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# Feeding periodicity, diet composition, and food consumption of subyearling rainbow trout in winter

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**Abstract** Although winter is a critically important period for stream salmonids, aspects of the ecology of several species are poorly understood. Consequently, we examined the diel feeding ecology of subyearling rainbow trout (*Oncorhynchus mykiss*) during winter in a central New York stream. Rainbow trout diet was significantly different during each 4-h interval and also differed from the drift and benthos. Feeding was significantly greater during darkness (i.e. 20:00 h – 04:00 h) than during daylight hours (i.e. 08:00 h – 16:00 h), peaking at 20:00 h. Daily food consumption (1.9 mg) and daily ration (3.4 %) during winter were substantially lower than previously reported for subyearling rainbow trout in the same stream during summer. These findings provide important new insights into the winter feeding ecology of juvenile rainbow trout in streams.

**Keywords** Rainbow trout · Winter · Diel · Feeding

## Introduction

Winter is generally considered a critical (Cunjak and Power 1986) and stressful (White and Harvey 2007; Anderson et al. 2016) period for stream salmonids. Moreover, during winter, the youngest age classes of fishes are thought to be the most at risk (Oliver et al. 1979). Although stream salmonids actively feed during winter there have been few studies done that have examined salmonid diet in the context of available prey (Anderson et al. 2016). In addition, for many salmonid species, it is unknown if their feeding ecology changes during winter in terms of feeding periodicity, diel variation in diet composition, and food consumption.

During winter, metabolic activity of stream salmonids decreases in response to changes in photoperiod and water temperature (Metcalfe and Thorpe 1992; Cunjak et al. 1998). Slower metabolic activity during winter includes reductions in both assimilation efficiency and gut evacuation rates (Cunjak et al. 1998) as well as reduced swimming ability and prey capture efficiency (Watz and Piccolo 2011). Consequently, food consumption of stream salmonids during winter is less than during other seasons. However, there are few studies that have examined the food consumption during winter by a salmonid species in relation to other seasons in a natural stream setting.

Subyearling rainbow trout (*Oncorhynchus mykiss*) have been shown to exhibit seasonal patterns of diel periodicity in food consumption. Soon after emergence in early June, rainbow trout/steelhead fed most intensely during the day (i.e. 08:00 h – 20:00 h) in three Lake Ontario tributaries (Johnson et al. 2013). However, later in the summer, subyearling rainbow trout have been found to feed most actively from 20:00–24:00 h (Johnson and McKenna 2015). Furthermore, subyearling rainbow trout have been observed to feed more actively from the drift than the benthos in streams

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during summer (Riehle and Griffith 1993; Dedual and Collier 1995; Johnson and McKenna 2015). However, how these aspects of the feeding ecology of stream salmonids vary between winter and other seasons is often poorly understood for most species (Anderson et al. 2016) including rainbow trout.

We examined the winter feeding ecology of subyearling rainbow trout in a stream where the summer feeding ecology had previously been described (Johnson and McKenna 2015). Specifically we sought to determine (1) diel feeding periodicity, (2) diel variation in diet composition, (3) foraging strategy (benthic or drift), and (4) food consumption of subyearling rainbow trout, during winter. Furthermore, we sought to compare and contrast this information to aforementioned summer feeding ecology information available for subyearling rainbow trout from the stream.

## Materials and methods

Subyearling rainbow trout were collected with a backpack electroshocker in Grout Brook, Cortland County, NY, in late January. Grout Brook supports a naturalized migratory population of rainbow trout that spawn in the stream, spending two years as juveniles before outmigrating to Skaneateles Lake, one of the Finger Lakes in central New York. The stream provides high quality spawning and nursery habitat with summer water temperatures seldom exceeding 20 °C (Johnson and McKenna 2015). Winter stream discharge ranges from 0.10 $m^3 s^{-1}$ to 0.27 $m^3 s^{-1}$ (Johnson and Douglass 2009). Stream temperature during fish collections was 2 °C. A minimum of 25 subyearling rainbow trout were collected at 4-h intervals over a 24-h period. Trout were collected over a 0.5 km stream reach with samples of fish at each successive 4-h time interval made starting 10 m up-stream of where collections ended for the previous 4-h interval. Fish collections at each 4-h interval generally took 20 min. Upon collection, fish were immediately preserved in 10 % buffered formalin. Collections made at night (i.e. 20:00 h, 24:00 h, 04:00 h) were facilitated by the use of head-lamps on the electroshocking crew. Food availability was assessed using a Surber sampler (benthos) and drift nets (drift). Five Surber samples (0.09 $m^2$; mesh size 0.75 mm) and five drift samples (aperture 30.5 cm × 30.5 cm; mesh size 0.60 mm) were taken concurrent with fish collections. Both Surber samples and drift samples were taken immediately above the section where fish were collected. Drift nets were set approximately 3 h prior to fish collections so each represented 3 h of invertebrate drift and immediately above the area where Surber samples were taken in order to prevent contamination of the drift from the benthic sampling. Available prey samples were taken in areas where the stream habitat (depth, velocity, and substrate) was similar to where peak densities of subyearling rainbow trout occurred. These areas were generally transition areas between riffles and runs.

In the laboratory rainbow trout were measured (total length, mm) and weighed (nearest 1.0 mg) prior to stomach removal. Stomachs were removed and weighed (full and empty) to help determine feeding periodicity. The weight of the stomach contents divided by the weight of the fish was used as the index of stomach fullness at each 4-h interval, which was used to estimate feeding periodicity over the 24-h period. Aquatic taxa were identified to the lowest practical taxon (usually family), whereas terrestrial taxa were identified to order. Dry weight estimates (24 h at 105 °C) were derived for all prey taxa in order to determine their contribution in the diet. Diet composition over the 24-h period was determined using diet composition estimates at each 4-h interval that were weighted by the respective periodicity values for the same interval. The mean of these values was used to determine the 24-h diet.

Food consumption during each 4-h interval was estimated using the equation of Elliott and Persson (1978),

$$C_t = \frac{(S_t - S_o e^{-Rt})}{1 - e^{-Rt}}$$

where $C_t$ is the amount of food consumed in $t$ h, $S_t$ is mean stomach contents at the end of the interval, $S_o$ is mean stomach contents at the beginning of the interval, and R is the exponential rate of gastric evacuation. These food ingestion rates were then summed to obtain an estimate of the daily food consumption. Subyearling rainbow trout feed more or less continuously, but $S_o$ of the first interval was unknown. We used the last observed stomach content ($S_t$) value for the initial $S_o$. This is more reasonable than assuming stomachs began empty, but assumes the consumption is roughly similar from one day to the next at this time of year. Values for R were derived from Hayward and Weiland (1998). Daily food consumption (based on wet weights in mg) of rainbow trout was estimated by summing interval values for the

24-h period. Daily ration was expressed as total daily food consumption divided by fish weight.

Bootstrapping cluster analysis (McKenna 2003) was used to evaluate differences in the diet of subyearling rainbow trout among 4-h intervals over the 24-h period. The cluster analysis objectively uses the Bray-Curtis similarity index, UPGMA linkage method, and 1000 bootstrap samples to test for significant differences between linked groups, based on diet at each 4-h interval. Because the Shapiro-Wilks test showed that diet data were not normally distributed, we assessed the significance of diet composition differences between each time period using Kruskal-Wallis one-way analysis of variance (Statistix 8.0 Analytical Software, Tallahassee, Florida). The Linear Food Selection Index of Strauss (1979) was used to quantify prey selection by subyearling rainbow trout in relation to the drift and benthos. Coefficient values range from −1 (avoidance) to +1 (preference). A significance level of $\alpha = 0.05$ was used for all comparisons.

## Results

A total of 194 subyearling rainbow trout were examined. Mean total length was consistent among the sampling periods (71.1–78.9 mm), and averaged 74.5 mm (Table 1). Only two rainbow trout (1.0 %) had empty stomachs. Except for 20:00 h when chironomids (31.0 %) dominated the diet, ephemeropterans (34.4 %) were the major prey of subyearling rainbow trout in Grout Brook (Fig. 1). Ephemerellids and heptageniids were the major families of ephemeropterans consumed comprising 18.0 % and 15.0 % of the 24-h diet, respectively. Trichopterans (19.9 %), dipterans (19.6 %), and plecopterans (12.4 %) all contributed at least 10 % of the 24-h diet. The trichopterans consumed consisted mainly of hydropsychids (7.4 %) and brachycentrids (4.5 %), the dipterans were mainly chironomids (11.7 %) and tipulids (6.4 %), and the plecopterans were primarily perlids (6.6 %) and capniids (5.2 %) (Fig. 1). Fish (slimy sculpin) were a minor component (3.0 %) of the diet of rainbow trout.

The diet composition of subyearling rainbow trout varied over the 24-h period. The contribution of ephemeropterans (25.3 % at 20:00 h - 46.7 % at 08:00 h), trichopterans (9.4 % at 20:00 h - 29.0 % at 04:00 h), dipterans (5.6 % at 04:00 h - 36.4 % at 20:00 h), and coleopterans (1.5 % at 20:00 h-10.7 % at 16:00 h) in the diet varied greatly over the 24-h period (Fig. 1). Consumption of some taxa (plecopterans 6.3 % at 08:00 h - 15.3 % at 24:00 h) was more uniform over the 24-h period. The consumption of some individual families of aquatic insects also varied widely including ephemerellids (2.9 % at 20:00 h to 31.7 % at 24:00 h), heptageniids (3.7 % at 24:00 h to 21.7 % at 20:00 h), and chironomids (2.2 % at 04:00 h to 31 % at 20:00 h).

**Table 1** Number of subyearling rainbow trout examined and mean length (mm, ±SE) of subyearling rainbow trout examined for diet analysis at 4-h intervals in Grout Brook in January

| Time (hours) | Number | Mean length |
|---|---|---|
| 1200 | 25 | 78.9 ± 2.0 |
| 1600 | 25 | 75.1 ± 2.1 |
| 2000 | 30 | 71.1 ± 2.4 |
| 2400 | 30 | 72.7 ± 2.4 |
| 0400 | 28 | 73.9 ± 1.7 |
| 0800 | 30 | 71.2 ± 1.1 |
| 1200 | 26 | 78.6 ± 2.1 |

Coleopterans (32.1 %) were the major benthic (Surber samples) prey taxon and consisted of elmids (21.7 %) and psephenids (10.4 %) (Fig. 1). Ephemeropterans (21.4 %, mainly ephemerellids-14.0 %), dipterans (20.4 %, mainly tipulids-10.4 %), and trichopterans (15.5 %, consisting of many families) all made up at least 10 % of the benthic invertebrate community. Ephemeropterans (29.2 %, mainly ephemerellids-13.2 % and oligoneuriids-11.0 %), trichopterans (27.7 %), dipterans (23.4 %, mainly tipulids 7.8 % and simuliids 7.7 %), and plecopterans (13.9 %, mainly capniids-9.0 %) were the major components of the invertebrate drift in Grout Brook (Fig. 1).

The diet of subyearling rainbow trout differed significantly among all 4-h intervals (Fig. 3). Moreover, the diet of trout during each of the 4-h intervals was also significantly different than the composition of the benthos (Surber samples) and the drift. Rainbow trout diets during daylight hours (i.e. 08:00 h, 12:00 h, 16:00 h) and nighttime hours (i.e 20:00 h, 24:00 h, 04:00 h) were more similar as a group (Fig. 2). Similar to the cluster analysis, electivity analysis for prey taxa did not yield strong evidence to suggest either a drift or benthic foraging pattern by subyearling rainbow trout in winter. When comparing the 24-h diet to the composition of the drift and Surber samples there was positive selection for

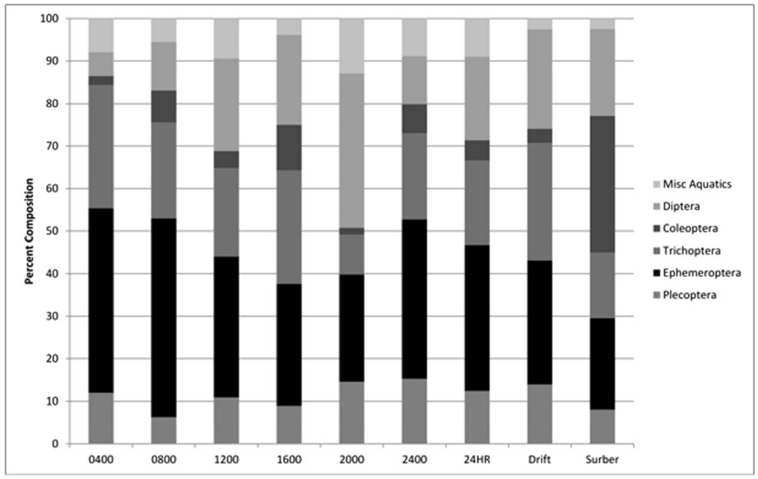


**Fig. 1** Percent dry weight diet composition of subyearling rainbow trout at 4-h intervals and over 24-h in Grout Brook in January

several families of aquatic insects for both sets of available prey samples including, brachycentrids, corydalids, chironomids, elmids (adults), ephemerellids, heptageniids, leptocerids, perlids, phryganeids, and polycentropids (Fig. 3). Hydroptilids, oligoneurids, simuliids, and tipulids were negatively selected compared to both sets of available prey samples. Prey taxa which differed in their selection between drift and bottom samples included capniids (−0.27 drift, 0.22 benthos), elmid larvae (0.43 drift, −0.79 benthos), and limnephilids (−0.84 drift, 0.10 benthos) (Fig. 3).

Subyearling rainbow trout in Grout Brook in January fed heaviest during periods of low light (Fig. 4). Feeding intensity greatly increased from 16:00 h-20:00 h, peaking at 20:00 h. Feeding intensity remained high until 04:00 h and was lowest at 08:00 h. Food consumption from 20:00 h-04:00 h was significantly greater than during other time intervals (Fig. 4). Daily food consumption and daily ration of subyearling rainbow trout was estimated at 1.9 mg and 3.4 %, respectively.

## Discussion

Previous investigators have documented that trout in streams actively feed throughout the winter, albeit at lower levels compared to warmer months (Cunjak and Power 1987; White and Harvey 2007; Anderson et al. 2016). Our observations are consistent with these findings. Johnson and McKenna (2015) reported that daily food consumption and daily ration of subyearling

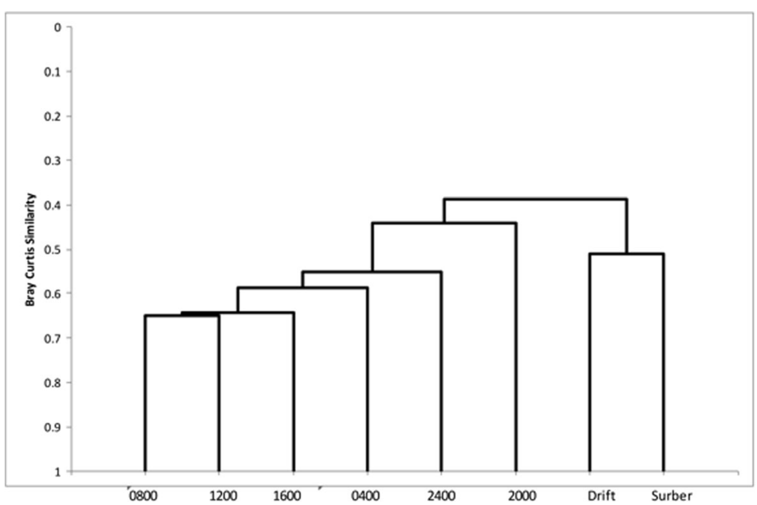


**Fig. 2** Dendrogram of cluster analysis results for the diet of subyearling rainbow trout at 4-h intervals and available prey in Grout Brook. Bray-Curtis similarity values are provided along the ordinate. All group linkages were significantly different ($p < 0.05$)

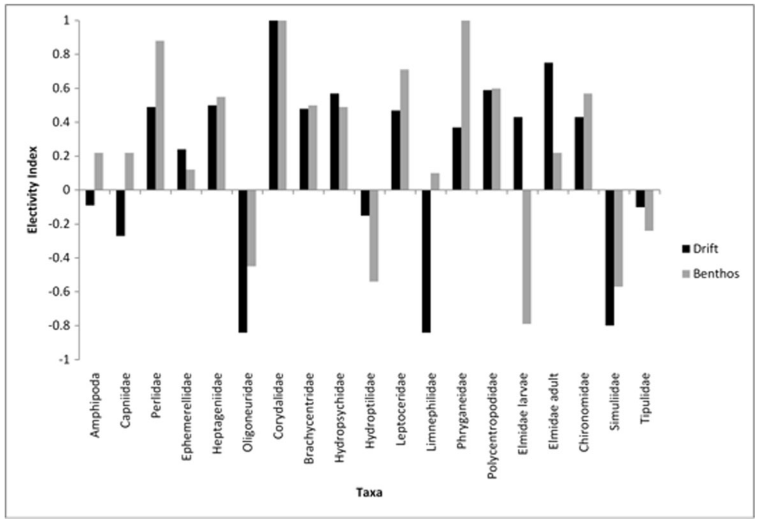


**Fig. 3** Subyearling rainbow trout prey selection values for drifting and benthic prey. Values range from 1 to −1, with positive values suggesting a food preference and negative values suggesting a food avoidance

rainbow trout in Grout Brook during summer was 5.3 mg and 13.3 %, respectively. These values are substantially higher than the daily food consumption (1.9 mg) and daily ration (3.4 %) values observed in this study during winter. It should be noted, however, that the average size of rainbow trout in this study (i.e. $x$ = 74.5 mm, 5.1 g) was larger than the previous study (54.5 mm, 1.6 g) (Johnson and McKenna 2015). The percentage of empty stomachs (1.0 %) we observed in rainbow trout in Grout Brook in January was lower than the 4.4 % reported for brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in winter in the Credit River in Ontario, Canada (Cunjak and Power 1987), but similar to that reported for juvenile rainbow trout in an Idaho stream (Riehle and Griffith 1993).

Similar to our observations, previous studies of the diet of juvenile rainbow trout in streams have not documented a consistent relationship with either the composition of the benthos or drift. Harvey and Railsback (2014) observed that inclusion of both drift and benthic feeding in an individual based model provided better estimates of individual fish mass for rainbow trout than scenarios where fish fed only from the drift. Riehle and Griffith (1993) found a poor association between the diet of juvenile rainbow trout with the drift in fall and winter in Silver Creek, Idaho. Similarly, Johnson (2007) reported that subyearling steelhead (migratory rainbow trout) fed equally from the drift and benthos during the first year of a study on the Salmon River, NY but fed more from the benthos during the second year. Johnson and McKenna (2015) found that the diet of subyearling rainbow trout was more similar to the drift than the benthos in Grout Brook in summer. However, that study was done in the

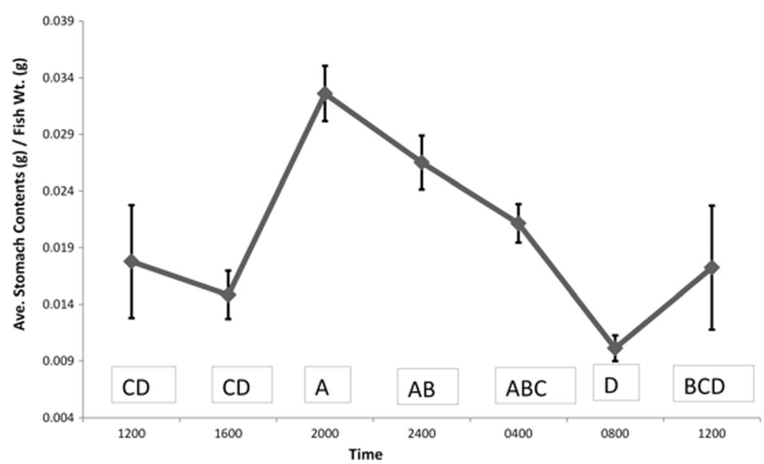


**Fig. 4** Feeding periodicity estimates (± standard error) for subyearling rainbow trout in Grout Brook, New York, during January. Different letters along the x-axis represent significant differences in feeding intensity among 4-h intervals

presence of subyearling Atlantic salmon, which had been stocked into Grout Brook to examine resource partitioning between the species. Johnson and Waldt (2014) have shown that the presence of Atlantic salmon can cause subyearling rainbow trout to shift to a more drift feeding pattern. Consequently, in the absence of sympatric Atlantic salmon in Grout Brook during this study, subyearling rainbow trout fed equally from the drift and benthos with no tendency toward either.

Although the presence of Atlantic salmon could have played a role in the different observations of rainbow trout feeding strategies between this study and the previous one conducted during summer on Grout Brook, another possibility is the absence of terrestrial insects in the winter diet and available prey samples. Terrestrial insects often comprise a large percentage of the summer diet of stream salmonids as well as composition of the drift (Allen 1978; Dedual and Collier 1995; Johansen et al. 2010). However, at the northern latitudes where most trout streams occur, terrestrial insects are dormant during the winter (Hynes 1972). When they are found in the diet of stream fishes, terrestrial insects are generally regarded as an indication of drift feeding (Zaret and Rand 1971; Johnson and Ringler 1980), because they are seldom found in benthic samples. With the absence of allochthonous prey taxa during winter, such as terrestrial insects that are clearly associated with the drift, both drift and bottom samples at this time are exclusively autochthonous. Consequently, the absence of virtually an exclusively drift oriented prey group such as terrestrial insects during the winter may make ascribing fish diet to either drift or benthic feeding patterns more difficult.

Although available prey samples were collected in habitats that corresponded with peak subyearling rainbow trout densities, all habitats where fry were collected were not sampled to quantify available prey. Since even in small streams such as Grout Brook invertebrate densities can vary based on microhabitat characteristics (Hynes 1972), these density differences could influence site-specific trout diet. Of the major families of aquatic insects consumed ephemerellids, heptageniids, hydropsychids, brachycentrids, and chironomids were positively selected when considering both the drift and bottom available prey samples. Only two families, oligoneurids and simuliids were negatively selected. These findings are in general agreement with those of Laudon et al. (2005) who reported positive selection by rainbow trout for brachycentrids, hydropsychids, and chironomids, whereas simuliids were not selected. Some investigators have used electivity values to ascribe drift versus bottom feeding strategies of stream salmonids (Griffith 1974; Tippets and Moyle 1978). In Grout Brook, there was general agreement between selectivity values derived for major prey taxa between both the drift and bottom samples. Consequently, similar to the cluster analysis, electivity values were unable to elucidate a linkage between rainbow trout diet and the composition of the drift or benthos. Several studies have found a low correlation between rainbow trout diet with invertebrate drift in streams (Bisson 1978; Tippets and Moyle 1978; Johnson 2007). We also found a low association between the diet of subyearling rainbow trout and the diet in Grout Brook in this study, which could be partially due to low drift rates during winter at northern latitudes (Brittain and Eikeland 1988).

Diel variation in both the diet composition and feeding periodicity has been previously reported for juvenile rainbow trout (Bisson 1978; Angradi and Griffith 1990; Johnson and McKenna 2015). However, none of these studies were conducted during winter. Generally terrestrial insects are more active during diurnal periods in warmer months and at this time terrestrials contribute more to the diet than during nocturnal periods (Angradi and Griffith 1990; Johnson and McKenna 2015). Although some studies of juvenile rainbow trout feeding activity have found no diel changes in stomach fullness (Dedual and Collier 1995), most studies have reported a late afternoon or early evening increase in feeding activity during summer (Johnson and Johnson 1981; Riehle and Griffith 1993; Johnson and McKenna 2015). Riehle and Griffith (1993) examined seasonal trends in feeding periodicity of juvenile rainbow trout and found that in October peak feeding was at midnight and in January during the early morning. Our findings in this study, in conjunction with the previous work done on Grout Brook (Johnson and McKenna 2015), suggest that subyearling rainbow trout feeding activity is triggered by low light. During summer, rainbow trout feeding activity sharply increased after 20:00-h, peaked at 24:00-h, and remained high throughout the night (Johnson and McKenna 2015). In January, this exact same pattern occurred except it was moved forward by four hours. Rainbow trout feeding intensity sharply increased at 16:00 h, peaking at 20:00 h, and remaining high throughout the night. In Grout Brook, subyearling rainbow trout feeding activity increased at the onset of darkness during both summer (20:00 h – 24:00 h) and winter (16:00 h – 20:00 h) and remained high until daylight. Not only do juvenile salmonids become more nocturnal under low light conditions, their efficiency to capture prey is also reduced (Watz et al. 2014). An increase in feeding activity during darkness is often considered a predator avoidance behavior (Railsback et al. 2005). Consequently, the feeding activity of subyearling rainbow trout in Grout Brook may be influenced by the risk of predation during both summer and winter.

This study provides valuable insights into the winter-feeding ecology of subyearling rainbow trout in streams. Estimates of daily food consumption and daily ration were low, substantially lower than values derived from the same stream population of trout from previous work (Johnson and McKenna 2015). Moreover, the close association between the diet of rainbow trout with the composition of the drift that occurs during summer, was not observed. Trout diet among all 4-h intervals was significantly different as were comparisons of trout diet to the composition of the drift and benthos. Increased feeding activity was associated with periods of darkness and may reflect predator avoidance behavior. These findings collectively are important contributions to better understand the ecology of stream salmonids during winter.

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All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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