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**INVERTEBRATE PHENOLOGY AND PREY SELECTION OF THREE
SYMPATRIC SPECIES OF SALMONIDS;
IMPLICATIONS FOR INDIVIDUAL FISH GROWTH**

A Thesis Presented

by

JEFFREY VEIKKO OJALA

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTERS OF SCIENCE

February 2008

Wildlife and Fisheries Conservation

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SYMPATRIC SPECIES OF SALMONIDS;
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ABSTRACT

INVERTEBRATE PHENOLOGY AND PREY SELECTION OF THREE SYMPATRIC SPECIES OF SALMONIDS; IMPLICATIONS FOR INDIVIDUAL FISH GROWTH

FEBUARY 2008

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Growth plays an important roll in the survival of individual salmonid fish. Diet inevitably plays a significant role in the determination of salmonid growth, with these diets consisting primarily of aquatic macroinvertebrates, predominately insect taxa. Aquatic insects have a complex life history with most having a short, aerial adult period and an aquatic juvenile stage(s). The periodicity of this juvenile stage (voltinicity) can take a few months to a few years, with the vast majority lasting a single year. These numerous and overlapping phenologies therefore have a significant impact on the availability of prey that salmonid fish find profitable.

Variation in the availability and use of macroinvertebrate prey may be an important determinant of growth variation in stream salmonids. However, few studies possess the requisite information to make these links explicitly, particularly for more than one co-occurring species. Drift and benthic invertebrate availability and selection were measured for three sympatric species of stream salmonids (Atlantic salmon, brook trout, and brown trout) in a long-term study site at West Brook, Whately MA through out 2003.

Benthic macroinvertebrates were found to have a strong seasonal cycle of size and abundance in West Brook. Consistent with the numerical domination of univoltine

aquatic insects in this stream, relatively few large, individuals are present in the spring

prior to the peak of adult emergence, with many small, individuals in the fall. This

phenology combined with abiotic factors (discharge, temperature) has significant effect

on the availability of profitable salmonid prey.

Examining the role of prey selection revealed that salmonid fish were able to

capitalize on this seasonal abundance. Additionally, salmonid species were shown to

change foraging tactics from drift feeding to the consumption of both benthic and

terrestrial derived prey. These results suggest that spring is a period of high prey

abundance producing a common pattern of high consumption and growth for all three

species. Among-species differences in diet are most manifest during periods of resource

scarcity. These results indicate that seasonal dynamics in physical conditions and

invertebrate phenology may combine to produce a critical period for individual growth in

stream salmonids.

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SEASONAL VARIATION IN ABUNDANCE, DIVERSITY, AND SIZE

DISTRIBUTIONS OF MACROINVERTEBRATES

Abstract

Variation in the availability of macroinvertebrate prey may be an important determinant of growth variation in stream salmonids. I measured drift and benthic invertebrate availability for three sympatric species of stream salmonids (Atlantic salmon, brook trout, and brown trout) in a long-term study site at West Brook, Whately MA. Drift and benthic invertebrates were collected during sampling bouts spaced at three-month intervals within an eight day window for each bout, at three times of day. Benthic macroinvertebrates were found to have a strong seasonal cycle of size and abundance in West Brook. Consistent with the numerical dominance of univoltine aquatic insects in this stream, relatively few, large, late-instar individuals are present in the spring prior to the peak of aquatic insect emergence, with many, small, early-instar individuals in the fall. The propensity of benthic invertebrates to leave the benthos and enter the drift was effectively predicted by the Rader (Rader 1997) drift model, indicating that the habitat and behavior of invertebrates was critical in determining their availability to drift-feeding salmonids. Consistent with seasonal variation in the growth rates of all three salmonid species, drift biomass (biomass per time) was low in summer, in spite of high numerical invertebrate abundance, because invertebrates were small and stream discharge was low. Conversely, during high salmonid-growth periods in the spring, drift biomass flux rates were significantly higher. These results indicate that seasonal dynamics in physical conditions

(flow, temperature) and invertebrate phenology may combine to produce a highly

seasonal pattern of growth in stream salmonids.

<u>Introduction</u>

Reflecting the highly seasonal nature of north temperate stream environments, growth of

stream-dwelling salmonid fishes differs greatly among seasons (Letcher *et al.* 2002).

Low temperatures, low light levels, and consequent low invertebrate productivity

generally result in low or negative growth during the north temperate winter (Metcalfe &

Thorpe 1992). However, there appears to be considerable variation with respect to when

maximum growth rates occur, even when temperature is considered. Frequent sampling

of individually-marked fish with high capture rates has enabled estimation of unbiased

growth rates of three sympatric salmonid species in the long-term study at West Brook,

Massachusetts, USA (Carlson & Letcher 2003, Letcher & Gries 2003). These studies

clearly demonstrate that growth in all three species is highly concentrated in the spring,

between April and June, with growth rates declining to near zero throughout the rest of

the year. Interestingly, these high growth rates occur when frequently high and

occasionally turbid flows may increase foraging costs (Nislow *et al.* 1999, Sweka &

Hartman 2001). Although inter-annual variation exists, in individual fish growth rates,

the underlying pattern has been consistent for close to a decade (Letcher personal

communication).

Seasonal variation in the availability of invertebrate prey may be an important

determinant of salmonid growth variation in West Brook and other small coldwater

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streams where aquatic insects are the major prey items (Allan 1981). Growth of salmonid fish has been shown to correspond to the abundance of drifting invertebrate prey populations (Wilzbach *et al.* 1986, Erkinaro & Niemelä 1995). As salmonids are opportunistic (feed on abundant prey), size selective (tend to feed on larger prey items) and visual foragers (Allan 1981), invertebrate phenology and diel periodicity can strongly influence availability to salmonids.

The low annual survival rates as well as high fecundity and taxonomic diversity of aquatic insects has led to varied and overlapping seasonal phenologies that strongly influence patterns of size and abundance (Merritt & Cummins 1996). Additionally, variation in species emergence times can change insect community density, biomass and diversity rapidly. Further, the Allan paradox suggests that autochthonous production is insufficient to support apparent fish growth in most streams (Waters 1988). Without accounting for seasonal variation and aquatic and terrestrial derived resources, the influence of prey on salmonid growth opportunity may be underestimated.

Invertebrates also vary in their availability to salmonids via differences in their propensity to enter the water column via drift. Drift feeding is the dominant mode of foraging for most stream salmonids (Allan 1981, Rader 1997). Drift propensity varies by taxa, density, and environmental conditions, therefore seasonal variation should strongly influence drift availability. To account for these influences, Rader (1997) developed a model to predict taxon-specific drift propensity. The model takes into consideration; propensity to intentionally drift, likelihood of being accidentally dislodged by the current,

drift distance, adult drift, benthic exposure, and body size to arrive at a base score which is then modified by an abundance factor. Taxa with high scores are predicted to be found frequently in the drift and, as a consequence, to be strongly represented in salmonids diets. Propensity to drift would then be an appropriate proxy for the likelihood of a prey type to be encountered and potentially consumed during visual foraging. Field testing of this model has been conducted in Colorado, by Rader, and California by Esteban and Marchetti (2004). Esteban and Marchetti found drift propensity scores to be correlated with stomach contents but not to drift densities. Variations in regional invertebrate dynamics and stream bed geomorphology could have an impact on the applicability of the drift propensity model. To date no test of the drift propensity model has been conducted in the northeastern US or over multiple seasons. In addition to the behavioral, morphological, and life-history factors that influence propensity to drift, it has been long established that many invertebrates drift more frequently at night (Brittain & Eikeland 1988), with the largest (and potentially most attractive to salmonid predators) having the most pronounced diel patterns. There is little known about how diel variation in drift differs among seasons. However, given this uncertainty, it is essential to effectively characterize and encompass diel variation in any study of seasonal variation.

This study quantified seasonal and diel variation of instream macroinvertebrate assemblages with respect to taxonomic composition, size structure and biomass. Further, it measured seasonal and diel variation in invertebrate flux (numerically and in biomass) for the drifting fraction of the population. Comparisons were made between variation found in these populations to the seasonal variation in individual fish growth rates.

Finally, it evaluated the ability of the Rader drift propensity model to predict the drifting portion of the total insect population of West Brook.

Methods

Study Site

West Brook is a 6.3 km long, third order stream in the middle Connecticut river basin located near the town of Whately, Massachusetts, USA (42°25', 72°40'). This stream is described in Letcher & Gries (2003) and has an average gradient of 2% and an annual median discharge of 0.7 m^3/s. The study section is located approximately 3 km downstream of a drinking water reservoir, making the numerous small tributaries below the dam the primary source for summer flows. Flow regime is typical of New England streams, with high spring flows, low summer flows (which are exacerbated by the presence of a water supply dam upstream of the study area), rising and more variable flow in the fall, followed by low flow with variable ice cover in the winter. Summer temperatures are moderated by groundwater influence and shading, rarely exceeding a daily average of 18˚ C. The brook consists predominantly of long stretches of riffle and glide interspersed with short pools. The long-term study site at West Brook (the data source for season-specific salmonid growth rates) consists of a 1 km study section and associated 1-2nd order tributary streams. In order to avoid impact on the long-term study, the invertebrate sampling was conducted in a 520 m section of stream approximately 1.75 km downstream of the long-term site. These study sections were broken into four 100 m sample sites with an approximately 40 m buffer between each sampled section. The sites were generally similar in physical characteristics except in one area where a dirt road

runs the length of the river right bank, occasionally leaving only a few meters between it and the stream. Consequently, there are large open canopy patches and periodic inputs of fine sediment and road salt in that area. These open patches are in the bounds of the study site but are found within the 40 m buffer section and not the sampled stream segments.

Three species of salmonids, Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) co-occur in West Brook and make up over 95% of the fish in the stream with a few blacknose dace (*Rhinichthys atratulus*) encountered in both the long term and diet study sites. Slimy sculpin (*Cottus cognatus*) and American eel (*Anguilla rostrata*) are present but infrequent in either site. Resident brown trout and brook trout are maintained by natural reproduction. Anadromous Atlantic salmon, originally native to the Connecticut river basin, were extirpated in the 1850's due to the installation of large scale hydro-electric dams (Gephard & McMenemy 2004). At West Brook, each spring, Atlantic salmon fry (~ 26 mm fork length) are stocked into the stream. Stocks are from regional hatcheries and are added at a density of approximately 50/100 m^2. Atlantic salmon smolts leave the system, on average, after two years in the stream with no naturally occurring breeding population (Letcher *et al.* 2002). Three species of aquatic salamanders are also present but are not common.

<u>Invertebrate phenology & diel periodicity</u>

Collections of stream invertebrates were taken in five sampling efforts over an average of five days (range 2 - 8 days) from April to December of 2003 (Table 1.1). For each date,

one 100 m section was sampled at each time period; sun up, mid-day, sun down and midnight. A ~ 40 m buffer between sections was created where no sampling activity occurred. Due to low water temperatures (< 1° C) in December, only two separate mid-day samples were conducted for this sampling.

At each sampling section a 500 μm mesh drift net was deployed for 20 minutes in a representative riffle habitat at the top of the sampled stream section. In order to determine the water volume sampled, measurements were conducted at the net opening for water depth by hand ruler, and water velocity measured with a Swoffer 2100-14 flow meter (Swoffer Instruments Inc. Seattle WA 98188). At the same time, a sample of the benthic invertebrate fauna was collected slightly downstream from the drift net. The sample was collected with a Surber sampler (0.3 m^2 frame size, mesh size 500 μm) by hand washing all of the cobble within the sample frame and stirring fine substrate, also by hand, for two minutes. Invertebrate samples were placed in storage containers with stream water and kept cool until returning to the lab. Upon return to the lab (approximately 0.5 hr trip) field samples were frozen in a -5° C freezer, allowing for the preservation of the samples without altering tissue structure or size (Benke *et al.* 1999). Aquatic invertebrates were identified, to family, under a dissecting microscope as described by Peckarsky *et al*. (1990); terrestrial-derived prey were identified to family as described in the bug guide network (Bartlett 2002) Individuals were measured for total body length (excluding cerci) to the nearest tenth of a millimeter by one of two comparable methods. Depending on equipment availability, some animals were measured by ocular micrometer, while others were digitally imaged by microscopy and

measured with the use of Image Tool (UTHSCSA v 3.0, 2002), image analysis software. Invertebrate dry mass was calculated using length-weight regressions from Benke *et al.* (1999) and Sabo *et al.* (2002). Individuals from a given sample were transferred into vials of the same family and preserved with 70% EtOH. Unless otherwise stated, insects identified in this study were in their juvenile (larval or nymphal) stage.

Hypotheses and statistical analyses

H1: Abundance, size and diversity of benthic and drift invertebrates will be greatest when salmonid growth rates are highest

To test this hypothesis an analysis of variance (ANOVA) was conducted, with Tukey's test for unequal n for post-hoc comparisons of significant results. In order to meet the assumptions of normality, variables were log-transformed, except for sample diversity where an arc-sin transformation was used.

Individual fish growth is measured by calculating the difference in size at capture less its size at the previous capture. This study used growth data from the long term population study at West Brook providing measures of growth over the course of a year at approximately two month intervals. As a result the invertebrate response variables were compared among monthly samples (April, June, September, and December) and also between early season (the high fish growth interval, April and June combined) and late season (the low fish growth interval, September and December combined). Invertebrate assemblage attributes were expressed in several different ways. Numerical density is the

number of individuals per unit area (m^2) for benthic invertebrates, or per unit volume (m^3) for drift. Individual size is an important attribute, as trout are generally size-selective in their foraging (Allan 1981). In this study it was expressed as mean individual length (mm), across invertebrate taxa for a given sampling bout. Biomass density (mg m^{3-1} drift, mg m^{2-1} benthic) integrates numerical density and individual size. Invertebrate drift flux was calculated in two ways, biomass flux (mg hr^{-1}) and numerical flux (# hr^{-1}), which can be more relevant than drift density as a measure of drift prey availability to salmonids. Invertebrate diversity was calculated using the Shannon - Wiener index (H):

$$H = -\sum p_i \log p_i$$

where p_i is the proportion of any given taxon (Hauer & Lamberti 1996). Richness (S) as the taxa count and evenness of the invertebrate community (E) was assessed with the Tramer (1969) method:

$$E = H / \log S$$

H2: Abundance, size and diversity of benthic and drift invertebrates will be greatest at night when aquatic insect drift has been shown to be most frequent.

To test this hypothesis, an analysis of co-variance (ANCOVA) was used, combing the methodology and metrics described above with the addition of time of day as a co-variant. In instances where no seasonal variation was detected, sample month was removed creating a more parsimonious ANOVA model. A bootstrap resampling was performed for these analyses (SYSTAT 11) as only one sample was collected at each time of day.

H3: Rader drift propensity model will accurately predict drift assemblages at West Brook

To examine the role of drift propensity in salmonid diets, the Rader (1997) drift propensity model was used to test whether the propensity of invertebrate taxa to enter the drift is an important determinant of salmonid diet choice in West Brook. If this model was unable to accurately predict the portion of the benthic community likely to be found in the drift, its ability to predict salmonid diets would be less likely. Drift propensity is the likelihood that a given taxon will be found in the water column as opposed to the benthos. This likelihood is based on morphological and behavioral traits of a given taxon that influence the probability of entrainment in the stream flow. Propensity base scores for a large range of taxa are given in Rader (1997). In some instances the model calls for identification to genus: as this study only identified drifting invertebrates to family, an average for the entire family was used. This approach was justified as variation among genera, within families is minimal. Final drift propensity scores are derived from base scores that are multiplied by an abundance factor. The abundance factor was calculated from the collected benthic data and gives weight to those taxa commonly encountered; this ranking was based on monthly densities. Rare taxa were those found with ten or fewer individuals. In order for a taxon to be considered abundant, it had to fit two criteria: 1) the taxon is present in all samples for the given month. 2) The number of individuals belonging to that taxa were greater then the mean number of individuals in all taxa of that month. Taxa with counts greater than ten but not meeting the abundant criteria were classified as common. In evaluating the effectiveness of the Rader model

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for West Brook, a Spearman's rank correlation analysis was used. This analysis

correlated invertebrate abundance in drift samples with the drift propensity score.

Significantly positive rank correlations indicate that the model is an effective predictor of

invertebrate drift.

Results

Invertebrate abundance, size and diversity

Benthic

Benthic macroinvertebrates demonstrated among sample month variation in both density

($F = 31.85$, $df = 3, 3$, $P = 0.009$) and size ($F = 108.941$, $df = 3, 1968$, $P < 0.001$). The

pattern revealed fewer (mean 185.0 m^{-2}) larger (mean 5.2 mm) late-instar individuals in

April and many (2011.7 m^{-2}, Tukey's $P = 0.008$) smaller (3.4 mm, Tukey's $P < 0.001$)

individuals in August, with intermediate values in June, returning to few (383.3 m^{-2})

larger (7.7 mm) individuals in December (Fig. 1.1). Sample biomass was relatively

uniform at around 215 mg m^{-2} (SE 57.9) ($F = 5.0$, $df = 3, 3$, $P = 0.108$), except in August

when the large number of early instar individuals greatly increased biomass to 1018.9 mg

m^{-2} (SE 325.8). Invertebrate diversity was higher during the June and August samples

than at other times of the year ($F = 44.538$, $df = 3, 3$, $P = 0.005$, Tukey's $P \leq 0.048$, Fig.

1.2). Numerically the population was dominated by chironomid midges (Diptera:

Chironomidae) and typically one or two families of mayflies (Ephemeroptera) through

out the year. Otherwise all taxa present were found in low numbers regardless of time of

year (Table A-1).

Drift

Drift numerical density (number m^{-3}) and numerical flux (number hr^{-1}) showed no statistically significant among sample month variation ($F = 0.807$, $df = 3$, 10, $P = 0.518$ and $F = 1.00$, $df = 3$, 10, $P = 0.432$ respectively), with an average of 8 m^{-3} (SE 1.8) and 534 hr^{-1} (SE 2.0). Similarly, drift biomass density (mg m^{-3}) was not statistically significant among sample months ($F = 2.65$, $df = 3$, 10, $P = 0.448$). The overall drift biomass density trend demonstrated that small incremental declines, from the April maxima, are continuous through the year (Fig. 1.3); with a mean biomass of 4.4 mg. Drift diversity was not statistically significant among sample months ($F = 1.27$, $df = 3$, 10, $P = 0.332$) with a mean Shannon-Wiener index of 26.5 (Fig. 1.2). In contrast, length of drifting prey varied significantly across sample months ($F = 25.42$, $df = 3$, 2354, $P < 0.001$), being highest in April and December (mean 4.2 mm, SE 0.2 Tukey's $P = 0.912$) declining in June (mean 3.6 mm, SE 0.1) with the lowest values in August (mean 3.1 mm, SE 0.1, Tukey's $P < 0.001$). As a consequence, biomass flux (mg hr^{-1}) demonstrated significant seasonal variation when early sample periods were compared to late ones ($F = 9.44$, $df = 1$, 12, $P = 0.010$, Fig. 1.4). The mean biomass flux rate in the early season (April and June) was 480.0 mg hr^{-1} (SE 1.6) and 75% lower in the late season (August and December, mean 120.0 mg hr^{-1}, SE 0.6).

Diel variation

No statically significant diel variation was found for any sample month for benthic samples. Drift densities and flux rates did not differ among sample months. Some significant diel variation in invertebrate size was observed, but differences were not

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consistent across sample months. In April size was highest in mid-day samples (mean

5.8 mm, SE 0.28) with all other times of day equal to one another (Tukey's $P \geq 0.695$).

In June mean length was highest in mid-day samples (mean 4.2 mm, SE 0.24), lower but

equal in morning and midnight samples and lowest in evening samples (mean 2.78 mm,

SE, 0.06, Tukey's $P \leq 0.030$). Mean invertebrate size in August was highest at midnight

(mean 4.2 mm, SE 0.26) with other sample periods shown to be the same (Tukey's $P \geq$

0.853). In December size was larger in the morning sample than at mid-day ($F = 20.30$,

$df = 1, 153, P < 0.001$, Fig. 1.5).

<u>Drift propensity</u>

The Rader drift propensity model was an effective predictor of drift density in every

month but December (Table 1.2). Excluding December, the Spearman's rank correlation

mean ρ was 0.566 (range 0.564 – 0.567 $P < 0.001$). During the December sample the

correlation between drift density and drift score was very low ($\rho = 0.155$) and not

statistically significant ($P = 0.5$). Only four taxa were inconsistent with the model. Two

of these (capniid stoneflies and glossosomatid caddis) were found in only a single drift

sample. Elmid beetles and ephemerellid mayflies which were found more frequently,

were consistently assigned a higher drift propensity rank then warranted by drift

abundance.

Discussion

The results of this research show that distinct seasonal trends in macroinvertebrate

abundance and diversity exist at West Brook. This pattern is consistent with expected

patterns of a system dominated by univoltine insects as described by Merritt & Cummins (1996) with few, large individuals present in the spring prior to adult emergence, contrasting many small recently hatched, early instar individuals during the summer, returning to fewer larger individuals, as cohorts thin, through the winter and following spring. The spike in biomass is likely due to these numerous recently hatched individuals. The rapid decrease in biomass, due to departure of large mature individuals, is consistent with other studies as described by Merritt & Cummins (1996) (life history-pp 41-73) and references therein. Greater diversity during the June sample is possibly driven by hyporheic species nearing the substrate surface in preparation for emergence (Merritt & Cummins 1996).

As the benthic macroinvertebrate community is considered the source of the drift assemblage, seasonal patterns found in the benthic population were expected to be found in the drifting. There were no significant differences in drift density among sample months in West Brook, and no differences in numerical flux rate. However, there were significant differences in both the mean size of drifting invertebrates, and in biomass flux rates, that were largely concordant with the general pattern of salmonid growth. These findings are consistent with Allan *et al*. (1987) who found that drift rate (analogous to drift flux) is best predicted by discharge while density remains independent of discharge. These results suggest that the high rate of salmonid growth (Carlson & Letcher 2003, Letcher & Gries 2003) may be driven by the combination of influx of large prey size and high encounter rates associated with high spring flows. By contrast, during low-growth

periods, prey are frequently below salmonid detection limits, and low stream discharge reduces encounter rate.

Diel variation, other than individual length, in the drifting invertebrate population was not detected. This is in contrast to common results as summarized in Brittain & Eikeland (1988). Additional sampling across the range of the lunar cycle may be required to determine the true nature of diel variation of drifting insects at West Brook. Changes in individual length show that available prey are largest during the crepuscular periods in the early season when salmonid foraging is greatest (Allan 1981). An increase in size of prey during August evening samples is consistent with Allan (1984) and may also contribute to the nocturnal habits of Atlantic salmon found by Gries *et al*. (1997) and Johnston & Bergeron (2004).

The Rader (1997) drift propensity model was effective in predicting drift assemblages in all but the December sample. This suggests that it has the potential to predict the diets of drift foraging salmonids. Its inability to predict December drift assemblages is not unexpected as temperatures near freezing would significantly alter insect physiology and behavior (Merritt & Cummins 1996). The efficacy of this model could, potentially, be increased by the application of its reproductive components during the time of year when a given taxa is actively engaged in the reproductive life stage. Further an additional component that used stream discharge as a modifier similar to that of abundance may increase the ability of this model to predict taxa with intermediate base drift scores.

Predictive power of ephemerilld mayfly drift might improve with greater taxonomic resolution (Rader 1997).

The macroinvertebrate population at West Brook demonstrated trends that are indicative of univoltine dominated systems for the benthic community; however, the drift assemblages showed little of the anticipated variation. Although biomass flux is elevated in the spring, decreased capture success at higher current velocities could diminish the capacity of salmonid fish to detect and capture prey (Hill & Grossman 1993, Nislow *et al.* 1999). Collectively these elements suggested that invertebrate phenology, coupled with abiotic factors, may affect fish growth, but without accounting for prey selection, no direct link can be established.

Table 1.1. Summary of macroinvertebrate samples conducted at West Brook. Standard errors are listed in parentheses.

Median Sample Date	Mean Discharge $(cm*s^{-1})$	Benthic Biomass (mg)	Benthic Density (n)	Drift Biomass $(mg*m^{-3})$	Drift Flux Biomass $(mg*min^{-1})$	Drift Density $(n* m^{-3})$	Drift Flux Numerical $(n*min^{-1})$
26- April 2003	0.805	165.1 (93.82)	185.0 (58.33)	6.0 (2.96)	7.9 (1.69)	7.1 (3.37)	8.8 (2.90)
19-June 2003	0.197	226.2 (11.949)	898.3 (121.67)	5.3 (1.65)	8.1 (3.10)	11.4 (4.52)	15.1 (5.60)
25-Aug 2003	0.030	1018.9 (286.88)	2011.6 (201.67)	3.4 (1.19)	2.2 (0.87)	9.4 (3.74)	7.2 (4.32)
19-Dec 2003	0.338	349.1	383.3	0.7 (0.01)	1.45 (0.35)	1.8 (0.30)	3.9 (1.5)

Table 1.2. Spearman's rank correlation coefficients and probability estimates for drift samples and drift propensity score for each sample month for West Brook.

Sample Type	April		June		August		December	
	rho	P	rho	P	rho	P	rho	P
Drift	0.567	0.001	0.564	0.001	0.566	0.001	0.155	0.500

Figure 1.1. Monthly variation in benthic macroinvertebrate density and mean individual length collected at West Brook. Columns indicate density and the solid line indicates length. Asterisks indicate significant difference in length from the preceding month. Dashed line indicates non significant difference in density from the preceding month by Tukey's post hoc testing. Error bars are standard errors.

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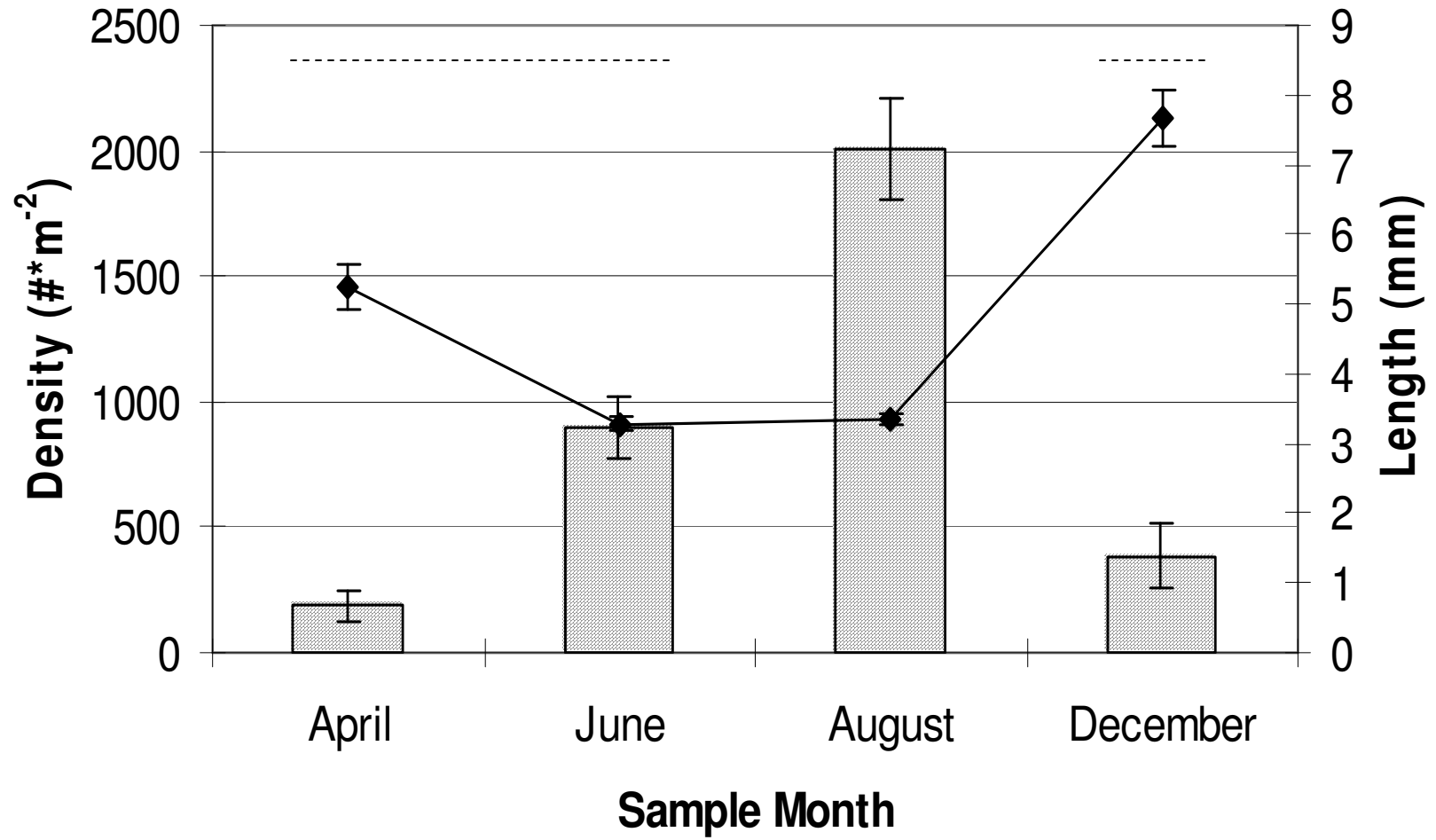
Figure 1.2. Monthly variation in macroinvertebrate Shannon – Wiener diversity index for both the benthic and drift communities from West Brook. Dashed line indicates non-statistically significant differences in benthic diversity by Tukey's post hoc testing. Error bars are standard error.
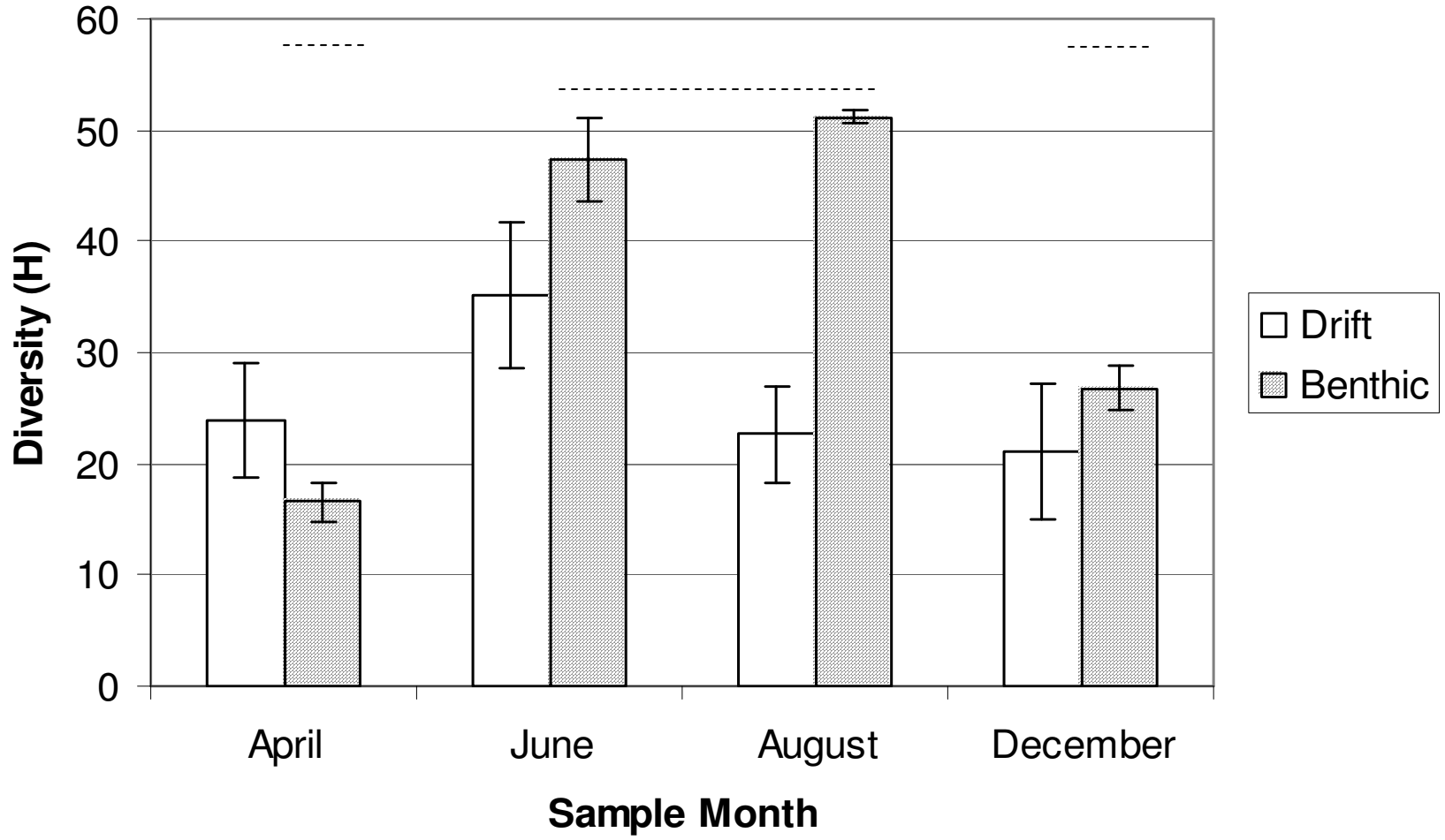
Figure 1.3. Monthly variation in drift biomass density in West Brook. Error bars are standard errors.
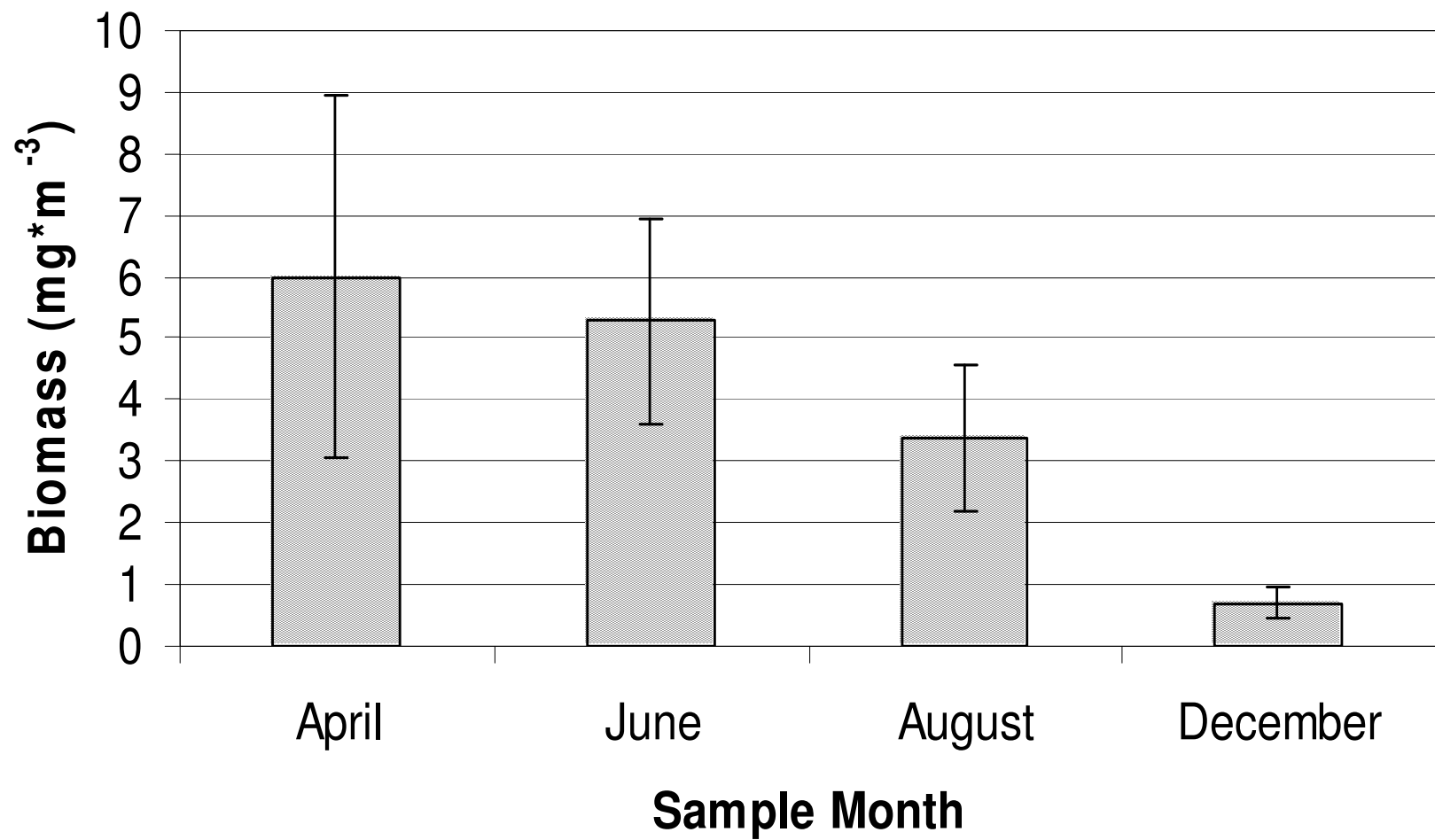
Figure 1.4. Monthly variation in drift flux by biomass (bars) and the mean individual length (line) of drifting macroinvertebrates from West Brook. Error bars are standard errors.
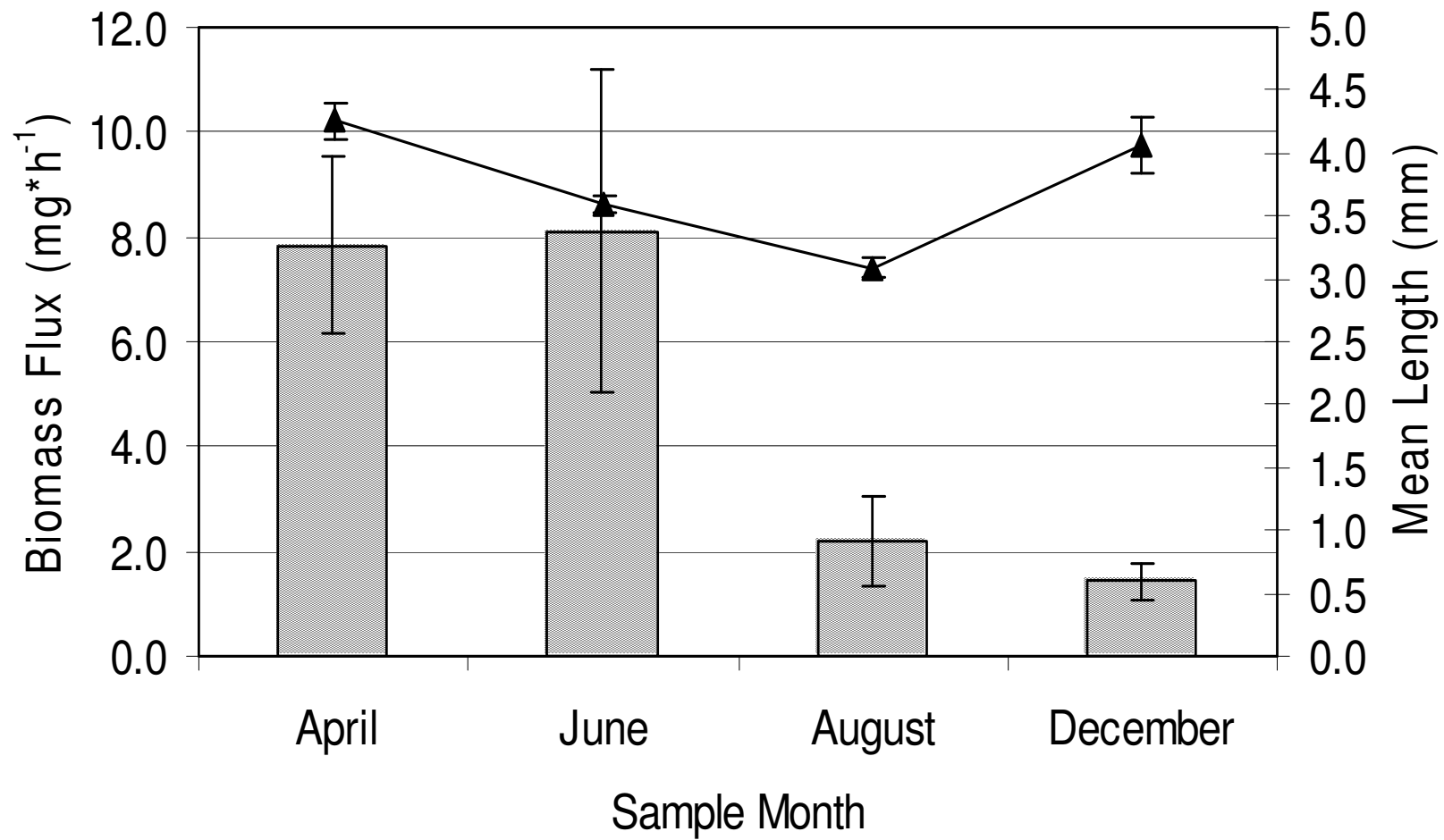
Figure 1.5. Variation in the mean individual length of drifting macroinvertebrates broken down into diel sample events from West Brook. Morning samples are labeled 'AM', mid-day samples 'MID_D' evening samples 'PM' and midnight samples 'MID_N'. Error bars are standard errors.
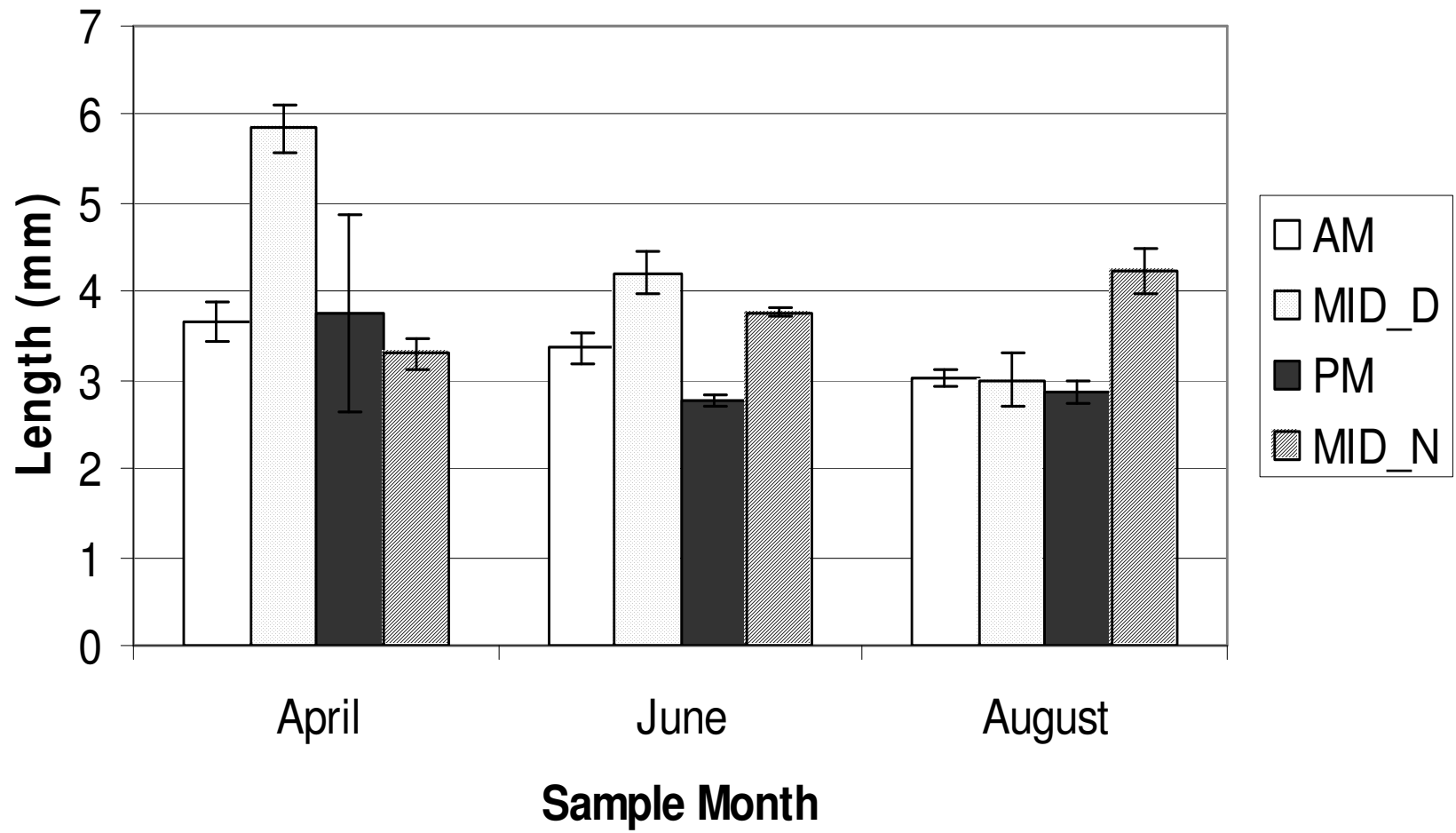
CHAPTER 2

SEASONAL VARIATION IN THE DIETS OF SYMPATRIC BROOK TROUT,

BROWN TROUT, AND ATLANTIC SALMON IN RELATION TO PREY

AVAILABILITY

Abstract

Variation in the selection of macroinvertebrate prey may be an important determinant of

growth variation in stream salmonids. However, few studies possess the requisite detailed

information (multiple recaptures of marked individual fish, frequent samples of

invertebrate prey availability and use) to make these links explicitly. We tested the

relationship between macroinvertebrate use and seasonal variation in the growth rates of

three sympatric species of stream salmonids (Atlantic salmon, brook trout, and brown

trout) in a long-term study site at West Brook, Whately MA. Drift and benthic

invertebrate samples and fish stomach contents were collected at three month intervals,

within an eight day window, and for three time periods at each interval. I found that

positive selection of prey taxa was limited to few (typically one) taxa for any given

month. Dietary overlap among salmonid species and gut fullness of all three species was

greatest during high salmonid-growth sample periods. During high-growth periods, drift

propensity was a strong predictor of the importance of invertebrate taxa in the diets of all

three salmonid species. In contrast, during the summer, as the availability of aquatic-

insect derived drift was reduced, all three species underwent diet shifts. Brook trout and

brown trout used a higher proportion of terrestrially-derived prey, while Atlantic salmon

diets contained a high proportion of benthic invertebrates which were rarely found in the

drift, suggesting that they were feeding directly on the benthos. These results suggest that spring is a period of high prey resource abundance (invertebrate drift) producing a common pattern of high consumption and growth for all three species. Among-species differences in diet, likely reflecting differences in habitat and behavior were most manifest during periods of resource scarcity.

Introduction

Reflecting the highly seasonal nature of north temperate stream environments, growth of stream-dwelling salmonid fishes differs greatly among seasons (Letcher *et al.* 2002). There is general consensus that low temperatures, low light levels, and consequent low invertebrate productivity result in low or negative growth during the north temperate winter (Metcalfe & Thorpe 1992). However, there appears to be considerable variation with respect to the time when maximum growth rates occur, even when temperature is considered. Complicating this issue, most studies use apparent growth (change in mean individual size) as a proxy for real growth (changes in individual size over time), with consequent biases associated with size-selective mortality (Juanes *et al.* 2000). Studies that measure individual growth of a large unbiased sample of a population are rare, despite their ability to increase understanding of the causes and consequences of salmonid growth variation. Further, most studies focus on single populations, with detailed studies of co-occurring species conspicuously lacking. Without accounting for species interactions, single population growth models may underestimate the role of prey during periods of low availability (Hurlbert 1978).

Frequent sampling of individually-marked fish with high capture rates has enabled estimation of unbiased growth rates of three sympatric salmonid species in the long-term study at West Brook, Massachusetts, USA (Letcher & Gries 2003, Carlson *et al.* 2004). The study has clearly demonstrated that growth in all three species is highly concentrated in the spring, between April and June, with growth rates declining to near zero through the rest of the year. Interestingly, these high growth rates occur when frequently high and occasionally turbid flows may increase foraging costs (Nislow *et al.* 1999, Sweka & Hartman 2001). Although some inter-annual variation exists, the underlying pattern has been consistent for close to a decade (Letcher personal communication).

Aquatic insects are the major prey items in north temperate streams (Allan 1981), and drift feeding is the dominant mode of foraging for most stream salmonids (Allan 1981, Rader 1997). The propensity for aquatic insects to drift varies by taxa, density, and environmental conditions; therefore seasonal variation should strongly influence drift availability. To account for these influences, Rader (1997) developed a model which predicts taxon-specific drift propensity. The model takes into consideration propensity to intentionally drift, likelihood of being accidentally dislodged by the current, drift distance, adult drift, benthic exposure, and body size to arrive at a base score which is then modified by an abundance factor. Taxa with high scores are predicted to be found frequently in the drift, and as a consequence, to be strongly represented in salmonid diets. Propensity to drift would then be an appropriate proxy for the likelihood of a prey type to be encountered and potentially consumed. Field testing of this model has been conducted in Colorado, by Rader, and in California by Esteban and Marchetti (2004). In California

drift propensity scores were correlated with stomach contents but not with drift densities (Esteban & Marchetti 2004). While the Rader model has the potential to be widely applicable, variations in regional invertebrate dynamics, hydroclimatology and stream geomorphology require region specific tests. To date no test of the drift propensity model had been conducted in the northeastern United States or in multiple seasons in any region.

Previous studies examining the interactions between salmonid prey choice, consumption and growth have yielded a range of results. Cada *et al*. (1987) found that during the summer, invertebrate drift rates were low and trout switch primarily to terrestrially-derived prey. Further, they suggest that this leads to a period of limited growth during summer for rainbow trout in southern Appalachian streams. Sotiropoulos *et al*. (2006) found similar trends for brook trout in some New England streams where they were the only salmonid species present. Kreivi *et al*. (1999) found that brown trout rations in Finnish streams were highest in June and August and declined through the rest of the year. Additionally they found an effect for time of day where brown trout fed at crepuscular periods, when invertebrate availability was highest. Without the use of mark recapture, the above studies are limited to the use of apparent growth, when considering the impact of diets on the respective fish populations. Cunjak (1992), using tattoo marking that indicated the initial location of an individual fish, was able to narrow growth estimates by excluding the effect of immigrants. Atlantic salmon parr showed maximum fullness in June, with a decrease through the rest of the year. It was not possible, however, to distinguish losses from survival or emigration potentially biasing

late season results. Grader & Letcher (2006) studied juvenile Atlantic salmon in West

Brook and found a direct correlation between seasonal drift availability, gut fullness and

individual salmon growth. These studies provide an excellent framework in which to

correlate fish diets to individual growth but did not consider resource competition among

salmonid species.

In this study, the goal is to determine the relationship between salmonid prey selection

and salmonid growth in West Brook, by linking seasonal variation in prey choice and

prey consumption with observed growth patterns for the co-occurring species.

To achieve this goal the following objectives were investigated: 1) Evaluate seasonal

variation in salmonid diets and gut fullness. 2) Test the ability of the Rader drift

propensity model to predict prey importance in this system.

Methods

Study site

West Brook is a 6.3 km long, third order stream in the middle Connecticut river basin

located near the town of Whately, Massachusetts, USA (42°25', 72°40'). This stream is

described in Letcher & Gries (2003) and has an average gradient of 2% and an annual

median discharge of 0.7 m^3/s. The study section is located approximately 3 km

downstream of a drinking water reservoir, making the numerous small tributaries below

the dam the primary source for summer flows. Flow regime is typical of New England

streams, with high spring flows, low summer flows (which are exacerbated by the

presence of a water supply dam upstream of the study area), rising and more variable

flow in the fall, followed by low flow with variable ice cover in the winter. Summer

temperatures are moderated by groundwater influence and shading, rarely exceeding a

daily average of 18° C. The brook consists predominantly of long stretches of riffle and

glide interspersed with short pools. The long-term study site at West Brook (the data

source for season-specific salmonid growth rates) consists of a 1 km study section and

associated 1-2nd order tributary streams. In order to avoid conflicts with the long-term

study, the diet sampling was conducted in a 520 m section of stream approximately 1.75

km downstream of the long-term sites. For this study, sections were broken into four 100

m sample sites with an approximately 40 m buffer between each sampled section. The

sites are generally similar in physical characteristics, except where a dirt road runs the

length of the river right bank, occasionally leaving only a few meters between it and the

stream. This results in large open canopy patches and periodic inputs of fine sediment

and road salt. These open patches are in the bounds of the study site but are found within

the 40 m buffer section and not the sampled stream segments.

Three species of salmonids, Atlantic salmon (*Salmo salar*), brook trout (*Salvelinus*

fontinalis) and brown trout (*Salmo trutta*) co-occur in West Brook and make up over 95%

of the fish in the stream. A few blacknose dace (*Rhinichthys atratulus*) were encountered

in both the long term and diet study sites. Slimy sculpin (*Cottus cognatus*) and American

eel (*Anguilla rostrata*) are present but infrequent in either site. Resident brown trout and

brook trout are maintained by natural reproduction. Anadromous Atlantic salmon,

originally native to the Connecticut river basin, were extirpated in the 1850's due to the

installation of large scale hydro-electric dams (Gephard & McMenemy 2004). At West

Brook, each spring, Atlantic salmon fry (~ 26 mm fork length) are stocked into the stream. Stocks are from regional hatcheries and are added at a density of approximately 50/100 m^2. Atlantic salmon smolts leave the system, on average, after two years in the stream with no naturally occurring breeding population (Letcher *et al.* 2002). Three species of aquatic salamanders are present but are not common. Macroinvertebrate communities are dominated by aquatic insects, representing all aquatic orders, with crayfish and freshwater mollusks rarely encountered (see chapter 1).

Field collection

Collections of stream invertebrates and salmonid gut contents were taken in five sampling efforts, lasting an average of five days (range 2 - 8 days), from April to December 2003 (Table 2.1). For each date one 100 m section was sampled at each time period; sun up, mid-day, sun down and midnight. A ~ 40 m buffer between sections was created where no sampling activity occurred. Due to low water temperatures (< 1° C) in December only two separate mid-day samples were conducted for this sampling.

After completion of invertebrate sampling, the section was electro-fished with a backpack electroshocker for a single pass in a downstream to upstream direction. All overyearling (≥80 mm fork length) salmonids were retained in buckets of stream water and held in live cages submerged in the stream. If a single pass did not collect a minimum of 30 individuals, a second pass was conducted until 30 were obtained. Shock effort, sample start time and duration, and water temperature were recorded. Total stream discharge data collected 2 km above this study site were provided from USGS-BRD collaborators.

Fish were taken from in-stream pens to a stream-side work station, where they were anaesthetized in a solution of clove oil and stream water (0.04 ml L^{-1}) (Cho & Heath 2000), identified to species, weighed to the nearest tenth of a gram, and measured for fork length to the nearest millimeter. Fish were then gastricly lavaged by methods described by Sotiropoulos *et al*. (2006). Guts contents were retained in zipper style bags with a fish data tag and kept on ice until returned to the lab. Fish were then placed back into live wells, allowed to recover until they were actively swimming, and then returned throughout the study section.

Laboratory procedures

Upon return to the lab (approximately 0.5 hr trip) field samples were frozen in a -5° C freezer, allowing for the preservation of the samples without altering tissue structure or size (Benke *et al.* 1999). Aquatic invertebrates were identified, to family, under a dissecting microscope as described by Peckarsky *et al*. (1990); terrestrial-derived prey were identified to family as described in the bug guide network (Bartlett 2002). Dietary items that were unidentifiable due to an advanced state of digestion were excluded from the sample. Individuals were then measured for total body length (excluding cerci) to the nearest tenth of a millimeter by one of three comparable methods. Depending on equipment availability, some animals were measured by ocular micrometer, while others were digitally imaged by microscopy and measured with the use of image analysis software. One lab set up included the Image Pro application (Media Cybernetics Inc v 4.5, 2002) while the other used Image Tool (UTHSCSA v 3.0, 2002). Invertebrate dry mass was then calculated using length-weight regressions from Benke *et al*. (1999) and

Sabo *et al*. (2002). Individuals from the given fish were then transferred into vials of the same family and preserved with 70% EtOH. Unless otherwise noted, the identified insect taxa were in immature (larval or nymphal) form.

Hypotheses and statistical analyses

H1: Gut fullness and prey consumption will be greatest during high growth intervals

To test the hypothesis that gut fullness and consumption rates differed significantly across months, analysis of variance (ANOVA) was used. The contribution of diet to seasonal growth variation was examined by comparing the changes in dietary metrics, of each salmonid species to known patterns in seasonal fish growth. Variation was assessed monthly, with the months of April and June considered to be part of the high growth period and August and December the low growth period (Carlson & Letcher 2003, Letcher & Gries 2003). In order to account for the expected increase in prey size and stomach volume with increasing fish size consumption metrics were divided by the wet weight of fish.

Response variables include abundance (number gut^{-1} gram (of fish)$^{-2}$), gut mass (mg gut^{-1} gram (of fish)$^{-2}$), individual prey size and diet diversity. Diet diversity was calculated using the Shannon - Wiener index (H):

$$H = -\sum p_i \log p_i$$

where p_i is the proportion of any given taxon (Hauer & Lamberti 1996). Richness (S) is the taxa count, and evenness of the diet (E) was assessed with the Tramer method (Tramer 1969):

$$E = H / \log S$$

Consumption rates were also calculated in both number (number per gram (of fish)$^{-1}$ per hour^{-2}) and biomass (mg per gram (of fish)$^{-1}$ per hour^{-2}). Consumption rate was calculated given the number of prey and the mass found in guts and the rate of gastric evacuation. Gastric evacuation rates were estimated through the use of two temperature dependent equations. Because salmonid diets consist of a mix of relatively soft-bodied (chironomids and some caddisflies) and harder-bodied (mayflies, stoneflies) prey, the calculation temperature-specific gastric evacuation rates are estimated by calculating the mean value between the MacNeil *et al*. (2001) amphipod model (appropriate for hard-bodied prey) and the Windell *et al*. (1976) oligochaete model (appropriate for soft-bodied prey) for the water temperature recorded at each sample. The calculated gastric evacuation rate was then applied to all fish caught at that water temperature, regardless of species.

Among-species differences in diet was assessed with Schoener's overlap index:

$$P_{jk} = [\Sigma(\text{minimum } p_{ij}, p_{ik})] \, 100$$

Where P_{jk} is the overlap, expressed as a percent, between species j and k and p_{ij}, p_{ik} = the proportion of resource i to the total resources used by species j and k. Values greater than 0.6, on the 1 point scale, were considered significant (Hurlbert 1978).

H2: Invertebrate taxa and size differ in their relative importance in fish diets.

H3: Fish select certain invertebrate taxa and size classes disproportionately to their abundance in benthic and drift samples.

Understanding the importance of specific types and sizes of prey is key to understanding the contribution of prey phenology to salmonid growth. To assess if fish select prey items on the basis of abundance, size or drift propensity, three approaches were used.

1) To test the hypothesis that prey size differed significantly across months, an analysis of co-variance (ANCOVA) was used. The contribution of prey size to seasonal growth variation was examined by comparing the changes in mean prey item size of each salmonid species by month (April, June, August, December), to known patterns (chapter 1) in variation of available prey. In tests where the covariate of fish size was not show to be statistically significant the more parsimonious ANOVA tests were conducted.

2) Cortés (1997) presented a modification of the index of relative importance (IRI) for dietary data. His modification was to make the IRI relative to itself so that it would be based on a percentage of the total index (%IRI). This allows for the direct comparison of one index to another. Cortes suggested that comparisons between elasmobranch species could then be made for items of dietary importance. Although the use of compound indices have been debated, Liao *et al*. (2001) found that the %IRI provided an optimal approach to diet analysis. This index was then used to test prey selectivity and is described by Cortés (1997):

$$IRI = (\%N + \%W)\ \%O\ \text{ and}$$

$$\%IRI = 100 * IRI\ /\ \Sigma\ IRI$$

Where the index for a given taxa is: $\%N$ – the percent number, $\%W$ – percent weight, and $\%O$ - percent occurrence of a given taxa found in fish guts. Use of this hybrid index, compared to its constituent parts, assures that no one metric over represents its importance. If a given taxa is highly abundant but very small, a percent number alone may over-represent its actual importance to fish diet.

3) Taxa that had a $\%IRI$ value of 10 or greater were then included for the calculation of the second index, Chesson's alpha. Chesson's alpha (Chesson 1978) is defined as:

$$\alpha = (r_i/p_i)\ /\ \Sigma(r_i/p_i)$$

Were r_i – the number of a given category i consumed and p_i – is the number of category i available. Values of alpha over the value of $1/k$ (k = total number of categories) indicate taxa consumed more often than would be expected by encounter rates alone. Alpha values were calculated for both the drift and the benthos to insure coverage of both prey sources. As a number of taxa can be present in either location, the drift propensity score was used to separate these groups (see below).

H4: Drift propensity increases the relative importance of invertebrates in fish diets.

To examine the role of drift propensity and salmonid diets, the Rader (1997) drift propensity model was used to test whether the propensity of invertebrate taxa to enter the drift is an important determinant of salmonid diet choice in West Brook. Drift propensity

is the likelihood that a given taxon will be found in the water column as opposed to the benthos. This likelihood is based on morphological and behavioral traits of a given taxon to, intentionally or unintentionally, become actively entrained in the stream flow. Propensity base scores for a large range of taxa are given in Rader (1997). In some instances the model calls for genera identification. As this study only identified drifting invertebrates to family, an average for the entire family was used. Final drift propensity scores are derived from base scores that are multiplied by an abundance factor. The abundance factor was calculated from the collected benthic data and gives weight to those taxa commonly encountered; this ranking was based on monthly densities. Rare taxa were those found with ten or fewer individuals. In order for a taxon to be considered abundant it had to fit two criteria: 1) The taxon was present in all samples for the given month. 2) The number of individuals belonging to that taxon were greater than the mean number of individuals in all taxa of that month. A taxon with counts greater then ten but not meeting the abundant criteria was classified as common. In evaluating the effectiveness of the Rader model for West Brook, a Spearman's rank correlation analysis was used. This analysis correlates invertebrate abundance in drift and gut samples with the drift propensity score. Significantly positive rank correlations indicate that invertebrates with a higher propensity to drift are more selected as prey items.

<center>**Results**</center>

Gut fullness and prey consumption

Gut biomass and consumption rate by biomass

Sample month was found to be a factor in gut biomass (mg gut^{-1} gram (of fish)$^{-2}$) variation in Atlantic salmon ($F = 7.996$, $df = 3$, 119, $P < 0.001$, Fig. 2.1). Gut mass was highest in April (mean 1.9 mg g^{-1}, SE 0.22) with steady declines to August (mean 0.21 mg g^{-1}, SE 0.07). December rebounded slightly to levels similar to June (mean 1.0 mg g^{-1}, Tukey's $P = 0.987$). No variation in gut biomass was detected in brook trout ($F = 0.954$, $df = 3$, 55, $P = 0.421$) with an annual mean of 2.14 mg g^{-1} (SE 0.396). Brown trout also showed no statistically significant variation in gut biomass ($F = 1.557$, $df = 3$, 194, $P = 0.201$) with an annual mean of 2.52 mg g^{-1} (SE 0.784). Although April rates were ~3 mg g^{-1} higher, this was not a statistically significant result.

Sample month was found to be a factor in rate by biomass (mg g^{-1} hr^{-2}) variation of Atlantic salmon ($F = 13.520$, $df = 3$, 119, $P < 0.001$, Fig. 2.2). Here consumption rate was highest in early sample periods (April and June, mean 4.40 mg g^{-1} hr^{-2}, SE 0.399) and 75.9% lower in later periods (August and December, mean 1.06 mg g^{-1} hr^{-2}, SE 0.323). Brown trout also demonstrated rate by biomass variation among sample months ($F = 2.894$, $df = 3$, 193, $P = 0.036$). In this instance the rate was highest in April (mean 7.27 mg g^{-1} hr^{-2}, SE 1.034), lower and equal in June and August (mean 4.15 mg g^{-1} hr^{-2}, SE 0.903) and lowest in December (mean 0.85 mg g^{-1} hr^{-2}, SE 0.435). Brook trout did not show any statistically significant variation in consumption rate by biomass ($F = 1.008$, $df = 3$, 55, $P = 0.396$) with an annual mean of 8.06 mg g^{-1} hr^{-2} (SE 1.882).

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Gut density and numeric consumption rate

Gut density (number gut^{-1} gram (of fish)$^{-2}$) exhibits among sample variation in all salmonid species ($P \leq 0.013$, see table 2.2 and Fig. 2.3). Atlantic salmon exhibit a pattern where density is highest in the early season (mean 0.88 # g^{-1}, SE 0.107) and 71.5% lower in the late season (mean 0.25 # g^{-1}, SE 0.040, Tukey's $P \leq 0.055$). In brook trout, gut density is highest in April with a mean of 1.07 # g^{-1} (SE 0.220) lower, but not statistically significant, in June (mean 0.45 # g^{-1}, SE 0.12, Tukey's $P = 0.094$) with August and December equal to June (Tukey's $P \geq 0.837$) but lower then April (Tukey's $P \leq 0.033$). Brown trout show a pattern where density is highest in April (mean 0.98 # g^{-1}, SE 0.086) lowering incrementally to an August minimum (mean 0.19 # g^{-1}, SE 0.082) with rates in December covering a range equal to all other sample periods (Tukey's $P \geq 0.205$).

Consumption rate by number (number gram (of fish)$^{-1}$ hour^{-2}) showed monthly variation among Atlantic salmon ($F = 6.739$, $df = 3, 119$, $P < 0.001$, Fig. 2.4). Here the pattern showed that consumption rate is high in the early season (mean 3.02 # g^{-1} hr^{-2}, SE 0.400) compared to late (mean 1.03 # g^{-1} hr^{-2}, SE 0.214). Brown trout consumption rate by number also demonstrated monthly variation ($F = 4.097$, $df = 3, 193$, $P = 0.008$). Here the pattern showed the rate highest in April (mean 2.63 # g^{-1} hr^{-2}, SE 0.231) incrementally declining to the December minimum (mean 0.28 # g^{-1} hr^{-2}, SE 0.088). Tukey's post hoc comparisons show that April is larger then August and December with all other times having shown no statistically significant differences for brown trout. Brook trout demonstrated no monthly variation in consumption rate by number ($F = 1.435$, $df = 3, 55$, $P = 0.243$).

Empty stomachs (guts devoid of prey) were encountered during every sample event. The percentage of fish with empty guts varied seasonally within and among salmonid species (Table 2.3). Of all fish lavaged, 9.0% were found without gut contents. A Chi^2 test showed that emptiness is unequal between the high growth (April & June) and low growth (August & December) interval ($P < 0.001$). For all species emptiness was lowest in April (mean 3.4%, range 0 – 8.8 per species) and highest in August (mean 26.3%, range 17.4 – 32.4).

Diet diversity

All measures of diet diversity showed monthly variation in Atlantic salmon ($P \leq 0.001$, see table 2.4). For all metrics the pattern was the same as that of diversity, which showed high diversity in the early season (mean 3.70, SE 0.443) and low late diversity (mean 1.37, SE 0.241, Fig. 2.5). Brook trout also exhibited this variation ($P \leq 0.008$) and pattern with mean early season high of 3.90 (SE 0.611) and late season low of 1.26 (SE 0.361). Brown trout exhibited monthly variation in diversity metrics ($P < 0.001$) but showed a slightly different pattern. Here diversity was maximized in the early season (mean 3.67, SE 0.315), minimized in August (mean 0.75, SE 0.161) while rebounding slightly in December (mean 2.15, SE 0.638).

Dietary overlap

Dietary overlap varied seasonally with overlap among all three species highest in April (range 0.63 – 0.78, Table 2.10). In June overlap ranged from 0.35 – 0.63 with the overlap of Atlantic salmon and brown trout shown to be significant (> 0.60). Overlap was never

found to be significant in August (range 0.29 – 0.51). December overlap ranged from

0.42 – 0.59, showing highest rates of overlap between Atlantic salmon and brown trout.

Prey selection

Size

Invertebrates found in salmonid guts were larger on average than invertebrates in drift

and benthic samples ($P \leq 0.001$, Fig. 2.6). Prey length (Fig 2.7) varied monthly for

Atlantic salmon ($F = 27.851$, $df = 3$, 1474, $P < 0.001$). Prey were largest in April (mean

6.4 mm, SE 0.131) with length similar in June and August (mean 4.5 mm, SE 0.175) with

December samples showing a large variance making it similar to both April and August

(Tukey's $P \leq 0.168$). Prey length varied seasonally for brown trout ($F = 20.016$, $df = 3$,

2127, $P < 0.001$) with prey length largest in December (mean 9.1 mm, SE 1.535), lowest

in June (mean 5.9 mm, SE 0.127) with intermediate and similar values in April and

August (Tukey's $P = 0.836$). Brook trout did not show any significant variation in prey

item size ($F = 1.985$, $df = 3$, 521, $P = 0.115$). Prey size was dependent on fish fork length

for brook trout ($P = 0.036$) and brown trout ($P < 0.001$) but not for Atlantic salmon ($P =$

0.700).

Index of relative importance

Using a %IRI value of 10 as a threshold value, many prey categories contributed little to

salmonid diets (Table A-3). Vertebrate prey items were excluded from this analysis as

their large mass overrepresented them in the calculations for %IRI for biomass. No taxon

was found to be of dietary importance throughout the duration of the study among or

within fish species. Taxa that ranked high were often the same among salmonids for a given sample period (Table 2.5) and were therefore used in the calculations of Chesson's alpha for that month. In April, all species showed ephemerellid mayflies to be of high importance (>23 %IRI). Heptageniid mayflies were also important in April to Atlantic salmon (38.1 %IRI) and brown trout (17.5 %IRI) but not for brook trout. In June, emergent mayflies were important to all species (>18 %IRI), while baetid mayflies were important to Atlantic salmon (60.1 %IRI) and brown trout (26.3 %IRI) only. Helicopsychid caddisflies were shown to be important to all salmonids in August (>10.8 %IRI). Terrestrial derived prey was also important to brook (65.4 %IRI) and brown trout (45.2 %IRI) at that time of year. In December, chironomid flies were important to all species (>10.7 %IRI). Also in December ephemerellid mayflies were shown to be important to Atlantic salmon (48.2 %IRI) and brown trout (38.6 %IRI), while glossosomatid caddisflies were shown to be important to Atlantic salmon (13.1 %IRI) and brook trout (17.4 %IRI).

Prey selection by Chesson's alpha

Prey taxa were most often consumed in proportion to, or slightly less than, their availability (i.e. abundance in drift and invertebrate samples). Positive selection was consistent across fish species and often limited to a single taxon at a given sample period; glossosomatid caddisflies in December, helicopsychid caddisflies in August, emergent mayflies in June. In April, Atlantic salmon and brown trout showed positive selection for heptageniid mayflies, while brook trout selected siphlonurid mayflies (Fig. 2.8 a-d). In December, neutral selection was shown for hydropsychid caddis by all fish species and

for brachycentrid caddis in brook trout. Fish showed negative selection for all other taxa included in these analyses.

Non- drift associated prey

Using the Rader (1997) drift propensity model as a guide, post hoc, a list was developed containing taxa that were not prone to drift and therefore were most likely to be encountered by fish only in the benthos (Table 2.6). Taxa with a base drift propensity score of 41 or less were considered for the list. This value classified stone cased caddis with the benthic group while free living caddis were excluded. Several taxa meet this criteria due to missing values in categories where characteristics were undefined by Rader (1997). In order to properly classify these taxa the collected drift and benthic sample data were used. A ratio of the number of a given taxon found in the drift to the benthos was calculated and those taxa with values less then one were considered benthic.

These benthic-associated prey often made up a significant portion of salmonid diets. To calculate the contribution of benthic prey to salmonid diets, the abundances of all taxa meeting the benthic-associated criteria were added together. The %IRI of this group was then tallied for among-sample comparisons. Gut samples in April and June showed low numbers of benthic-associated prey with a mean composite %IRI of 8.3 (range 0.9 – 17.5). In August, the mean rose substantially to %IRI 33.5 (range 22.2 – 44.2), with levels remaining high in December (Table 2.7).

A special category of non-drift associated prey involved consumption of vertebrates, including aquatic salamanders and non-salmonid fish. Consumption of highly mobile vertebrate prey was rare. Vertebrate prey were observed in the guts of seven individual fish (Table 2.8), encompassing four discrete prey species. Six instances were found in the largest brown trout (> 179 mm in fork length), three in April, one in August and two in December, accounting for 17.6% of brown trout in this size class. An Atlantic salmon consumed a slimy sculpin in December, the only instance of vertebrate consumption for this species.

Drift propensity

Drift propensity score correlations were always lowest in December for all groups (mean $\rho = 0.200$, range $0.144 - 0.358$, Table 2.9). Atlantic salmon gut densities were well correlated with drift scores ($P < 0.05$) throughout the year ranging from an April high ($\rho = 0.528$) to a December low ($\rho = 0.344$) (mean $\rho = 0.587$). Brook trout diets were also favorably predicted by drift score ($P < 0.02$, mean $\rho = 0.464$). Brown trout guts were accurately predicted for April and June (mean $\rho = 0.471$) but not for August (Table 2.9).

Discussion

Results of the diet analysis show that peak fullness for the three salmonid species is at or near maximum in the early season (April & June), corresponding to the peak in fish growth found by Letcher & Gries (2003) and Carlson & Letcher (Carlson & Letcher 2003). Diet diversity also showed this pattern for the trout species with no seasonal variation detected for Atlantic salmon. These seasonal patterns were also found (Cunjak

1992, Nislow *et al.* 1999, Grader & Letcher 2006) for Atlantic salmon; brown trout, (Allan 1981); (Jobling & Baardvik 1994) and for brook trout. In studies from northern Europe, the seasonal patterns in fullness differ from those found here, but correspond to periods of increased growth rates in those systems (Kelly-Quinn & Bracken 1990).

Drift propensity was an accurate predictor of salmonid diets except in the month of December. Given water temperatures are at or near the freezing point, it would be unrealistic to expect this model to accurately predict diets for this sample. The other notable exception was for brown trout in the month of August. As brown trout diets were accurately predicted in other samples and the model was effective for other species in this month, it seems unlikely that this failure is a defect in the model. This study shows that the Rader (1997) model can be effectively used in the region.

Prey items selected by salmonid fish consistently showed that the mean item length selected was larger than that of the available invertebrate community. Seasonal changes in selected prey size were proportional to seasonal changes in the mean size of available prey. In Atlantic salmon prey size was independent of fish size, as was found by Keeley & Grant (1997), in a New Brunswick stream. Given that month to month variance in prey length of salmonids was small (< 2.0 mm), fish size, and size-related gape limitation, was unlikely to be a factor.

Important and selected prey taxa were markedly similar among salmonid fish in each sample month. In April, salmonid fish prey selectivity tended to be highest for mayflies

by %IRI. The high importance of the ephemerellid family was largely driven by its great

abundance (both in number & biomass) in the drift (chapter 1). Mayfly families that

were low in drift abundance showed two different patterns. The first showed that taxa

with low intentional drift scores (likely poor swimmers (Rader 1997)) were positively

selected. Conversely, fish showed negative selection for the family Baetidae, a taxon of

strong swimmers that were frequently found in diets. In June, positive selection was

limited to emergent mayflies. During the emergence process most mayfly taxa drift

through the water column with little ability to change trajectories (Rader 1997). Baetid

mayflies were the most abundant taxon in June drift samples; this abundance is reflected

in their high level of relative dietary importance. Dietary overlap among salmonid

species is at its greatest levels during these two sample periods.

Prey selection in August, when prey were in short supply, changed in different ways for

each salmonid species. Atlantic salmon show positive selection for epibenthic prey

during the August sample with the %IRI showing the importance of both epibenthic and

drift prey. This is consistent with (Gries *et al.* 1997, Nislow *et al.* 1998, Amundsen *et al.*

1999) and may be indicative of, the benthic oriented holding station of Atlantic salmon

(Höjesjö *et al.* 2005) or the change to nocturnal activity. Metcalfe *et al.* (1999) suggest

that this change in activity patterns may decrease drift-feeding efficiency for these sight-

based predators. In contrast, Brook trout show that both drifting and terrestrially derived

prey are of high importance. Both (Sotiropoulos *et al.* 2006) and (Allan 1981) found the

same pattern in the reliance on terrestrial derived prey in other brook trout populations.

Finally, it appeared that brown trout abandon drift foraging, as the drift propensity model

fails to predict August diets, in favor of both benthic and terrestrial derived prey. As the drift propensity model was shown to be effective for other salmonids at this time of year and for brown trout at other times of year, it is unlikely that this result is from a failure of the model. Important prey cover both terrestrial and benthic prey with positive selection limited to helicopsychid caddis. These results are consistent with Bridcut (2000) for terrestrial prey and Kreivi *et al*. (1999) for benthic prey. Prey selection in December shows that benthic foraging continues for all species, but this may be due to the movement of fish to over-winter habitat close to the substrate surface (Huusko *et al.* 2007).

These diet shifts are not without consequence as the percentage of guts that were found empty increased significantly in the fall. The increase in emptiness in later time periods has been found previously for all three salmonid species ((Kreivi *et al.* 1999) brown trout; (Sotiropoulos *et al.* 2006) brook trout; (Simpson *et al.* 1996) Atlantic salmon). Further, even if fish are able to successfully capture epibenthic prey, this foraging mode may be more energetically costly (Fausch K.D. *et al.* 1997). Anecdotal evidence also suggests that certain epibenthic prey, particularly stone cased caddis larvae often pass through a fish undigested.

These results demonstrate a potentially strong link between invertebrate dynamics and seasonal variation in individual fish growth. During seasons when availability of appropriate (large) drifting prey was high all three species adopted a common drift foraging strategy, which yielded high consumption rates and a low percentage of fish

with empty stomachs. The results also show that a diet switch, to less profitable and harder to capture prey, occurs in the low growth periods of August and December. In contrast, during the low growth period, empty stomachs were common, consumption rates were low, and differences among species were marked. These results underscore the importance of assessing prey dynamics, fish foraging strategies and interspecific interactions over entire seasonal cycles, and under different levels of resource availability. Further investigation using multiple systems and the use of gut contents from individually marked fish would aid in the understanding of the role of diet selection on salmonid growth.

Table 2.1. Summary of fish captured for the diel samples collected from West Brook.

Median Sample Date	Time of Day	Mean Water Temperature (deg C)	Fish Species	Mean Length (mm)	Mean Weight (g)	Number of Fish (n)
21-Apr-03	Day	8.5	Atlantic salmon	99	12.2	15
			Brook trout	91	8.5	7
			Brown trout	106	16.2	39
30-Apr-03	Night	9.3	Atlantic salmon	91	9.8	22
			Brook trout	107	19.9	9
			Brown trout	100	13.5	43
18-Jun-03	Day	15.0	Atlantic salmon	128	28.9	20
			Brook trout	126	25.7	6
			Brown trout	145	44.6	34
20-Jun-03	Night	15.0	Atlantic salmon	126	25.6	21
			Brook trout	228	69.9	9
			Brown trout	149	46.6	31
25-Aug-03	Day	15.5	Atlantic salmon	142	33.2	16
			Brook trout	128	27.2	10
			Brown trout	171	66.6	34
26-Aug-03	Night	18.0	Atlantic salmon	126	25.6	29
			Brook trout	109	18.3	18
			Brown trout	152	44.3	19
19-Dec-03	Day	0.6	Atlantic salmon	120	18.1	18
			Brook trout	118	19.9	7
			Brown trout	117	19.9	16

Table 2.2. ANOVA summary statistics for the three salmonid species at West Brook.

Species	F - ratio	P - value	df
Atlantic salmon	6.769	>0.001	3, 132
Brook trout	3.200	0.019	4, 60
Brown trout	8.387	>0.001	4, 211

Table 2.3. Summary of stomach emptiness for each salmonid species at each sample month from West Brook. Percentage is reported for each species at the listed sample month. Emptiness is defined as stomach without prey.

	Atlantic salmon	Brook trout	Brown trout	*Mean*
April	8.8%	None	1.2%	*3.0%*
June	2.5%	15.4%	1.6%	*3.3%*
August	32.4%	17.4%	29.3%	*21.4%*
December	12.5%	None	23.1%	*12.2%*
Mean	*13.7%*	*10.2%*	*8.5%*	Global 9.4%

Table 2.4. ANOVA summary statistics for the mean annual diet diversity metrics of the three species of salmonid fish at West Brook. Shown are the P-values, F ratio and the degrees of freedom from 1-way ANOVA.

	Atlantic salmon		Brook trout		Brown trout	
	F	*P*	*F*	*P*	*F*	*P*
Diversity	13.473	0.000	3.738	0.026	9.859	0.000
Evenness	17.145	0.000	4.866	0.010	12.547	0.000
Richness	10.786	0.000	3.655	0.028	12.129	0.000
df	3,57		3,22		3,105	

Table 2.5. Percent index of relative importance of significant dietary taxa (value > 10) of the salmonid species from West Brook. These calculations are based on Cortes (1996) and do not include vertebrate prey items. Items marked with an asterisk (*) are shown for comparative purposes only and are not considered a significant portion of the diet.

		%IRI		
Month	Taxon	Atlantic salmon	Brook trout	Brown trout
April	Ephemerellidae	43.01	23.49	50.21
	Heptageniidae	38.13	8.11*	17.50
	Siphlonuridae	5.36*	25.47	12.55
June	Baetidae	60.06	7.27*	26.25
	Emergent	18.83	81.78	50.97
August	Helicopsychidae	10.74	15.94	24.77
	Rhyacophilidae	11.46	0.00*	16.47
	Terrestrial	3.37*	65.41	45.21
December	Chironomidae	12.51	10.70	20.34
	Ephemerellidae	48.17	6.75*	38.56
	Brachycentridae	0.00*	17.93	0.00*
	Glossosomatidae	13.14	17.43	5.11*

Table 2.6. Taxa, found in West Brook, associated exclusively with the benthos.

Order	Family
Coleoptera	Elmidae
	Psephenidae
Diptera	Chironomidae
	Ceratopogonidae
	Empididae
	Tabanidae
	Tipulidae
Megaloptera	Corydalidae
	Sialidae
Plecoptera	Leuctridae
	Peltoperlidae
	Taeniopterygidae
Trichoptera	Glossosomatidae
	Helicopsychidae
	Hydropsychidae
	Limnephilidae
	Philopotamidae
	Polycentropodidae
	Psychomyiidae
Class-	Bivalva
Class-	Gastropoda

Table 2.7. Percent index of relative importance of benthic prey for the three salmonid fish species from West Brook. These calculations are based on Cortes (1996) and are cumulative totals of taxa associated strictly with the benthos as listed in table 2.6.

Month	Fish Species	Benthic %IRI
April	Atlantic salmon	7.4
	Brook trout	17.5
	Brown trout	9.8
June	Atlantic salmon	7.3
	Brook trout	0.9
	Brown trout	6.9
August	Atlantic salmon	44.2
	Brook trout	22.2
	Brown trout	34.0
December	Atlantic salmon	33.3
	Brook trout	43.5
	Brown trout	41.4

Table 2.8. Incidence of vertebrate consumption by salmonid fish from West Brook. Size is shown for each prey item, this measurement varies by prey type. Fish, including black nose dace and slimy sculpin are measured as fork length. Salamanders are measured from snout tip to the last tail vertebra. The month of the occurrence, the consumer species and fork length are listed.

Month	Fish species	Fork Length	Prey type	Size
April	Brown trout	147	Blacknose dace	11.2
	Brown trout	162	Dusky salamander	67.3
	Brown trout	194	Two lined salamander	70.1
August	Brown trout	190	Black nose dace	27.3
December	Brown trout	142	Two lined salamander	24.8
	Atlantic salmon	155	Slimy sculpin	30.0
	Brown trout	178	Two lined salamander	56.2

Table 2.9. Monthly Spearman's rank correlation coefficients and probability estimates between drift propensity score and diets of the three salmonid fish species from West Brook. Values marked by dagger (†) indicate non-statistically significant result.

	April		June		August		December	
Sample Type	rho	P	rho	P	rho	P	rho	P
Atlantic salmon	0.528	0.001	0.408	0.010	0.482	0.002	0.344†	0.050
Brook trout	0.438	0.005	0.483	0.002	0.578	0.001	0.358	0.020
Brown trout	0.509	0.001	0.433	0.005	0.230†	0.200	0.144†	0.500

Table 2.10. Monthly measure of diet overlap between salmonid species (ATS – Atlantic salmon, BKT – brook trout, BNT- brown trout). Overlap was calculated using Schoener's formula (1970). Values marked by and asterisk (*) indicate significant overlap (values >0.60).

Month	ATS - BKT	ATS - BNT	BKT - BNT
April	*0.63	*0.78	*0.73
June	0.35	*0.63	0.55
August	0.36	0.29	0.51
December	0.50	0.59	0.42

Figure 2.1. Monthly variation in gut biomass of the three salmonid fish species from West Brook. Legend indicates Atlantic salmon (ATS), brook trout (BKT) and brown trout (BNT). Dashed line indicates non-statistically significant differences in Atlantic salmon gut biomass by Tukey's post hoc testing. Error bars are standard errors.
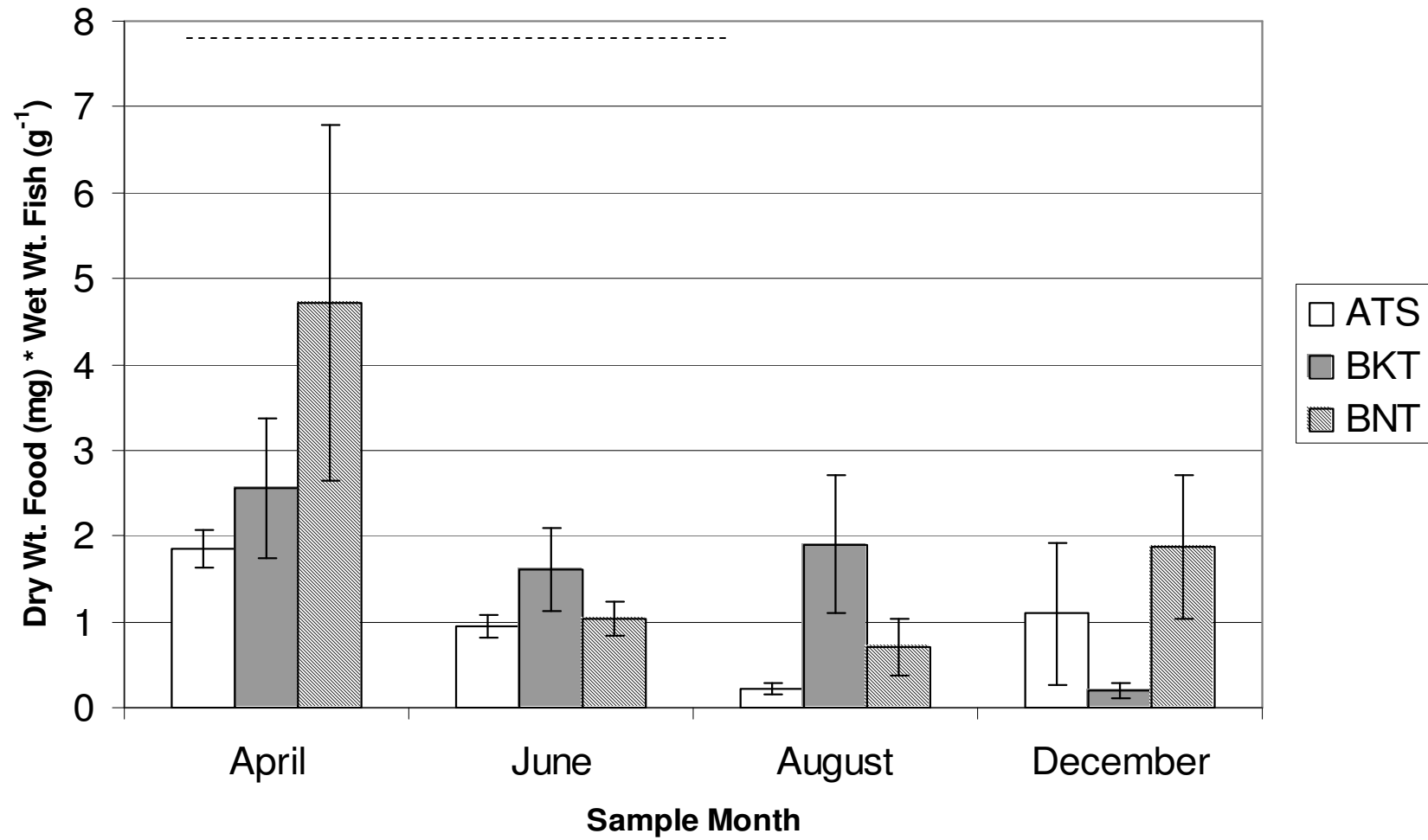
Figure 2.2. Monthly variation in consumption rate by biomass of the three salmonid fish species from West Brook. Legend indicates Atlantic salmon (ATS), brook trout (BKT) and brown trout (BNT). Dashed line indicates non-statistically significant differences in Atlantic salmon consumption rate by biomass by Tukey's post hoc testing. Error bars are standard errors.
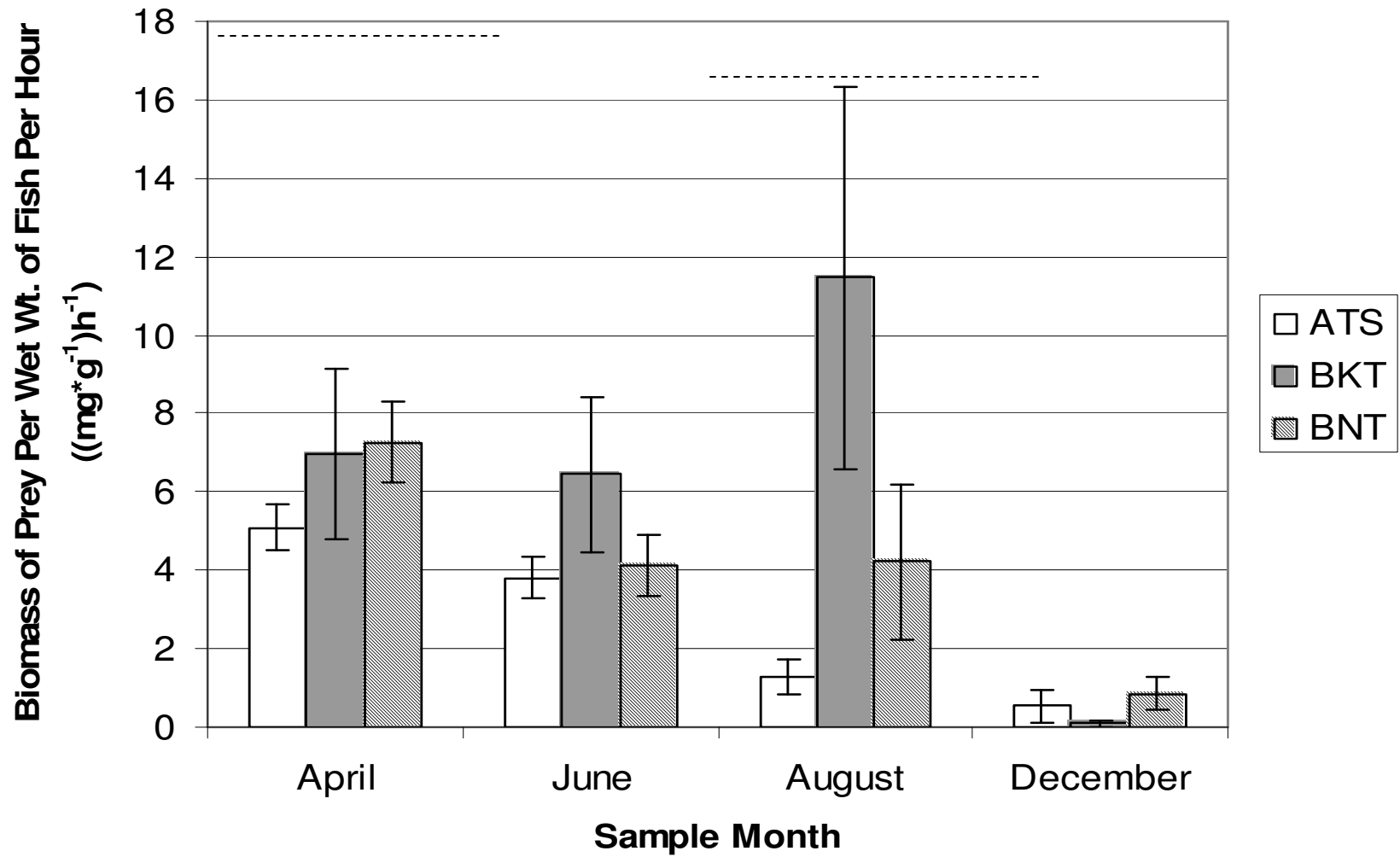
Figure 2.3. Monthly variation in gut density of the three salmonid fish species from West Brook. Legend indicates Atlantic salmon (ATS), brook trout (BKT) and brown trout (BNT). Dashed line indicates non-statistically significant differences in Atlantic salmon gut biomass by Tukey's post hoc testing; solid line- brook trout, dotted line- brown trout. Error bars are standard errors.
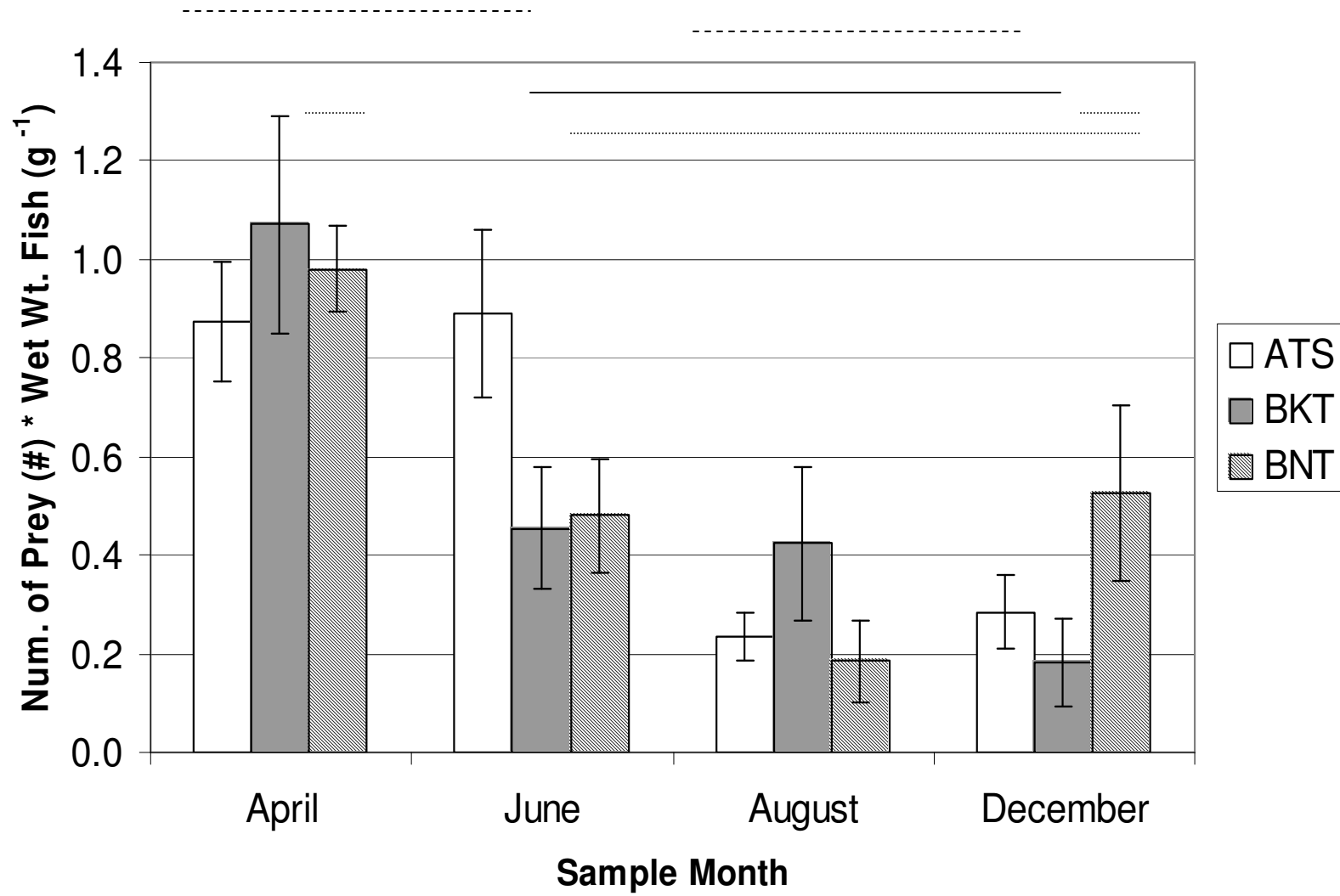
Figure 2.4. Monthly variation in consumption rate by number of the three salmonid fish species from West Brook. Legend indicates Atlantic salmon (ATS), brook trout (BKT) and brown trout (BNT). Dashed line indicates non-statistically significant differences in Atlantic salmon gut biomass by Tukey's post hoc testing; solid line- brown trout. Error bars are standard errors.
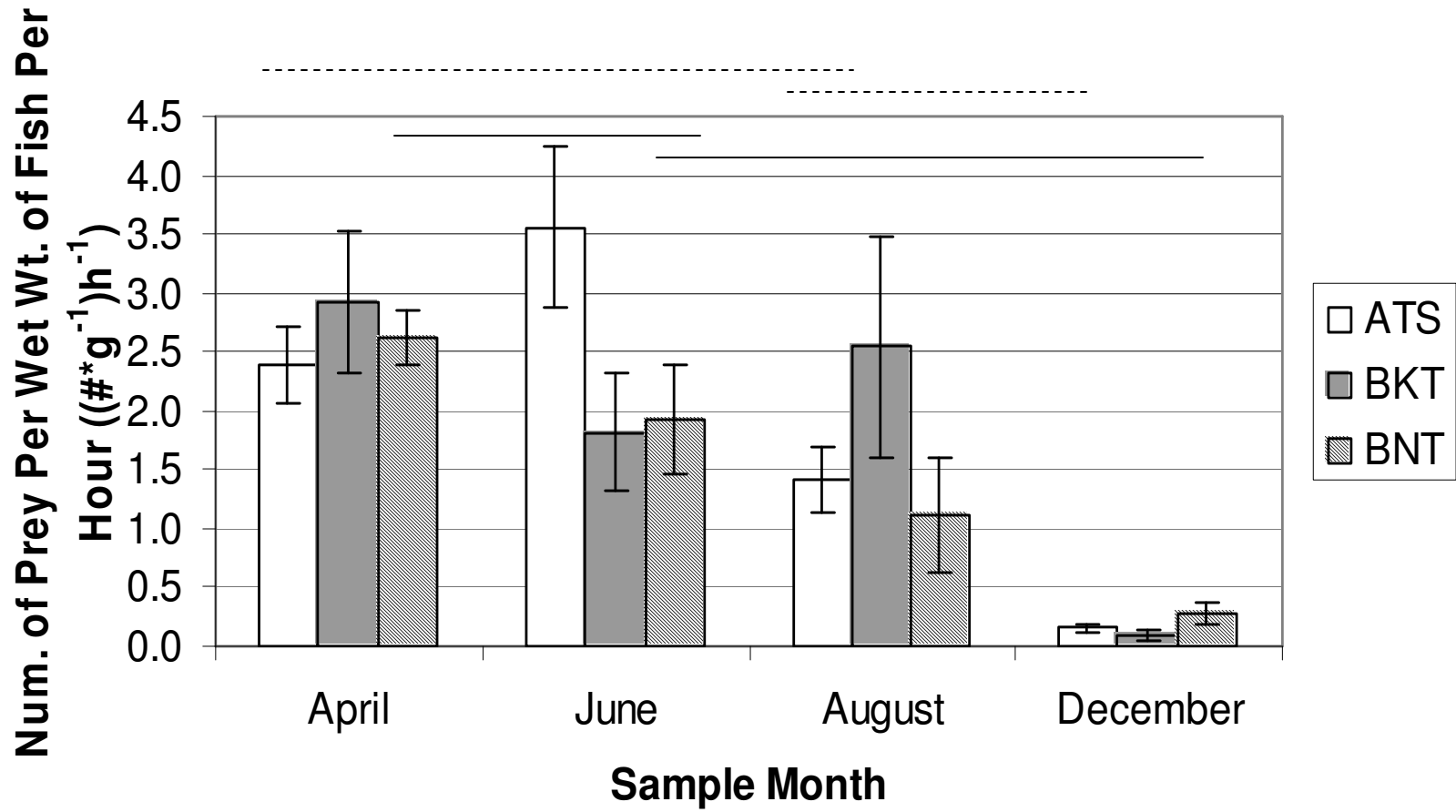
Figure 2.5. Monthly variation in the Shannon-Wiener index of diet diversity for the three salmonid fish species from West Brook. Legend indicates Atlantic salmon (ATS), brook trout (BKT) and brown trout (BNT). Error bars are standard errors.
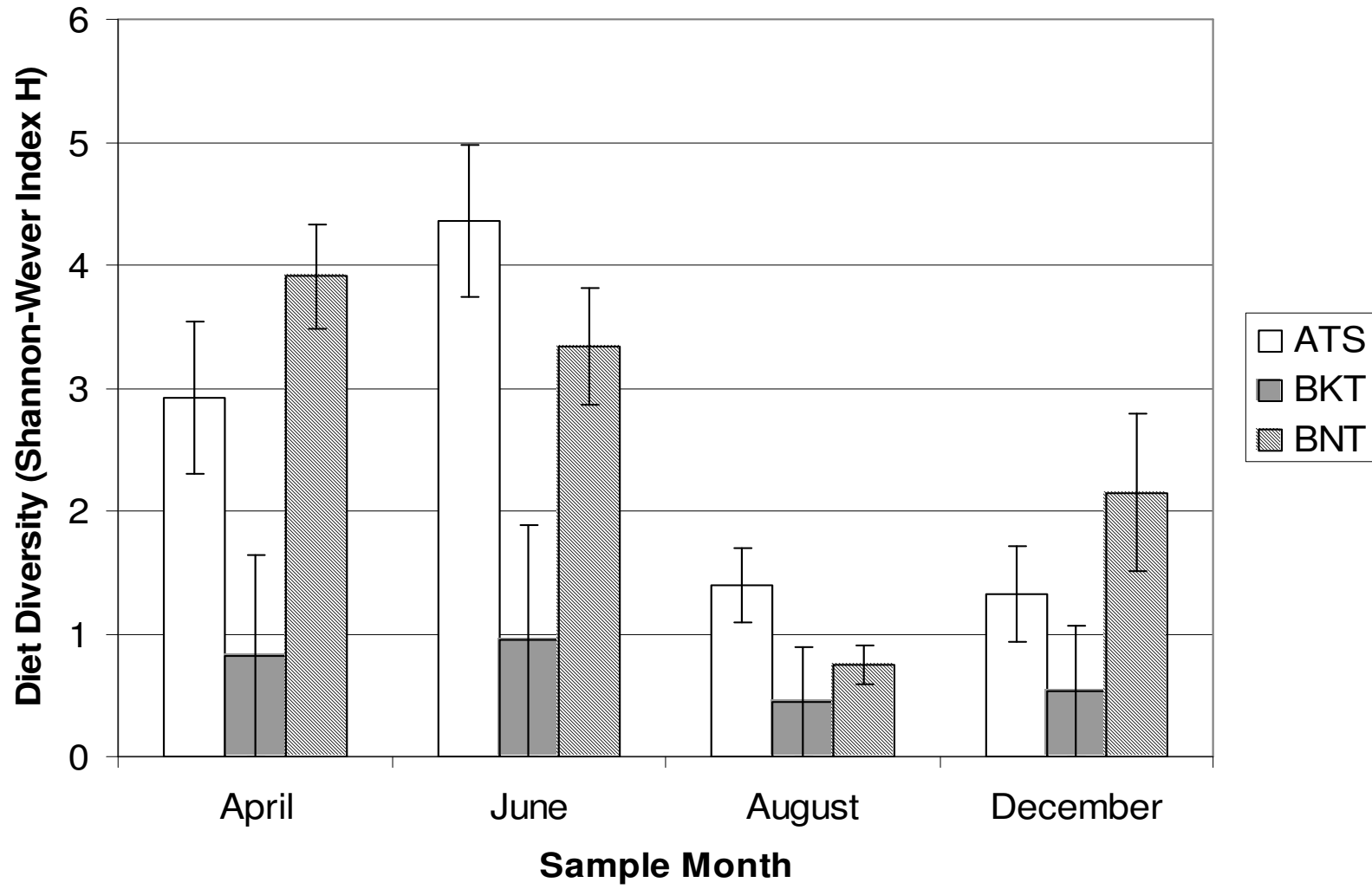
Figure 2.6. Monthly variation in mean item size for salmonid guts and drift samples from West Brook. Error bars are standard errors.
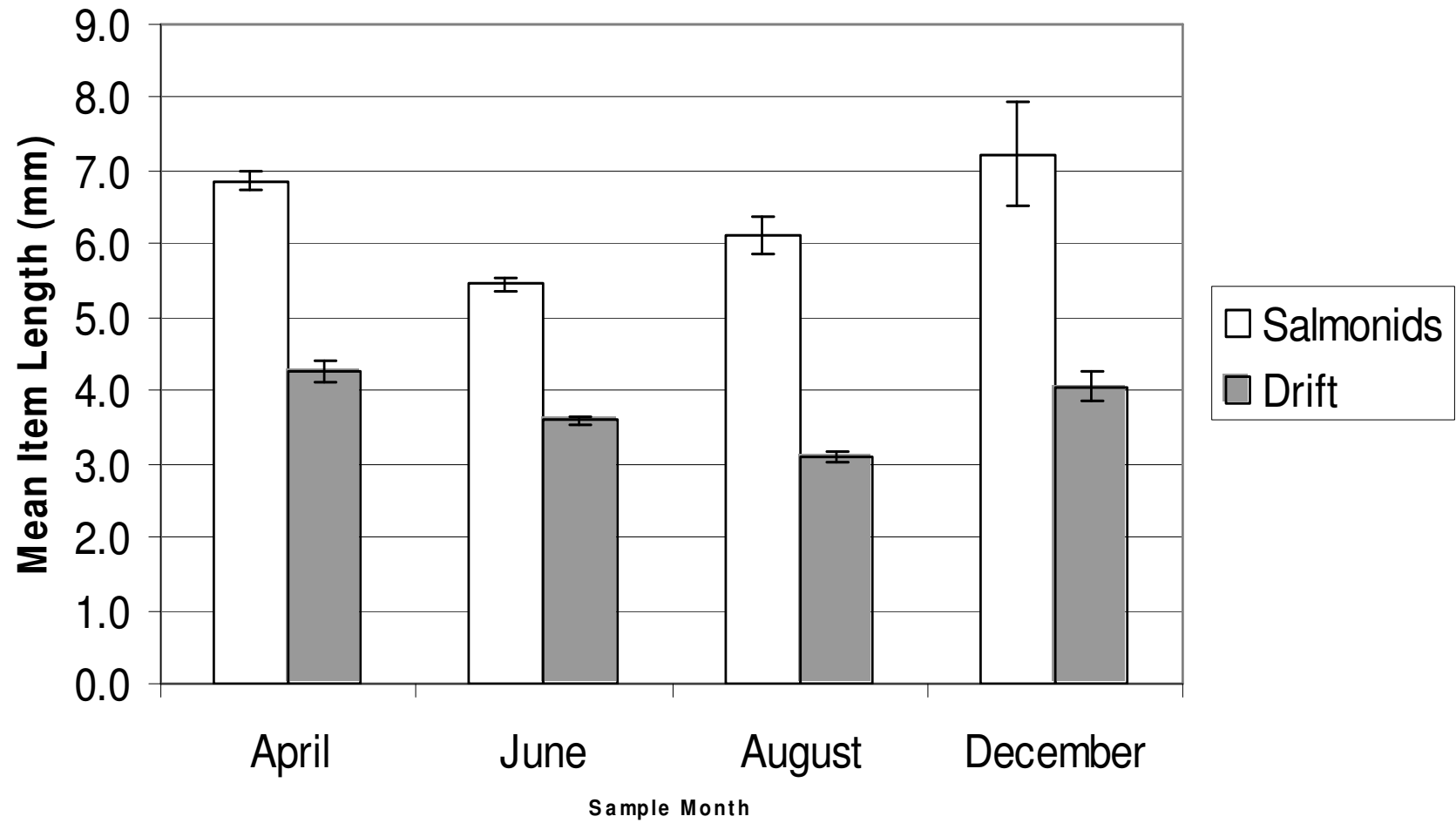
Figure 2.7. Monthly variation in prey item length of Atlantic salmon and brook trout from West Brook. Legend indicates Atlantic salmon (ATS), brook trout (BKT) and brown trout (BNT). Dashed line indicates non-statistically significant differences in Atlantic salmon gut biomass by Tukey's post hoc testing; solid line- brown trout. Error bars are standard errors.
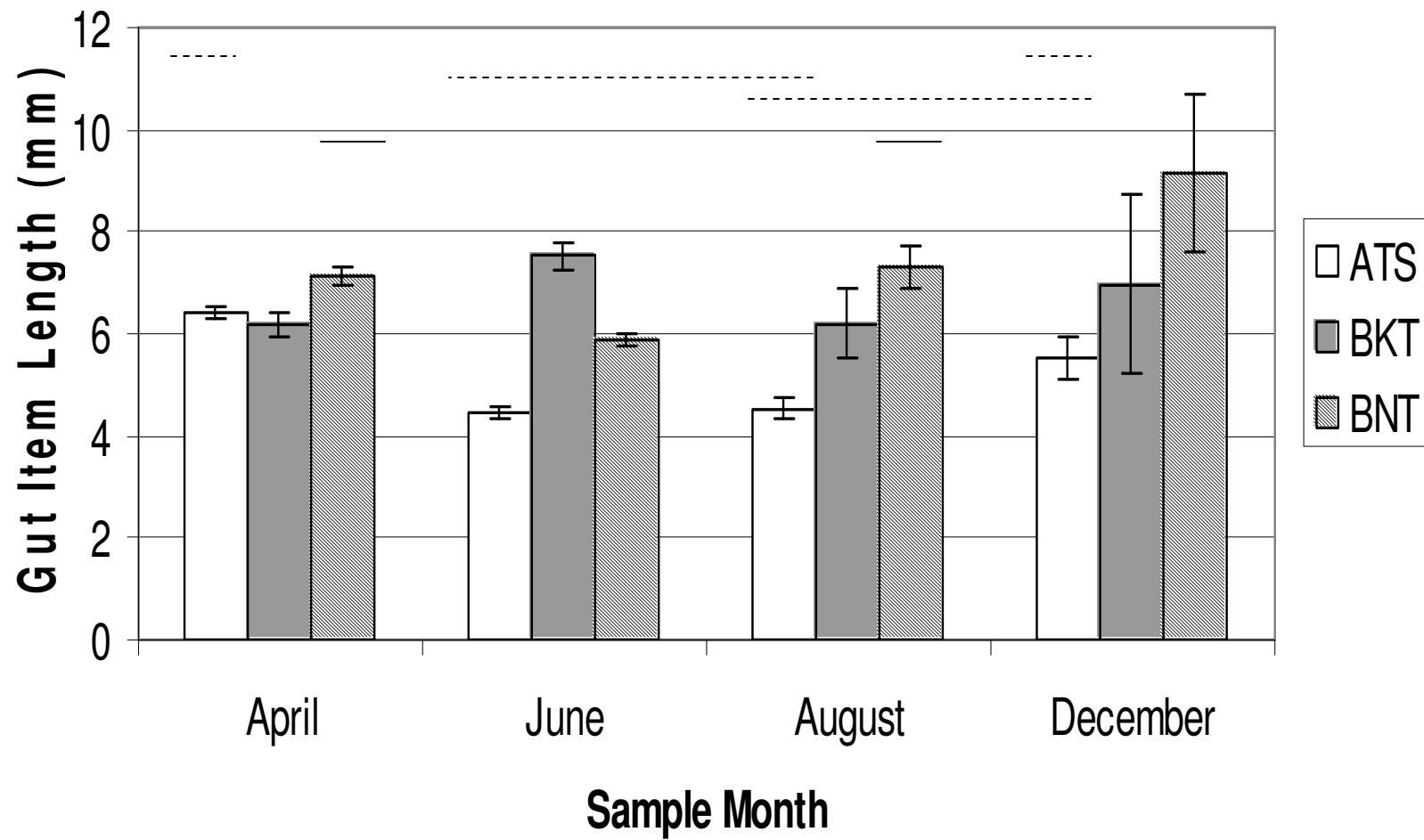
Figure 2.8a. April Chesson's alpha values for taxa with a percent index of relative importance greater then 10 for the three salmonid fish species from West Brook. Legend indicates fish species; Atlantic salmon (ATS), brook trout (BKT) and brown trout (BNT). The dotted line indicates the value of 1/k, values over this line are considered positively selected for.
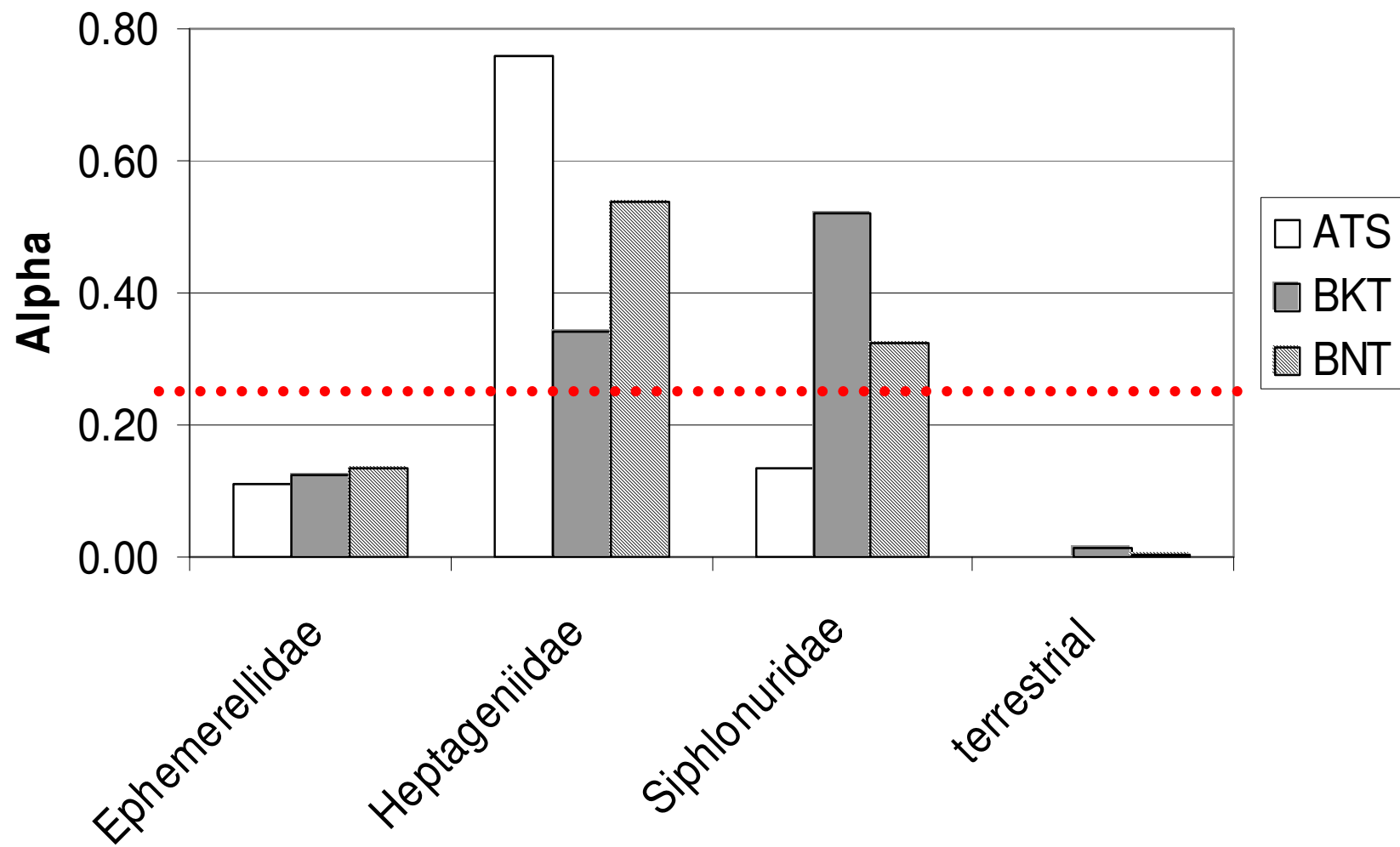
Figure 2.8b. June Chesson's alpha values for taxa with a percent index of relative importance greater then 10 for the three salmonid fish species from West Brook. Legend indicates fish species; Atlantic salmon (ATS), brook trout (BKT) and brown trout (BNT). The dotted line indicates the value of 1/k, values over this line are considered positively selected for.
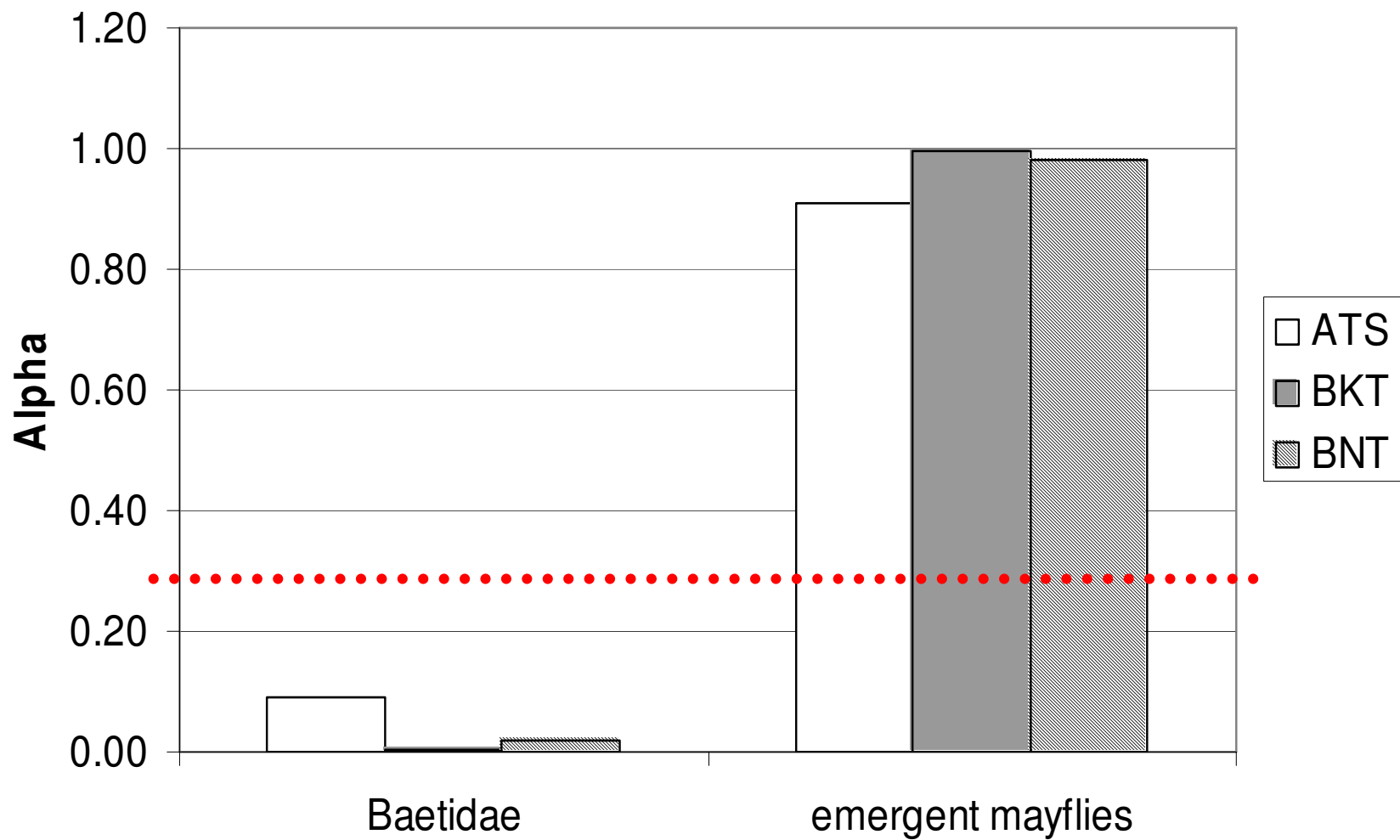
Figure 2.8c. August Chesson's alpha values for taxa with a percent index of relative importance greater then 10 for the three salmonid fish species from West Brook. Legend indicates fish species; Atlantic salmon (ATS), brook trout (BKT) and brown trout (BNT). The dotted line indicates the value of 1/k, values over this line are considered positively selected for.
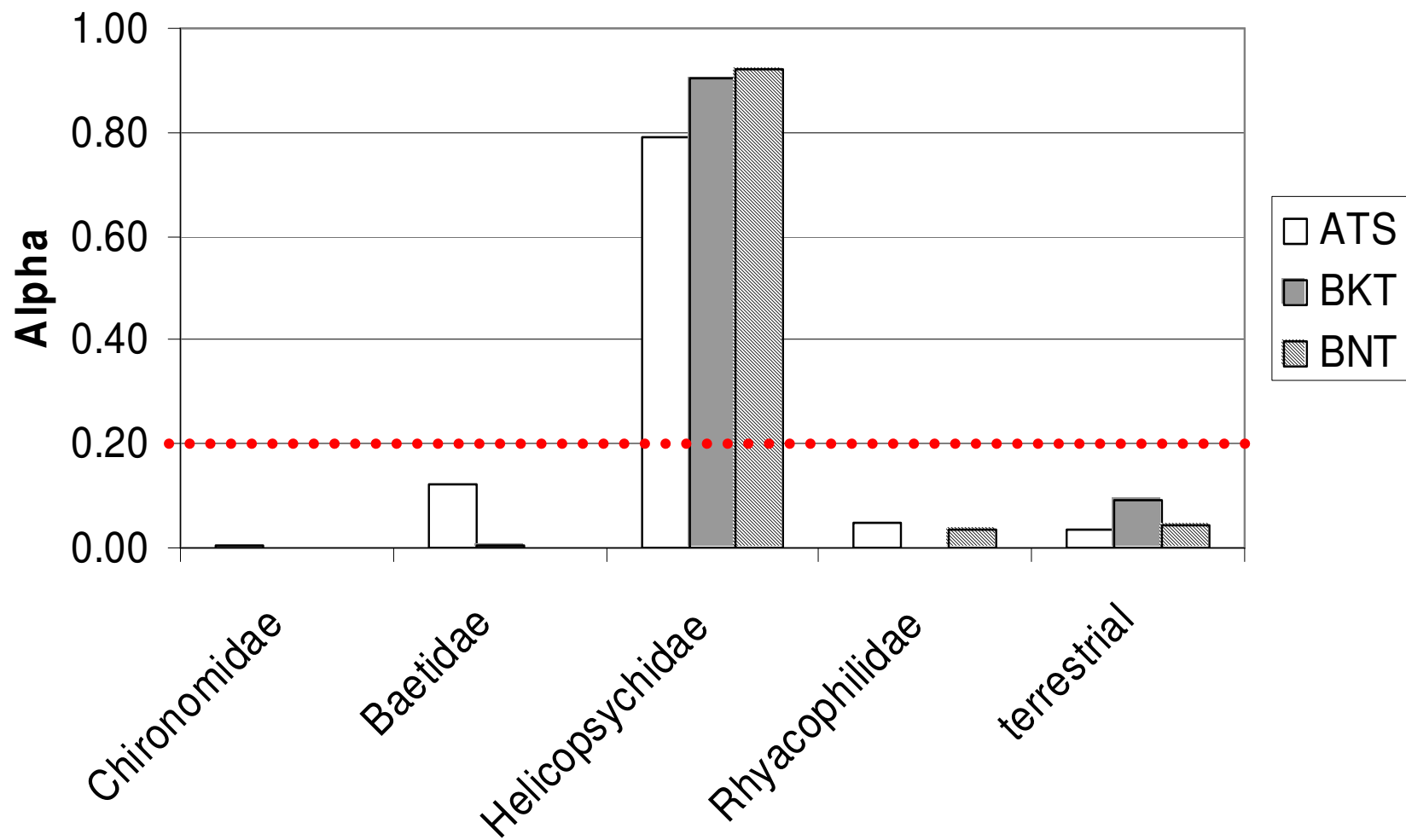
Figure 2.8d. December Chesson's alpha values for taxa with a percent index of relative importance greater then 10 for the three salmonid fish species from West Brook. Legend indicates fish species; Atlantic salmon (ATS), brook trout (BKT) and brown trout (BNT). The dotted line indicates the value of 1/k, values over this line are considered positively selected for.
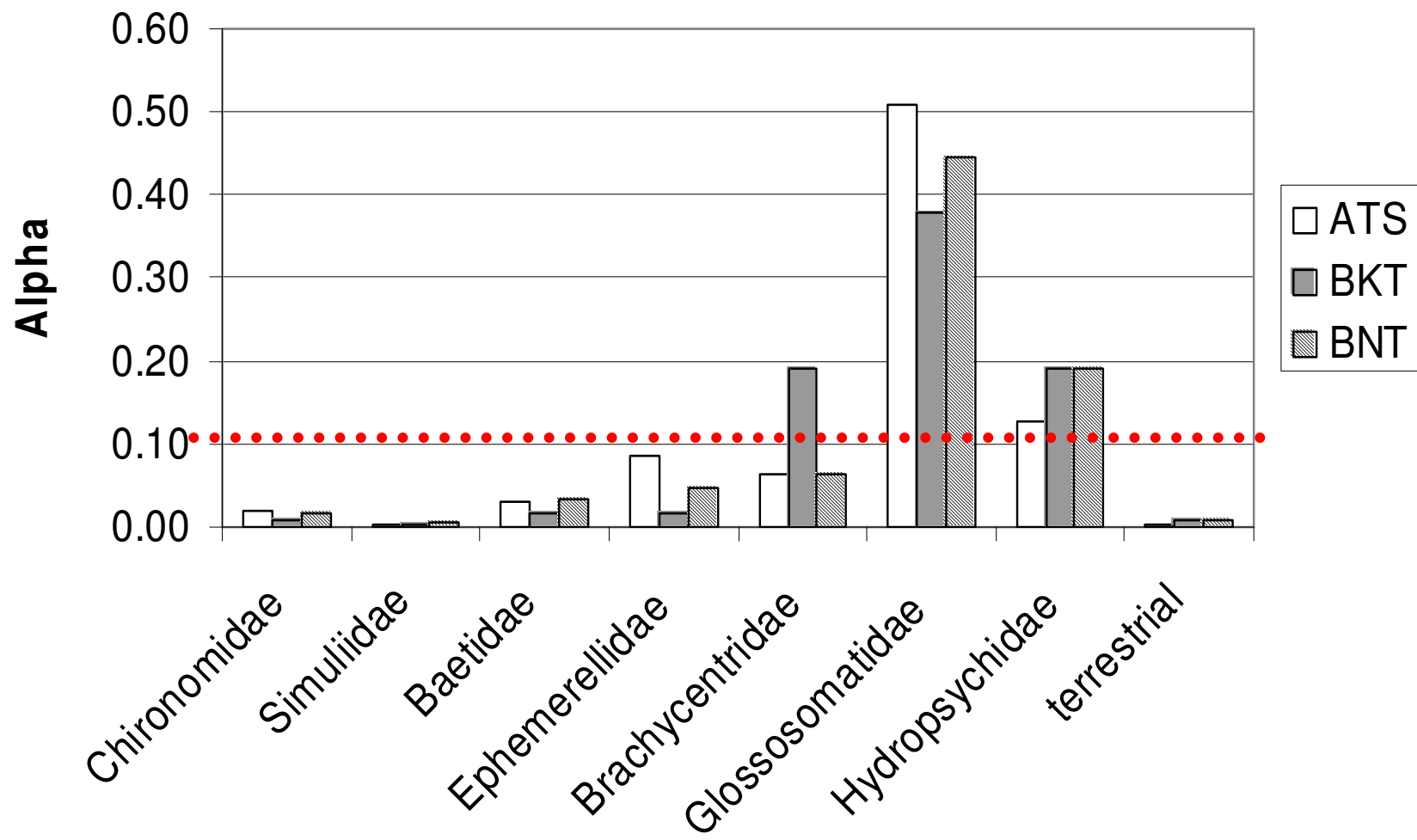
Figure 2.9. Conceptual model of the seasonal diet switch exhibited by the three species of salmonid fish from West Brook.
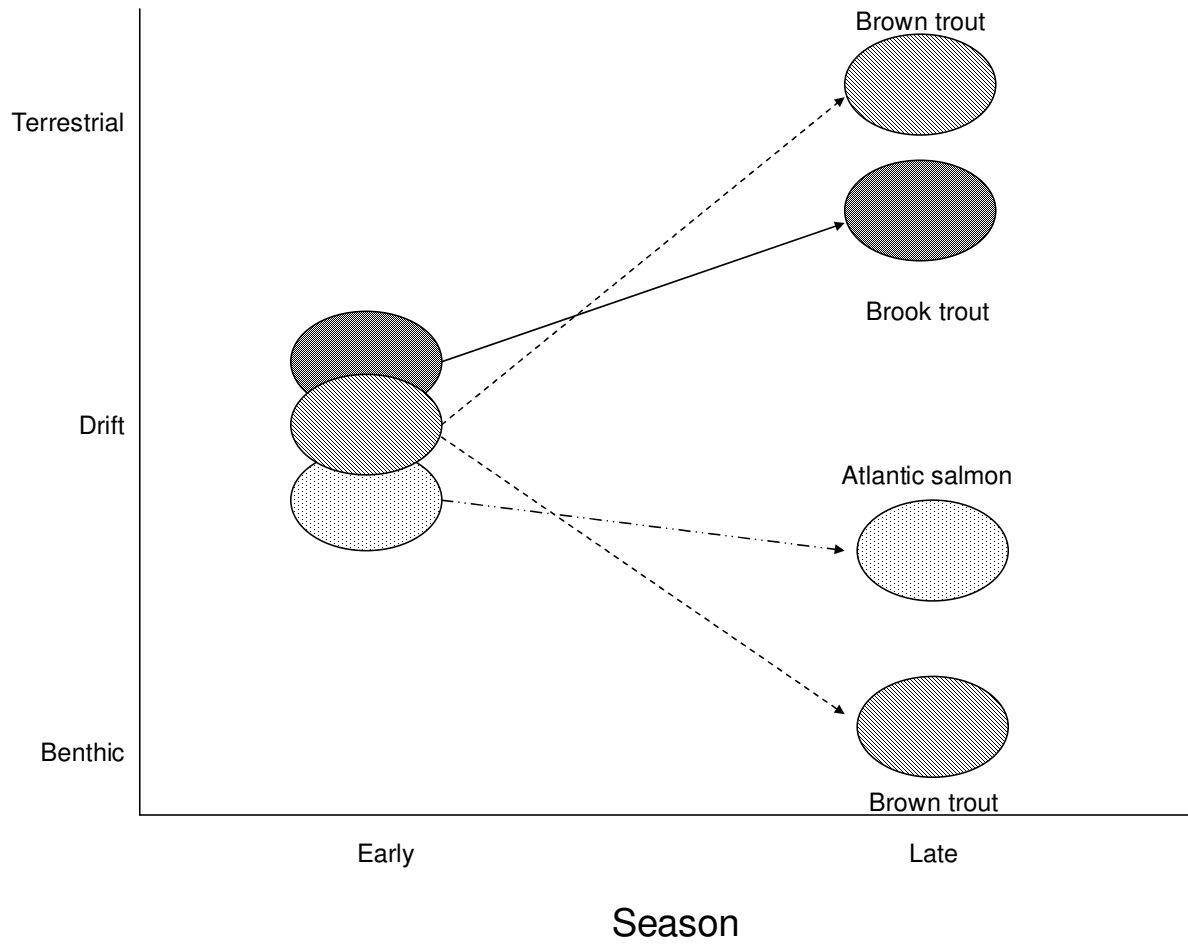
Brown trout

Brook trout

Atlantic salmon

Brown trout

Terrestrial

Drift

Benthic

Foraging Strategy
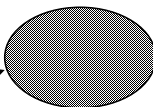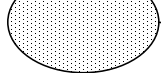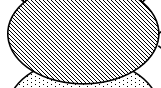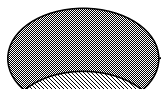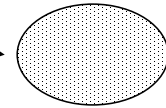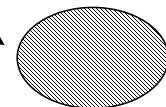
Early

Late

Season

Appendix A
Invertebrate Population Data

Table A-1. Mean density (#) and biomass (mg) of the drift and benthic samples for West Brook. Three diel drift samples are given per cubic meter (m^{-3}), with the benthic sample per square meter (m^{-2}). Totals are a mean value for benthic and morning drift samples, while the two other drift samples are single sample totals. Blank spaces indicate that no individuals of that taxa where captured.

April 2003	Day		Night		Midnight		Benthic	
Taxa	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
Coleoptera								
Elmidae	0.17	0.10	0.02	0.01	0.21	0.08	2.70	1.22
Others								
Diptera								
Chironomidae	1.38	0.17			1.13	0.10	9.60	0.95
Simuliidae	0.30	0.12	0.02	0.00	0.10	0.00		
Tipulidae	0.05	0.04			0.03	0.01	3.00	0.70
Others	0.60	0.64	0.03	0.00	2.13	0.76	2.70	0.64
Ephemeroptera								
Baetidae	0.02	0.03	0.02	0.00	0.52	0.08	0.60	0.37
Ephemerellidae	0.40	0.69	0.08	0.02	0.24	0.06	2.40	5.41
Heptageniidae	0.04	0.04			0.07	0.06	2.40	1.70
Leptophlebiidae	0.02	0.01			0.07	0.01		
Siphlonuridae	0.04	0.04			0.10	0.09	0.30	0.18
subimago								
Others								
Plecoptera								
Capniidae	0.49	2.41						
Chloroperlidae	0.04	0.06						
Perlodidae							0.90	2.50
Taeniopterygidae	0.02	0.09						
Others	0.16	0.19	0.03	0.00			0.30	0.00
Trichoptera								
Glossosomatidae								
Helicopsychidae								
Hydropsychidae	0.04	0.10					0.30	0.01
Lepidostomatidae	0.06	0.13	0.02	0.00				
Leptoceridae	0.06	0.03	0.02	0.01	0.03	0.00		
Limnephilidae			0.02	0.47	0.03	1.19	0.60	7.84
Philopotamidae								
Psychomyiidae	0.02	0.01						
Rhyacophilidae	0.02	0.01	0.02	0.00	0.03	0.03	2.70	8.04
Others	0.34	0.90						
Terrestrial Derived Insect - Others	1.18	0.29	0.02	0.00	0.48	0.12	4.50	0.02
Non-Insect Invertebrates							0.30	0.15
Mean Total	9.25	10.24	1.70	3.29	15.10	7.58	55.50	49.54

Table A-1 (cont.)

June 2003	Day		Night		Midnight		Benthic	
Taxa	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
Coleoptera								
Elmidae	0.23	0.14	0.26	0.05	0.39	0.27	30.90	12.36
Others	0.13	0.23			0.04	0.95	0.60	0.28
Diptera								
Chironomidae	0.63	0.11	0.26	0.02	1.48	0.40	30.60	2.44
Simuliidae	0.10	0.02	0.04	0.00	0.39	0.25	0.30	0.07
Tipulidae	0.05	0.05	0.04	0.02	0.04	0.01	5.70	4.03
Others	1.28	0.28	0.21	0.09			4.80	1.53
Ephemeroptera								
Baetidae	2.50	0.29	8.59	0.64	20.03	3.17	23.70	1.21
Ephemerellidae	0.28	0.24	0.13	0.10	0.23	0.35	8.70	8.97
Heptageniidae			0.04	0.01	0.08	0.26		
Leptophlebiidae	0.09	0.04			0.08	0.06	1.20	0.51
Siphlonuridae	0.21	0.16	0.21	0.02	0.27	0.19		
subimago	0.33	2.11						
Others	0.18	0.92			0.62	1.26	0.30	0.63
Plecoptera								
Capniidae								
Chloroperlidae	0.02	0.01	0.04	0.00	0.08	0.02	1.20	0.10
Perlodidae	0.02	0.10					10.20	2.04
Taeniopterygidae								
Others	0.09	0.07	0.04	0.00	0.08	0.05	6.00	0.13
Trichoptera								
Glossosomatidae	0.07	0.02	0.13	0.01	0.12	0.02	7.80	1.03
Helicopsychidae							0.90	0.20
Hydropsychidae							0.30	1.42
Lepidostomatidae							0.30	0.02
Leptoceridae	0.09	0.01						
Limnephilidae	0.02	3.83					1.50	0.02
Philopotamidae	0.13	0.11	0.04	0.01	0.04	0.03	0.90	0.41
Psychomyiidae							0.90	0.41
Rhyacophilidae					0.08	0.03	1.20	0.91
Others					0.04	0.01	7.20	0.92
Terrestrial Derived	0.27	0.91	0.09	0.07	0.27	0.48	14.10	0.47
Insect - Others	0.09	0.26			0.12	0.45	1.20	0.31
Non-Insect Invertebrates	0.04	0.00					1.20	0.31
Mean Total	8.48	10.12	11.80	1.21	31.45	10.95	269.52	67.87

Table A-1 (cont.)

August 2003	Day		Night		Midnight		Benthic	
Taxa	Density	Biomass	Density	Biomass	Density	Biomass	Density	Biomass
Coleoptera								
Elmidae	0.20	0.07					28.80	34.54
Others	0.08	0.03					3.90	6.84
Diptera								
Chironomidae	4.12	0.16	13.36	5.18	0.78	0.44	72.00	6.35
Simuliidae	1.02	0.12			0.33	0.29	0.30	0.01
Tipulidae	0.04	0.36					5.70	3.14
Others	0.69	0.30					8.70	1.51
Ephemeroptera								
Baetidae	0.21	0.02	0.49	0.30	1.99	0.79	8.40	0.52
Ephemerellidae	0.60	0.03	0.33	0.02	0.11	0.01	76.50	3.23
Heptageniidae	0.20	0.00					4.80	0.29
Leptophlebiidae	0.10	0.00			0.22	0.03	20.70	0.78
Siphlonuridae subimago					0.11	0.01	1.50	0.53
Others	0.07	0.02			0.11	0.12		
Plecoptera								
Capniidae							0.90	0.17
Chloroperlidae							7.20	1.56
Perlodidae	0.18	0.11			0.11	0.08	2.40	0.71
Taeniopterygidae								
Others	0.31	0.07	0.16	0.00	0.22	0.61	12.90	1.66
Trichoptera								
Glossosomatidae	0.24	0.03	0.16	0.07			6.30	23.50
Helicopsychidae					0.11	0.00	12.30	0.87
Hydropsychidae	0.67	0.39	0.16	0.01	0.22	0.01	39.00	17.19
Lepidostomatidae								
Leptoceridae							0.90	0.09
Limnephilidae	0.04	0.00					0.90	22.44
Philopotamidae			0.16	0.02	0.11	0.09	2.10	1.03
Psychomyiidae							0.60	0.18
Rhyacophilidae	0.39	0.10	0.16	0.01			12.90	11.64
Others	0.04	0.40					11.10	11.07
Terrestrial Derived	0.20	1.07	0.65	0.75	0.22	0.12	3.30	0.02
Insect - Others	0.08	0.04					2.10	3.48
Non-Insect Invertebrates							15.60	19.71
Mean Total	10.95	2.81	4.80	1.96	2.10	1.17	603.55	305.71

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Table A-1 (cont.)

December 2003	Day		Benthic	
Taxa	Density	Biomass	Density	Biomass
Coleoptera				
Elmidae	0.06	0.07		
Others	0.02	0.07		
Diptera				
Chironomidae	0.49	0.16	5.70	4.47
Simuliidae	0.31	0.04	2.40	0.78
Tipulidae			0.90	3.58
Others	0.12	0.16	1.80	1.06
Ephemeroptera				
Baetidae	0.16	0.02	1.80	0.51
Ephemerellidae	0.14	0.04	5.70	11.39
Heptageniidae	0.05	0.01	2.10	4.24
Leptophlebiidae	0.06	0.02	0.90	0.94
Siphlonuridae			0.30	0.09
subimago				
Others				
Plecoptera				
Capniidae	0.05	0.01	0.30	0.36
Chloroperlidae	0.03	0.02	0.90	0.55
Perlodidae				
Taeniopterygidae	0.04	0.01	1.50	0.70
Others	0.03	0.00	0.60	0.14
Trichoptera				
Glossosomatidae				
Helicopsychidae			0.30	0.02
Hydropsychidae				
Lepidostomatidae	0.04	0.04		
Leptoceridae				
Limnephilidae				
Philopotamidae			0.60	0.84
Psychomyiidae				
Rhyacophilidae			0.60	0.78
Others			0.30	0.95
Terrestrial Derived	0.36	0.16	7.80	0.03
Insect - Others				
Non-Insect Invertebrates	0.04	0.00		
Mean Total	3.88	1.44	543.05	391.78

Appendix B
Salmonid Prey Composition Data

Table B-1. Percent composition by weight, number, frequency of occurrence and index of relative importance of Atlantic salmon gut contents from West Brook. Values are based on mean prey consumed of each species therefore percentages may equal more then 100.

	April 2003			
Taxa	%Number	%Weight	%Occurrence	%IRI
Coleoptera				
Elmidae	0.62	0.17	1.61	0.07
Other				
Diptera				
Chironomidae	7.39	1.92	8.81	3.49
Simuliidae	1.91	2.68	3.64	0.71
Tipulidae				
Other	0.62	0.09	1.61	0.06
Ephemeroptera				
Baetidae	7.63	6.67	8.64	5.04
Ephemerellidae	33.26	20.07	19.60	37.26
Heptageniidae	27.98	14.33	24.24	36.41
Leptophlebiidae	0.62	0.02	1.61	0.05
Siphlonuridae	6.80	8.35	9.35	5.56
subimago				
Other	1.23	0.69	3.23	0.32
Plecoptera				
Capniidae	1.32	0.53	2.06	0.15
Chloroperlidae	1.12	0.61	2.06	0.14
Perlodidae	1.74	4.54	4.48	1.90
Taeniopterygidae	5.75	4.89	6.08	4.77
Other	6.17	4.10	11.29	2.52
Trichoptera				
Glossosomatidae	0.62	1.00	1.61	0.13
Helicopsychidae	1.01	22.86	2.50	1.91
Hydropsychidae	1.13	34.25	2.59	4.41
Lepidostomatidae				
Leptoceridae				
Limnephilidae				
Philopotamidae				
Psychomyiidae	0.62	1.72	1.61	0.19
Rhyacophilidae	1.74	4.93	2.86	0.71
Other	0.00	0.00	0.00	0.00
Terrestrial Derived	1.63	1.13	4.11	0.22
Insect - Others	0.62	1.75	1.61	0.20
Non-Insect Invertebrates				

Table B-1 (cont.)

Taxa	%Number	%Weight	%Occurrence	%IRI
		June 2003		
Coleoptera				
Elmidae	0.87	0.11	2.73	0.13
Other				
Diptera				
Chironomidae	1.07	0.44	3.49	0.28
Simuliidae	1.00	0.19	2.73	0.15
Tipulidae	1.44	0.73	4.84	0.66
Other	1.51	0.76	5.76	0.26
Ephemeroptera				
Baetidae	40.79	5.04	17.57	38.60
Ephemerellidae	3.28	1.96	7.51	2.21
Heptageniidae	5.75	11.24	9.62	8.57
Leptophlebiidae	1.06	0.36	2.73	0.18
Siphlonuridae	5.75	1.41	5.12	1.91
subimago	23.34	34.11	10.79	30.53
Other	2.50	8.49	3.89	3.25
Plecoptera				
Capniidae	0.26	0.39	1.61	0.07
Chloroperlidae	0.74	1.26	1.87	0.20
Perlodidae	0.26	1.17	1.61	0.15
Taeniopterygidae	1.47	5.57	3.85	0.97
Other	0.13	10.48	0.81	0.54
Trichoptera				
Glossosomatidae	2.68	1.40	4.96	1.18
Helicopsychidae	1.11	0.28	3.34	0.22
Hydropsychidae	1.61	5.42	4.55	1.99
Lepidostomatidae				
Leptoceridae				
Limnephilidae	1.45	4.04	3.94	0.89
Philopotamidae	0.39	0.20	1.61	0.06
Psychomyiidae	0.39	4.11	2.42	0.69
Rhyacophilidae	3.90	18.35	8.70	12.82
Other	3.47	5.35	8.54	1.31
Terrestrial Derived	4.27	16.47	6.28	3.28
Insect - Others	0.13	0.44	0.81	0.03
Non-Insect Invertebrates	2.47	1.09	3.54	0.46

Table B-1 (cont.)

Taxa	%Number	%Weight	%Occurrence	%IRI
		August 2003		
Coleoptera				
Elmidae	1.90	0.08	4.76	0.64
Other				
Diptera				
Chironomidae	7.93	4.81	9.13	7.51
Simuliidae	9.78	2.33	4.56	3.32
Tipulidae				
Other	4.35	1.94	5.56	1.76
Ephemeroptera				
Baetidae	19.76	3.42	17.06	24.74
Ephemerellidae	13.74	0.96	7.14	6.80
Heptageniidae	3.81	0.32	7.14	1.98
Leptophlebiidae				
Siphlonuridae	5.37	3.81	4.17	2.80
subimago	4.35	54.90	5.56	16.62
Other	4.58	2.15	5.82	2.25
Plecoptera				
Capniidae				
Chloroperlidae				
Perlodidae				
Taeniopterygidae	4.35	2.81	5.56	2.01
Other	13.52	4.06	21.83	8.05
Trichoptera				
Glossosomatidae	2.86	33.44	4.76	11.63
Helicopsychidae	9.74	11.01	9.39	12.50
Hydropsychidae	5.78	4.45	7.14	4.39
Lepidostomatidae	2.17	0.21	3.57	0.49
Leptoceridae	10.48	0.03	4.76	3.36
Limnephilidae				
Philopotamidae				
Psychomyiidae	0.95	0.12	2.38	0.17
Rhyacophilidae	9.65	21.68	9.52	25.08
Other	0.95	0.12	2.38	0.17
Terrestrial Derived	9.01	12.63	7.41	4.49
Insect - Others	4.35	13.12	5.56	4.90
Non-Insect Invertebrates	9.51	19.10	13.14	7.54

Table B-1 (cont.)

Taxa	%Number	%Weight	%Occurrence	%IRI
		December 2003		
Coleoptera				
Elmidae				
Other				
Diptera				
Chironomidae	14.86	0.40	11.36	14.41
Simuliidae				
Tipulidae				
Other				
Ephemeroptera				
Baetidae	2.70	0.03	4.55	1.03
Ephemerellidae	20.27	2.58	18.18	34.52
Heptageniidae	6.76	0.13	11.36	6.50
Leptophlebiidae	6.76	0.86	6.82	4.32
Siphlonuridae	4.05	0.43	4.55	1.69
subimago				
Other	4.05	0.21	4.55	1.61
Plecoptera				
Capniidae	8.11	0.29	4.55	3.17
Chloroperlidae	2.70	0.12	4.55	1.07
Perlodidae				
Taeniopterygidae				
Other	4.05	0.26	6.82	0.81
Trichoptera				
Glossosomatidae	9.46	1.58	9.09	8.33
Helicopsychidae				
Hydropsychidae	1.35	0.90	2.27	0.43
Lepidostomatidae				
Leptoceridae				
Limnephilidae	9.46	0.56	4.55	3.78
Philopotamidae				
Psychomyiidae				
Rhyacophilidae				
Other	4.05	2.17	4.55	1.17
Terrestrial Derived Insect - Others				
Non-Insect Invertebrates				

Table B-2. Percent composition by weight, number, frequency of occurrence and index of relative importance of Brook trout gut contents from West Brook. Values are based on mean prey consumed of each species therefore percentages may equal more then 100.

Taxa	April 2003			
	%Number	%Weight	%Occurrence	%IRI
Coleoptera				
Elmidae				
Other				
Diptera				
Chironomidae	9.72	2.79	7.98	6.94
Simuliidae	5.88	1.29	3.85	2.37
Tipulidae	2.17	14.30	6.25	6.44
Other	3.63	3.73	7.18	1.59
Ephemeroptera				
Baetidae	3.48	14.01	5.26	5.63
Ephemerellidae	22.18	3.33	9.89	15.55
Heptageniidae	9.93	13.64	12.92	15.76
Leptophlebiidae	3.87	7.62	6.87	4.45
Siphlonuridae	12.83	6.90	12.12	15.00
subimago				
Other	13.73	1.01	7.69	9.74
Plecoptera				
Capniidae	3.21	3.14	4.48	2.04
Chloroperlidae	3.33	0.82	3.33	0.67
Perlodidae	1.96	2.55	3.85	1.49
Taeniopterygidae	12.40	5.15	8.89	13.11
Other	9.66	8.84	18.97	12.73
Trichoptera				
Glossosomatidae	2.17	1.96	6.25	1.62
Helicopsychidae	13.04	3.95	6.25	6.65
Hydropsychidae	3.33	4.61	6.67	2.55
Lepidostomatidae				
Leptoceridae				
Limnephilidae				
Philopotamidae	1.96	0.45	3.85	0.80
Psychomyiidae	1.67	1.49	3.33	0.51
Rhyacophilidae	2.17	50.11	6.25	20.45
Other	5.59	3.37	11.03	2.66
Terrestrial Derived Insect - Others	7.99	21.10	9.52	9.87
Non-Insect Invertebrates				

Table B-2 (cont.)

Taxa	%Number	%Weight	%Occurrence	%IRI
		June 2003		
Coleoptera				
Elmidae	0.61	0.36	2.86	0.14
Other	5.82	4.26	9.05	2.43
Diptera				
Chironomidae	1.29	0.13	3.81	0.20
Simuliidae	0.61	0.03	2.86	0.09
Tipulidae	1.96	0.31	4.76	0.31
Other	0.61	0.28	2.86	0.13
Ephemeroptera				
Baetidae	10.80	0.30	22.86	7.09
Ephemerellidae	4.27	0.91	8.57	2.23
Heptageniidae	3.66	3.28	8.57	2.98
Leptophlebiidae				
Siphlonuridae	1.22	0.04	2.86	0.18
subimago	68.05	70.42	22.86	78.82
Other	7.08	4.84	5.24	3.25
Plecoptera				
Capniidae				
Chloroperlidae	1.96	1.26	4.76	0.45
Perlodidae				
Taeniopterygidae				
Other				
Trichoptera				
Glossosomatidae	0.61	0.05	2.86	0.09
Helicopsychidae	1.22	0.82	5.71	0.59
Hydropsychidae	1.96	2.70	4.76	0.65
Lepidostomatidae	1.83	0.15	2.86	0.28
Leptoceridae	0.61	0.03	2.86	0.09
Limnephilidae	3.92	0.15	9.52	1.13
Philopotamidae	1.96	16.10	4.76	2.50
Psychomyiidae				
Rhyacophilidae				
Other	0.61	7.50	2.86	1.16
Terrestrial Derived Insect - Others	3.09	12.48	20.32	6.02
Non-Insect Invertebrates				

Table B-2 (cont.)

Taxa	%Number	%Weight	%Occurrence	%IRI
		August 2003		
Coleoptera				
Elmidae	2.00	2.16	3.13	1.24
Other				
Diptera				
Chironomidae	3.78	11.52	6.76	5.18
Simuliidae	5.35	8.73	8.71	4.48
Tipulidae				
Other	7.00	3.48	13.13	3.63
Ephemeroptera				
Baetidae	5.17	0.51	6.70	2.48
Ephemerellidae	4.00	4.80	6.25	5.25
Heptageniidae	4.00	0.17	6.25	2.48
Leptophlebiidae	6.00	0.09	6.25	3.63
Siphlonuridae				
subimago	5.00	25.92	10.00	11.08
Other	8.35	17.10	11.83	11.61
Plecoptera				
Capniidae	4.35	0.37	7.14	0.85
Chloroperlidae				
Perlodidae				
Taeniopterygidae				
Other	10.35	63.55	16.52	21.52
Trichoptera				
Glossosomatidae				
Helicopsychidae	39.00	3.04	16.25	35.08
Hydropsychidae	7.50	2.60	9.69	6.43
Lepidostomatidae				
Leptoceridae				
Limnephilidae				
Philopotamidae				
Psychomyiidae	5.00	3.09	10.00	2.90
Rhyacophilidae				
Other	21.35	25.71	20.27	11.48
Terrestrial Derived	28.62	24.20	25.03	33.32
Insect - Others	4.00	0.42	3.13	1.32
Non-Insect Invertebrates	4.00	2.21	6.25	1.85

Table B-2 (cont.)

Taxa	%Number	%Weight	%Occurrence	%IRI
		December 2003		
Coleoptera				
Elmidae				
Other				
Diptera				
Chironomidae	10.00	0.64	11.76	9.33
Simuliidae				
Tipulidae				
Other				
Ephemeroptera				
Baetidae				
Ephemerellidae	5.00	9.13	5.88	6.19
Heptageniidae	10.00	0.47	5.88	4.59
Leptophlebiidae	5.00	1.87	5.88	3.01
Siphlonuridae	5.00	12.78	5.88	7.80
subimago				
Other				
Plecoptera				
Capniidae				
Chloroperlidae	5.00	0.86	5.88	2.57
Perlodidae	5.00	8.98	5.88	6.13
Taeniopterygidae				
Other	15.00	7.93	11.76	10.05
Trichoptera				
Glossosomatidae	15.00	2.45	11.76	15.30
Helicopsychidae				
Hydropsychidae	5.00	14.84	5.88	8.70
Lepidostomatidae				
Leptoceridae				
Limnephilidae				
Philopotamidae				
Psychomyiidae				
Rhyacophilidae				
Other	15.00	40.02	17.65	24.12
Terrestrial Derived	5.00	0.02	5.88	2.20
Insect - Others				
Non-Insect Invertebrates				

Table B-3. Percent composition by weight, number, frequency of occurrence and index of relative importance of Brown trout gut contents from West Brook. Values are based on mean prey consumed of each species therefore percentages may equal more then 100.

Taxa	%Number	%Weight	%Occurrence	%IRI
		April 2003		
Coleoptera				
Elmidae	0.27	7.02	0.67	0.41
Other	0.25	1.46	0.57	0.09
Diptera				
Chironomidae	5.53	0.20	8.09	3.29
Simuliidae	1.70	0.41	2.67	0.45
Tipulidae	0.29	2.25	0.77	0.14
Other	2.28	14.50	1.91	0.94
Ephemeroptera				
Baetidae	5.72	0.72	8.46	3.64
Ephemerellidae	30.52	13.26	14.92	42.68
Heptageniidae	13.82	5.61	12.58	16.06
Leptophlebiidae	1.61	0.69	3.42	0.80
Siphlonuridae	12.08	9.47	11.04	15.77
subimago	3.24	2.34	2.31	0.95
Other	3.26	1.82	4.33	1.31
Plecoptera				
Capniidae	3.81	3.76	3.60	1.89
Chloroperlidae	1.69	4.73	3.14	1.65
Perlodidae	1.51	3.25	2.09	0.95
Taeniopterygidae	5.14	2.77	4.04	5.65
Other	3.84	2.66	8.11	0.72
Trichoptera				
Glossosomatidae	2.54	1.14	2.52	0.63
Helicopsychidae	1.05	8.49	1.52	1.02
Hydropsychidae	0.76	9.26	1.52	1.13
Lepidostomatidae	0.77	3.76	0.95	0.33
Leptoceridae	0.25	0.12	0.57	0.02
Limnephilidae	0.99	0.58	0.57	0.08
Philopotamidae	1.26	1.54	1.49	0.20
Psychomyiidae	0.63	0.01	1.49	0.05
Rhyacophilidae	0.86	0.27	2.08	0.16
Other	3.29	7.83	6.44	0.91
Terrestrial Derived Insect - Others	1.59	0.25	2.96	0.22
Non-Insect Invertebrates	1.44	11.59	2.23	0.82

Table B-3 (cont.)

Taxa	%Number	%Weight	%Occurrence	%IRI
		June 2003		
Coleoptera				
Elmidae	1.07	2.99	3.23	1.22
Other	1.34	1.49	3.29	0.63
Diptera				
Chironomidae	1.73	0.39	4.63	0.78
Simuliidae	0.50	0.04	1.73	0.06
Tipulidae	1.22	0.34	2.70	0.22
Other	3.64	1.21	9.26	0.46
Ephemeroptera				
Baetidae	20.08	2.04	11.07	16.67
Ephemerellidae	3.45	1.46	6.02	1.44
Heptageniidae	4.04	7.61	6.27	5.03
Leptophlebiidae				
Siphlonuridae	6.05	1.66	6.80	2.92
subimago	28.19	30.86	18.68	43.64
Other	17.08	19.83	10.06	11.58
Plecoptera				
Capniidae				
Chloroperlidae	0.66	1.23	2.06	0.29
Perlodidae	0.58	1.75	2.06	0.39
Taeniopterygidae				
Other	0.66	0.11	2.15	0.07
Trichoptera				
Glossosomatidae	5.98	6.54	5.72	8.77
Helicopsychidae	2.74	0.82	3.29	0.53
Hydropsychidae	0.17	0.21	0.66	0.02
Lepidostomatidae				
Leptoceridae	0.49	0.01	1.49	0.05
Limnephilidae	3.52	16.69	2.63	3.59
Philopotamidae	0.66	0.31	2.15	0.16
Psychomyiidae	0.17	0.40	0.66	0.03
Rhyacophilidae	2.39	11.46	5.71	6.47
Other	2.56	1.86	5.86	0.36
Terrestrial Derived	2.64	14.64	5.62	3.88
Insect - Others	1.16	0.83	4.12	0.20
Non-Insect Invertebrates	2.23	3.70	8.26	0.62

Table B-3 (cont.)

Taxa	August 2003			
	%Number	%Weight	%Occurrence	%IRI
Coleoptera				
Elmidae	1.18	98.81	5.26	18.25
Other				
Diptera				
Chironomidae	4.02	0.15	9.43	1.88
Simuliidae	0.75	0.02	2.08	0.10
Tipulidae				
Other	3.01	0.22	6.25	0.42
Ephemeroptera				
Baetidae	5.38	0.05	6.60	1.80
Ephemerellidae	1.18	0.01	5.26	0.22
Heptageniidae				
Leptophlebiidae				
Siphlonuridae	1.18	0.15	5.26	0.24
subimago				
Other	12.26	21.16	10.76	11.59
Plecoptera				
Capniidae	0.75	0.14	2.08	0.12
Chloroperlidae				
Perlodidae				
Taeniopterygidae				
Other	3.01	0.26	4.17	0.84
Trichoptera				
Glossosomatidae	4.51	4.15	4.17	2.23
Helicopsychidae	41.50	0.02	16.28	37.10
Hydropsychidae	0.75	0.01	2.08	0.10
Lepidostomatidae				
Leptoceridae				
Limnephilidae	2.26	0.17	2.08	0.31
Philopotamidae				
Psychomyiidae				
Rhyacophilidae	22.77	13.76	5.76	14.00
Other	13.76	13.73	18.40	10.34
Terrestrial Derived	21.84	28.20	31.23	37.95
Insect - Others	3.10	2.31	12.61	1.34
Non-Insect Invertebrates	12.26	14.20	17.36	8.74

Taxa	%Number	%Weight	%Occurrence	%IRI	
Coleoptera					
Elmidae		1.45	0.05	2.27	0.300789
Other					
Diptera					
Chironomidae	9.33	14.49	0.40	13.64	17.88534
Simuliidae		1.45	0.07	2.27	0.304256
Tipulidae		1.45	0.36	2.27	0.362301
Other		2.90	0.24	2.27	0.629
Ephemeroptera					
Baetidae		2.90	0.03	4.55	1.171012
Ephemerellidae	6.19	11.59	2.65	13.64	17.10553
Heptageniidae	4.59				
Leptophlebiidae	3.01	2.90	0.31	4.55	1.282326
Siphlonuridae	7.80				
subimago					
Other		10.14	1.28	9.09	9.146639
Plecoptera					
Capniidae		5.80	0.12	2.27	1.184007
Chloroperlidae	2.57				
Perlodidae	6.13				
Taeniopterygidae		2.90	0.39	4.55	1.315372
Other	10.05	7.25	0.22	9.09	3.892178
Trichoptera					
Glossosomatidae	15.30	8.70	0.44	4.55	3.654837
Helicopsychidae					
Hydropsychidae	8.70	1.45	2.26	2.27	0.74317
Lepidostomatidae					
Leptoceridae					
Limnephilidae		1.45	0.21	2.27	0.331673
Philopotamidae					
Psychomyiidae					
Rhyacophilidae					
Other	24.12	17.39	12.52	11.36	6.978144
Terrestrial Derived Insect - Others	2.20	2.90	0.00	4.55	1.160574
Non-Insect Invertebrates					

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