Fisheries Session

Fall and Winter Brook Trout Prey Selection and Daily Ration

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Abstract: Most studies examining salmonid diets and their relationship to invertebrate drift are confined to periods from spring through early fall. Invertebrate drift generally decreases from spring through summer and fall seasons and is greatest during diel periods of low light. Salmonid feeding efficiency is reduced under low light conditions and several studies have found them to feed primarily through the daylight hours. Drift feeding salmonids are also size selective. The purpose of this study was to determine if patterns of invertebrate drift and brook trout feeding seen during warmer times of the year hold during the post-spawning fall and winter for brook trout *(Salvelinus fontinalis)* in the central Appalachians. The general diel pattern of invertebrate drift and salmonid feeding found during spring and summer months in other studies was less obvious during the post-spawning fall and winter for brook trout. Total invertebrate drift density did not follow a diel pattern. Brook trout diet composition was not correlated to the composition of invertebrate drift and brook trout may feed from the benthos more frequently than previously suspected for stream salmonids. There appeared to be no diel effect on brook trout feeding. Brook trout daily ration during the fall and winter were extremely low and may have been below maintenance ration during the fall.

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Stream-dwelling salmonids are generally believed to be opportunistic, visual predators feeding primarily on invertebrate drift (Rader 1997). Being opportunistic, the composition of salmonid diets shows a correlation to the composition of the drift (Elliot 1973, Allan 1981). However, several studies also note that prey size, in addition to abundance in the drift, is an important determinant of diet. Larger taxa are over represented in the diet and underrepresented in the drift (Allan 1981, Sagar and Glova 1988, Forrester et al. 1994). This size selectivity may be reduced at night (Sagar and Glova 1988, Angradi and Griffith 1990).

Diel changes in prey consumption may be related to prey visibility. Decreased light intensity has been shown to decrease the feeding efficiency of stream-dwelling salmonids (Wilzbach et al. 1986). In addition, several studies have shown diel patterns of prey consumption with lower consumption during nighttime hours (Allan 1981, Sagar and Glova 1988, Angradi and Griffith 1990, Forrester et al. 1994). Contrary to these studies Elliot (1973) found increased feeding of brown trout *(Salmo trutta)* at night when invertebrate drift was greatest. Invertebrate drift typically follows a diel pattern with drift densities increasing at night (Waters 1972). This is believed to be a predator avoidance mechanism in benthic invertebrates. If fish predators are visually oriented, benthic invertebrates have adapted by drifting when the feeding efficiency of the predator is reduced. Also, within invertebrate taxa, larger individuals, who are most detectable by fish predators, restrict their drifting behavior to periods of darkness (Douglas et al. 1994). Rader (1997) presented a conceptual model of the relationships among light intensity, trout feeding, efficiency, and invertebrate drift over a diel period. In general, as light intensity decreases, salmonid feeding efficiency decreases, and invertebrate drift increases.

Most studies of salmonid feeding and invertebrate drift have been restricted to the seasons of late spring through early fall (May–Oct.) (Reed and Bear 1966, Elliot 1973, Allan 1981, Sagar and Glova 1988, Forrester et al. 1994, Young et al. 1997). An exception is Bridcut and Giller (1995) in a study with brown trout. Seasonal trends in invertebrate drift and salmonid diets show that total drift density and daily consumption are greatest in the spring and both decline through the summer months (Wipfli 1997, Allan 1981). Also, terrestrial invertebrates become a larger portion of the diet proceeding from spring through summer (Wipfli 1997, Young et al. 1997). Knowledge concerning the late fall and winter salmonid diet habits and prey availability is lacking.

The purpose of this study is to describe post-spawning prey availability and diet composition of stream dwelling brook trout in the central Appalachian Mountains and to determine if the general trends of invertebrate drift and trout diet seen during summer months hold during the fall and winter. The importance of this study to management lies in furthering our knowledge of the trophic basis of brook trout production during critical periods often overlooked in similar studies. In this paper, we investigate (1) the correlation between invertebrate drift composition and brook trout diet composition, (2) the diel variability in invertebrate drift and brook trout diets, (3) size-selectivity in brook trout diet, and (4) daily ration of brook trout during the fall and winter.

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Methods

Study Site

Brook trout diets and invertebrate drift were sampled from Stonecoal Run, Randolph County, West Virginia. Stonecoal Run is a second order tributary of the Middle Fork River. The stream has an average gradient of 3.7, a wetted width of 3.75–5 m, and a pool:riffle ratio of 0.2. The substrate is largely composed of small to large cobble. Stonecoal Run supports a locally high brook trout population density (as compared to other streams within the Middle Fork watershed) of approximately 45–50 adult brook trout per 100 m (Sweka and Hartman, unpubl. data). Since 1995, the West Virginia Division of Natural Resources and the Department of Environmental Protection has been adding annually limestone sand to Stonecoal Run to mitigate the effects of acid mine drainage and acid precipitation. Currently, pH remains near neutral year round.

Invertebrate Drift

Invertebrate drift and brook trout diets were sampled on 12–13 November 1999 (fall) and 26–27 February 2000 (winter). The fall sampling was after peak spawning activity (mid Oct) and after leaf fall in the region. Sunrise and sunset were 0658 hours and 1708 hours during the fall and 0657 hours and 1808 hours during the winter. Invertebrate drift and brook trout diets were sampled during 4 equally spaced time intervals over a 24 hour period. These periods ran from 2100–0300, 0300–0900, 0900–1500, and 1500–2100 hours. The average daily stream temperature during fall was 8.82 C (range: 8.25–9.33 C) and was 7.15 C (range: 6.65–7.84 C) during the winter. Winter stream temperatures would normally be lower, but winter sampling was conducted during an unseasonably warm period, and thus average winter stream temperatures at the time of sampling were within 2° of those in the fall. Only 1 24-hour period was sampled each season, which may constitute a lack of replication in our study. However, we felt that seasonal variability would overwhelm within seasonal variability.

Invertebrate drift was sampled with 6 drift nets placed at the tails of riffles and heads of pools. We felt this would be the most appropriate location to sample prey available to brook trout, assuming that most brook trout hold in pools and the majority of invertebrate drift would be coming from riffles. The mouth of the nets was 56×30 cm and the mesh size was 250-µm. The bottom of each net was in contact with the substrate and the tops were above the water level. Water depth and average current velocity were measured at three equally spaced points across the front of each net at the time of deployment and prior to retrieval. Nets were left in the stream for approximately 6 hours. Beginning and ending depths and current velocities were used to calculate average filtration volumes over the 6 hour period. Contents of the drift nets were rinsed into a 250-µm sieve and then transferred to 95% ethanol. Nets were then placed back into the stream for the next time interval. Wading was not permitted in the stream 20–30 m above each net to minimize increases in accidental drift due to human disturbance.

Brook Trout Diets

Brook trout diets were sampled 4 times during each diel cycle. These 4 sampling periods were centered on 0300, 0900, 1500, and 2100 hours. During each sampling period we collected at least 15 brook trout (>100 mm total length) using a pulsed DC backpack electrofishing unit. Stomach contents were immediately sampled following collection. The fish were anesthetized with 120 mg/liter clove oil (Anderson et al. 1997), total lengths measured (nearest mm), and weighed (nearest g). Stomach contents were sampled by gastric lavage (Wipfli 1997) with stream water and contents were collected in a 250-µm sieve, and then transferred to 95% ethanol. Ten brook trout were kept and frozen as soon as possible (within 30 minutes) each season and taken to the lab to determine the effectiveness of the gastric lavage technique and for dry weight estimation. Brook trout from the same stream segment were not sampled more than once during a season.

Laboratory Procedures

Aquatic invertebrates in both diet and drift samples were identified under a dissecting microscope to the family level when practical (Borror et al. 1989, Merrit and Cummins 1996). Extremely small (<0.25 mm head width) or rare taxa, were identified to order. Terrestrial invertebrates were identified to order, and in some cases family. Head widths and lengths of all organisms were measured to at least the nearest 0.1 mm (0.04 mm for the smallest taxa) with an ocular micrometer. Because both invertebrate drift and brook trout diets were preserved in 95% ethanol, dry mass (mg) of each individual was determined using published head width-mass or length-mass equations for each taxa (Rogers et al. 1976, Smock 1980, Sample et al. 1993, Benke et al. 1999).

Frozen brook trout were thawed in the lab and their stomach excised and any remaining contents identified as described above. The stomach and fish were then measured to the nearest mm, wet weighed to the nearest 0.0001 g, and dried at 80 C to a constant mass (>48 hours). Percent dry weight was calculated as dry weight divided by wet weight×100.

Statistical Analysis

Invertebrate drift density was calculated in terms of number and/or biomass per $100 \cdot m^3$ of water for each sample. We used a split-plot analysis of variance (ANOVA) to identify seasonal and diel differences in invertebrate drift density, with seasons (fall and winter) as the main plots and time intervals as the subplots. We log transformed the head widths of invertebrates to more closely approximate a normal distribution. Again, a split-plot ANOVA was used to evaluate the effect of season and time of day on drift size and Fisher's least significant difference test was used as a multiple comparison test if significance was found by the *F*-test for either season or time of day.

To determine if prey availability was an indicator of prey use, we correlated percent composition of the drift with percent composition of the diet. Fish from all time periods within a season and drift samples from all time periods within a season were pooled to determine percent composition data. Percent composition of the diet and drift were arcsine transformed and Pearson correlation coefficients were determined for each season for taxa present in both drift and diet.

Selectivity for individual taxa was determined using the forage ratio (Krebs 1999). Forage ratios were calculated for taxa present in both drift and diet as the percent composition of diet divided by the percent composition of the drift. The forge ratios of each taxa were then regressed on the median head width of each taxa to determine if brook trout exhibited size selection.

The stomach contents of each fish were standardized on a dry weight of prey per dry weight of fish ($g \cdot g^{-1}$, DW) basis. Dry weight (DW) of each fish in the field was calculated with a total length (TL) to dry weight regression equation derived from the sample brook trout dried in the lab ($DW = 0.000002398 \cdot TL^{2.91}$; n = 20; $R^2 = 0.96$). We sampled a relatively large size range of fish during each season (range: 9–61 g in the fall; 9–47 g in the winter); therefore, we needed to correct the dry weight of prey in each fish's stomach to account for any allometric influences on observed stomach content weight. The overall mean dry weight of all fish from both seasons was 4.11 ± 0.2245 (95%CI) and the slope (CB = –0.307) of the allometric consumption equation ($C = CA \cdot W^{CB}$) for lake trout *(Salvelinus namaycush*; Stewart et al. 1983) was used to standardize the dry weight of food in each individual brook trout's stomach to the overall mean weight of all brook trout. Again, a split-plot ANOVA was used to determine differences in the weight of stomach contents between seasons and time intervals within a season.

Daily ration for each season was calculated as in Elliot and Persson (1978):

$$C_d = 24 \cdot SR$$

where C_d is the daily ration ($g \cdot g^{-1} \cdot d$), S is the mean dry weight of food in the stomach over a 24-hour period, and R is the rate of gastric evacuation. This equation assumes a constant rate of consumption throughout the day, which holds true for brook trout in our study (see results). The rate of gastric evacuation (Sweka and Hartman, unpubl. data) was determined by experiments with hatchery-raised brook trout (n = 25) in the lab at similar water temperatures experienced in the field during the fall and winter according to the methods described in Elliot (1972). R is a coefficient in an exponential gastric evacuation model:

$$Y_x = Y_o \cdot e^{-R \cdot X}$$

where: Y_o is the initial amount of prey in a fish's stomach, X is time in hours, Y_x is the amount of prey remaining after time X, and R is the sample regression coefficient or the exponent for the exponential curve and is the constant relative rate of gastric evacuation, which is equal to the proportion of remaining stomach contents evacuated per unit time.

Field estimates of daily ration were compared to predictions of maintenance ration from a bioenergetics model for brook trout (Hartman and Sweka 2001). The model was fit to temperatures encountered in the field during the fall and winter. Brook trout energy density was determined from % dry weight of brook trout using

Table 1. Mean drift density (95% CI) (n·100 m^{-3}) of major groups of invertebrates. Different letters indicate significant difference between time intervals.

	Group	2100–0300	0300–0900	0900–1500	1500–2100
Fall	Ephemeroptera	1.04 (0.83)	1.26 (0.82)	1.51 (1.80)	2.00 (1.09)
	Plecoptera	15.55 (13.86)	8.42 (5.64)	14.89 (18.89)	30.07 (13.04)
	Trichoptera	0.92 (0.78)	1.11(0.75)	1.66 (1.15)	2.24 (1.12)
	Adult aquatic	0.20 (0.20)	1.08 (3.78)	1.31 (1.73)	0.47 (0.49)
	Other aquatic	1.34 (0.82)	1.43 (0.92)	1.84 (1.27)	1.77 (0.93)
	Terrestrial	1.50 (0.94)	3.77 (2.30)	11.26 (14.83)	8.81 (6.63)
	Total drift	20.30 (15.80)	15.71 (9.36)	31.82 (35.10)	45.21 (16.24)
Winter	Ephemeroptera	2.85 (0.64)	5.85 (3.05)	4.11 (1.56)	3.81 (1.73)
	Plecoptera	63.42 (18.98)^{a}	77.86 (36.86)^{ab}	30.89 (7.09)^{b}	39.05 (20.99)^{b}
	Trichoptera	3.85 (1.80)	4.92 (1.89)	3.37 (1.18)	2.31 (1.21)
	Adult aquatic	0.67 (0.47)	0.63 (0.52)	0.91 (0.59)	1.21 (0.46)
	Other aquatic	10.90 (7.89)	15.92 (4.71)	12.57 (1.55)	10.51 (4.22)
	Terrestrial	2.26 (2.62)	4.09 (2.63)	26.30 (26.95)	3.93 (2.34)
	Total drift	83.73 (28.46)	109.07 (46.29)	78.01 (28.56)	60.62 (29.04)

the salmonid equation in Hartman and Brandt (1995). Brook trout energy density was 3,949 j·g^{-1} during the fall and 3,895 j·g^{-1} during the winter. We assumed the diet was 100% aquatic invertebrates with an energy density of 4000 j·g^{-1} (wet weight) which is in the range for Ephemeroptera (Cummins and Wuycheck 1971).

Results

Invertebrate Drift

Total drift density (n·100 m^{-3}) was significantly higher in the winter than in the fall ($P<0.01$). However, there was no difference in total drift between time intervals within a season ($P = 0.22$). Ephemeroptera, Plecoptera, and Trichoptera all had higher drift densities during the winter ($P<0.01$ in all cases) (Table 1). The diel effect was significant for Plecoptera during the winter where drift density was highest during the period from 0300–0900 hours ($P = 0.01$).

Total biomass in the drift (mg·100 m^{-3}) showed a similar pattern to numbers in the drift. Drift biomass was greatest during the winter ($P = 0.04$) and there was no diel effect ($P = 0.44$). Mean drifting biomass during the fall and winter were 130.98 ± 55.92 mg·100 m^{-3} and 223.28 ± 42.84 mg·100 m^{-3}, respectively. Among major groups of invertebrates, only the biomass of Ephemeroptera was significantly higher in the winter ($P = 0.04$). Mean drifting biomass of Ephemeroptera during the fall and winter were 7.99 ± 1.89 mg·100 m^{-3} and 13.99 ± 6.66 mg·100 m^{-3}, respectively. An increase in the biomass of "other" aquatic invertebrates accounts for the increase in total drifting biomass from fall to winter ($P<0.01$) (fall mean: 9.70 ± 1.77 mg·100 m^{-3}; winter mean: 53.65 ± 9.96 mg·100 m^{-3}). This group was comprised of Diptera, Coleoptera, Oligochaeta, and Anisoptera. No group showed a diel effect ($P>0.05$ in all cases) on biomass in the drift.

Table 2. Percent composition of the invertebrate drift and brook trout diets by number and biomass.

		Drift			Diet		
	Group	*N*	% Number	% Mass	*N*	% Number	% Mass
Fall	Ephemeroptera	166	5	6	40	6	6
	Plecoptera	2068	62	64	112	16	8
	Trichoptera	188	6	7	201	28	20
	Adult aquatic	42	1	2	67	9	17
	Other aquatic	212	6	8	87	12	16
	Terrestrial	657	20	13	202	28	34
	Total	3333	100	100	709	100	100
Winter	Ephemeroptera	396	5	7	93	7	7
	Plecoptera	4803	65	47	353	25	18
	Trichoptera	316	4	6	341	24	16
	Adult aquatic	63	1	3	213	15	31
	Other aquatic	1104	15	24	226	16	12
	Terrestrial	737	10	13	172	12	16
	Total	7419	100	100	1398	100	100

The Plecoptera dominated the total drift during the diel cycle both in terms of numbers and biomass for both seasons. In the fall, Plecoptera comprised 62% of the fall invertebrate drift by number and 64% by biomass. In the winter, Plecoptera comprised 65% of the fall invertebrate drift by number and 47% by biomass (Table 2).

Invertebrate size (in terms of head width in mm) in the drift differed seasonally and throughout the day within a season ($P<0.01$). However, this pattern differed between major taxonomic groups (Fig. 1). Drifting Trichoptera were larger during the winter ($P<0.01$). They also showed a diel effect during the fall where the smallest mean size occurred during the daylight hours of 0900–1500 ($P<0.01$). However, the smallest mean size of drifting Trichoptera during the winter occurred during the nighttime hours of 2100–0300 ($P<0.01$). The mean size of drifting Plecoptera was also larger during the winter than in the fall ($P<0.01$). In both seasons, the smallest size occurred during the daylight hours of 0900–1500 ($P<0.01$ in both cases). There were no seasonal ($P = 0.58$) or diel effects ($P = 0.07$) on the mean size of drifting Ephemeroptera.

Brook Trout Diets

Percent composition of the diet and drift were arcsine root transformed and Pearson correlation coefficients of % composition of the diet and % composition of the drift were not significant for either season (fall $r = 0.24$, $P = 0.15$; winter $r = -0.04$, $P = 0.81$). Plecoptera comprised the majority of the drift in terms of both density and biomass, but made up a much lower portion of brook trout diets (Table 2). Conversely, adult aquatic invertebrates and Trichopterans comprised a small proportion of the drift, but a much larger proportion of the brook trout diets.

Regression of the forage ratio (% composition of diet / % composition of drift) on median head widths of the prey taxa showed a positive relationship during both the fall and winter. Although R^2 values were low, the forage ratio increased significantly as median head width increased for both seasons ($P<0.01$ in both cases) (Fig. 2).

Seasonal and diel effects were observed for the mean size of individual prey in the brook trout diets (Fig. 3). Overall, invertebrate prey was larger during the winter than in the fall ($P<0.01$). A diel effect was seen during the fall when the mean head width of prey was smallest at 1500 hours ($P<0.01$). All other time periods were equivalent. In the winter sample, the smallest mean head width of prey occurred during the night (0300 hours).

The specific mass of stomach contents ($g \cdot g^{-1}DW$) was significantly greater during the winter than during the fall ($P<0.01$). The daily average of specific stomach mass was 0.003 ± 0.001 $g \cdot g^{-1}$ during the fall and 0.013 ± 0.002 $g \cdot g^{-1}$ during the winter. Time of the day had no significant effect on specific stomach mass in either season ($P = 0.13$) although specific stomach mass tended to be higher during the daylight hours in the winter (Fig. 4). As the specific stomach mass did not significantly change throughout the course of a day, we assumed a constant feeding rate for brook trout and calculated daily consumption as 24 multiplied by the mean specific stom-

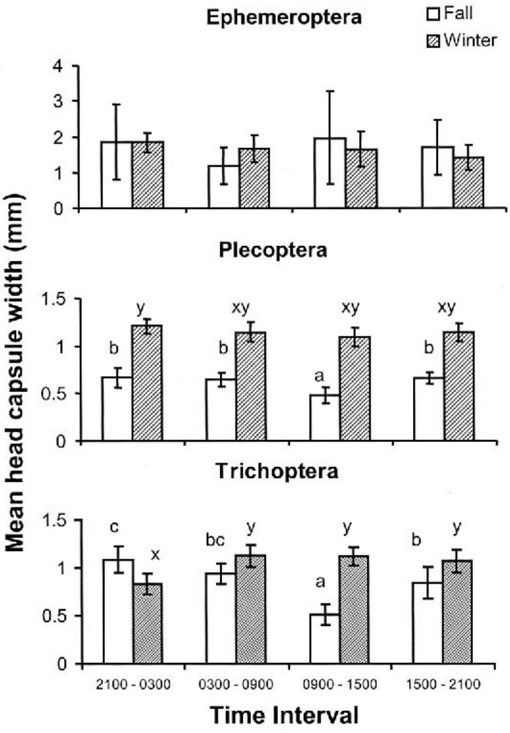

Figure 1. Mean sizes of individuals in the invertebrate drift. Error bars correspond to 95% confidence intervals. Different letters denote significant differences between time intervals throughout the day. Note: nontransformed means are shown. Statistical analysis was conducted on log transformed values.

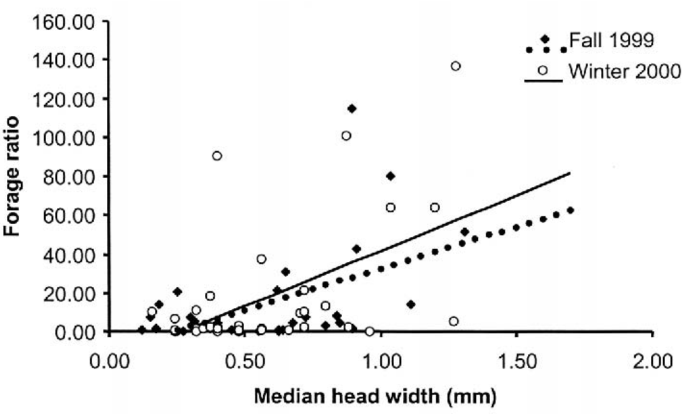

Figure 2. Relationship between the forage ratio and the size of invertebrate prey. Fall: Y=–10.19+42.71·X; R^2=0.28. Winter: Y =–15.65+57.02·X; R^2=0.30.

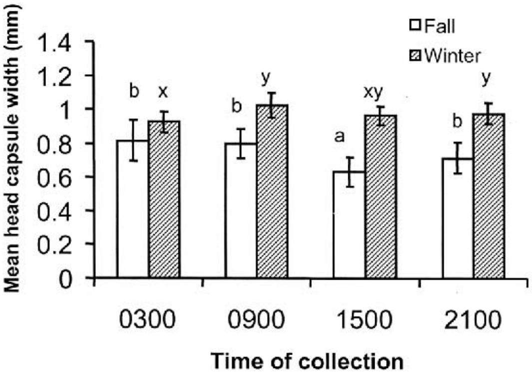

Figure 3. Mean size of prey in brook trout diets. Error bars correspond to 95% confidence intervals. Different letters denote significant differences between times of collection. Note: non-transformed means are shown. Statistical analysis was conducted on log transformed values.

ach mass and the gastric evacuation rate. The gastric evacuation rate (R) that we determined in the lab with hatchery brook trout was 0.0275 ± 0.012 g dry weight/hour (± 95%CI). Daily ration in the fall was lower than that in the winter. Daily ration in the fall was 0.002 ± 0.0005 $g \cdot g^{-1} \cdot d$ (95%CI) and 0.008 ± 0.0016 $g \cdot g^{-1}$)d in the winter. Maintenance ration predicted by the bioenergetics model was 0.0027 $g \cdot g^{-1} \cdot d$ during the fall and 0.0019 $g \cdot g^{-1} \cdot d$ during the winter. Thus, field estimates of daily ration were below maintenance ration during the fall.

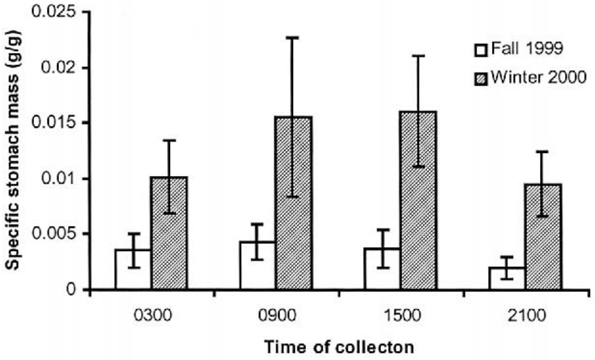

Figure 4. Mean specific stomach mass (g·g^{-1},DW) of brook trout. Error bars correspond to 95% confidence intervals.

Discussion

Patterns of Invertebrate Drift

The drift of aquatic invertebrates declines from spring through summer months, and reaches a low in the late summer and early fall (Young et al. 1997, Allan 1981). Adult aquatic invertebrate emergence during the spring and summer reduce abundance in the drift by the fall (Wipfli 1997). Our findings of the lowest invertebrate drift during the fall support these ideas. Fall drift sampling was conducted shortly after leaf fall when yearly benthic production is beginning. By the winter samples the overall number of drifting invertebrates increased most likely due to a greater time since leaf fall. The major energy source for invertebrate production in low order streams comes from allochthonous inputs in the form of leaf fall (Vannote et al. 1980).

We did not observe a diel effect on total drift density or biomass. Only the Plecoptera showed a diel effect on drift density and this only occurred during the winter and no group showed a diel effect on drifting biomass. The generality that drift density increases during low light levels associated with nighttime hours (Rader 1997) does not seem to hold following leaf fall in the later fall and winter. The greatest drift density of Plecopterans occurred from 0300–0900 hours and a portion of this time period occurred during daylight hours. Others have found invertebrate drift to be greatest following dusk (Elliot 1973, Allan 1981, Rader 1997), not during dawn and early morning as found for Plecoptera here. High variation between samples and lack of statistical power may explain why a diel effect was not observed for other taxa.

Although diel effects were not seen for drift density or biomass, time of day did influence the average size of individuals of major taxonomic groups in the drift. When a diel effect was observed, the mean size of Plecoptera and Trichoptera was generally lowest during daylight hours. Fish predation can suppress daytime drift and most daytime drift is considered accidental (Waters 1972, Douglas et al. 1994). Larger individuals, which are most detectable by predators, restrict intentional drift to periods of low light and decreased predator feeding efficiency (Douglas et al. 1994). When accidental drift occurs, larger individuals may be more efficient swimmers and have better reattachment capabilities than smaller individuals (Rader 1997). Thus, once in the drift, smaller individuals may drift greater distances and be proportionately higher during daytime drift than larger individuals.

Brook Trout Diets

Abundance of a given prey taxa in the drift was a poor predictor of abundance in the brook trout diets during both seasons. Percent composition of the diet was not correlated with percent composition of the drift. Studies with other salmonids during other times of the year found significant overlap between abundance in the drift and diet (Elliot 1970, Allan 1981, Young et al. 1997). However, Forrester et al. (1994) suggest that salmonids are selective for certain taxa. Most studies agree that salmonids show size selectivity (Allan 1978, 1981; Grant and Noakes 1986, Forrester et al. 1994).

If salmonids are size selective, then larger taxa should be over-represented in the diet and underrepresented in the drift. The forage ratio (% composition of the diet/% composition of the drift) increased significantly during both seasons as the median head width of prey increased, which indicates size selectivity for drifting prey taxa. Larger sized taxa such as Trichoptera: Limnephilidae (both fall and winter) and Plecoptera: Taeniopterygidae (winter) comprised a high percentage of the diet in terms of numbers and biomass, yet were a small component of the drift. Two assumptions of the relationship between the forage ratio and the size of prey taxa are that the propensity to drift is equal among all taxa, and that brook trout feed exclusively from the drift. These assumptions may be invalid.

The propensity of various taxa to drift depends on morphology, behavior, habitat associations, and exposure to flow. Rader (1997) ranked many taxa according to their propensity to drift and availability as trout prey. Limnephilidae are cased caddis flies having a relatively low propensity to drift, which Rader (1997) scored as prey with a low availability to trout. Taeniopterygidae scored as largely unavailable prey due to their association with pool and depositional areas within a stream. The high composition of the diet, supposedly low propensity to drift, and observed low composition of the drift by both Limnephilidae and Taeniopterygidae suggests that the brook trout in this study were obtaining these prey by foraging from the benthos. Others have also suggested that consumption of cased caddis larvae such as Limnephilidae is the result of benthic foraging (Bisson 1978, Forrester et al. 1994). Brook trout may not rely on the drift for available prey to the degree as previously suspected, and perhaps 40% or more of the ingested biomass (combination of Limnephilidae and Taeniopterygidae) comes directly from the benthos.

Relative comparisons between total drift seasonally and through the seasonal diel cycle corroborates findings of specific stomach mass of food for the brook trout. The higher specific mass of stomach contents found during the winter than in the fall supports our findings that overall invertebrate drift density was greater during the winter. There was no diel effect on total drift density in either season and the same can be said for mean specific stomach mass in brook trout. The lack of any significant diel effect on the specific stomach mass during either season suggests that brook trout feed continuously throughout the day and that feeding efficiency is not compromised during the lower light intensity during the night. However, the lack of a diel effect is more likely due to a low gastric evacuation rate at lower seasonal temperatures. The gastric evacuation rate we found in the lab (at similar temperatures to the field) and used in calculating daily ration in the field, was only 0.0275 mg dry weight·hr^{-1}. Although this rate is low, it seems reasonable. Forrester et al. (1994) found a gastric evacuation rate of 0.051 g dry weight·hr^{-1} for brook trout at 16 C, and this would be expected to be lower at lower water temperatures. However, Elliot (1972) reports gastric evacuation rates of 0.122–0.126 g dry weight·hr^{-1} for brown trout at 7.6 C—higher than those for brook trout and also at a lower temperature. Inappropriate gastric evacuation rates may be a large source of error in estimating consumption in the field and these rates vary with temperature, fish size, and prey type.

Low gastric evacuation rates may also explain the dominance of Limnephilidae in the diet of the brook trout and over-representation when compared to the drift. Forrester et al. (1994) also noted that cased caddis larvae comprised a higher portion of brook trout diets than invertebrate drift. When consuming taxa such as Limnephilidae, the entire case is ingested which would likely slow digestion and gastric evacuation (Forrester et al. 1994). Longer time in the stomach as compared to other more digestible taxa may result in an overestimation of the relative contribution of such prey to the diet.

Brook trout daily ration during both the fall and winter was low compared to other salmonids at other times of the year in the literature (Elliot 1973, Amundsen and Klemetsen 1988, Sagar and Glova 1988, Forrester et al. 1994). The low daily ration (fall: 0.002 ± 0.0005 g·g^{-1}·d; winter: 0.008 ± 0.0016 g·g^{-1}·d) raises the question as to whether daily energy requirements can be met at such low rations. To answer this question, we ran bioenergetics model simulations (Hartman and Sweka 2001). The maintenance ration for a 23-g fish (average wet weight for brook trout in the field) during the fall would be 0.0027 g·g^{-1}·d and 0.0019 g·g^{-1}·d during the winter. Our field estimates of daily ration were slightly below the maintenance ration predicted by the bioenergetics model during the fall, but exceeded the maintenance ration predicted for the winter. Brook trout may experience negative growth during the fall and food limitation may be one mechanism responsible for low post-spawning survival in brook trout (Hutchings 1993).

Water temperatures during the winter sample were above normal conditions during this time of year, which may bring into question the daily ration estimates as being representative of winter conditions. Unseasonable warm temperatures could influence brook trout daily consumption if the fish had unlimited prey and were feeding near maximum consumption. If the fish were feeding at maximum consumption during both seasons, we would expect lower daily rations under normal conditions in the winter due to lower temperatures. Based on a bioenergetics model for brook trout (Hartman and Sweka 2001) the average sized brook trout could potentially consume 0.033 $g \cdot g^{-1} \cdot d^{-1}$ at 4 C—a typical winter temperature. However, our estimates for daily ration were well below maximum consumption predicted for a fish of similar size to those in our study. Brook trout are opportunistic feeders in lowly productive systems and it is unlikely that they come close to ever eating at maximum consumption levels. In this study, daily ration estimates are probably much less affected by water temperature than by prey availability.

Conclusions

General relationships between invertebrate drift and salmonid diets appear to be less obvious during the post-spawning fall and winter when compared to other studies conducted from spring through early fall seasons. The observed lack of a diel effect on brook trout feeding may be indicative of constant feeding throughout all times of the day, but is most likely due to low rates of gastric evacuation during these cooler periods of the year. Brook trout showed size selectivity and consumed disproportionately larger prey than what was available in the drift. A high degree of consumption of taxa with a low propensity to drift suggests that benthic foraging may be greater than previously suspected for stream-dwelling salmonids. Daily ration was below maintenance ration levels predicted by bioenergetics models during the fall and this may be one factor that contributes to apparent low post spawning survival of adult brook trout.

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