

## What's on the Menu? Evaluating a Food Availability Model with Young-of-the-Year Chinook Salmon in the Feather River, California

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**Abstract.**—We adapted a salmonid food availability model by Rader to the Feather River in California and evaluated the ability of the model and two alternative measures of invertebrate abundance to predict the diet of young-of-the-year salmonids. We compared the stomach contents of 240 Chinook salmon *Oncorhynchus tshawytscha* with the model rankings and the taxonomic abundances in the benthos and drift. Rader's model did not adapt well to the Feather River. The model was correlated with the stomach contents of Chinook salmon but not with invertebrate drift, as theorized by the model's conceptual framework. Invertebrate abundance alone was a better indicator of salmonid feeding, and salmonid diet was correlated with both benthic and drift abundances. We urge caution in applying the model to novel regions and taxa without first examining the correlations between the drift and benthos. Observational studies of salmon foraging behavior, coupled with stomach content and invertebrate collections, may provide more information about food availability in little-studied systems.

Food availability plays an important role in the survival, growth, and reproduction of salmonids (Nislow et al. 1998; Bradford and Higgins 2001). Growth during freshwater rearing is thought to affect success both during out-migration and while at sea (Nislow et al. 1999). Abundance, growth, and survival vary considerably between rivers, and studies suggest that underlying differences in invertebrate biomass or drift contribute to some of this variation (Cada et al. 1987; Filbert and Hawkins 1995; Nislow et al. 1998; Nislow et al. 1999). Since large body size and the advantages it confers increase a fish's chance of survival (Holtby et al. 1990), it is important to consider food availability when examining the suitability of salmonid habitat (Nislow et al. 1998). While there is evidence for food limitation in many rivers (Poff and Huryn 1998), the fish community as a whole consumes only a small portion of the total benthic invertebrate production (Waters 1988). Food preferences and prey availability affect diet choices (Strauss

1979), and consequently benthic invertebrate biomass is often a poor indicator of the amount of food available to higher trophic levels (Poff and Ward 1991; Power et al. 1996; Wootton et al. 1996; De Crespino de Billy and Usseglio-Polatera 2002).

Rader (1997) created a model to predict prey availability to drift-feeding salmonids based on invertebrate life history traits. As salmonids are primarily visual, opportunistic drift feeders (Everest and Chapman 1972; Filbert and Hawkins 1995; Rader 1997), Rader based prey vulnerability estimates largely on each taxon's likelihood of entering the drift. He assigned aquatic invertebrates numerical scores in 11 life history categories: propensity to intentionally drift, habitat preference, flow exposure, overall mobility, an index of drag, average drift distance, daily activity patterns, benthic exposure, emergence behavior, oviposition behavior, and overall size. He then ranked each taxon's availability to salmonids as food based on the sum of these scores weighted by a measure of taxon abundance. His objective was to provide criteria for classifying invertebrates into guilds based on their propensity to drift and their importance as food for salmonids (Rader 1997). His model is a first step in predicting the amount of energy available to salmonids and could provide the framework for a biotic index to evaluate the impact of changes in invertebrate community structure on higher trophic levels. Rader's model is attractive as a bio-monitoring tool, as it requires a relatively simple level of taxonomic resolution, provides a single, dimensionless number that allows for comparisons, and uses data that is currently collected for routine rapid bioassessment protocols.

Rader (1997) created his model for trout streams in the foothills of the central Rocky Mountains and evaluated its performance with adult brook trout *Salvelinus fontinalis* and Colorado River cutthroat trout *Oncorhynchus clarki pleuriticus*. The model is based on general invertebrate life history, and the defined traits, categories, and criteria should allow for a similar ranking procedure for trout streams in multiple ecoregions (Rader 1997).

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Our goal was to adapt the Rader model to the Feather River in California and evaluate its success at predicting drift and the diet of young-of-the-year (age-0) Chinook salmon *O. tshawytscha*.

Salmonid populations in the Central Valley have declined sharply (Fisher 1994). Water development for hydroelectric generation, irrigation, flood control and domestic water supply has eliminated or restricted much of their formerly available habitat (Fisher 1994). Reclaiming lost habitat is often not an option and therefore it is critical to manage remaining stocks to full advantage. In addition to the direct effect of habitat loss, dams have been shown to diminish the amount of energy available to higher trophic levels by shortening the trophic links leading to predatory fishes (Wootton et al. 1996). Although young-of-the-year salmonids may spend limited time in freshwater, survival to the estuarine phase can be greatly affected by growth and the amount of energy stored during early rearing (Higgs et al. 1995). If Rader's (1997) model successfully predicts drift and diet in the Feather River, it may provide a cost-effective method for scientists to evaluate the impact of management practices on food availability for salmonids.

### Study Area

The Feather River is a flow-regulated river in the northern end of the Central Valley of California (Figure 1). The Oroville Dam impounds the river, and below the dam, the river is divided into two reaches: the low-flow channel (river kilometer [rkm] 95–108) and the high-flow channel (rkm 95 to the confluence with Sacramento River). The low-flow channel (13.7 km long) flows from the fish barrier dam to the Thermalito Afterbay outlet (Figure 1) and has a constant discharge of 17 m<sup>3</sup>/s except when the flows are occasionally raised for flood control. The majority of the water bypasses this reach and is shunted through a series of shallow bays (forebay and afterbay) and power generation facilities before rejoining the main channel via the Thermalito Afterbay outlet (Figure 1). Below this outlet (the start of the high-flow channel), discharge varies between 34 and 481 m<sup>3</sup>/s. The high-flow channel is generally more turbid than the low-flow channel and has warmer water temperatures in the spring and summer.

Fall-run Chinook salmon in the Feather River display an ocean-type life history strategy (Healey 1983), and most juveniles emigrate long before smolting (<50 mm) (CWDR 2002). Out-migration

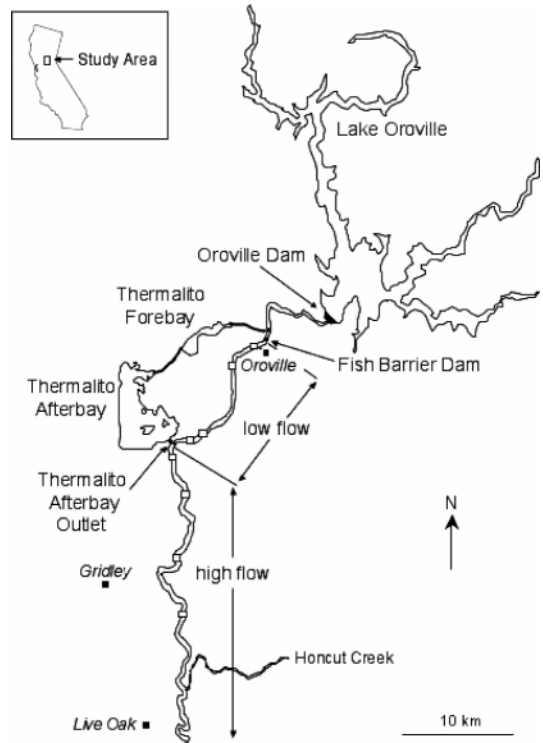


FIGURE 1.—Map of the Feather River, California, showing the study area and the Oroville Dam complex. Open boxes indicate sample sites. In the low-flow channel, samples were taken from both the main and side channels at each site.

begins in November and continues until June, with peak numbers leaving the river in February.

We set up 12 permanent sample sites. Four sites were located in the main river channel of each section (low-flow channel: rkm 107, 99.6, 98.2, and 96.7; high-flow channel: rkm 94.1, 89.3, 86.1, and 76) and four additional sites were situated in side channels adjacent to the sites in the low-flow channel. We collected all of our samples from riffles because past research suggests that riffle habitats have more diverse invertebrate fauna and because riffle sampling is routinely used for environmental sampling (Hughes 1975). We sampled each site twice in 2001: once between January 2 and 18 and once between April 9 and 26. In January, the river had an average temperature of 9.4°C and discharge in the high-flow channel was between 61 and 69.5 m<sup>3</sup>/s. In April, the low-flow channel and high-flow channel temperatures averaged 11.7°C and 16.7°C, respectively, and high-flow channel discharge was 35.5 m<sup>3</sup>/s.

TABLE 1.—Traits and scores used to classify stream invertebrates based on their availability to age-0 Chinook salmon in the Feather River, California. All parameters except size and habitat are the same as in Rader (1997); the former are reproduced with permission. Size-category scores were modified based on data from Rondorf et al. (1990) to accommodate age-0 versus juvenile or adult fish. "Reservoir" was added as a habitat classification (score = 9) to account for the addition of zooplankton to the river by reservoirs. Invertebrates inhabiting the hyporheic or depositional zones were not scored in the remaining four accidental drift categories; NA = not available.

Categories	Scores				
	0	1	3	6	9
Intentional active drift	No/catastrophic	Rare	Occasional		Frequent
Accidental drift					
Habitat	Hyporheic	Depositional			Erosional/reservoir
Flow exposure	Avoiders/NA	Obligates		Facultatives	
Mobility	Sessile/NA	Attached	Crawlers		Swimmers
Drag index	NA	<6.0	6.0–12.0	>2.0	
Drift distance	Passive sinkers/NA	Active swimmers	Active settlers	Passive floaters	
Adult drift					
Emergence behavior	Winter/NA		Crawl to bank	Drift/swim to surface	
Oviposition behavior	Overhanging vegetation/NA		Crawl underwater/dropped	Run across/land on surface	
Diel activity	NA	Nocturnal		Diurnal	
Benthic exposure	Buried/hyporheic	Concealed	Exposed		
Size (mm)		<1 or >10	1–2/8–10		2–8

## Methods

**Fish collection.**—We collected 10 age-0 Chinook salmon from each site in January ( $n = 120$ ) and in April ( $n = 120$ ). Based on a preliminary study of feeding periodicity in June 2000, which indicated that the highest relative prey weight (dry weight stomach contents/fish weight) in stomachs occurred between 1400 and 1600 hours, we collected fish between 1330 and 1600 hours. We collected all fish immediately after drift sampling, slightly downstream from where the drift nets were set.

We collected fish by seining (15 m long, 0.5-cm mesh) except in April at rkm 107, where the fish were collected by backpack electrofishing (Smith-Root Model 12B). We deeply anesthetized the fish with tricaine methanesulfonate (MS-222) and preserved them in a 10% solution of formalin. In the laboratory, we measured the standard length, wet weight, and percent stomach fullness for each fish. Stomach fullness was estimated visually to the nearest 5%. We dissected the stomachs and identified the contents to the taxonomic level required by Rader's (1997) model. Body parts were sorted by taxon, and we determined the minimum number of individuals in the stomach by estimating the least number of organisms needed to make up the parts. We did not count material that was digested beyond recognition. We calculated the

percent composition by number of each prey type by dividing the counts for each taxon by the total number of individuals in the stomach. We averaged the results from all 10 fish taken at each time and site.

**Invertebrate collection.**—We collected two drift samples and three benthic fauna samples at each site during each sampling period. We collected the drift samples by placing two nets (1.0 m high  $\times$  0.5 m wide  $\times$  1 m long; 360- $\mu$ m mesh) in the main current at the tail end of the riffle for 15 min each. We combined the catch from both nets into one composite sample preserved in 90% ethanol. We measured water depth and velocity (Marsh-McBirney Flowmate Model 2000) in front of each net and used the averages to calculate the catch of drifting invertebrates per unit volume of water. The drift samples were collected between 1330 and 1600 hours on the day before the benthic collections, just downstream from where the benthic sampling would take place.

We collected the benthic invertebrate samples with modified Surber samplers (1.0 m high  $\times$  0.5 m wide  $\times$  1 m long; 360- $\mu$ m mesh; with a 0.75-m<sup>2</sup> sampling grid) based on an adaptation of the California Department of Fish and Game's (1999) protocol for rapid bioassessment. At each site, we collected three samples (one in the middle and one near each bank) along three, randomly chosen tran-

TABLE 2.—The subcategory scores of invertebrates collected in the Feather River, California, in January and April of 2001. Scores were assigned using a modification of the procedures outlined in Rader (1997). Only taxa that comprised at least 0.01% of the average benthic abundance were included in the model. Taxa were assigned to abundance categories based on their average benthic density in the Feather River in both January and April (A = abundant [ $>1,000$  individuals/m<sup>2</sup>]; C = common [99–1,000 individuals/m<sup>2</sup>]; R = rare [ $<99$  individuals/m<sup>2</sup>]). Blank cells indicate subcategories that were not applicable to the specific taxon. The total score was calculated with an abundance-based multiplier and was used in Spearman's rank correlation analysis.

Taxon	Active drift	Habitat	Flow exposure	Mobility	Drag index	Drift distance	Emergence behavior
Acari	3	1					
Amphipoda	9	9	6	9	6	1	
Cladocera	9	9	6	9	1	6	
Coleoptera							
Elmidae	0	9	6	3	1	3	3
Collembola	0	1				6	
Copepoda	9	9	6	9	1	6	
Diptera							
Ceratopogonidae	0	1					6
Chironomidae	0	9	0	3	1	6	6
Empididae	0	9	0	3	1	6	6
Simuliidae	9	9	6	1	1	3	6
<i>Antocha</i>	0	9	0	3	6	6	3
Ephemeroptera							
<i>Acentrella/Baetis</i>	9	9	6	9	1	1	6
Ephemerellidae	1	9	6	3	1	3	6
Leptohyphidae	1	1					6
Gastropoda	0	1					
Hydroida	9	1					
Isopoda		9	6	3	1		
Lepidoptera							
<i>Petrophila</i>	3	9	1	1	6	3	6
Oligochaeta	0	1					
Ostracoda	1	1					
Pelecypoda	0	1					
Plecoptera							
Perlodidae	1	9	6	3	3	3	3
Trichoptera							
Glossosomatidae	0	9	6	3	1	0	6
Hydropsychidae	3	9	1	1	6	3	6
Hydroptilidae	0	9	1	0	1	0	6
Psychomyiidae	3	9	1	1	3	3	6
Turbellaria	0	9	6	3	1	6	

sects running perpendicular to the flow. We brushed the rocks in the sample grid clean and disturbed the underlying substrate. To standardize our collections, we sampled at each net for 10 min. We combined the three samples from each transect into one composite sample preserved in 90% ethanol. We sorted and identified the sample from each transect separately and averaged the numbers to calculate a site mean.

In the laboratory, we drained the sample of alcohol (300- $\mu$ m-mesh sieve) and laid the material out in a thin, homogeneous layer on a metal tray divided into 54 4-cm<sup>2</sup> grids. Under a dissecting microscope, we removed all invertebrates from

randomly selected grids until at least 500 (benthic) or 300 (drift) individuals were collected (California Department of Fish and Game 1999). Each selected grid was completely sorted, even if more than 500 or 300 individuals were found. We enumerated the number of taxa in each sample and calculated benthic or drift densities (number/m<sup>2</sup> for benthic samples and number/m<sup>3</sup> for drift samples).

*The Rader model.*—We ranked the availability of Feather River invertebrates to age-0 Chinook salmon by use of a modified version of the model described in Rader (1997; Tables 1, 2). We only included taxa that comprised over 0.01% of the

TABLE 2.—Extended.

Taxon	Oviposition behavior	Diel activity	Benthic exposure	Size (mm)	Size score	Abundance	Total score
Acari		6	3	0.4–3	3	A	16
Amphipoda			3	5–12	3	R	23
Cladocera			3	0.2–3	3	C	69
Coleoptera							
Elmidae	3	0	1	2–8	9	R	19
Collembola				<1	1	R	4
Copepoda			3	<0.5–2	3	C	69
Diptera							
Ceratopogonidae	6	6	1	1–5	9	R	14.5
Chironomidae	6	6	1	2–8	9	A	70.5
Empididae	6	6	1	2–7	9	R	23.5
Simuliidae	6	6	3	1–5.5	9	A	88.5
<i>Antocha</i>	0	6	1	12–24	1	C	42
Ephemeroptera							
<i>Acentrella/Baetis</i>	3	6	3	4–8	9	A	93
Ephemerellidae	6	6	1	5–9	9	C	61.2
Leptohyphidae	6	6	0	4–8	9	C	29
Gastropoda			1	4–12	9	C	11
Hydroida			3	1–25	1	R	7
Isopoda		1	1	5–20	1	R	11
Lepidoptera							
<i>Petrophila</i>	3	1	1	11–25	1	R	17.5
Oligochaeta			0	2–20	1	C	2
Ostracoda		6	3	<1	1	R	6
Pelecypoda			0	2–8	9	C	10
Plecoptera							
Perlodidae	6	1	1	8–20	1	R	18.5
Trichoptera							
Glossosomatidae	3	1	3	3–8	9	C	49.2
Hydropsychidae	3	1	1	10–28	1	A	52.5
Hydroptilidae	3	1	3	1–5	9	C	39.6
Psychomyiidae	3	1	1	4–8	9	R	20
Turbellaria			1	5–10	9	C	42

mean total benthic abundance in our samples. We eliminated rare taxa from the data set because correlation coefficients are strongly affected by large numbers of zeros (Krebs 1999), and the many ties caused by rare taxa inflate estimates of agreement (Angradi and Griffith 1990).

In cases when our sampled taxa were the same as those found by Rader (1997), we used his scores, except that we modified the size and abundance categories. We classified invertebrate fauna specific to the Feather River (Acari, Cladocera, Copepoda, Hydroida, Isopoda, and Ostracoda) with procedures from Rader (1997) and life history information from publications on aquatic inver-

tebrate biology (Usinger 1963; McCafferty 1981; Schram 1986; Thorp and Covich 1991; Merritt and Cummins 1996; Smith 2001). We then created a new habitat classification (reservoir; score = 9; Table 1) to account for the high abundance of zooplankton added to the river channel drift by the upstream reservoirs.

We adjusted prey size scores to reflect age-0 Chinook salmon foraging. Past research suggests that the optimum size of prey consumed by salmonids increases in direct proportion to fork length (Wankowski and Thorpe 1979), and many studies have found that smaller fish eat smaller prey (Bannon and Ringler 1986; Hubert and

TABLE 3.—Standard length, weight, and percent stomach fullness of age-0 Chinook salmon ( $n = 40$  per section in each month) collected from three reaches of the Feather River, California, in January and April 2001 (with the size of the 95% confidence intervals [CIs]). The fish were measured after preservation in a 10% solution of formalin. Stomach fullness was estimated visually to the nearest 5%.

Month	Section	Standard length (mm)		Weight (g)		Stomach fullness (%)	
		Mean	95% CI	Mean	95% CI	Mean	95% CI
Jan	Low-flow main channel	30.7	0.5	0.4	0.02	50	10
	Low-flow side channel	30.7	0.4	0.4	0.02	40	10
	High-flow channel	30.6	0.6	0.4	0.03	30	5
Apr	Low-flow main channel	46.3	2.9	1.3	0.3	40	5
	Low-flow side channel	48.6	3.0	1.6	0.3	60	5
	High-flow channel	57.6	2.1	3.7	0.4	50	5

Rhodes 1992; Keeley and Grant 1997). We assigned availability scores for prey size based on data from Rondorf et al. (1990) (Table 1). Rondorf et al. (1990) observed that subyearling Chinook salmon in the Columbia River fed mostly on prey ranging from 1 to 10 mm and actively selected invertebrates between 2 and 8 mm. Invertebrates measuring 1–2 mm and 8–10 mm were eaten less often, and those smaller than 1 mm or larger than 10 mm were rarely seen in the stomachs.

We adjusted the scores assigned for abundance to reflect invertebrate density in the Feather River. We assigned invertebrates to abundance categories based on the average density of the taxa in the January and April benthic samples. Invertebrate taxa with over 1,000 individuals/m<sup>2</sup> were considered abundant, those with 99–1,000 individuals/m<sup>2</sup> were considered common, and those with fewer than 99 individuals/m<sup>2</sup> were deemed rare.

**Ranking procedure.**—The taxonomic resolution (order, family, or genus) at which invertebrates were grouped was determined by similarity of the fauna within the taxon. Taxa with different habitats or that differed by two or more parameters were divided (to family or genus level) and classified separately (Table 2). Invertebrates with different habitats were classified separately because habitat had a large influence on total score. Invertebrates inhabiting the hyporheic or depositional zones were not scored in the accidental drift categories (flow exposure, mobility, drag index, and drift distance), which substantially lowered their total score. As was done by Rader (1997), we grouped all life stages (larvae, pupae, and adults) into one taxonomic category and based classification on the traits of late-instar juveniles and the oviposition and emergence behaviors of adults. We considered winged adults of amphibiotic insects as aquatic. We did not include terrestrial invertebrates or aquatic vertebrates in the model.

Invertebrate taxa were ranked according to their total score summed across all categories and multiplied by a factor expressing the effect of abundance on prey availability. Higher scores denote greater availability as prey. Abundance was used as a multiplier because it interacts with the other traits to influence prey availability (Rader 1997). The subtotals for rare taxa were multiplied by 0.5. Subtotals for abundant and common taxa with scores lower than average were multiplied by 1.0. Subtotals for abundant and common taxa with scores greater than average were multiplied by 1.5 and 1.2, respectively (Table 2).

**Statistical analysis.**—We used Spearman's rank correlation analysis (SAS Institute 2000) to cross-compare the abundances of invertebrates in the benthic, drift, and stomach content samples and the invertebrate rankings predicted by the Rader model. We averaged the results from the four sites in each reach (low-flow main channel, low-flow side channel, and high-flow channel) and performed our analyses on the mean densities of benthic (individuals/m<sup>2</sup>) and drift (individuals/m<sup>3</sup>) invertebrates and the stomach contents (percentage by number) for each reach, over each sample period (January and April). Statistical correlations were considered significant at an  $\alpha$  level of 0.05.

## Results

All the fish in this study fed mainly on autochthonous organisms. Terrestrial organisms comprised between 0% and 6% of the total diet in each section. The fish appeared to be actively feeding at the time of sampling (Table 3), as many of the items in the stomach contents were fresh (intact) and very few fish had empty stomachs (January: 12/120; April: 1/120).

The data were highly intercorrelated (Table 4). For all reaches and dates, benthic invertebrate density was correlated with stomach contents, drift

density, and the rankings of the Rader model. Stomach contents were correlated with drift density except in the low-flow main channel in January, and with the rankings of the model.

The Rader model rankings were not correlated with the density of drifting invertebrates in any of the study reaches (Table 4). Simuliids composed a lower proportion of the drift than the model predicted, whereas mites (Acari), oligochaetes, and cladocerans all drifted in higher abundances than expected from Rader's predictions. Removal of zooplankton and mites did not change the correlations. As the model forecasted, baetid mayflies (*Acentrella/Baetis*) and chironomids were both common in the water column.

A few invertebrate taxa dominated the benthic, drift, and stomach content samples (Table 5). Mites, chironomids, simuliids, baetid mayflies (*Acentrella/Baetis*), and hydropsychids dominated the benthos, comprising between 60% and 92% of the total number of taxa in each reach. Mites, cladocerans, chironomids, baetids, and oligochaetes comprised 60–90% of the total drift in each section. Chinook salmon in all reaches in January and in the low-flow main channel in April fed primarily on chironomids and baetids. In the low-flow side channel in April, Chinook salmon ate numerous hydropsychids in addition to chironomids and baetids. In the high-flow channel, Chinook salmon primarily consumed chironomids and cladocerans.

### Discussion

The model of invertebrate availability to salmonids that was proposed by Rader (1997) did not adapt well when applied to age-0 Chinook salmon in the Feather River. To be efficient at ranking the availability of invertebrates to drift-feeding salmonids, the model should be positively correlated with the ranked abundances of taxa in both the gut and drift samples (Rader 1997). While the model was correlated with the stomach contents of Chinook salmon, it was not correlated with invertebrate drift. Furthermore, since the abundances of taxa in the benthos, drift, and stomach contents were all intercorrelated (Table 4), the model may have been correlated with the stomach contents merely through a shared correlation with benthic abundance. Since all stomach contents were correlated with the benthos, overall invertebrate abundance was a good predictor of age-0 salmonid diet. It appears that the fish ate what was most commonly available.

The lack of correlation between Rader's index and the drift indicates that, even if the model did

predict invertebrate availability to salmonids, it did not do so the way Rader intended. In his test, Rader (1997) did not look for correlation between the model's ranks and drift, so it is unknown whether the original model predicted the proportions of drifting invertebrate taxa. It is therefore impossible to determine whether this problem is specific to our adapted model or was also present in the original model.

There are several possible explanations why the index rankings and drift abundances were not correlated in this study. First, the Rader model rankings may not correlate to invertebrate drift in any system. If, however, the lack of correlation is specific to the Feather River, it is possible that river regulation has changed invertebrate drift dynamics. Oroville Dam impounds the river, and past research has shown that flow regulation can modify invertebrate drift rates (Minshall and Winger 1968; Irvine and Henriques 1984; Poff and Ward 1991). Both river reaches (low flow and high flow) used in this study experience manipulated flow regimes and have therefore likely altered invertebrate distribution and behavior. Chironomids, baetids, and oligochaetes were all common in the Feather River drift, and oligochaetes drifted more than the model predicted. Previous studies have shown that these genera often respond to changes in flow rate with increased drift (Minshall and Winger 1968; Irvine and Henriques 1984; Irvine 1985). We propose that measurement of invertebrate response to flow fluctuations may help clarify drift patterns in regulated rivers.

Alternatively, the model may not have adapted well to the addition of invertebrates from the reservoirs to the river. Zooplankton was common in the Feather River, but absent from the system that Rader (1997) studied. Zooplankton often dominates the drift below reservoirs (Brittain and Eikeland 1988), and Hubert and Rhodes (1992) found that the diet of trout below dams was dominated by zooplankton, whereas trout in unregulated reaches fed predominately on chironomids. We created a new habitat category to account for the addition of large numbers of zooplankton to the Feather River drift from the upstream reservoirs (Lake Oroville, Thermalito Forebay, and Thermalito Afterbay); however, the model still underestimated the abundance of zooplankton in the drift and the importance of cladocerans in the April diet of Chinook salmon. Removal of cladocerans, copepods, and mites (taxa not included in Rader's original model) did not, however, increase corre-

TABLE 4.—Results of Spearman’s rank correlation analysis comparing benthic samples, drift samples, and Chinook salmon stomach content samples collected from the Feather River, California, in January and April 2001. Each sample type is also compared with the Rader (1997) model. Results in bold italics are significant at  $\alpha = 0.05$ .

Month	Section	Drift vs. benthos		Stomach vs. benthos		Stomach vs. drift	
		rho	P-value	rho	P-value	rho	P-value
Jan	Low-flow main channel	<b>0.67</b>	<b>0.0001</b>	<b>0.57</b>	<b>0.0021</b>	0.36	0.063
	Low-flow side channel	<b>0.55</b>	<b>0.0029</b>	<b>0.43</b>	<b>0.026</b>	<b>0.68</b>	<b>&lt;0.0001</b>
	High-flow channel	<b>0.58</b>	<b>0.0017</b>	<b>0.45</b>	<b>0.019</b>	<b>0.56</b>	<b>0.0025</b>
Apr	Low-flow main channel	<b>0.62</b>	<b>0.0005</b>	<b>0.60</b>	<b>0.001</b>	<b>0.48</b>	<b>0.012</b>
	Low-flow side channel	<b>0.60</b>	<b>0.001</b>	<b>0.55</b>	<b>0.0033</b>	<b>0.49</b>	<b>0.0096</b>
	High-flow channel	<b>0.69</b>	<b>&lt;0.0001</b>	<b>0.51</b>	<b>0.0064</b>	<b>0.49</b>	<b>0.0092</b>

TABLE 5.—Abundance of invertebrate taxa in the benthos (BEN; number/m<sup>2</sup>), drift (DRI; number/m<sup>3</sup>) and Chinook salmon stomach content (STM; percent by number) samples collected from three sections of the Feather River, California, in January and April 2001. Blank spaces indicate zero values.

Taxon	January								
	Low-flow main channel			Low-flow side channel			High-flow channel		
	BEN	DRI	STM	BEN	DRI	STM	BEN	DRI	STM
Acari	2,139.1	3.9		552	3.8	0.5	189.0	0.2	
Amphipoda	10.8		0.6	2.9		1.3	4.0		
Cladocera	239.8	1.3	1.5	50.2	1.7	0.7	22.0	0.2	0.3
Coleoptera									
Elmidae	5.7			3.3					
Collembola	4.6	0.1		2.7			2.8		0.2
Copepoda	119.7	0.4		35.7	0.8	0.6	14.7	0.2	0.2
Diptera									
Ceratopogonidae									
Chironomidae	2,713.7	1.3	29.6	997.6	1.2	47.3	3,807.3	0.3	54.0
Empididae	6.6		0.2	6.9			1.0		
Simuliidae	5,648.6	0.3	8.6	3,074.1	0.2	6.3	1,950.9		5.0
<i>Antocha</i>	115.8			189.8			22.7		
Ephemeroptera									
<i>Acentrella/Baetis</i>	3,902.8	1.2	47.5	4,487.5	1.9	33.2	2,892.8	0.2	24.2
<i>Serratella</i>	3.0						1.3		
Leptohyphidae	82.7			169.7			91.0		
Gastropoda	120.2	0.1		93.2	0.1		41.2		
Hydroida									
Isopoda				41.0	0.1	0.7			
Lepidoptera									
<i>Petrophila</i>	18.3			16.7			25.9		
Oligochaeta	215.4	0.3	0.2	341.7	1.0		102.6	0.1	
Ostracoda	24.7			2.7					
Pelecypoda	79.9			86.9			127.5		
Plecoptera									
<i>Isoperla</i>	8.3			23.3			121.6		
Trichoptera									
Glossosomatidae	268.4			404.3			86.2		
Hydropsychidae	1,072.8		0.3	2,700.6			5,859.4	0.1	2.5
Hydroptilidae	2.4			2.2			45.7		
Psychomyiidae							12.7		
Turbellaria	50.8			167.1			73.9		
Terrestrials	15.3	0.1	0.4	45.2	0.4	1.5	44.4	0.1	0.8

TABLE 4.—Extended.

Month	Section	Model vs. benthos		Model vs. drift		Model vs. stomach	
		rho	<i>P</i> -value	rho	<i>P</i> -value	rho	<i>P</i> -value
Jan	Low-flow main channel	<b>0.49</b>	<b>0.0091</b>	0.29	0.14	<b>0.51</b>	<b>0.0065</b>
	Low-flow side channel	<b>0.43</b>	<b>0.026</b>	0.15	0.47	<b>0.50</b>	<b>0.0086</b>
	High-flow channel	<b>0.42</b>	<b>0.031</b>	0.37	0.055	<b>0.59</b>	<b>0.0012</b>
Apr	Low-flow main channel	<b>0.53</b>	<b>0.0043</b>	0.24	0.23	<b>0.56</b>	<b>0.0023</b>
	Low-flow side channel	<b>0.48</b>	<b>0.011</b>	0.078	0.70	<b>0.40</b>	<b>0.037</b>
	High-flow channel	<b>0.59</b>	<b>0.0012</b>	0.32	0.11	<b>0.52</b>	<b>0.0057</b>

TABLE 5.—Extended.

Taxon	April								
	Low-flow main channel			Low-flow side channel			High-flow channel		
	BEN	DRI	STM	BEN	DRI	STM	BEN	DRI	STM
Acari	7,370.6	3.2	2.5	10,521.0	10.4	0.5	1,407.4	1.4	9.2
Amphipoda	2.7		0.6	1.6		0.9	6.0		
Cladocera	1,104.5	4.2	6.5	976.7	4.5	2.2	3,757.9	54.8	21.8
Coleoptera									
Elmidae	9.0			9.0			3.0		
Collembola				1.6			16.8		
Copepoda	244.8	0.8	0.1	116.5	1.1		273.4	4.8	
Diptera									
Ceratopogonidae	4.8		0.2	18.0		0.2			1.3
Chironomidae	5,812.8	0.9	50.0	6,890.0	2.9	46.3	5,853.8	1.0	422.1
Empididae				5.1		0.2			
Simuliidae	5,809.2	0.4	9.1	3,924.3	0.3	11.1	640.0	0.1	1.5
<i>Antocha</i>	145.4			69.6			50.9		
Ephemeroptera									
<i>Acentrella/Baetis</i>	5,913.7	0.7	12.9	6,723.1	0.6	12.3	3,543.4	0.3	10.2
<i>Serratella</i>	197.5		0.1	453.7			4,905.1	0.2	
Leptohyphidae	119.3		0.4	121.0		0.6	22.8		0.1
Gastropoda	164.4	0.3		300.9	0.5		51.6		
Hydroida					0.1		31.1		
Isopoda				24.2		0.1			
Lepidoptera									
<i>Petrophila</i>	40.0		0.7	3.0		0.1	21.1		0.3
Oligochaeta	581.2	1.0	0.1	956.4	6.3	5.4	301.9	0.5	
Ostracoda	33.4			57.0	0.1	1.0	5.9	0.1	
Pelecypoda	185.3			164.5			82.9		
Plecoptera									
<i>Isoperla</i>	5.8			6.0			3.0		
Trichoptera									
Glossosomatidae	178.2		0.2	299.3		0.7	83.4		0.3
Hydropsychidae	590.6		2.2	507.3		12.0	3,277.9	0.2	5.0
Hydroptilidae	8.7		0.3	37.6		1.0	76.4		2.3
Psychomyiidae			0.2				35.2		0.4
Turbellaria	152.1			273.3			108.4		
Terrestrials	54.4	0.2	6.4	96.9	1.0	3.8	286.0	0.2	4.1

lation to the drift or change any of the other correlations we found.

The time of sampling may also have affected our results. Studies suggest that drift, diet, and the relationship between the two change throughout the day (Sagar and Glova 1988; Angradi and Griffith 1990). For consistency, we collected all drift and stomach samples at approximately the same time. We based our sampling schedule around the feeding patterns of Chinook salmon in the Feather River rather than on patterns of invertebrate drift. Small sample sizes and restricted spatial and temporal scales may exclude important taxa, but gut analysis should still reflect the ranked order of availability of captured prey and exclude relatively unavailable taxa (Rader 1997). Our sampling regime was therefore likely sufficient to portray Chinook salmon diet. However, we may not have adequately sampled the drift, and collection of multiple samples from each site at various times might have led to higher correlation between the model and the drift and changed the relationship between the benthos and the drift. Further study would be needed to confirm this.

High correlations among the stomach content, drift, and benthic samples could, however, reflect nonselective foraging by age-0 Chinook salmon in the Feather River. Most studies suggest that age-0 salmonids feed opportunistically from the drift (Becker 1970; Everest and Chapman 1972; Petrusso and Hayes 2001), though many papers report some degree of epibenthic foraging (Angradi and Griffith 1990; Nislow et al. 1998). It is impossible to determine from correlation results whether the fish in the Feather River are feeding from both the drift and benthos or whether correlation to both merely reflects an association between the drift and benthos. Further observational studies would help clarify the feeding habits of age-0 Chinook salmon in the Feather River.

Rader (1997) theorized that not all benthic invertebrates are equally available as prey and created his model to rank taxa according to their likelihood of entering the drift and hence their vulnerability to drift-feeding salmonids. In the Feather River, however, diet was closely correlated to both benthic and drift composition, suggesting invertebrate availability was determined by invertebrate abundance. The other life history traits identified by the model were not helpful in ranking invertebrates according to their importance in the diet of salmonids. We believe the model formulated by Rader (1997) has merit as an evaluative tool, but we urge caution in applying the model

to novel situations, regions, and taxa without first examining correlations between the drift and the benthos.

The Rader model is very attractive. It is relatively easy to use, requires low taxonomic resolution, and condenses the large amount of species-specific data collected in routine benthic samples into one number that expresses the amount of food available to salmonids. The model also provides a conceptual framework for evaluating the types of traits that make prey available to higher trophic levels, and allows predictions on how changes in invertebrate community structure will affect fish. Unfortunately, the very traits that make the model appealing may also cause difficulties. Salmon are plastic, opportunistic feeders, capable of changing their foraging tactics in response to habitat, prey density, and time of day (Rondorf et al. 1990; Nislow et al. 1998; Poff and Huryn 1998). Invertebrates are also adaptable, shifting their behavior and life history (Malmqvist 1992; Culp and Scrimgeour 1993; Peckarsky et al. 2002) to suit their environment and the risk of predation. Without a thorough knowledge of the study system, it is difficult to create a model to sum up this dynamic relationship. Observational studies of foraging, coupled with stomach content and invertebrate collections, may provide more information about food availability in little-studied systems.

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### References

- Angradi, T. R., and J. S. Griffith. 1990. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. *Canadian Journal of Fisheries and Aquatic Sciences* 47:199-209.

- Bannon, E., and N. H. Ringler. 1986. Optimal prey size for stream resident brown trout (*Salmo trutta*): tests of predictive models. *Canadian Journal of Zoology* 64:704–713.
- Becker, C. D. 1970. Feeding bionomics of juvenile Chinook salmon in the central Columbia River. *Northwest Science* 44:75–81.
- Bradford, M. J., and P. S. Higgins. 2001. Habitat-, season-, and size-specific variation in diel activity patterns of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 58:365–374.
- Brittain, J. E., and T. J. Eikeland. 1988. Invertebrate drift: a review. *Hydrobiologia* 166:77–93.
- Cada, G. F., J. M. Loar, and M. J. Sale. 1987. Evidence of food limitation of rainbow and brown trout in Southern Appalachian soft-water streams. *Transactions of the American Fisheries Society* 116:692–702.
- California Department of Fish and Game. 1999. California stream bioassessment procedure. California Department of Fish and Game, Water Pollution Control Laboratory, Sacramento.
- CDWR (California Department of Water Resources). 2002. Emigration of juvenile Chinook salmon in the Feather River, 1998–2001. CDWR, Sacramento.
- Culp, J. M., and G. J. Scrimgeour. 1993. Size-dependant diel foraging periodicity of a mayfly grazer in streams with and without fish. *Oikos* 68:242–250.
- De Crespín, de Billy, V., and P. Usseglio-Polatera. 2002. Traits of brown trout prey in relation to habitat characteristics and benthic invertebrate communities. *Journal of Fish Biology* 60:687–714.
- Everest, F. H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile Chinook salmon and steelhead trout in two Idaho streams. *Journal of the Fisheries Research Board of Canada* 29:91–100.
- Filbert, R. B., and C. P. Hawkins. 1995. Variation in condition of rainbow trout in relation to food, temperature, and individual length in the Green River, Utah. *Transactions of the American Fisheries Society* 124:824–835.
- Fisher, F. W. 1994. Past and present status of central valley Chinook salmon. *Conservation Biology* 8: 870–873.
- Healey, M. C. 1983. Coast wide distribution and ocean migration patterns of stream- and ocean-type Chinook salmon, *Oncorhynchus tshawytscha*. *Canadian Field Naturalist* 97:427–433.
- Higgs, D. A., J. S. Macdonald, C. D. Levings, and B. S. Dosanjh. 1995. Nutrition and feeding habits in relation to life history stage. Pages 161–315 in C. Groot, L. Margolis, and W. C. Clarke, editors. *Physiological ecology of Pacific salmon*. UBC Press, Vancouver.
- Holtby, L. B., B. C. Andersen, and R. K. Kadowaki. 1990. Importance of smolt size and early ocean growth to interannual variability in marine survival of Coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* 47:2181–2194.
- Hubert, W. A., and H. A. Rhodes. 1992. Sizes of prey consumed by age-0 brown trout in Douglas Creek, Wyoming. *Journal of Freshwater Ecology* 7:277–282.
- Hughes, B. D. 1975. A comparison of four samplers for benthic macroinvertebrates inhabiting coarse river deposits. *Water Research* 9:61–69.
- Irvine, J., and P. Henriques. 1984. A preliminary investigation on effects of fluctuating flows on invertebrates of the Hawea River, a large regulated river in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 18:283–290.
- Irvine, J. 1985. Effects of successive flow perturbations on stream invertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1922–1927.
- Keeley, E. R., and J. W. A. Grant. 1997. Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* 54:1894–1902.
- Krebs, C. 1999. *Ecological methodology*, 2nd edition. Benjamin Cummings, Menlo Park, California.
- Malmqvist, B. 1992. Stream grazer responses to predator odour: an experimental study. *Nordic Journal of Freshwater Research* 67:27–34.
- McCafferty, W. 1981. *Aquatic entomology: the fisherman's and ecologists' illustrated guide to insects and their relatives*. Science Books International, Boston.
- Merritt, R. W., and K. W. Cummins. 1996. *An introduction to the aquatic insects of North America*, 3rd edition. Kendall/Hunt, Dubuque, Iowa.
- Minshall, G. W., and P. V. Winger. 1968. The effect of reduction in stream flow on invertebrate drift. *Ecology* 49:580–582.
- Nislow, K. H., C. L. Folt, and D. L. Parrish. 1999. Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. *Ecological Applications* 9:1085–1099.
- Nislow, K. H., C. Folt, and M. Seandel. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 55:116–127.
- Peckarsky, B. L., A. R. McIntosh, B. W. Taylor, and J. Dahl. 2002. Predator chemicals induce changes in mayfly life history traits: a whole-stream manipulation. *Ecology* 83(3):612–618.
- Petrusso, P. A., and D. B. Hayes. 2001. Invertebrate drift and feeding habits of juvenile Chinook salmon in the upper Sacramento River, California. *California Fish and Game* 87:1–18.
- Poff, N., and A. Huryn. 1998. Multiscale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. *Canadian Journal of Fisheries and Aquatic Sciences* 55:201–217.
- Poff, N. L., and J. V. Ward. 1991. Drift response of benthic invertebrates to experimental streamflow variations in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 1926–1936.

- Power, M., W. Dietrich, and J. Finlay. 1996. Dams and downstream aquatic biodiversity: potential food web consequences of hydrologic and geomorphic change. *Environmental Management* 20:887–895.
- Rader, R. B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1211–1234.
- Rondorf, D. W., G. A. Gray, and R. B. Fairley. 1990. Feeding ecology of the subyearling Chinook salmon in riverine and reservoir habitats of the Columbia River. *Transactions of the American Fisheries Society* 119:16–24.
- Sagar, P. M., and G. J. Glova. 1988. Diel feeding periodicity, daily ration, and prey selection of a riverine population of juvenile Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). *Journal of Fisheries Biology* 33:643–653.
- SAS Institute. 2000. JMP statistical software user's guide, version 4. SAS Institute, Cary, North Carolina.
- Schram, F. R. 1986. Crustacea. Oxford University Press, New York.
- Smith, D. G. 2001. Pennak's freshwater invertebrates of the United States: porifera to Crustacea, 4th edition. Wiley, New York.
- Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Transactions of the American Fisheries Society* 108:344–352.
- Thorp, J. H., and A. P. Covich. 1991. Ecology and classification of North American freshwater invertebrates. Academic Press, San Diego, California.
- Usinger, R. C. 1963. Aquatic insects of California. University of California Press, Berkeley.
- Wankowski, J. W. J., and J. E. Thorpe. 1979. The role of food particle size in the growth of juvenile Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology* 14:351–370.
- Waters, T. F. 1988. Fish production–benthos production relationships in trout streams. *Polskie Archiwum Hydrobiologii* 35:545–561.
- Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. *Science* 273:1558–1561.