9 97.9	44.2 83.8	91.8 86.1	53.9 67.0	56.2 73.3
Terrestrial										
Adults										
Misc. Terr.	1.4 0.5		98.6 89.1	4.4 67.4	0.0 2.4	0.0 0.7	51.9 8.4	6.8 4.6	46.1 33.0	38.2 19.6
Annelida										
Total	1.4 0.5	0.0 0.0	98.6 89.1	4.4 67.4	90.6 2.7	0.1 1.4	1.2 6.3	1.4 9.3	46.1 33.0	5.5 5.8
Number of Fish	8	0	3	3	8	6	2	2	2	1 1
% Empty	62.5		0.0	33.3	12.5	16.7	0.0	0.0	0.0	0.0
H'	1.12	N/A	0.34	0.63	1.67	0.81	1.27	0.96	1.39	1.92
Variance of H'	0.00	N/A	0.14	0.04	0.10	0.23	0.70	0.54	0.16	0.03

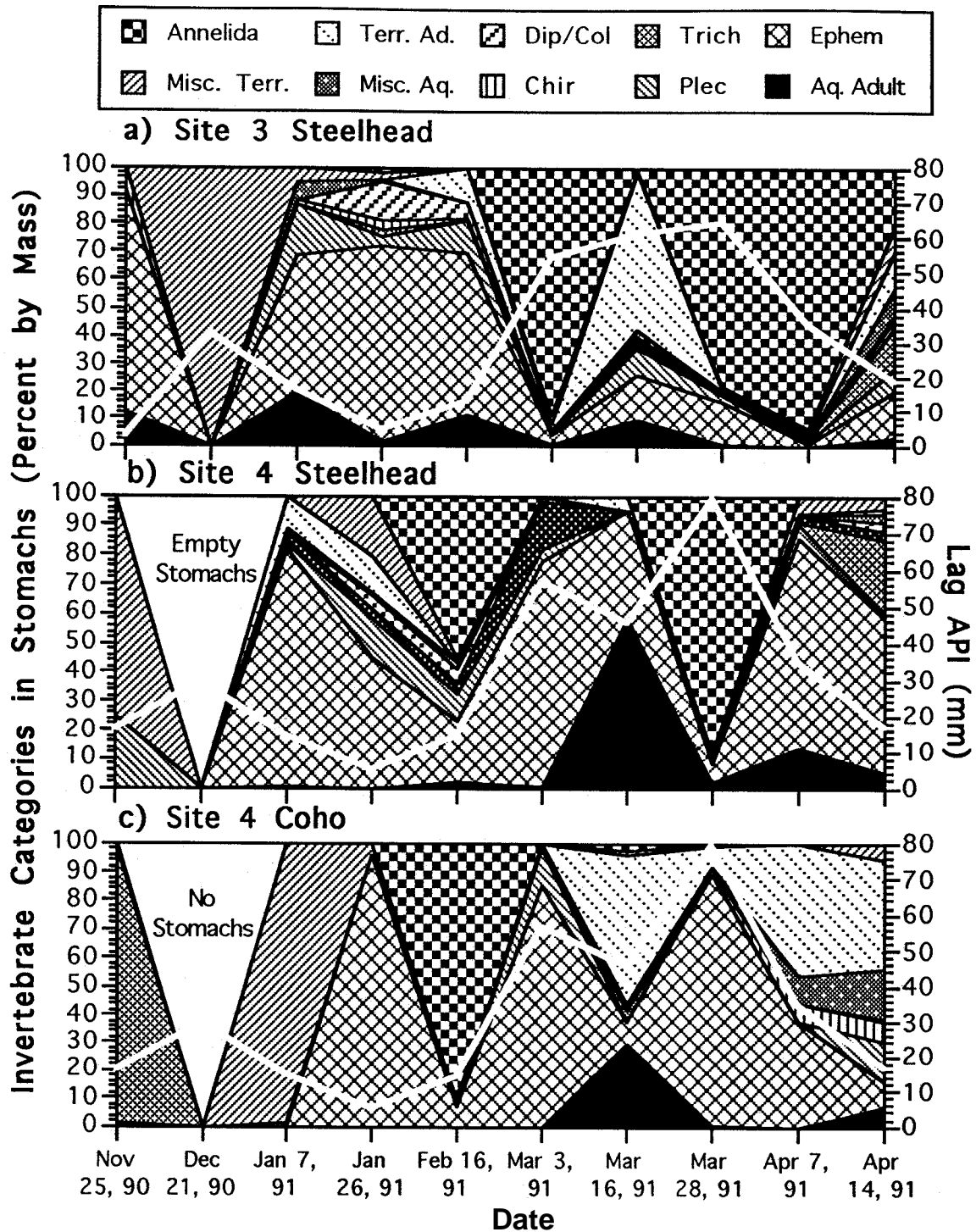


Figure 13. Diet composition, shown as % mass of invertebrate food categories, of juvenile steelhead and coho salmon in sites 3 and 4 from November 24, 1990 to April 14, 1991 in Pudding Creek, California. Solid white line indicates lag API (mm) for sample dates. Aq. Adults = Aquatic Adults, Ephem = Ephemeroptera, Plec = Plecoptera, Trich = Trichoptera, Chir = Chironomidae, Dip/Col = Diptera (other than Chironomidae) and Coleoptera, Misc. Aq. = Miscellaneous Aquatics, Terr. Ad. = Terrestrial Adults, Misc. Terr. = Miscellaneous Terrestrials, and Annelids.

Table 12. Overlap values of juvenile salmonid diets and drift sampled from November 1990 to April 1991 in Pudding Creek, CA. NS = no samples were collected, S3 = Site 3, S4 = Site 4, STL = Steelhead.

Sample Date	S3 STL vs. S3 Drift	S4 STL vs. S4 Drift	S4 Coho vs. S4 Drift	S4 STL vs. S4 Coho	S3 STL vs. S4 STL
Nov 24-25, 1990	0.1355	0.0282	0.0021	0.0132	0.0057
Dec 20-21, 1990	0.1204	NS	NS	NS	NS
Jan 6-7, 1991	0.4875	0.2396	0.0316	0.1337	0.8198
Jan 26-27, 1991	0.2003	0.0724	0.0916	0.7301	0.8364
Feb 16-17, 1991	0.1538	0.1451	0.0143	0.8616	0.3856
Mar 2-3, 1991	0.0367	0.9588	0.9382	0.9750	0.0392
Mar 16-17, 1991	0.3175	0.2178	0.1144	0.5275	0.3314
Mar 28 -29, 1991	0.0728	0.0495	0.3674	0.0717	0.9871
Apr 7, 1991	NS	NS	NS	NS	NS
Apr 13-14, 1991	0.5618	0.5971	0.1596	0.2366	0.5828
mean	0.2318	0.2885	0.2149	0.4437	0.4985

Evidence for Competition?

Evidence of competition could be exhibited as decreased condition, growth, or stomach fullness or in partitioning of food resources for one or both of the sympatric species. No strong trends in growth, condition, or stomach fullness clearly indicate competition between steelhead and coho salmon. Partitioning of food resources might be indicated in overlap values between species. Values greater than 0.60 are considered significant. Overlap values range from 0.0132 to 0.9750 for sympatric steelhead and coho salmon and from 0.0057 to 0.9871 for allopatric and sympatric steelhead. High overlap values between sympatric and allopatric steelhead might indicate sympatric steelhead feeding habits are not influenced by coho salmon, if drift composition is similar in both sites. Trends in overlap values are not explained by lag API, water temperature, or average daily drift density. Dates with the highest overlap correspond to the date with highest drift density (March 2-3, 1991).

DISCUSSION

The wide range of stream flows and temperatures in the winter of 1993 provided an opportunity to study the effects of food abundance and availability on overwintering juvenile steelhead and coho salmon in northern California. The study period included the coldest days on record (December 20-21, 1990), seasonally large floods, and low-flow periods, all of which I sampled.

Distribution and Abundance

Coho salmon were found only in the upper study site, Site 4, which may be attributed to increased habitat complexity. Site 4 had a higher quantity of woody debris which increased the habitat complexity of sample units and made the units smaller in length and surface area. Coho salmon have a higher affinity for woody debris than steelhead especially in winter (Hartman 1965, Bustard and Narver 1975, Tschaplinski and Hartman 1983, McMahon and Hartman 1989, Shirvell 1990). Differences in woody debris, instream cover, and average habitat length may explain why coho salmon were not found in both reaches. Despite differences in fish species composition, the two study sites had similar densities of total numbers of fish, although on average, Site 4 had 19% higher fish densities (0.43 fish/m²) than Site 3 (0.36 fish/m²).

Juvenile fish biomass and density in this study were within the ranges reported in the literature. Density in this study ranged from 0.21 to 0.68 fish/m² for allopatric steelhead (Site 3), 0.21 to 0.40/m² sympatric steelhead (Site 4), and 0.07 to 0.21 fish/m² sympatric coho salmon (Site 4). Other winter studies reported values from 0.01 to 0.34 fish/m² for coho salmon in southeastern Alaska (Murphy et al. 1984b); 0.02 to 0.66 fish/m² for steelhead and 0.24 to 0.73 fish/m² for coho salmon in small streams in British Columbia (Mundie and Traber 1983); 0.2 to 1.6 fish/m² for coho salmon in pools in coastal streams on the Oregon coast (Nickelson et al. 1992). For

summer studies on coastal streams in Northern California values ranged from 0.03 to 0.45 fish/m² for coho salmon and from 0.47 to 1.37 fish/m² for steelhead (Burns 1971). Cederholm and Reid (1987) summarized eight studies in the Pacific Northwest and found the mean coho salmon biomass ranged from 0.78 to 2.88 g/m²; whereas, Chapman (1965) found in Oregon streams that juvenile coho salmon biomass ranged from 4.0 to 27.0 g/m². During the summer, juvenile steelhead had a biomass of 0.14 to 0.26 g/m² in Northern California (Burns 1971).

Food Availability and Diet

Mild coastal California winters made stream temperatures warmer than those measured in other northern or higher elevation winter studies where stream temperatures approximately range from 0 to 6°C from November to April (Hartman et al. 1982; Koski 1982; Beschta et al. 1987). Only during the December cold snap did stream temperatures dip down around 2°C; for the rest of the study temperatures ranged from 5 to 10°C. During the cold snap fish appeared inactive since it was difficult to collect an adequate sample size, and fish that were collected had either empty stomachs or low food volume. However, during the remainder of the study period fish were observed swimming, feeding and there was a higher proportion of fish collected with food in their stomachs.

Although winter stream temperatures were warmer than temperatures in more northern regions they were still low. The low temperature regime reduced digestion and I assume that observed stomach contents represent the diet in the last 24 hours. Half of the samples were collected when water temperatures were below 7° C and the remaining samples were collected at temperatures below 10° C. Elliott (1973) found that at water temperatures below 7° C the stomach contents of brown and rainbow trout represented a daily ration. Koski and Kirchhofer (1982) estimated gastric evacuation rates of coho salmon were slow at low stream temperatures.

Food availability, as measured by drift samples, was low throughout the study with the exception of a peak on the first major storm event. Stomach fullness was not strongly correlated to drift. For example, food availability and stomach fullness were initially low from December to early February. The first large storm event of the season, March 2-3, 1991, introduced a temporary pulse of drift into the stream. Afterwards, food availability dropped back to levels lower than before the storm; whereas, stomach fullness remained relatively high. Low drift after the March 2-3, 1991 storm may have been because scouring and high flows depleted the aquatic invertebrate population. Differences between stomach fullness and drift may be attributed to several factors. First, although drift appears relatively low, perhaps food was not limiting for fish. Comparison of drift values between streams can be difficult because of the lack of a standard measure, differences in measuring techniques, and natural variability (Waters 1969). Nevertheless, drift densities measured in Pudding Creek were at the low end of values reported elsewhere (0.22 to 2.5 animals/m³ in southeastern Alaska; Kirchhofer 1982; and 0.1 to 1.0 animals/m³ in British Columbia; de Leeuw 1982). If food was not limiting, then other environmental factors (such as water temperature or stream discharge) influenced the ability of the juvenile salmonids to capitalize on drifting invertebrates.

The second possible explanation for discrepancies between measured food availability and stomach fullness is that the stream temperature and flow regimes were both higher during the second half of the study period. Differences in water temperature and stream flow can influence fish behavior in several ways. Faster and more turbid water reduces the ability of visual predators to capture food and may provide visual protection of juveniles from other predators. The increased stream temperatures may make more food available. Bustard and Narver (1975) found that with a combination of cold temperatures (<7°C) and increased stream discharge steelhead and coho salmon fed more actively than at tower discharge and similar temperatures. Higher temperatures

influence the activity of fish and may have accelerated the emergence rate and life cycles of invertebrate populations.. Or the increased discharge in combination with warmer temperatures may have had a positive effect on fish activity. At higher temperatures, more fish appear to occupy higher velocities (Smith and Li 1983; Hill and Grossman 1993). Hill and Grossman (1993) suggest that at higher temperatures, stream fishes have an increased ability to capture prey and higher velocities increase prey availability.

The third possibility for differences between measured food availability and observed stomach fullness is that drift may not have been the only source of food for the juvenile salmonids. Salmonids are known to be opportunists and can take advantage of a variety of food sources (Waters 1969). Perhaps they were feeding more on the benthos and terrestrial items which were locally available on the edges of habitats or in inundated vegetation. Although drift density alone was a poor predictor of stomach fullness, lag API, drift density, and water temperature combined were good predictors of sympatric and allopatric steelhead stomach fullness. These variables were poorer predictors for coho salmon. Reimers (1957) suggests that in some streams there may be higher benthic invertebrate populations during the winter than the summer. Maciolek and Needham (1952) also observed, in a winter study, that trout feeding was associated with flood events.

For allopatric and sympatric steelhead but not for coho salmon there was a shift in diet and an increase in diversity after early-February when stomach fullness increased. Shifts in diet composition and stomach fullness may be explained by shifts in behavioral patterns in response to flooding. Elwood and Waters (1969) suggested that severe storms in small streams cause loss of fish and invertebrates through flooding and scouring. However, where there is instream cover and small storms events, juvenile salmonids may move into inundated vegetation, floodplains, and other sources of refuge (Tschaplinski and Hartman 1983) and take advantage of alternative food sources.

During high flows, I collected fish in inundated vegetation and floodplains which coincided with high stomach fullness.

Patterns of type and abundance of organisms consumed were highly variable for both fish species. Ephemeroptera, when available, was the only food item consistently preferred by all fish. Dietary preferences of coho and steelhead shifted to seasonally abundant organisms such as miscellaneous terrestrials, annelids, terrestrial adults, and aquatic adults when they were available. During periods of low-flow miscellaneous terrestrials were preferred; whereas, during high flows annelids were preferred. Since miscellaneous terrestrials is a conglomerate of several organisms, such as amphipods, Cladocera, copepods, Hemiptera, water mites, ostracods, and snails this categorization could be misleading.

Diet diversity of coho salmon was lower than that of sympatric or allopatric steelhead. Coho salmon also had a larger component of terrestrial invertebrates. Coho salmon diet diversity decreased on dates with the highest API and streamflows. This may be attributed to preferred food items becoming more abundant and available to coho salmon. Koski and Kirchhofer (1982) found that coho salmon were selective in their food choices and thought the presence or absence of desired prey influenced the density and growth of coho salmon. Maciolek and Needham (1952) indicated a difference in general winter feeding and ice-laden water feeding of rainbow trout. They noted there was a greater consumption of mayflies, stoneflies, and caddisflies in ice-laden water, whereas during the remainder of the winter more flies, beetles, and oligochaetes were ingested.

Condition and Growth

Overall, fish condition and growth had increased by the end of the study. As might be expected, condition and growth remained somewhat steady from December to mid-February for both species. During this period food availability and stomach

fullness were low. Relative condition and growth of allopatric and sympatric steelhead were high from mid-February to early April then declined slightly; whereas, coho salmon growth rate and relative condition fluctuated and then slightly increased at the end.

No single variable or combination of variables (stomach fullness, average daily drift, lag API, or stream temperature) could accurately predict fish condition. Condition was weakly correlated with stomach fullness for allopatric steelhead and poorly for sympatric steelhead and coho salmon. Stream temperature was somewhat correlated with condition of sympatric steelhead and sympatric coho salmon but not for allopatric steelhead.

Riparian vegetation has been shown to explain the greatest amount of variation on trout population size (Wesche et al. 1983). The riparian zones of stable streams have vegetation that harbors terrestrial insects, which can become part of the fish food resource (Reiser and Bjornn 1979). Large woody debris increases the complexity of the stream channel and enhances instream cover which is critical to fish (Bryant 1983; Murphy et al. 1986; Fausch and Northcote 1992). Small streams play an important role in the Pacific Northwest as nursery streams for juvenile salmonids (Bryant 1983).

Evidence for Competition

There was no clear evidence for competition between steelhead and coho salmon. There were sample dates with extremely high or low diet overlap values for sympatric steelhead and coho salmon; however, this does not necessarily indicate competition for a food resource, if the resource is not limited. Competition may have been difficult to detect in this study because of the short time scale and different densities of sympatric and allopatric fish (Fausch 1988).

Conclusions

Juvenile coho and steelhead in Pudding Creek grew and maintained biomass during winter conditions which were milder than in more northern coastal climates. Food supplies were lower than those measured in other winter studies yet quantities appeared adequate for the low densities of fish present. Winter floods may play an important role in overwintering survival. Flooding allows juvenile salmonids access to a wider range of food resources and fish had fuller stomachs during high flow conditions than at other times. However, this can only occur if riparian zones have been maintained which protect the integrity of the stream as well as facilitate the addition and recruitment of large woody debris into the stream channel. In a stable stream, with adequate instream cover, floods are important for food supply and sustaining growth and condition.

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Appendix 1

Order, common name, and family of organisms found in drift and stomach samples.

Order	Common Name/Family	Order	Common Name/Family	Order	Common Name/Family
Aced	-miles & ticks	Diptera	-flies	Isopoda	-isopods
	Halacarkae		Asilidae		unknown
	unknown		Athercidae	Isoptera	-termites
Amphipoda	-scuds		Bibionidae		unknown
	TalRridae		Carabidae	lepidoptera	-moths & butterflies
Annelids	-earthworms		Cecidomyidae		Tortricidae
	Lranbrickae		Geratopppgonidae		Pyralidae
Anoplura	-sucking hoe		Chironomidae	MaNophaga	-chewing lice
	unknown		Cuckae		unknown
Araneda	-spiders		Dbddae	Megaloptera	-dobsordiles, fishflies, akierfliss
	Araneae		Dolictropodidae		Corydiadidae
Chebneithida	-Psuedoscolopion		Empididae		Sialidae
Chikipoda	centipedes		Ephydridae		unknown
	unknown		Middae	Nematode	-roundworms
Cladocera	-water fleas		Muscidae		unknown
	Daphnia		Mycetophagidae	Nematomorpha	-horsehair worms
Coelenerata	-sponge		sMycetophilidae		unknown
	Hydra		Phoridae	Odonata	-dragonflies
Caleoptera	rtes		Psychodidae		Gomphidae
	Bostrichidae		Sdaddae	Ostraooda	-seed shrimp
	CarNharidae		SimuAidae		unknown
	Carabidae		Tabanidae	Plecoptera	-stoneflies
	Cerambycidae		T'pukdae		CaprAdae
	thrysomelidae		unknown		Chloroperbdae
	Cisidae	Ephemeroptera	-mayflies		Leuctridae
	Coocinellidae		Baetidae		Nemouridae
	Cucujidae		Ephemerellidae		Pedidae
	CurouliaHeptagenkae				Perfodidae
	Demrestidae		Leptophlebiidae		Ptemarycidae
	Dryapidae		Sphionuridae		Taeniopterygidae
	Dytiscidae		Tricorythidae		unknown
	Elatidae	Gastropods	-snails	Psoooptera	-barMice and bookGce
	Emidae		unknown		Psocidae
	Gelastocordidae	Hemiptera	-true bugs		unknown
	Gyrktidae		Anthocoridae	Siphonoptera	-fleas
	Halipfidae		Berytidae		Dolidapsyllidae
	Histeddae		Lygaeidae	Tardigradi	-water bears
	Hydraenidae		Redwiidae		unknown
	Hydrophilidae		Tingidae	Thysanoptera	-thrips
	Lknnichidae		Velndae		Thrpidae
	N'rtidukdae		unknwon	Trictwptera	-caddisflies
	Pselaptddae	Homoptera	-aphids & loppers		Brachycemridae
	Ptilidae		Aleyrodidae		Calamoceratidae
	Salpingidae		Aphidae		Glossomatidae
	Scarabaeidae		Cicadoidea		Hydropsychidae
	Sciomyzidae		Cicadefidae		Hydroptilidae
	Scirtidae		Delphackaa		Lepidostomatidae
	Scolytidae		unknwon		Leptoceddae
	Staphylinidae	Hymenoptera	-ants, wasps, & bees		Umnephilidae
	unknown		Encyrtidae		Philopotamidae
CoNembola	-spring tails		Eulophidae		Polycemropodidae
	Emomobryidae		Mymaridae		RhyacophiAdae
	Hypogastruidae		Pteromalkae		unknown
	Isotomidae		Tdchogrammatdae		invertebrate eggs
	Onychiuridae		Cynpidae	Miscellaneous unidentified	
	Poduridae		Braconidae		
	Sminthuridae		Ichneumonidae		
	unknown		Geraphronidae		
Copepoda	-copepods		Diaprfidae		
	Cyclopidae		Platygasteridae		
	Ergasilus		Scelionidae		
	unknown		Formicidae		
Dermaptera	-earwigsunknown				
	unknown				