PREDICTING PREY AVAILABILITY FOR STREAM SALMONIDS

By

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A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

of the Requirements for the Degree
Master of Science
in Natural Resources: Fisheries

May, 2007

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ABSTRACT

Predicting Prey Availability for Stream Salmonids

John J. Matousek

In this study I evaluated the effectiveness of the percentage by mass of behaviorally drifting invertebrates within drift samples to serve as an index of a stream's capacity to support salmonid growth. I tested hypotheses over seasonal timeframes that: 1) the taxonomic composition of stream salmonid diets corresponds more closely with the composition of the drift than of the benthos; 2) the percentage by mass of behaviorally drifting invertebrates in salmonid diets corresponds with the percentage of behaviorally drifting invertebrates in drift samples; and 3) salmonid growth is positively correlated with the percentage by mass of behavioral drift. The study was conducted in two 100-m reaches in each of six 2nd - 3rd order streams within the Smith and Klamath River basins in coastal northern California. Stream reaches received experimental manipulations of canopy opening and salmon carcass addition that produced sites differing in salmonid production. Within each reach, invertebrate benthos, drift, and diets from resident cutthroat trout (*Oncorhynchus clarki*), and rainbow trout (*Oncorhynchus mykiss*) were sampled three times each during summer and winter base flow conditions and seasonal measurements of salmonid growth from PIT-tagged individuals were obtained. Taxonomic composition of the salmonid stomach samples was not substantially similar to either the drift samples or the benthic samples. Salmonids did not appear to be actively selecting for behaviorally drifting invertebrates and no relationship was observed between the growth of juvenile salmonids and the percentage of behaviorally drifting invertebrates in the drift. As such, the relative percent of behavioral drift was found to be insufficient as an index of prey availability. Contributing to the difficulty of assessing prey availability was stream flow variability, seasonal and diel abundance of other prey sources, incomplete taxonomic classification, and the opportunistic feeding behavior of juvenile salmonids.

ACKNOWLEDGEMENTS

My success in this lengthy endeavor has depended on the efforts, knowledge and support of many individuals. First, I would like to thank the members of my committee: Dr. Bret Harvey, for his assistance with all things statistical; Dr. Kenneth Cummins, for his love of aquatic entomology and his ability to share it with others; Dr. Terry Roelofs, for fisheries advice, both scientific and recreational; and especially my major advisor Dr. Peggy Wilzbach, for providing me with this practical and meaningful project and seeing me through to the final draft. Individually, and as a group, they have given their time and guided me through this sometimes daunting step in my career, and for this I am extremely grateful.

Funding for this project was provided by a grant to Dr. Wilzbach from the National Council for Air and Stream Improvement. I would like to acknowledge students and staff of the USGS California Cooperative Fish Research Unit for providing field assistance and resources necessary to successfully complete this project. Among many to whom I extend my sincere gratitude are Kay Brisby, Sarah Kleinschmidt, Craig Johnston, Ozvaldo Hernandez, and Michael Mettee.

Another partner in the success of this project was Green Diamond Resource Company who allowed us to locate our study sites on their property. In particular, I would like to thank Chris Howard for his assistance on numerous occasions transporting my sampling equipment to remote study sites.

Finally, I would like to thank my friends and family, especially my wife Bethany, for always being there to offer love and support to keep me moving toward my goals.

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INTRODUCTION

Although food availability and physical habitat are major factors affecting salmonid productivity in streams (Chapman 1966, Poff and Huryn 1998), restoration efforts for salmonids in the Pacific Northwest have focused largely on physical habitat alone. While food and habitat certainly interact to some degree in limiting salmonid production, failure to specifically consider food needs of the fish may limit restoration efforts. Several studies support the importance of food supply in affecting production (Filbert and Hawkins 1995, Richardson 1993). One study modified in-stream food supplies to juvenile Coho salmon (*Onchorhynchus kisutch)* and observed an increase in growth rates and lipid storage (Mason, 1976), while others showed that nutrient additions stimulating primary production could be correlated to increases in salmonid growth rates (Johnston et al. 1990, Peterson et al. 1993). Food availability has even been shown in artificial stream channels to be a greater factor in determining fish growth and residency than the amount of available cover (Wilzbach 1985, Boss and Richardson 2002). Also, maximum growth rates of juvenile salmonids have been measured in hatcheries where habitat diversity is negligible. Recent recognition of the need to consider food availability (Duncan 2001), has resulted in a management need for the development of a readily measured index for assessing adequacy of the food supply to support salmonid growth.

Despite its potential importance in fish production, food availability for juvenile salmonids is difficult to determine and is rarely assessed (Nislow et al. 1998, Fausch et al. 1988). This is partially due to the difficulty of determining what represents available prey for salmonids. The opportunistic nature of salmonids allows them to adjust their feeding habits in response to changes in habitat and food supply (Dill 1983, Grant and Noakes 1987, Bridcut and Giller 1995). At the same time, variability exists among invertebrate groups in their vulnerability to predation by salmonids due to differences in habitat, behavioral, and morphological characteristics (Rader 1997, de Crespin de Billy et al. 2000). Not all invertebrates in the drift or benthos are vulnerable to salmonid predation at all times and therefore, invulnerable groups have little or no impact on salmonid production (Rader 1997).

Sampling-related obstacles also contribute to the difficulty of assessing food availability. The clumped distribution pattern and seasonal phenology, which characterize benthic stream invertebrates, requires a larger number of samples and multiple sampling events (Elliott 1977). These samples must then be processed with a microscope which is a laborious procedure. Taxonomic identification is difficult, and taxonomy of immature aquatic insects is still poorly known incomplete (Rosenberg and Resh 1993, Merritt and Cummins 1996).

Establishing a relationship between growth or production of salmonids and benthic invertebrates has also been challenging, as exemplified by the “Allen Paradox”, in which estimated production of benthic invertebrates was found to be insufficient to support trout populations in the Horokiwi stream in New Zealand (Allen 1951). A lack of correspondence in production of benthic invertebrates and salmonids may arise for two reasons. First, the invertebrate benthos includes many forms that are not routinely available to salmonids, which feed predominately on drifting invertebrates (Elliott 1970, 1973, Waters 1972, Cada et al. 1987). Second, sampling of the benthos alone may overlook major community components important to fish feeding (Pringle and Ramirez 1998). In particular, the terrestrial invertebrate component of salmonid diets at certain times can represent a large and important source of food for stream fishes (Bridcut 2000, Kawaguchi et. al. 2003, Baxter et. al. 2005) and it is not adequately sampled in benthic collections although it would be in drift collections that sample the water surface.

Rader (1997) suggested that a first step in predicting the actual food or energy available for salmonids is to evaluate differences in availability among groups of aquatic taxa. Because availability of invertebrates is primarily defined by their general propensity to drift (Rader, 1997), this study examined the use of a measurement of the drifting invertebrates to predict prey availability for juvenile salmonids.

The drifting behavior of stream invertebrates is well-documented (Muller 1954, Waters 1965a, b). Drift may serve as a method of dispersal, escape from predation, and as a means of moving to more suitable habitats and food resources. Wilzbach and Cummins (1989) provided data suggesting a large portion of drifting invertebrates may be diseased. Although there is not a unique drift fauna per se (Waters 1972), some taxa are particularly abundant in the drift and may occur in drift samples with some pattern of diel periodicity. Most of these species exhibiting a diel periodicity in drift experience a peak in abundance in the drift shortly after dusk (Elliot 1967) or at dawn (Waters 1972). Although the mechanisms underlying diel periodicity in the drift are not yet fully understood, the phenomenon led Waters (1965) to propose a classification scheme that distinguishes between behavioral drift, constant or accidental, and catastrophic drift. Behavioral drift refers to drift occurring at a consistent period of the day, resulting from a behavior pattern characteristic of certain species. Constant or accidental drift of insects refers to the continuous occurrence in the drift of representatives of all species, in low numbers, and at all times of the day. Catastrophic drift occurs as a result of physical disturbance of benthic fauna from floods, and other scouring agents, but also from drought, high temperatures and toxic contaminants. Although they have not been previously classified on this basis, insects of terrestrial origin that are collected in the water column or water surface may be classified the same way. Most terrestrial invertebrates occur in streams when blown in by winds and could be considered accidental.

The significance of a distinction among drift categories to stream salmonids and other drift feeding fishes is that behaviorally drifting invertebrates represent a temporally predictable food supply, and potentially constitute a mainstay of salmonid diet in streams. Accordingly, I expected that the proportion of behaviorally drifting individuals in salmonid diets would correspond with the proportion of behaviorally drifting individuals in the drift samples. Constant or catastrophic drift may present windfall diet items, and are most abundant at high flows when fish foraging may be reduced (Nislow et al. 1998). As such they are not likely to form a predictable base of prey support for fish.

If behavioral drift represents a consistent component of fish diets, then differences in drift composition among streams should be detectable in fish growth. Salmonid growth is a function of food availability (the proportion of potential prey that can be detected, captured, and consumed), metabolic costs including those of obtaining and processing food, and the assimilability of the food (Fausch 1984). A positive relationship between salmonid growth and percent mass of behavioral drifters within drift samples was expected. If so, this would provide an effective index of prey availability for stream salmonids.

The objectives of this study were to test three specific hypotheses: 1) the taxonomic composition of stream salmonid diets corresponds more closely with the composition of the drift than the benthos; 2) the percent mass of behavioral drifting invertebrates in salmonid diets corresponds with the percent mass of behaviorally drifting invertebrates in drift samples; and 3) salmonid growth is positively correlated with the percent mass of behavioral drifters within the drift.

Hypotheses were tested over seasonal (winter and summer) timeframes. Biomass of invertebrate samples was used in all calculations because total prey biomass provides a better estimate of the invertebrate's contribution to a fish's energy gain, or production than does the number of individual prey (Bowen 1983, Mittelbach and Osenberg 1994).

MATERIALS AND METHODS

Study Site

The study was conducted in twelve 100-m reaches on six 2nd and 3rd order streams in coastal northern California (Figure 1). Two of the streams are located in the Lower Klamath River basin (Tectah and Tarup creeks) and the four remaining streams are in the Smith River basin (Peacock, South Fork Rowdy, Little Mill, and Savoy creeks). Stream reaches were similar in catchment area, gradient, and stream size (Table 1).

The regional climate is maritime with mild, dry summers and cool, wet winters. The typical annual rainfall for the Smith River sites is 168 cm, while the Klamath River sites receive approximately 205cm per year, most of which falls between November and March. Average air temperatures range between 16 and 20°C in the summer and between 4 and 10°C in the winter. Average water temperatures in the sites ranged between 11 and13°C in the summer and between 8 and 9°C in the winter (Ambrose et. al. 2004). Bedrock of all six study sites was of the Franciscan complex (California Division of Mines and Geology 1964) and soils were of the Hugo-Josephine association (United States Soil Conservation Service 1967a, b). Riparian vegetation was dominated by red alder (*Alnus rubra*) and the fish assemblages were dominated by resident coastal cutthroat trout (*Oncorhynchus clarki clarki*) and rainbow trout/steelhead (*Oncorhynchus mykiss*).

Figure 1. Location of the four study sites within the Smith River basin and the two study sites within the Klamath River basin in Northern California (From Wilzbach et al. 2005).

Table 1. Characteristics of open- and closed-canopy reach of the study sites. c = sites with carcasses added. Modified from Wilzbach et al. (2005)

				Mean bankfull width (m)		Gradient (%)	
Stream Site	Basin	Basin Area (km^2)	Latitude/Longitude	Open	Closed	Open	Closed
Savoy	Smith	5.0	41°54'14"N/124°5'12"W	8.0	8.6	4.7	5.6
South Fork Rowdy(c)	Smith	4.9	41°51'16"N/124°5'23"W	7.9	7.8	5.6	5.1
Peacock(c)	Smith	3.5	41°50'11"N/124°5'11"W	3.8	4.4	2.4	4.2
Little Mill	Smith	3.4	41°52'27"N/124°6'47"W	6.5	5.9	7.7	9.5
Tarup(c)	Klamath	4.9	41°27'45"N/123°59'32"W	7.9	7.2	2.8	1.8
Tectah	Klamath	7.9	41°15'47"N/123°57'52"W	6.0	7.2	2.9	1.7

My study was embedded in work described in Wilzbach et al. (2005), in which riparian canopy cover and salmon-derived nutrients were experimentally manipulated (Table 1). Riparian canopy was removed from a randomly selected 100-m reach within each of the six streams. A second 100-m reach in each stream maintained an intact riparian canopy. The two reaches were separated by 150-200m of stream channel. In three of the streams (South Fork Rowdy, Peacock, and Tarup creeks); carcasses of Chinook salmon (*Oncorhynchus tshawytscha*) were added (winters of 2002 and 2003) to both open and closed canopy reaches, at a loading of approximately 1 kg/m². This experimental design of canopy opening and salmon carcass additions produced sites differing in salmonid growth and constituted an advantageous design for testing the importance of the availability of invertebrate prey to salmonid growth.

Sampling Design

Each of the twelve study reaches was sampled three times during the period of summer through early fall (June – September) of 2002 and three times during the period of winter through early spring (January – April) of 2003. The former period constitutes the major emergence period for both spring-summer and fall-winter generations of stream invertebrates. The latter period is the growth, but non-emergence, period for fall-winter generations of stream invertebrates. On each sampling occasion, invertebrate drift, benthos, and fish gut contents were collected.

Drift sampling began approximately one hour before sunset and lasted for two hours. This time frame was used because it was assumed to capture the maximum daily abundance and diversity of aquatic drifting invertebrates (Allan and Russek 1985). Two 45cm wide rectangular drift nets of 250µm mesh netting were placed in tandem on right and left sides of the channel in randomly selected riffles of each study reach. The nets were anchored to the substrate with rebar, and were positioned to capture surface flow while sitting above the streambed. Thus, net placement allowed for the collection of drifting benthic insects as well as terrestrial insects that fell into the stream. Stream depth and current velocity were measured at the mouth of each of the drift nets. Water velocities at drift sampling locations averaged 0.18 m/s in the summer/early fall and 0.46 m/s in the winter/early spring. After the drift nets were in place for two hours, net contents were washed into a 250µm sieve, placed in collection vials, and preserved with a 70% ethanol.

Juvenile salmonids were sampled downstream of the nets by use of collapsible minnow traps and a back pack electro-fishing unit to obtain a minimum sample size of 10 fish over 60 mm in fork length for stomach content analysis. Fish were sampled during the period that drift was collected, but prior to the collection of benthic samples. Captured fish were anaesthetized with Alka-Seltzer tablets, identified, weighed to the nearest 0.01g, measured to the nearest millimeter in fork length, and their stomach contents were extracted by gastric lavage. Stomach samples were washed into Whirl Pac® bags and preserved with a 70% ethanol. Fish were allowed to recover before being released back to the site of capture.

Following collection of drift samples and fish stomach samples, two benthic samples were taken in each reach using a Surber sampler (.31m×.31m) with a 250µm mesh size net. These samples were taken immediately upstream from drift sampling points. The substrate was disturbed and the cobbles washed into the net. The contents were then washed into a 250µm sieve and into collection vials, and preserved with a 70% ethanol.

Fish growth data used in my analysis was acquired from data collected during a separate study by Wilzbach et al. (2005), which was in progress during my study. Fish were collected in each reach by multiple pass electro-shocking and all individuals over 70 mm in fork length were implanted with passive integrated transponder (PIT) tags used in recapture events to obtain an estimate of growth. Growth was estimated for the over-summer period (June 2002 – Oct 2002) and the over-winter period (Oct 2002 – June 2003).

Laboratory Procedures

All macroinvertebrates from benthos and drift samples (n = 144 each), and fish stomachs (n = 218) were identified, enumerated, and measured to the nearest millimeter in the lab. Length measurements were taken from the front of the head to the end of the abdomen excluding projections and cerci. Maximum shell length was measured for Mollusca. In samples in which the contents consisted of fragmented individuals the number of heads was counted and the size estimated by comparison to that of intact individuals of similar head size. The resolution of taxonomic identification applied for each taxon is described in Table 2. These levels of resolution were chosen as the highest level of resolution at which separation could be made for classification as behaviorally or accidentally drifting taxa.

Once identified, individuals from each sample were categorized according to their propensity for accidental or behavioral drifting. Differentiation between the two groups was determined from available literature. Table 3 lists the taxa classified as behaviorally drifting and the literature support for their classification as such. Table 4 shows the percentage that each behavioral drifter contributed to the drift samples by number and biomass. All other taxa identified during the study, which are listed in Appendix A, were considered to be accidentally drifting.

Biomass estimates were derived from taxon-specific length-mass regressions from Smock (1980) and unpublished data furnished by Dr. Ken Cummins and Dr. Margaret Wilzbach (Humboldt State University, Appendix B).

Table 2. The taxonomic level of resolution at which invertebrates found in the drift, benthos, and fish stomach samples were identified.

TAXA	LEVEL OF RESOLUTION
(i) Aquatic Insects	
Ephemeroptera	Genus
Plecoptera	Genus
Odonata	Family
Trichoptera	Genus
Hemiptera	Family
Megaloptera	Family
Coleoptera (larvae and adults)	Family
Diptera (except Chironomidae)	Family
Chironomidae (except Chironominae)	Subfamily
Chironominae	Tribe
(ii) Terrestrial Insects	
All specimens	Order
(iii) Other Aquatic Invertebrates	
Oligochaeta	Class
Crustacea	Order
Mollusca	Subclass
(iv) Other Terrestrial Invertebrates	
All specimens	Class

Table 3. Invertebrate taxa classified as behaviorally drifting and the literature support for each.

Behaviorally Drifting Macroinvertebrates	Supporting literature
Ameletus nymphs	Minshall and Winger, 1968 Coutant, 1964
Baetis nymphs	Waters, 1962 Minshall and Winger, 1968 Kohler, 1985 Allan et. al, 1986 Forrester, 1994
Paraleptophlebia nymphs	Reisen and Prins, 1972 Forrester, 1994 Grzybkowska et al., 2004
Chironomidae larvae and pupae (excluding *Tanypodinae*)	Reisen and Prins, 1972 Bridcut, 2000 Grzybkowska et al., 2004
Dixidae larvae	Waters, 1962 Elliott and Tullett, 1977
Simuliidae larvae	Waters, 1962 Bridcut, 2000
Amphipoda	Waters, 1962 Waters, 1972

Statistical Analyses

The Bray-Curtis index measure or dissimilarity (B), (Krebs 1999), was used to compare the taxonomic composition of salmonid diets to drift and benthic samples. This was estimated as:

$$B = (\sum |X_s - X_{db}|) / (\sum X_s + X_{db}),$$

Where X_s is the biomass of a particular taxon in the diet sample, and X_{db} is biomass of the same taxon in either the drift or the benthic sample. Values were expressed as a measure of similarity by using the complement of the Bray-Curtis measure (1.0 – B), with values ranging from 0(dissimilar) to 1(similar). A similarity index value was calculated for each drift and benthic sample for sampling events where at least 3 fish were collected for diet analysis. A paired two-tailed T-test was used to determine if similarity between diet and drift samples differed from similarity between diet and benthic samples.

The percent mass of behaviorally drifting invertebrates found in the diets was plotted against the percent mass of behaviorally drifting invertebrates found in drift samples to evaluate electivity by salmonids for this group of invertebrates. Because graphical analysis revealed a lack of apparent electivity, further statistical analysis was not warranted.

The relationship between seasonal salmonid growth and the percent mass of behaviorally drifting invertebrates collected in the drift was evaluated by linear regression. Specific growth rate (G) of recaptured salmonid individuals was measured as:

$$G = ((\ln W_t - \ln W_0) / t) * 100,$$

Where W_t is the final mass (g), W_0 is the initial mass (g), and t is the growth period, in days.

The relationship between specific growth rate (G) of salmonids and mass of invertebrates (g/m^3) in the drift samples was also evaluated by linear regression for the purpose of verifying correlations found in the relationship between salmonid growth and percent mass of behaviorally drifting invertebrates in the drift samples.

RESULTS

Composition of the drift, benthic and salmonid diet samples

Mean similarity index values between diet and drift samples (mean=0.21) differed from similarity index values between diet and benthic samples (mean=0.15), (paired t-test: p=0.02, df=27). Seasonal differences in similarity were not observed, so data were combined and presented on an annual basis. Ephemeroptera adults, Diptera adults, and Hymenoptera were commonly represented in both the drift and diet samples but were rarely found in any of the benthic samples. Several terrestrial taxa (e.g. Formicidae, Orthoptera, Isopoda, Plecoptera adults, and Trichoptera adults) were found almost exclusively in the diet samples. Although commonly found in all three sample types, large individuals of some taxa (e.g. Perlidae, Chloroperlidae, and Rhyacophilidae) represented a large percentage by biomass in some benthic samples.

Of the behavioral drifters, Chironomidae larvae and *Baetis* nymphs represented the largest percentages of the overall composition of the drift by both number of individuals and biomass (Table 4). Baetis nymphs comprised between one-tenth and one-third of both the numbers of individuals and the biomass within all drift samples. Total percentage of behavioral drifters was relatively low and made up approximately one-half of the drift samples by number of individuals but only between one-fourth and one-third of the drift samples by biomass. Non-behavioral drifters in the drift samples included many different taxa.

Table 4. Percent composition of behaviorally drifting macroinvertebrates found within drift samples.

Behaviorally Drifting Macroinvertebrates	% by number of individuals in drift samples (summer, 2002)	% by number of individuals in drift samples (winter, 2002)	% by biomass (g) in drift samples (summer, 2002)	% by biomass (g) in drift samples (winter, 2002)
Ameletus	0.71%	3.97%	2.86%	6.98%
Baetis	30.26%	25.40%	10.72%	14.15%
Paraleptophlebia	2.15%	2.66%	2.98%	3.98%
Chironomidae (excluding *Tanypodinae*)	11.26%	18.48%	3.27%	4.45%
Dixidae	3.12%	0.94%	1.64%	0.36%
Simuliidae	2.75%	1.00%	1.53%	2.9%
Amphipoda	0.03%	0.18%	.08%	0.75%
Total	50.28%	52.63%	23.08%	33.57%

Behavioral drifting invertebrates found within diet samples

Salmonids did not detectably select prey exhibiting behavioral drift (Figure 2). The proportion of behavioral drifters, as a percent of total biomass, found in salmonid diets was rarely higher than the proportion of behavioral drifters collected in drift samples. Seasonal differences were not observed, so data were combined and presented on an annual basis.

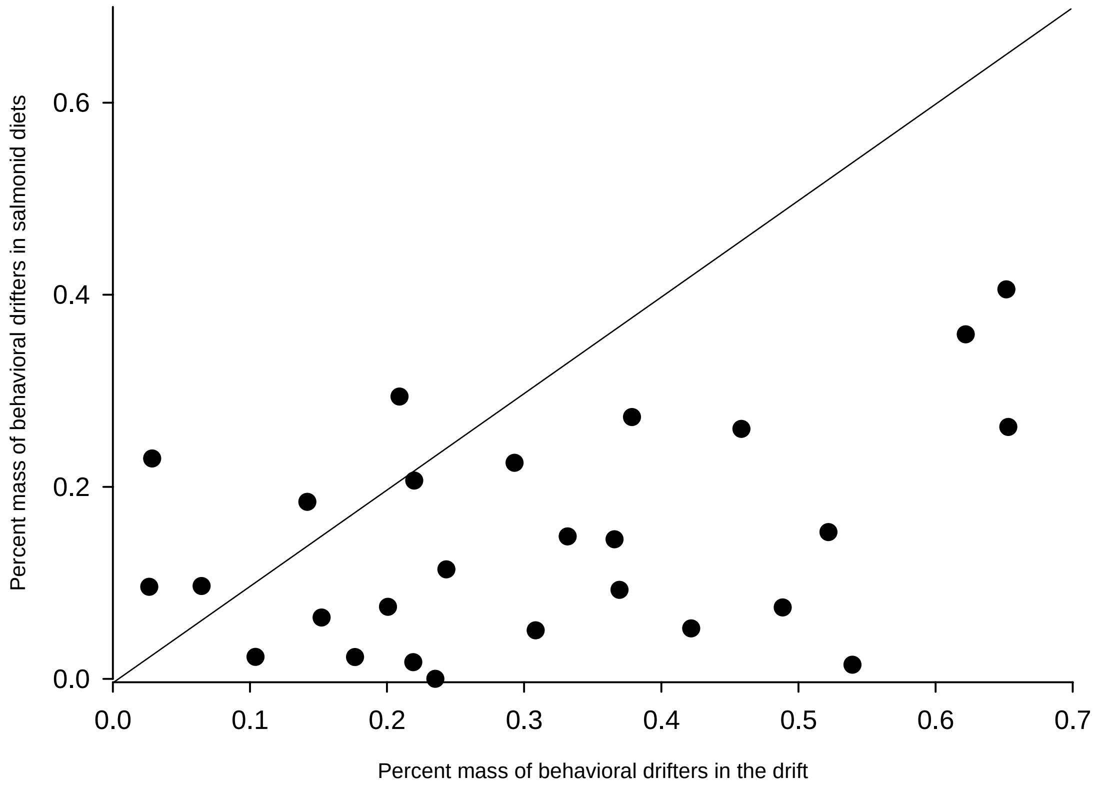

Figure 2. Mean percent mass of behaviorally drifting invertebrates in drift samples vs. mean percent mass of behaviorally drifting invertebrates in salmonid diets. Each point represents a sampling event in which 3 or more salmonids were collected for diet analysis (n = 27). A 45 degree line is included for reference to neutral electivity.

Relationship between salmonid growth and the abundance of behavioral drifting invertebrates in the drift

The percent mass of behaviorally drifting invertebrates in drift samples was positively correlated with salmonid growth rates in the summer/early fall of 2002 (R^2=0.43, Figure 3). A relationship was not found during the winter/early spring of 2003 (R^2= 0.026, Figure 4).

The relationships between salmonid growth and the total mass of drifting invertebrates (Figures 5, 6) and the mass of behaviorally drifting invertebrates (Figures 7, 8) were also examined, in an attempt to explain the seasonal significance found between the percent mass of behaviorally drifting invertebrates in the drift samples and the salmonid growth rates in the summer/early fall (Figure 3). No significance was found in any of these relationships. Inspection of Figures 3, 5, and 7 reveals that the highest growth – highest percent behavioral drift datum in Figure 3 corresponded with very low total drift (Figure 5) and an intermediate concentration of behavioral drift (Figure 7). For Figure 3, $R^2 = 0.43$ with the highest growth – highest percent behavioral drift datum included and $R^2 = 0.05$ with the datum excluded.

I concluded that the abundance of behaviorally drifting invertebrates was not an adequate predictor of salmonid growth within the streams in this study.

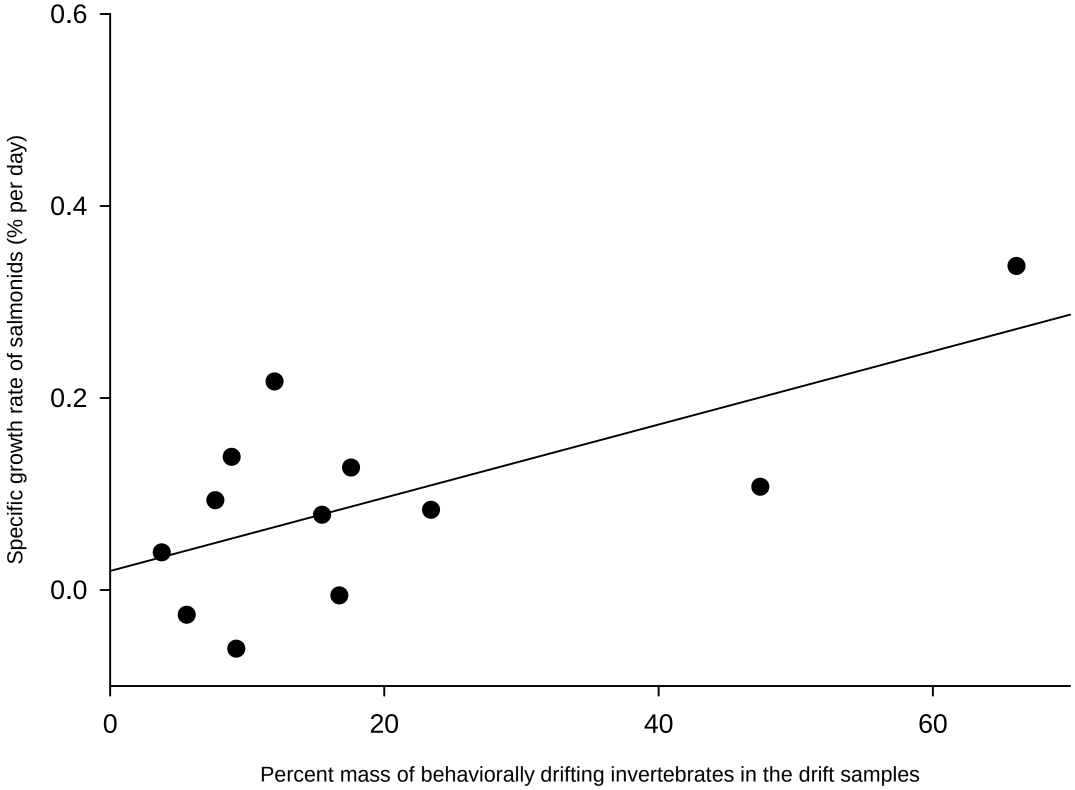

Figure 3. Relationship between the percent mass of behaviorally drifting invertebrates in the drift and the specific growth rates of salmonids during summer/early fall 2002. Each point represents a sampling reach (n=12). The percent mass of behaviorally drifting invertebrates represents the mean of 6 samples for each site.

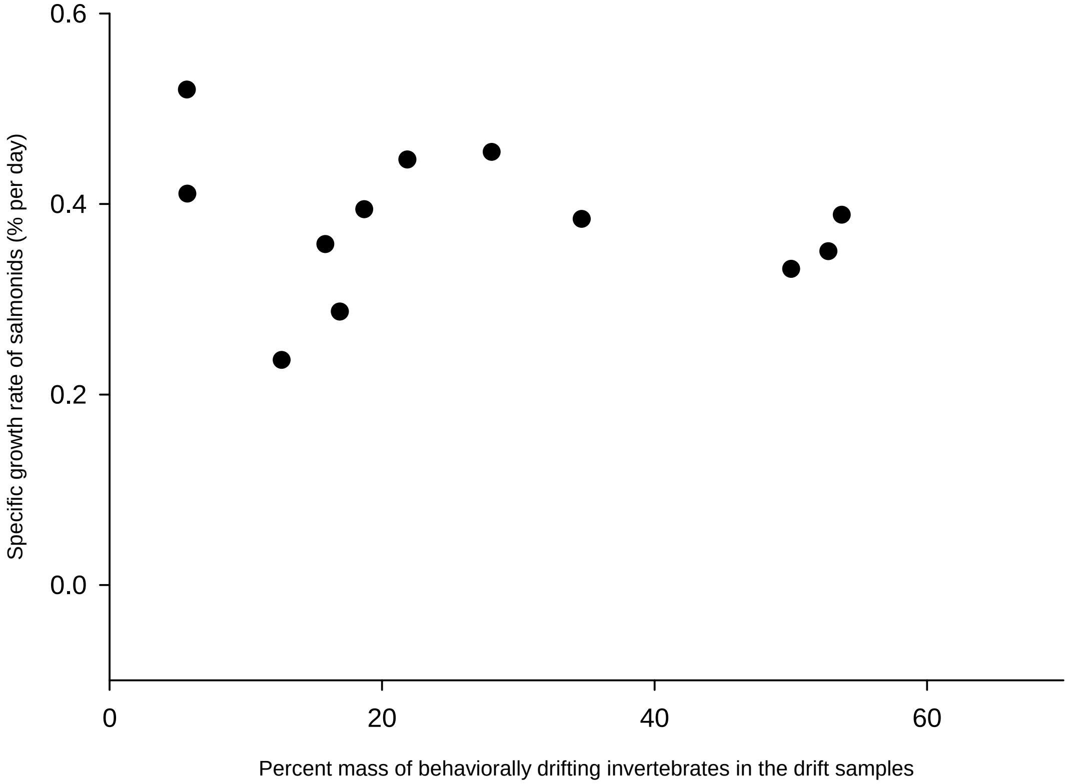

Figure 4. Relationship between the percent mass of behaviorally drifting invertebrates in the drift and the specific growth rates of salmonids during winter/early spring 2003. Each point represents a sampling reach (n=12). The percent mass of behaviorally drifting invertebrates represents the mean of 6 samples for each site.

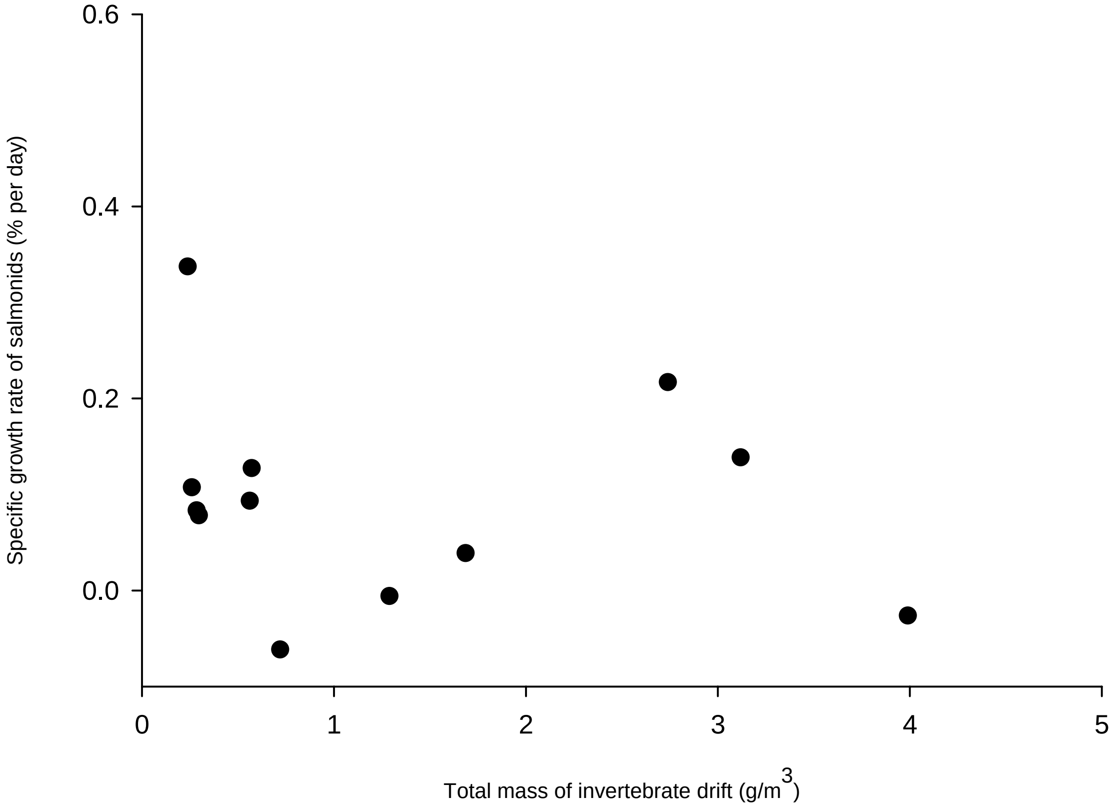

Figure 5. Relationship between the total mass of invertebrates in the drift and the specific growth rates of salmonids during summer/early fall 2002. Each point represents a sampling reach (n=12). The mass of drifting invertebrates represents the mean of 6 samples for each site.

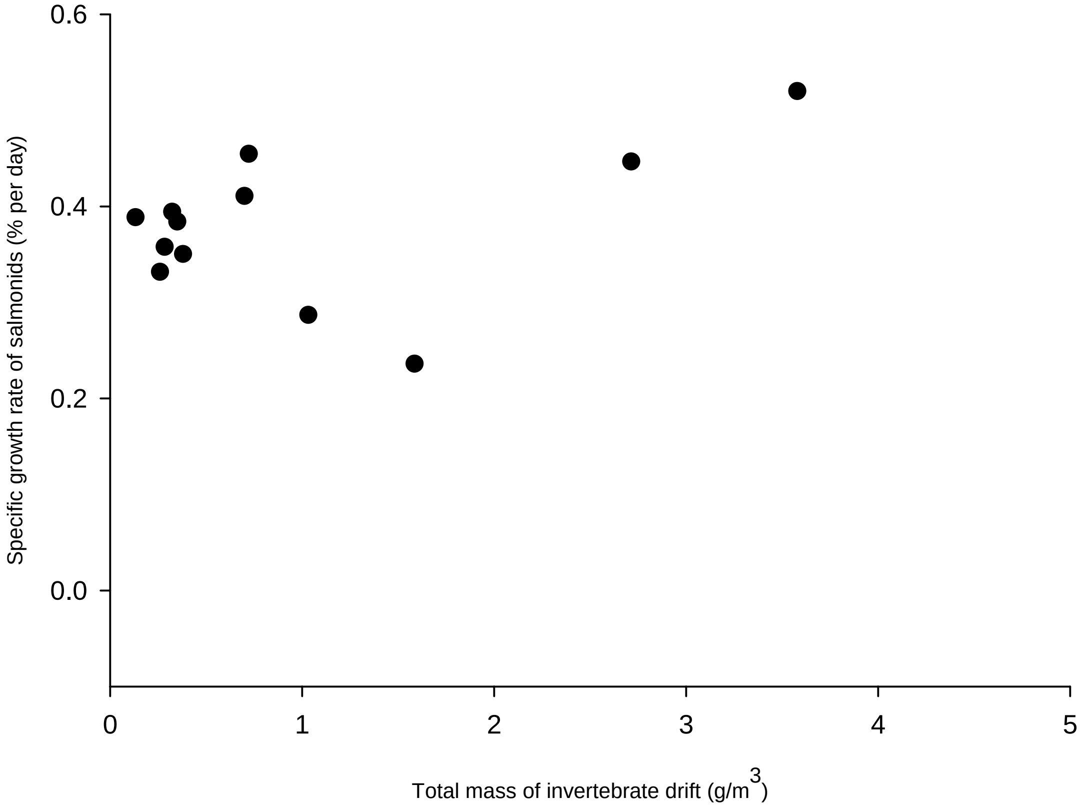

Figure 6. Relationship between the total mass of invertebrates in the drift and the specific growth rates of salmonids during winter/early spring 2003. Each point represents a sampling reach (n=12). The mass of drifting invertebrates represents the mean of 6 samples for each site.

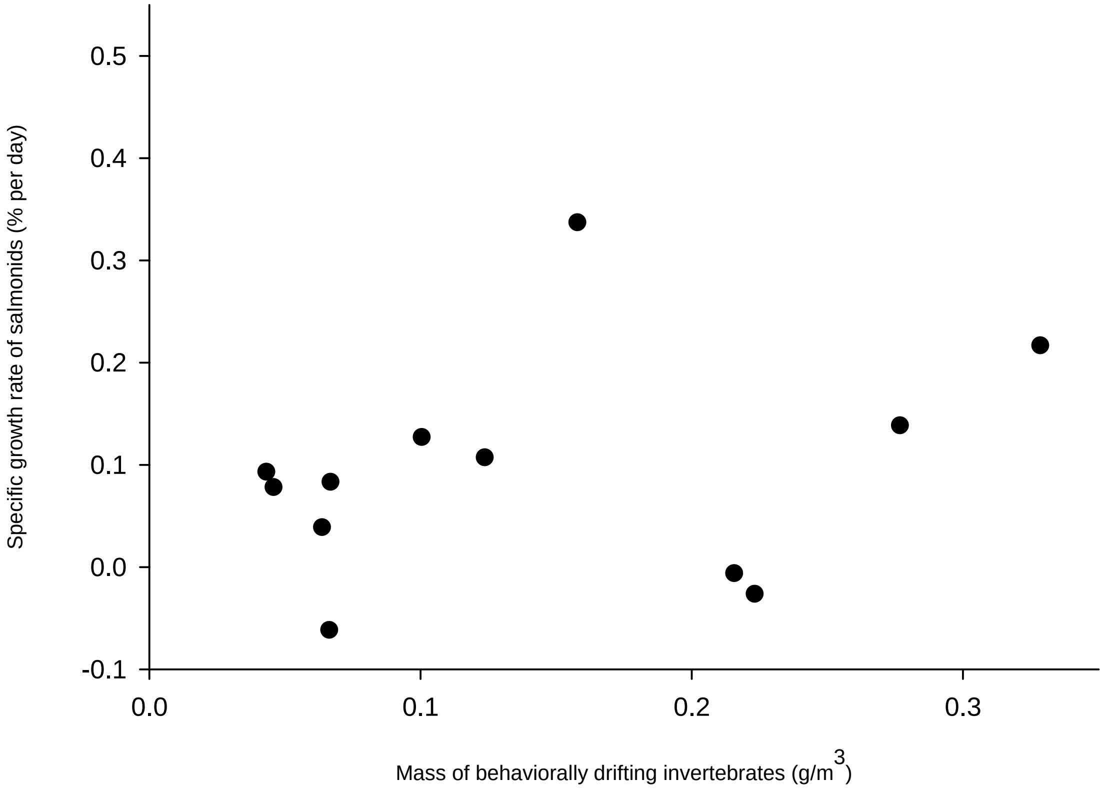

Figure 7. Relationship between the mass of behaviorally drifting invertebrates in the drift and the specific growth rates of salmonids during summer/early fall 2002. Each point represents a sampling reach (n=12). The mass of behaviorally drifting invertebrates represents the mean of 6 samples for each site.

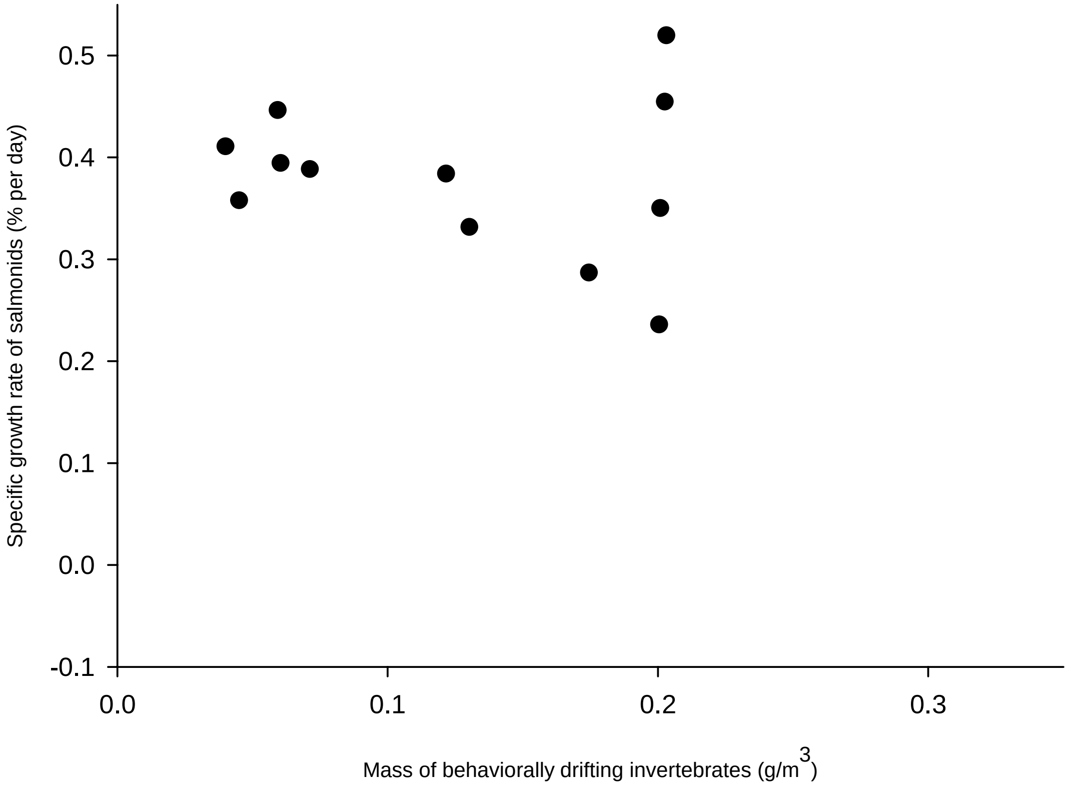

Figure 8. Relationship between the mass of behaviorally drifting invertebrates in the drift and the specific growth rates of salmonids during winter/early spring 2003. Each point represents a sampling reach (n=12). The mass of behaviorally drifting invertebrates represents the mean of 6 samples for each site.

DISCUSSION

Weak similarities between the salmonid stomach contents and either the drift or the benthic samples were found in these study sites, although taxonomic composition of salmonid diet samples was found to be more similar in composition to the drift than to the benthos. This is consistent with my first hypothesis that the contents of the salmonid diets would resemble the drift more so than the benthos, however, the similarity index values for both drift and benthos were relatively low indicating a weak biological significance. These low similarity values suggest that neither samples from the drift nor the benthos are able to fully depict the amount of food available to trout in the streams in this study. The insufficiency of benthic samples of macroinvertebrates to characterize the amount of food available to higher trophic levels is consistent with previous studies (Allen 1951, Poff and Ward 1991, Wootton et al. 1996, de Crespin de Billy and Usseglio-Polatera 2002). Other studies (Allan 1981, Angradi and Griffith 1990), have also found that macroinvertebrate drift is not well correlated with feeding activity of stream-dwelling salmonids. These studies suggest that opportunistic fish feeding behavior, terrestrial inputs and time of day that sampling is conducted may all contribute to this difficulty of precisely characterizing trout diets using either the macroinvertebrate community in the drift or the benthos.

Contrary to my hypothesis that the proportion of behaviorally drifting invertebrates in salmonid diet samples would correspond to the proportion found in the drift, on most sampling events salmonids did not appear to select for this particular group of invertebrates. Additionally, a correlation between the growth rate of the juvenile salmonids and the percent of behaviorally drifting invertebrates in the drift was not found. Lack of support for these hypotheses suggests that criteria other than diel predictability of occurrence, such as prey size and ease of capture, may be more important in prey selection by salmonids, or it may reflect limitations of the study.

Potential limitations of the study include inadequate numbers of diet and (or) drift samples, lack of correspondence between diet contents and fish consumption patterns, and incomplete designation of all behaviorally drifting taxa. For example, although I sought a minimum of 10 diet samples per reach on each sampling event, this goal was rarely met because of minnow trap inefficiency and failure to locate sufficient numbers of trout while electro-fishing. Given the opportunistic nature of salmonid feeding (Bridcut and Giller 1995, Grant and Noakes 1987, Dill 1983), the small number of samples analyzed was likely not representative of the fish population. Similarly, two drift samples per reach on each date may have been insufficient to adequately characterize drift composition. Allan and Russek (1985) found that 6-7 replicates were required to obtain 95% confidence limits ± 50% of the mean for an abundant mayfly (Baetis *bicaudatus*). Logistic constraints and the narrow stream width of the study sites made further replication problematic.

Another potential limitation of my study is that fish diet samples were taken only during the period of dusk. They may not have adequately represented fish feeding over a 24-hour period. For example, fish could have been selecting for the behaviorally drifting invertebrates during the 2 hour sampling period, but the stomach contents may have been dominated by invertebrates consumed earlier in the day. In a 24-hour trout diet study by Angradi and Griffith, 1990, an increase in the relative wet weight of stomach contents was shown during the time of day preceding the diel increase in invertebrate drift. Many of the invertebrates found in this study's diet samples were of terrestrial origin and can potentially contribute up to 91% of a salmonid's prey during certain times of the year (Kelly-Quinn and Bracken 1990, Bridcut and Giller 1995). This group of invertebrates, which potentially peak in availability earlier in the day (Elliot 1970), may have over shadowed any selectivity for behavioral drifting invertebrates during the sampling time period in my study. Further study of diel drift and salmonid feeding patterns is required to adequately evaluate the relationship between proportions of behavioral drifters in the drift and in fish diets.

A third potential limitation of this study is that incomplete classification of behaviorally drifting invertebrates may have also led to their underestimation in my analyses. Certain taxa or early instars of certain taxa (e.g. *Nemouridae, Lepidostoma*) that were frequently found in the diet samples may have been actively entering the water column but were not classified as behavioral drifters. Such behavior of their early instars has not been reported. Confirmation of this would necessitate collection of drift periodically over 24 hour periods. Categorizing all terrestrial insects as accidental drifters may also be problematic. I classified as terrestrial both those taxa in which all life stages are terrestrial and the adults of insects whose nymphal or larval stages are aquatic. Many aquatic insects, particularly within the orders Ephemeroptera, Plecoptera Trichoptera and Diptera emerge on a diel pattern and re-enter the water as spent adults with the same diel pattern (Leonard and Leonard 1962). Thus many adult aquatic insects should probably be classified as part of the behavioral drift as well.

Variable stream condition could also be a factor in the lack of predictable invertebrate drift patterns. Current velocity has been shown to have a strong effect on drift patterns of aquatic invertebrates (Elliot 1968, Borchardt and Statzner 1990). The streams in this study are characterized by low summer flows and turbid, higher velocity winter flows. The higher winter flows may be causing more catastrophic invertebrate drift and could allow the salmonids to feed on many different prey items, including those of terrestrial origin, that are not normally available in summer. Alternatively, low summer flows may be restricting the invertebrates' ability to actively enter the drift thus forcing the salmonids to focus on alternate prey sources.

In conclusion, this study has shown that invertebrate drift composition is not well correlated with salmonid stomach contents, macroinvertebrates currently classified as behaviorally drifting do not appear to be actively selected by salmonids, nor does their proportional representation in the drift account for salmonid growth. As such, the relative percent of behavioral drift is insufficient as an index of prey availability. The opportunistic feeding behavior of juvenile salmonids may preclude the use of a simple index of food supply. Adding to the difficulty of assessing prey availability is stream flow variability, seasonal and diel abundance of other prey sources, and incomplete taxonomic classification. A more complete understanding of these subjects is an essential step that needs to be taken in order to accurately predict availability of prey sources for juvenile salmonids.

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APPENDIX A
Species list with occurrence by site and sample.

Taxon	Streams	Drift	Benthos	Stomachs
Collembola	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Ephemeroptera				
Ameletidae				
Ameletus	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Baetidae				
Baetis	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Ephemerellidae				
Caudatella	Tectah,Savoy	X		
Drunella	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Ephemerella	Tectah,Peacock	X		
Serratella	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Timpanoga	Tectah,Peacock,Rowdy,Savoy	X	X	X
Heptageniidae				
Cinygmula	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Epeorus	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Ironodes	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Rhithrogena	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Stenonema	Tarup		X	
Leptophlebiidae				
Paraleptophlebia	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Odonata				
Gomphidae	Tarup,Peacock,Savoy	X	X	
Plecoptera				
Capniidae				
Eucapnopsis	Peacock,Rowdy		X	
Chloroperlidae				
Kathroperla	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	
Suwallia	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Sweltza	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Leuctridae				
Despaxia	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Moselia	Tectah,Little Mill,Peacock	X	X	X
Nemouridae				
Malenka	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Nemoura	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Zapada	Tarup,Tectah,Little Mill,Rowdy,Savoy	X	X	X
Peltoperlidae				
Sierraperla	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Soliperla	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X

Appendix A. Species list with occurrence by site and sample (continued).

Taxon	Streams	Drift	Benthos	Stomachs
Perlidae				
Calineuria	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Claassenia	Tectah,Peacock		X	
Perlodidae				
Calliperla	Tarup,Tectah,Peacock,Rowdy,Savoy	X	X	
Isoperla	Tarup,Tectah,Savoy			X
Pteronarcyidae				
Pteronarcys	Peacock,Rowdy,Savoy	X	X	
Hemiptera				
Gerridae	Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Veliidae	Tectah,Rowdy,Savoy		X	X
Megaloptera				
Sialidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Trichoptera				
Apataniidae				
Apatania	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Brachycentridae				
Micrasema	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Calamoceratidae				
Heteroplectron	Tarup,Tectah,Peacock,Rowdy,Savoy	X	X	X
Glossosomatidae				
Glossosoma	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Hydropsychidae				
Hydropsyche	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Parapsyche	Little Mill,Rowdy,Savoy		X	X
Hydroptilidae				
Hydroptila	Rowdy		X	
Palaeagapetus	Little Mill,Peacock,	X		
Lepidostomatidae				
Lepidostoma	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Limnephilidae				
Allocosmoecus				
Cryptochia	Tarup	X		
Dicosmoecus	Tectah,Little Mill,Savoy	X	X	X
Ecclisomyia	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Homophylax	Tarup,Tectah,Little Mill,Rowdy	X		X
Hydatophylax	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Philocasca	Little Mill,Rowdy	X	X	
Psychoglypha	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Odontoceridae				

Appendix A. Species list with occurrence by site and sample (continued).

Taxon	Streams	Drift	Benthos	Stomachs
Nerophilus	Tectah		X	
Philopotamidae				
Chimarra	Tarup,Tectah		X	
Dilophilodes	Tectah,Little Mill,Peacock,Rowdy	X	X	X
Polycentropidae				
Polycentropus	Tarup,Little Mill,Peacock	X	X	
Rhyacophilidae				
Rhyacophila	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Sericostomatidae				
Gumaga	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Uenoidae				
Neophylax	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Neothrema	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Coleoptera				
Carabidae	Peacock			X
Chrysomelidae	Tarup,Tectah,Little Mill,Peacock,Savoy	X	X	X
Curculionidae	Tectah,Rowdy,Savoy	X		X
Dytiscidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Elmidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Gyrinidae	Savoy	X		
Hydraenidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X		X
Hydrophilidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X		X
Psephenidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Staphylinidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Diptera				
Blephariceridae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Ceratopogonidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Chironomidae				
Chironomini	Tarup		X	
Diamesinae	Rowdy,Savoy	X		
Orthocladinae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Tanypodinae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Tanytarsini	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Culicidae	Savoy	X		
Dixidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Empididae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Pelecorhynchidae	Little Mill,Peacock,Rowdy,Savoy		X	X
Ptychopteridae	Little Mill			X
Psychodidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Simuliidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X

Appendix A. Species list and occurrence by site and sample (continued).

Taxon	Streams	Drift	Benthos	Stomachs
Tipulidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Other Aquatic and Terrestrial				
Pleuceridae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Pulmanota	Tectah,Little Mill,Rowdy			X
Amphipoda	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Aphidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Arachnidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Chilopoda	Tarup,Tectah,Little Mill,Peacock,Savoy	X	X	X
Cicadelidae	Tarup,Tectah,Peacock,Rowdy,Savoy	X		X
Copepoda	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	
Decapoda	Little Mill	X		
Diplopoda	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X		X
Formicidae	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy			X
Hirudenia	Tarup,Tectah,Rowdy		X	
Hydracarina	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy			
Hymenoptera	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X		X
Isopoda	Tarup,Little Mill,Peacock,Rowdy,Savoy	X		X
Oligochaeta	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Orthoptera	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X		X
Ostracoda	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	
Pentatomidae	Little Mill,Savoy	X		X
Pseudoscorpiones	Tarup,Little Mill,Peacock,Rowdy,Savoy	X		X
Psocoptera	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Salamander	Tarup,Rowdy,Savoy			X
Fish Fry	Tarup,Tectah,Peacock			X
Thysanoptera	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X		
Lepidoptera	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Ephemeroptera (Adults)	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X		X
Plecoptera (Adults)	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X
Trichoptera (Adults)	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X		X
Diptera (Adults)	Tarup,Tectah,Little Mill,Peacock,Rowdy,Savoy	X	X	X

APPENDIX B

Regression coefficients (a, b) used in estimation of biomass (W) from length (L) measurements of invertebrate taxa using the formula $W=aL^b$.

Coefficient a	Coefficient b	Invertebrate taxa (larvae, unless noted)
0.001230	3.580	Ephemeroptera (imagos, subimagos, nymphs) Ameletidae Baetidae Copepoda
0.001849	3.763	Leptophlebiidae
0.001849	3.457	Ephemerellidae
0.003857	3.253	Heptageniidae
0.002809	3.036	Plecoptera (adults) Leuctridae Capniidae Perlodidae Chloroperlidae Diplura Thysanoptera
0.002581	2.993	Nemouridae Collembola
0.004303	3.061	Perlidae Isopoda (terrestrial and aquatic) Diplopoda Chilopoda Amphipoda Decapoda
0.001043	3.246	Megaloptera Odonata
0.001282	3.265	Hydropsychidae Philopotamidae Lepidoptera (aquatic larvae)
0.002934	3.243	Brachycentridae Lepidostomatidae Odontoceridae
0.002299	3.079	Apataniidae Calamoceratidae Limnephilidae Uenoidae
0.000591	3.686	Rhyacophilidae

Appendix B. Regression coefficients (a, b) used in estimation of biomass (W) from length (L) measurements of invertebrate taxa using the formula $W=aL^b$ (continued).

Coefficient a	Coefficient b	Invertebrate taxa (larvae, unless noted)
0.006885	2.958	Glossosomatidae Hydroptilidae
0.001453	3.611	All Aquatic Coleopteran Larvae
0.005875	2.809	Lepidoptera (terrestrial larvae)
0.001210	3.371	Simuliidae
0.000115	3.478	Aquatic Diptera (pupae) Ptychopteridae Tipulidae
0.001135	2.7508	Aquatic Diptera (larvae) Blephariceridae Psychodidae Ceratopogonidae Dixidae Empididae Pelecorhynchidae Chironomidae Gastropoda
0.047360	2.681	All Aquatic Coleopteran Adults Carabidae (terrestrial adults)
0.037140	2.366	Diptera (aquatic adults) Arachnida (terrestrial) Psocoptera Aphidae
0.004651	2.4222	Chironomidae (adults) Chironomidae (pupae)
0.049887	2.27	Gerridae Veliidae Pentatomidae
0.036589	2.696	Orthoptera Cicadellidae
0.017792	2.572	Formicidae
0.020838	2.407	Lepidoptera (terrestrial pupae) Hymenoptera (terrestrial)
0.023969	0.356	Diptera (terrestrial larvae)
0.039726	2.761	Hydracarina Ostracoda Salamander Fish Fry

Appendix B. Regression coefficients (a, b) used in estimation of biomass (W) from length (L) measurements of invertebrate taxa using the formula $W=aL^b$ (continued).

Coefficient a	Coefficient b	Invertebrate taxa (larvae, unless noted)
0.044780	2.929	Pseudoscorpiones
0.085350	0.216	Coleoptera (terrestrial larvae)
0.017650	2.903	Lepidoptera (terrestrial adults) Trichoptera (adults) Trichoptera (pupae)
0.287200	1.000	Hirudinea Oligochaeta Turbellaria