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Spatial and temporal ranges of resource exploitation by stream-dwelling cutthroat trout

by

Hope W. Owens

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# Table of Contents

## Contents

- List of Figures.................................................................................................................. vi
- Abstract.............................................................................................................................. viii

## INTRODUCTION................................................................................................................ 1

## METHODS ...................................................................................................................... 7
- Behavioral observations .................................................................................................. 7
- Behavioral Analyses ...................................................................................................... 9
- Invertebrate Sampling ................................................................................................... 11
- Statistical analyses ..................................................................................................... 13

## RESULTS ...................................................................................................................... 15
- Foraging Behavior......................................................................................................... 15
- Size-related effects on foraging behavior ..................................................................... 17
- Social effects on foraging behavior ............................................................................. 18
- Invertebrate Abundance ............................................................................................. 18
- Stream temperature .................................................................................................... 19
- Stream light levels ....................................................................................................... 19

## DISCUSSION ................................................................................................................ 22

## CONCLUSIONS ............................................................................................................ 29

## LITERATURE CITED ..................................................................................................... 30

## FIGURES ....................................................................................................................... 43
List of Figures

**Figure 1. Map of three first-order streams in southeastern Idaho where cutthroat trout were observed in order to quantify foraging behavior.** Invertebrate sampling and video segments were captured at Inman Creek (latitude: 42.8213044, longitude: -112.2202474), Goodenough Creek (latitude: 42.65430557, longitude: -112.28583213) and Harkness Creek (latitude: 42.6579718, longitude: -112.1924671), in Bannock County, Idaho. __________ 43

**Figure 2.** Mean proportion of video with cutthroat trout present (+1 SE) during diurnal (open bar) and nocturnal (solid bar) periods, over four months (N=452). ____________________________ 44

**Figure 3.** Mean foraging rate (+1 SE) of cutthroat trout during diurnal (open bar) and nocturnal (solid bar) periods (N=97). ____________________________ 45

**Figure 4.** Mean foraging rate (+1 SE) of cutthroat trout during diurnal (open bars) periods or nocturnal (solid bars), and according to foraging location in the stream (N=452). ____________________________ 46

**Figure 5.** (A) Mean foraging distance (body lengths) (+1 SE), and (B) mean rejection rate of foraging behavior (+1 SE), measured diurnally (open bars) and nocturnally (solid bars) in a subset of video segments (N=10). __________ 47

**Figure 6.** Mean no. foraging attempts (+1 SE) during diurnal (open bar) and nocturnal (solid bar) periods, in a subset of video segments (N=10).__________ 48

**Figure 7.** Mean monthly foraging rate (±1 SE) of cutthroat trout observed during (A) diurnal periods or (B) nocturnal periods, and according to foraging intake location, (square = benthic, circles = water column, triangle = surface) (N=107). ____________________________ 49

**Figure 8.** Mean foraging rate (+1 SE) of cutthroat trout during (A) diurnal and (B) nocturnal periods, partitioned by fish size and according to foraging intake location (solid bars = benthic, open = water column, hatched = surface) (8A: N=270, 8B: N=171). ____________________________ 50

**Figure 9.** Mean foraging rate (+1 SE) of cutthroat trout during (A) diurnal and (B) nocturnal periods, partitioned by fish position in group and according to
FORAGING INTAKE LOCATION (SOLID BARS = BENTHIC, OPEN = WATER COLUMN, HATCHED = SURFACE) (9A: N=324, 9B: N=168).

**Figure 10.** Mean invertebrate abundance (± 1 SE) from (A) drifting and (B) benthic invertebrate measures, across summer and fall months. Right-hand vertical axis was provided as a reference for conversion to untransformed values of drifting and benthic invertebrates, (solid circles = nocturnal concentrations, open circles = diurnal concentrations) (10A: N=68, 10B: N=71).

**Figure 11.** Mean monthly stream temperatures (°C) (±1 SE), (diurnal periods = dashed line, nocturnal periods = solid line) (N=145).

**Figure 12.** Mean monthly diurnal stream light levels (lumens x m²) (±1 SE) in first-order Idaho streams, (dashed lines = minimum and maximum light levels) (N=145).

**Figure 13.** Mean estimated energy intake (±1 SE) of cutthroat trout by month, from the drift (solid lines) or benthos (dashed lines), (diurnal periods = open circles, nocturnal periods = solid circles) (N=456).

**Figure 14.** The comparison of the mean maximum daily ration of a 10 cm fish with mean monthly energy intake estimates for fish in this study (±1 SE), from the drift (solid lines) or benthos (dashed lines), (diurnal periods = open circles, nocturnal periods = solid circles). Monthly averaged maximum daily ration is shown by the dotted line (N=456).
Spatial and temporal ranges of resource exploitation by stream dwelling-cutthroat trout  
Thesis Abstract – Idaho State University (2020)

Salmonid fishes in streams are commonly thought to forage on drifting aquatic invertebrates during daylight hours. However, past studies indicate variation in foraging behavior despite the predominant view of salmonids as diurnal drift-foraging predators. I used in-stream videography to assess foraging mode and energy intake for stream-dwelling Yellowstone cutthroat trout (Oncorhynchus clarkii bouvieri). I recorded the foraging behavior of wild fish with a waterproof video camera and estimated energy intake based on fish size and known values for prey. Fish chiefly obtained food from drifting invertebrates during daytime hours; however, alternative behaviors also were found, with foraging towards the stream benthos and in nocturnal hours observed at moderate levels throughout the year. I found foraging behavior to have significantly more variation than has been previously estimated, with alternative strategies comprising up to 30% of energy intake. Several variables had a strong influence on foraging rate and intake location, including the time of day, season, and fish size. In terms of energy content, nocturnal and benthic behavior had less total energy contribution to the fish than diurnal drift foraging behavior. Energy intake was highest from diel drift foraging behavior, even exceeding fish’s modeled metabolic limit in October and November. These results indicate that despite cutthroat trout being primarily drift-foraging predators, cutthroat trout supplemental strategies are a part of foraging behavior and should be considered in salmonid ecology and bioenergetics.

Keywords: Foraging behavior, animal behavior, energy intake, salmonid, cutthroat trout, camera system.
INTRODUCTION

For heterotrophic organisms, food consumption is necessary for life. Food availability is a primary factor limiting the growth, survival, and reproduction of individuals (Boutin 1990; Newton 1998; Sibly and Hone 2002). Because animal abundance often is intrinsically related to food availability, density-dependent competition for food and space often is a factor regulating animal populations (Fowler 1981; Grant 1987; Anholt and Werner 1995). In some cases, populations have been observed to crash under food stress (Becker and Beissinger 2006) and may reach sufficiently small numbers to increase the risk of extinction or the loss of genetic variability. Understanding the dynamics of prey availability and exploitation strategies by predators is critical in predicting the abundance of organisms (Johnson and Sherry 2001; Searle et al. 2013; Prevedello et al. 2013).

Quantifying the availability of food in natural ecosystems requires an understanding of an organism’s ability to exploit prey. How effective prey are at predator avoidance, in turn, affects food availability to predator populations and the degree to which food limits predator abundance (Anholt and Werner 1995). Prey may avoid predation by using temporal and spatial asynchrony with predator activity, or by defense mechanisms against predators (Abrams 1984). In response, predators may optimize their energy intake by altering foraging behavior to increase prey consumption during different times of the day or season, or by moving to areas with greater prey abundance (Sih 1982; Sims et al. 2006). Alternative foraging behaviors may compensate for
temporal and spatial asynchrony and may be dependent on predators tracking local resource levels in an environment (Persson 1985; Thorpe et al. 1998).

Foraging strategies can be flexible to compensate for varying heterogeneity of habitat occurring at different temporal, regional, and seasonal scales (Dill 1983; Baird et al. 1992). By understanding the availability of food sources in a foraging animal’s environment, and the factors that restrict animal’s ability to exploit prey, such as temporal and spatial availability of prey, or behavioral or morphological limitations of forager, the ‘foodscape’ can be defined as the range of edible prey types available to foraging animals from the broader landscape it occupies (Searle et al. 2013). Given the relationship between food availability and population abundance, it is important to understand the specific sources and components of an organism’s energy budget.

Stream ecosystems occupy a minority of space among the world’s biomes but play a critical role in transporting water, purifying water supplies, and providing habitat for many exploited fish populations (Nilsson and Berggren 2000; Dudgeon et al. 2006; Allen and Castillo 2007). With difficulties in processing and transferring energy between trophic levels within the physical forces of moving fluids, life in flowing water faces different constraints than in other aquatic and terrestrial ecosystems (Hynes and Bernard 1971; Vogel 1994). Food availability, and the efficiency by which predators can consume it, are difficult to quantify in streams because aquatic organisms are constantly under pressure of being moved downstream by a dense, viscous medium. One of the most widely studied groups of fishes with a lifecycle often tied to streams are the salmonid fishes, or ray-finned fishes in the family Salmonidae, which include salmon, trout, char, freshwater whitefishes, and grayling (Elliott 1994; Quinn 2005; McPhail...
Food availability has long been thought to be one of the main limits to salmonids in streams (Chapman 1966; Grant and Kramer 1990; Allen and Castillo 2007; Railsback and Harvey 2011); however, variability in salmonid foraging behavior indicates plasticity in foraging strategies and causes uncertainty in how to quantify food requirements for salmonid fishes (Grant 1987; Rosenfeld et al. 2005; Hayes et al. 2018).

The predominant paradigm of foraging for stream-dwelling salmonid fishes is that they acquire energy by maintaining a foraging position in the stream current, known as a foraging station, and capture invertebrates drifting by (Hughes and Dill 1990; Keeley and Grant 1995; Gunnarsson and Steingrímsson 2011; Syrjänen et al. 2011; Piccolo et al. 2014). As visual predators, salmonids commonly are thought to be diurnal foragers, feeding during daylight hours when drift can be observed and targeted in the water column (Kreivi et al. 1999; Neuswanger et al. 2014; Di Prinzio et al. 2015). In contrast, aquatic invertebrates in streams often enter the water column in highest numbers as ‘drift’ after dark, presumably as a means of avoiding predation from drift-feeding fishes (Elliott 1970; Muller 1974; Brittain and Eikeland 1988; Allen and Castillo 2007).

Salmonids appear to have a reduced capacity for drift-feeding in low light and are thought to be less effective as predators after dark (Fraser and Metcalfe 1997; Rader 1997). Similarly, salmonids appear to have a lower efficiency feeding from the stream bottom as invertebrates can shelter among the interstitial spaces of the substrate (Bourassa and Morin 1995; Beisel et al. 1998) and because salmonids have a terminally oriented mouth, making it difficult to capture prey from the stream bottom. During summer months, drifting invertebrates appear in elevated concentrations as larval invertebrates depart from the benthic substrate during dispersal life stages, or through
stochastic events (Muller 1974). As a result, salmonids in streams often are thought to acquire the dominant proportion of their energy budget as diurnal drift-feeding predators during the summer, when stream temperatures allow for optimal digestive and metabolic processing of food (Paloheimo and Dickie 1966; Cunjak 1988; Amundsen et al. 1999).

Despite the importance of diurnal drift-foraging behavior during a spring-summer growing season, studies have found that salmonids may acquire energy using alternative feeding modes that could comprise a significant proportion of their energy budget. Salmonids may capture prey through nocturnal foraging during conditions of low water temperature (Heggenes et al. 1993; Fraser et al. 1995; Fraser and Metcalfe 1997; Railsback et al. 2005) or may forage from the stream benthos during periods of low drift abundance. For instance, studies of diet composition based on stomach content data indicate that salmonids forage on large invertebrates with low drift propensities in periods of low drift availability (Tippets and Moyle 1978; Di Prinzio et al. 2015), and behavioral observations have documented a shift towards benthic foraging behavior under experimentally reduced levels of drift abundance (Fausch et al. 1997). In addition, studies of nocturnal stomach composition have found salmonids to have significantly full stomachs over winter nights (Cunjak et al. 1987; Johnson et al. 2016), contradicting the paradigm of diurnal summer-based foraging behavior (Rimmer et al. 1983; Amundsen and Klemetsen 1988). Stomach composition studies are not conclusive in inferring benthic feeding behavior, as large invertebrates can enter the drift even in low numbers (Angradi and Griffith 1990). Nocturnal foraging behavior has been observed in several species of salmonids across a broad range of environmental
conditions, including Atlantic salmon (*Salmo salar*) (Fraser et al. 1993, 1995), Chinook salmon (*Oncorhynchus tshawytscha*) (Hillman et al. 1992), coho salmon (*O. kisutch*) (Hillman et al. 1992; Roni and Fayram 2000), brown trout (*Salmo trutta*) (Heggenes et al. 1993), rainbow trout (*O. mykiss*) (Riehle and Griffith 1993), bull char (*Salvelinus confluentus*) (Jakober et al. 2000), and cutthroat trout (*O. clarkii*) (Bonneau and Scarnecchia 1998; Jakober et al. 2000). While these departures from drift foraging behavior are acknowledged, the extent and importance to which they occur are unknown.

The cutthroat trout is a salmonid fish species native to western North America, and the Yellowstone cutthroat trout (*O. c. bouvieri*) is a subspecies of cutthroat trout with populations native to the upper Snake River and Yellowstone River draining portions of Idaho, Nevada, Utah, Wyoming, and Montana (Trotter et al. 2018). As is the case for other salmonid fishes, cutthroat trout appear to obtain food primarily from drifting invertebrates in streams (Nakano et al. 1992); however, departures have been documented, with fish displaying foraging behavior from the stream benthos and by nocturnal foraging behavior (Jakober et al. 2000). Yellowstone cutthroat trout have experienced significant declines in distribution and genetic purity over their range and are actively managed as a species of conservation concern (Al-Chokhachy et al. 2017). It is critical to understand the food sources of cutthroat trout populations for successful conservation efforts, with available resource levels largely driving the life history and population dynamics of this species.

In this study, I investigated departures from the drift foraging paradigm in salmonid fishes by quantifying the foraging behavior of Yellowstone cutthroat trout. In
doing so, I estimated the source and relative importance of prey availability in the energy intake rates of stream-dwelling cutthroat trout. I evaluated temporal and spatial variation in foraging behavior to determine if cutthroat trout are primarily predators of daytime drifting invertebrates, feeding during warmer summer months, or whether food intake occurs from other locations over different short and longer-term timescales. I examined seasonal variation in foraging throughout the summer-fall growing season and assessed the degree to which foraging occurs towards the benthos, water column, and surface, over during diurnal and nocturnal hours. Furthermore, I conducted measures of visual reactivity of trout to drifting objects, to understand the effectiveness of drift foraging behavior under different foraging conditions. I used these measures to estimate energy intake rates for different foraging modes and compared them with a maximum daily ration to understand the relative importance of each foraging strategy. These measures allowed me to analyze the relationship between salmonid fishes and their food sources.
METHODS

I quantified the foraging behavior of cutthroat trout in three first-order tributary streams to the Portneuf River in southeastern Idaho, USA (Figure 1). Inman Creek, Harkness Creek, and Goodenough Creek are on public lands and contain genetically pure populations of Yellowstone cutthroat trout as the only species of fish present. This ecosystem of mid-elevation streams (1670-2000 m asl) is a mix of sagebrush steppe and montane flora and fauna (Sleeter 2012). Streams follow typical high elevation seasonal patterns of run-off fed streams of this semi-arid region (Minshall 1973). Mean monthly air temperatures for this region range from -8.9 to 31°C, with a mean annual precipitation of 308.1 mm (National Oceanic & Atmospheric Administration, Pocatello, 2018).

Behavioral observations

To quantify the diel foraging behavior of cutthroat trout over the study period, I used a waterproof digital video camera controlled by a microcomputer and software that recorded at systematic intervals over a 24h period. To record focal animal observations, I placed the camera in a haphazard selection of locations where fish had been observed to forage, and I positioned the camera field of view to capture the cross-sectional area of a stream pool. In the three study streams, the maximum pool volume was about 2.6 m³, with a typical stream width of 0.5 - 1.5 m. The video camera system consisted of a single Go-Pro hero 3+® camera (GoPro, San Mateo, CA) and watertight housing that was bolted to a 5mm thick steel plate (40 cm by 40 cm) to anchor the camera in the stream current. To power the camera over a 24h period, I replaced the standard camera battery with a battery eliminator wired to pass through camera housing
with a water-tight seal and connected to a 10,000 mAh external battery pack that was placed outside the stream, 3-5 m away (Voltaic Systems, Brooklyn, NY). The external battery used Always-On® technology to prevent powering-down during periods of low current draw. The camera was triggered to record a 10 min video segment every hour over a 24h period using a raspberry pi® microcomputer (Raspberry Pi Foundation, Cambridge, UK) connected to the camera’s wireless signal with a coaxial cable that also passed through the camera housing. Video clips were recorded for the first 10 minutes of every hour over a 24h period, beginning after the original time of submersion, using a python computer program® (Python Software Foundation, Delaware, USA) that turned the camera on and off and recorded video at desired intervals. Video sessions could then be collected from the field after a single 24h period by removing the camera’s image storage card. Additional cards and batteries could be exchanged if the camera was deployed on consecutive days. A cell phone served as an external monitor during camera placement using the Go-Pro Capture® application.

To record behavior during nighttime hours, the factory-installed lens of the video camera was replaced with a lens sensitive to infrared light. A single set of eight LED infrared lights (wavelength = 850nm) was used to illuminate stream sampling locations during night, allowing the cameras to record the nocturnal behavior of fish. Lights were strong enough to allow the attenuation of infrared light through water. Salmonid fishes, as well as invertebrates, are unable to see the infrared spectrum, making this method a suitable study tool to sample behavior during nighttime and low light conditions (Heise 1992; Dirnwoeber et al. 2012). I considered the diel temporal period to be nocturnal when light levels were at less than 4.5 LUX (lumens·m⁻²), when the infrared light source
illuminated the camera’s field of view. A HOBO Pendant® Temperature/Light 8K Data Logger (Onset, Cape Cod, MA) was placed on the camera mount to capture LUX of light in the foraging area. This sensor captured light levels and water temperature in the stream thirty minutes after the initiation of each video segment. Water temperature, LUX levels, sunrise and sunset times, pool volume, as well as GPS coordinates were collected with each corresponding video session.

Behavioral Analyses

In the laboratory, video recordings were reviewed to quantify the foraging behavior of focal fish. For focal animal observations, a foraging attempt was defined as a sudden movement of the fish towards an object in their field of view, ending with the fish opening and closing its mouth to engulf a prey item. Foraging attempts were included in the total number observed per unit time, even if the prey item was rejected by fish and ejected. Foraging attempts were classified within the stream according to foraging location as being either benthic, water column or water surface. All foraging behavior present on-screen was identified throughout each 10-minute recording session for each focal animal observed. In instances where multiple fish were present on screen, fish were distinguished by their length and position in the group (Bachman 1984).

To study the effect of fish size and location on foraging behavior, I recorded several variables to identify individual fish. Fish location in a pool was used as a substitute for dominance rank, as upstream-positioned fish have more direct access to available food sources, potentially casting a “foraging shadow” or depletion of drift for downstream fish. Defense of optimal foraging positions often occurs by dominant
individuals (Hughes and Dill 1990; Hughes 1992; Keeley 2001). Foraging observations were attributed to the place held ranking position. For example, foraging was assigned to the third-ranking position throughout at a video rather than to the original third placed fish in the group. Additionally, to investigate possible ontogenetic shifts in behavior, fish size was estimated using a reference video segment collected immediately following camera placement, where a ruler was moved through the field of view of the pool and used to convert distances on the screen into distances in cm. Patterns of spotting on fish also helped discriminate individuals in larger groups.

For behavioral comparisons, each 24-hour video interval was divided by diurnal and nocturnal periods collected from a stream location as a single observation in data analyses, pooling daytime or nighttime samples within a 24-hour day into a day or night measure. As multiple fish were sometimes observed within each 10-minute video collected, I averaged measures of foraging behavior across all fish observed in each segment and used the average measure to ensure the independence of observations. A single sampling site was sometimes re-visited within the four-month period but were treated as statistically independent observations when they did not occur within the same month. A total of 3 or 4 pools were filmed from each stream within a month. The foraging rate of each fish was calculated as the number of foraging attempts per minute.

Eq. 1: \( \text{foraging attempts per minute} = \frac{\text{no. of foraging attempts}}{\text{total minutes on screen}} \)

Behavioral observations were only included in data analyses if fish were present for greater than sixty seconds. Foraging behavior was then further calculated as overall monthly, diurnal, and nocturnal measures.
To estimate reaction distance and the probability of prey capture according to time of day and season, I measured foraging distance in body lengths, the rejection rate of prey items, and the number of investigatory movements made by fish. Measures of foraging distance and rejection rate (Grant 1987) were collected from a subsample of video containing equal diel ranges of fish presence and had sufficient water clarity to judge whether a fish retained a prey item or rejected it. To control for differences in fish size, foraging distance was estimated in body lengths, measured from the initial position of the fish’s snout to the location of in the stream where the prey item was captured. The rejection rate of food items was quantified by noting whether the fish ejected the item out after moving back to the foraging station, and the number of investigatory movements were measured as the number of directed movements made by fish away from their foraging station to drifting objections in the stream current.

Invertebrate Sampling

In each of the streams, I estimated food availability by sampling invertebrates from the stream current and the stream substrate. Invertebrate sampling occurred in habitats directly downstream of areas used for videography, with daytime sampling used to represent diurnal food availability and nighttime samples representing nocturnal food availability. I estimated drifting aquatic invertebrate abundance by anchoring a drift net in the center of the stream for 30 minutes. The drift net was constructed from a rectangular metal collar (25 cm × 25 cm) and attached to an elongated net 75 cm in length with a mesh size of 300 µm. Diurnal invertebrate drift samples were collected within a period ranging from 2 hours after sunrise until 2 hours before sunset. Nocturnal samples were collected beginning one half-hour after sunset, initiated during
astronomical twilight. At this time, the horizon line is visible, but details in the environment are not distinguishable by the observer. Sampling ended in the period of true night. The two sampling periods were selected to capture differences between diurnal and nocturnal invertebrate availability. While diurnal drift samples were collected daily from each pool the day following filming, a single nocturnal measurement represented a week of observations from a given stream. Benthic invertebrate samples were collected using a 0.072 m² Hess sampler placed onto the substrate, fitted with a 0.20 mm mesh net, following the methods described by Delong and Brusven (1998). Drifting invertebrate abundance was calculated as the number per meter cubed of water sampled, and benthic invertebrate abundance was calculated as the number per meter squared of stream substrate. Estimates of invertebrate abundance are based on the equations by (Smock 1996).

Eq. 2: Drifting invertebrate density (no. per m³)

\[
\text{Drifting invertebrate density} = \frac{\text{no. invertebrates sampled}}{\left(\text{net area (m}^2\right) \times \left(\text{current velocity (m/sec)}\right) \times \left(\text{sample time (1800 sec)}\right)}
\]

Eq. 3: Benthic invertebrate density (no. per m²) = \frac{\text{no. invertebrates captured}}{\text{benthic area sampled (m}^2\right)}

Following collection from the stream, all invertebrate samples were placed in plastic bags, preserved with 5% formalin, and returned to the laboratory for counting and identification. In the lab, the taxonomy of each invertebrate was identified to taxonomic family or order and measured for maximum length and width (±0.1 mm) using a dissecting microscope and digitizing system.
Statistical analyses

To test for differences between the main effects of diel period (diurnal versus nocturnal) on foraging rate, I used a t-test to compare means of daytime and nighttime foraging rate replicated across sampling sites. To investigate combined factors of foraging location (surface, water column, and benthos) as well as seasonal changes in foraging rate (July to November), I used a multifactor analysis of variance (ANOVA) approach to test for differences in foraging rate. I used measures of foraging rate based on individuals observed at sampling locations over 24-h sampling periods. I separated sampling observations over the three different study streams such that no sampling location on a single stream was observed on consecutive days, and no stream was observed for more than three consecutive days before a different stream was visited. In doing so, I assume the behavior of focal animal observations made at individual pools was independent of other pools in the set of observations.

To compare the relative importance of foraging effort from different areas of the stream, I estimated energy intake (joules • minute⁻¹) based on foraging rate from stream surface, water column, and benthos. Energy intake levels were estimated using location and time-specific foraging rates, multiplied by the average energy content of prey items encountered from the stream and by estimated prey rejection rates observed.

Eq. 4: Estimated energy intake

\[ \text{Estimated energy intake} = \text{foraging rate (number} \times \text{minute}^{-1}) \times \text{prey energy content} \times \text{capture probability} \]
Prey energy content, based on invertebrate length, was calculated using the following equation derived from, (Cumminns and Wuycheck 1971; Smock 1980).

Eq. 5: Prey energy content (joules × prey\(^{-1}\))

\[
= 0.3818(\text{mean length of prey size class (mm)})^{2.46}
\]

I also compared estimated energy intake with maximum intake rates based on Elliott’s (1975) model of maximum ration (Cmax) for brown trout. Because ration size is strongly dependent on fish size, I used a commonly observed fish length from my study streams (10 cm), converted to mass by the following equation (Jenkins and Keeley 2010).

Eq. 6: fish mass (g) = \(10^{3.1843(\log_{10}(\text{fish fork length(cm)})-5.242)}\)

Fish mass was then used to calculate Cmax from Elliott’s (1975) model using the following equations.

Eq. 7: if temp < 6.6\(^\circ\)C, \(C_{\text{max}} = (2.902)(\text{fish mass}(g))^{0.762}(e^{0.418(\text{temperature} \ ^\circ\text{C})})\)

Eq. 8: if temp > 6.6\(^\circ\)C, \(C_{\text{max}} = (15.018)(\text{fish mass}(g))^{0.759}(e^{0.171(\text{temperature} \ ^\circ\text{C})})\)

Daily Cmax was then converted to intake rate by dividing the ration by the number of minutes in a 24-hour period.
RESULTS

A total of 76, 24-hour intervals of video were collected from 31 different pool sites over the three study streams, producing about 304 hours of video with 1052 diurnal and 971 nocturnal 10 min video segments (n = 1076 in 2017; n = 948 in 2018). Sampling occurred from the beginning of August through November in 2017 and from the beginning of July through November in 2018. Of the video collected during the study, fish were observed onscreen in half of the segments (1094 or 51%). Video sometimes had more than one fish present on screen, with the largest groups reaching five fish. However, 719 (61.5% of onscreen observations) had one fish, and 149 (11.5% of observations) had two fish. The average duration of fish presence onscreen was 7.1 minutes (± 1.7 minutes) for each 10-minute interval. A total of 930 focal animal observations were scored and analyzed in this study with fish comprising a broad range of sizes. The smallest size class of fish observed were young of the year cutthroat trout (3-5 cm), occurring in 85 videos, or 15.6% of observations. Larger fish, ranging from 20 to 30 cm, appeared in 23 videos, or 3.25% of observations. The most common sizes of fish observed measured 5-10 cm in fork length, which occurred in 434 videos, or 57.7% of fish observations.

Foraging Behavior

I observed trout occupying foraging positions in the stream both diurnally and nocturnally, as well as throughout summer and fall seasons. In video segments with fish present, individuals occurred in relatively similar proportions diurnally and nocturnally (Figure 2), with fish maintaining foraging positions in 69.7% of total time in diurnal hours, and 67.7% nocturnally. While cutthroat trout were observed to forage
during both day and night periods, foraging rate was 71.2% higher during the day versus nighttime (± 9.5%) (Figure 3; t_{96.304} = 6.401, p < 0.05). Location of foraging effort differed among areas of the stream (Figure 4; ANOVA, F_{2, 452} = 68.57, p < 0.05) and according to diel period. Diurnally, drift foraging was primarily located in the water column and served as the predominant foraging location (Figure 4, ANOVA, F_{1, 198} = 67.71, p < 0.05). A smaller proportion of daytime drift feeding occurred from the water surface, and when combined, diurnal drift foraging occurred at an average of 0.77 foraging attempts per minute (± 0.38 attempts/min), comprising 69% of the total foraging effort. A much smaller proportion of benthic feeding was also observed across study sites, in both diurnal and nocturnal periods (Figure 4). During nocturnal periods, cutthroat trout foraged at lower rates, which did not differ among benthic, water column, and surface locations (Figure 4; ANOVA, F_{2, 123} = 2.265, p = 0.108).

Differences in diel foraging distance and rejection rate were also observed. Diurnally, fish were found to move on average 0.89 body lengths to intercept food, compared to 0.7 body lengths during nocturnal periods (Figure 5a; t-test, t_{18.904} = 3.345, p < 0.05). Fish exhibited a rejection rate of 14.7% of food items diurnally and 71.7% nocturnally (Figure 5b; t_{11.759} = 3.584, p < 0.05). Additional movements from foraging stations were also different between the two periods. Fish made an average of 0.84 investigatory movements per minute diurnally, and 0.38 movements per minute nocturnally (Figure 6; t_{234.6} = 10.991, p < 0.05).

When compared over the four-month observation period, foraging rate in the water column remained significantly higher than benthic and surface foraging rates (Figure 7a and b; foraging location effect: ANOVA, F_{2, 283} = 66.21, p < 0.05), but
declined across all categories (benthic, water column, and surface foraging) from July to November (Figure 7a and b; month effect: ANOVA, F_{6,107} = 5.96, p < 0.05). In addition, foraging rates were higher during daylight hours (Figure 7a and b; diel effect: ANOVA, F_{6,107} = 29.59, p < 0.05), particularly for daytime water column foraging, producing a significant time by diel period interaction (ANOVA, F_{2,283} = 42.32, p < 0.05). Separate interactions of time by diel foraging location and time by foraging location had no significant effect after controlling for all other factors in the model (ANOVA, both F-values < = 1.65, both p-values > 0.14).

Size-related effects on foraging behavior

There were differences in frequency and location of foraging effort related to fish size. Young-of-the-year cutthroat trout (<5 cm) were observed predominately during diurnal hours (91.7%); whereas, fish larger than 10 cm were more frequently observed during nocturnal periods (50.4%). Over diurnal observations, fish size had no effect on foraging rate (Figure 8a; ANOVA, F_{4,270} = 0.175, p = 0.95). As before, drift-feeding from the water column was the principal location of foraging activity (Figure 8a). Similarly, during nocturnal observations, there was no overall effect of fish size on foraging rate (Figure 8b; ANOVA, F_{4,171} = 0.914, p = 0.46); however, size significantly influenced intake location (Figure 8b, ANOVA, F_{2,171} = 11.383, p < 0.05) as well as producing a significant interaction between foraging location foraging rate and fish size (Figure 8b, ANOVA, F_{8,171} = 5.209, p < 0.05). During nocturnal periods, a higher frequency of surface foraging behavior was found in the largest size class of fish.
Social effects on foraging behavior

In terms of observed group size, single fish were the most common assemblage found on-screen, occurring in 458 (59%) of diurnal fish observations, and 261 (68%) nocturnally. Groups of two fish appeared in 101 (11%) of diurnal observations, and 47 (13%) nocturnally. Fish groups numbering three, four, and five fish occurred at lower levels, being 52 (6%) of diurnal and 9 (2%) of nocturnal observations. Ranking position did not influence foraging rate in both diurnal and nocturnal periods (Figure 9a; ANOVA, $F_{3, 324} = 0.004, p = 0.999$), (Figure 9b; ANOVA, $F_{3, 168} = 5.102, p = 0.942$). During diurnal hours, however, ranking position affected foraging intake location (Figure 9b; ANOVA, $F_{2, 324} = 81.164, p < 0.05$). Nocturnal foraging behavior was not found to shift in intake location with increasing position (Figure 9b; ANOVA, $F_{6, 168} = 0.842, p = 0.539$), and occurred at a significantly lower frequency than diurnal behavior.

Invertebrate Abundance

Estimates of food availability for cutthroat trout varied over the study period and according to diel period. Based on a total of 43 diurnal drifting invertebrate samples and 27 nocturnal drifting invertebrate samples, invertebrate abundance exhibited a significant seasonal decline over both diel periods (Figure 10a, ANOVA, $F_{3, 68} = 7.59, p < 0.05$). However, there was no significant diel difference in drifting invertebrate concentrations when integrated over the four-month period (Figure 10a, ANOVA, $F_{1, 68} = 0.33, p = 0.327$). Drifting invertebrate abundance was higher during August and September but decreased during October, and remained at consistent levels during diurnal periods in November, producing no significant month by diel period interaction (Figure 10a; ANOVA, $F_{3,68} = 1.43, p = 0.242$). Similarly, benthic invertebrate abundance
also exhibited a seasonal decline over both diel periods (Figure 10b, ANOVA, F\(_{3, 71}\) = 4.63, p = 0.0054). Benthic invertebrate abundance tended to be higher during nocturnal periods in August and September, but was lower during nocturnal periods in September and October, producing no significant difference between diel periods (Figure 10b, ANOVA, F\(_{1, 71}\) = 0.01, p = 0.94), or a significant month by diel interaction (Figure 10b, ANOVA, F\(_{3, 71}\) = 1.03, p = 0.39). Drift abundance was found to be positively correlated with benthic invertebrate abundance over the seasonal period: (drift vs. benthic invertebrates, r = 0.24, p < 0.05), (log\(_{10}\) drift vs. log\(_{10}\) benthic, r = 0.28, p < 0.05).

Stream temperature

As expected, stream temperatures varied both seasonally and between diel periods. When averaged over four-month observations, diurnal temperatures occurred at an average of 11.2 °C (± 2.5 °C) compared to 8.4 °C (± 1.7 °C) nocturnally (Figure 11). Temperature declined over the four months of observations, dropping from 14.8 °C (range = 12.5 - 15.1 °C) during the day and 13.2 °C (range = 11.7 - 14.6 °C) at night in August, to 5.2 °C during the day (range= 3.9 - 6.1 °C) and 2.6 °C at night (range= 2.2 - 4.8 °C) in November (Figure 10, ANOVA, F\(_{3, 145}\) = 12.46, p < 0.0001). However, due to overlap in temperature between diel periods there was no significant difference in temperature between periods (Figure 11; ANOVA, F\(_{1, 145}\) = 0.582, p = 0.45), as well as no interaction between month and diel period (Figure 11; ANOVA, F\(_{3, 145}\) = 0.413, p = 0.74).

Stream light levels

The number of daylight hours declines predictably each year in the Northern hemisphere, and the decreasing proportion of daylight hours were reflected in this
study, starting at 53% in August and decreasing to 42% in November. Outside of seasonal declines in the number of daylight hours, further decreases occurred in the intensity of light levels. A significant decline in daylight intensity was observed with seasonal change. November light levels were half the diurnal LUX levels illuminating streams in August (Figure 12, ANOVA $F_{3,145} = 7.18$, $p < 0.0001$).

Estimated measures of energy intake

    Drift-foraging comprised the greatest proportion of foraging effort. It accounted for the largest component of energy intake per minute, being greater than nocturnal drift foraging and benthic foraging behaviors. Energy consumption from drift foraging differed between day and night periods due to differences in foraging rate between the two periods as well as nocturnal hours having a reduced capture probability (Figure 13). A seasonal decline in energy intake was observed in drift foraging, with November level being the lowest levels of energy intake, with an average of 2.1 (joules·min$^{-1}$) diurnally and 0.24 nocturnally, compared to 3.7 and 1.2 in August ($\pm 0.36$ joules·min$^{-1}$). Drift foraging was found to be the most important foraging mode for cutthroat trout in my study. Benthic foraging accounted for a smaller proportion of energy intake and did not differ between day and night periods or across months.

    To understand the implications of energy intake for fish throughout the study period, the maximum daily ration was estimated for a 10 cm fish. Maximum daily energy intake was significantly higher in August, starting at 13.9 joules·min$^{-1}$, before steeply dropping into winter months (Figure 14). Estimated energy intake from diurnal and nocturnal drifting and benthic foraging remained less than the maximum daily ration in August and September; however, diurnal drift foraging became higher than this value
during October and November, remaining at consistent levels. Energy consumed during October and November through drift foraging was higher than the metabolic processing limit in salmonid fishes.
DISCUSSION

This study aimed to understand foraging behavior in fluvial cutthroat trout and identify the degree to which foraging behavior departs from the diel drift foraging paradigm. Results of this and earlier research support diurnal drift foraging as the primary foraging mode for wild cutthroat trout populations (Fraser and Metcalfe 1997; Gunnarsson and Steingrímsdóttir 2011; Tunney and Steingrímsdóttir 2012; Piccolo et al. 2014; Fingerle et al. 2016). However, in this study, nocturnal and benthic foraging were found to occur at moderate levels. Several factors affected the foraging rate and intake location, including diel period, season, size class, and fish position. While departures to drift foraging behavior have been documented previously, the extent to which they occur had not been investigated. Deviations from the drift foraging paradigm are of ongoing interest to scientists, with food abundance serving as the base for salmonid ecology and foraging models (Nislow et al. 1999; Fausch 2014).

As salmonids in streams often swim against the stream current to maintain a holding station and capture drifting invertebrate prey, they have long been described as drift-feeding predators (Hughes and Dill 1990; Keeley and Grant 1995; Gunnarsson and Steingrímsdóttir 2011; Syrjänen et al. 2011; Piccolo et al. 2014). Additional observations have led researchers to question whether diurnal drift-feeding is the primary source of feeding activity and energy intake. Both benthic and nocturnal foraging behavior have been observed in many salmonid fish species including Atlantic salmon (Fraser et al. 1993, 1995; Fraser and Metcalfe 1997), Chinook salmon (Hillman et al. 1992), coho salmon (Hillman et al. 1992; Roni and Fayram 2000), brown trout (Heggenes et al. 1993), rainbow trout (Tippets and Moyle 1978; Riehle and Griffith 1993; Di Prinzio et al. 1993),
2015; Johnson et al. 2016), bull trout (Jakober et al. 2000), brook trout (Cunjak et al. 1987), cutthroat trout (Bonneau and Scarnecchia 1998; Jakober et al. 2000), Dolly Varden, and white-spotted charr (Fausch et al. 1997). These observations contradict the paradigm of diurnal-summer based drift foraging behavior (Rimmer et al. 1983; Amundsen and Klemetsen 1988). In this study, cutthroat trout were found to forage from the stream benthos at a rate of 0.1 attempts per minute, or 15.6% of their total energy budget, and to forage nocturnally at 0.265 attempts per minute, or 24% of their energy budget. However, while foraging was found to occur in both diurnal and nocturnal periods, diurnal foraging occurred two to three times more frequently than nocturnal foraging. While these challenges to current energetic models are significant, it is also important to understand the context of this foraging behavior within the complex stream environment.

In stream ecosystems, several factors have been documented to influence foraging behavior of wild trout. With physiological and environmental limits to food intake, diel period, seasonal change, invertebrate abundance, temperature, diel light levels, fish size, ranking position, and stream locality are thought to influence foraging behavior (Muller 1974 p. 1; Smith and Griffith 1994; Gries et al. 1997; Fraser and Metcalfe 1997; Jakober et al. 2000; Hansen and Closs 2005; Gregory 2011). In this study, foraging behavior was found to be significantly impacted by season throughout the four-month study period, supporting a summer based foraging season (Paloheimo and Dickie 1966; Cunjak 1988). Foraging intake locations in the stream were biased towards diurnal drift foraging behavior, reinforcing the drift foraging paradigm (Kreivi et al. 1999; Neuwanger et al. 2014; Di Prinzio et al. 2015). During diurnal hours, drift
Foraging was the predominant foraging mode, however, during nocturnal foraging observations, fish foraging was directed approximately equally towards all areas in the stream system, including the benthos and water surface. In terms of overall importance, fish size did not affect foraging rate throughout a diel period, which is consistent with current foraging models (Fausch 1984, 2014). However, fish size influenced the foraging intake location in the stream. Similarly, fish ranking position did not impact foraging rate throughout a diel period but had a significant effect on stream intake location in diurnal hours. While food sources for salmonid populations were found to decline throughout the study period, invertebrate concentrations, diel temperature and light levels did not influence foraging behavior, despite a gradual seasonal decrease in all measures. In these study streams, a single pool supported a population of many fish, it is possible that mean foraging rates do not reflect the foraging requirements of individuals, with fish readily occupying open foraging sites throughout the year.

Many North American salmonid populations have experienced significant declines in abundance in the last 100 years (Nehlsen et al. 1991; Meffe 1992; Bradford and Irvine 2000). Through conservation action, fisheries managers attempt to mediate the loss of habitat and other threats to fisheries populations (Rieman et al. 2001; Solomon et al. 2003; Tsuboi et al. 2013). Foraging models have been implemented in a wide range of conservation actions. Uses for energetic models include habitat restoration, alteration of flow regimes, reestablishment of fish populations, and other proactive measures (Nislow et al. 1999; Urabe et al. 2010; Fausch 2014; Hayes et al. 2018). Foraging models are critical in ecology, as food sources directly relate to
population health and long-term fitness of individuals (Boutin 1990; Anholt and Werner 1995; Newton 1998). It is critical to understand foraging needs in fish populations as these needs reflect conservation requirements for animals. For realistic bioenergetic models, it is important to consider the full spectrum of foraging behaviors used by salmonid fishes (Fausch 2014).

Bioenergetic models are a critical tool used in salmonid conservation; however, it is possible that current salmonid foraging models underestimate food sources available to fish populations (Searle et al. 2013). The current understanding of salmonid foraging ecology is a diurnal, visual, drift foraging strategy, where fish are thought to maintain a stationary position in the stream current and capture drifting invertebrates suspended in the water column (Hughes and Dill 1990; Keeley and Grant 1995; Gunnarsson and Steingrímsson 2011; Syrjänen et al. 2011; Piccolo et al. 2014). In salmonid foraging models, the drift foraging paradigm is central in understanding energy intake and habitat quality (Dunbrack and Dill 1983; Fausch 1984; Hughes and Dill 1990). Food abundance for salmonids is only estimated using diurnal drifting invertebrate concentrations (Fausch 2014). However, for researchers, it is sometimes difficult to quantify food availability for animals in natural environments and to understand all food sources in energy intake (Searle et al. 2013). Cutthroat trout were found to deviate from the diurnal drift foraging model in 30% of total foraging behavior. Investigators have a better ability to quantify food sources using more intricate, scientifically nuanced models, which include alternative foraging strategies and environmental effects.
This research provides an example of how more extensive behavioral observations can impact an understanding of foraging habits. Interestingly, more nuanced measurements of behavior have been identified by being able to observe fish remotely across a diel and seasonal changes. Game cameras have been used extensively on land producing new insights and yielding a more comprehensive view of animal behavior (Trolliet et al. 2014). While inferences of salmonid foraging behavior have been long-established, direct behavioral observations of salmonids foraging in streams are limited (Vogel and Beauchamp 1999). Video techniques are appropriate for aquatic environments, overcoming natural barriers to observation (Vogel and Beauchamp 1999). Videography can be used to identify foraging behavior in streams and can be paired with environmental measures of habitat (Neuswanger et al. 2014, 2016).

As food in streams extends broadly beyond drifting invertebrates, alternative foraging strategies were not fully unexpected (Elliott 1970; Muller 1974; Brittain and Eikeland 1988; Allen and Castillo 2007). Aquatic invertebrates were found in the stream benthos at higher concentrations than stream drift, and these food sources exist at considerably lower concentrations in the water column (Elliott 1970; Muller 1974). Additionally, nocturnal foraging provides further opportunities for fish to acquire food ranging from 44% to 65% of a total diel period (Kronfeld-Schor and Dayan 2003). However, even with these supplemental food sources and strong selective pressures for food intake, diurnal drift foraging occurred at significantly higher levels than nocturnal and benthic foraging.
In terms of foraging effort, while salmonids in streams have commonly been observed to capture drifting invertebrates from the water during daylight hours, little is known about their nocturnal foraging activity. Measures of visual reactivity, including foraging distance, success, and the number of investigatory movements taken, were greatly reduced by nocturnal light levels. Anecdotally, with nocturnal foraging attempts being of a shorter distance and more arbitrarily directed, nighttime foraging seemed to rely on the use of the fish’s lateral line. Fish were often found to indiscriminately move towards non-food objects such as leaves or other organic matter, exhibiting a rejection rate of 14.7% of objects diurnally, compared to 71.7% in nocturnal hours.

Researchers have struggled to estimate energy intake for free-ranging animals (Fausch 2014). Using combined measures of foraging rate and capture success, energy intake was estimated from behavioral observations to better understand dietary impact in an integrative behavioral approach (Searle et al. 2013). In terms of estimated energy intake, both nocturnal and benthic behavior were less effective than diurnal drift foraging behavior, due to lower levels of foraging rate and capture success. Energy intake from drift foraging was so significant as to sometimes exceed the modeled metabolic processing limits for fish populations. During October and November, diurnal drift foraging behavior was maintained at consistent levels outside the bounds of metabolic processing limits for fish. In this study, fish were not able to be individually identified from within their larger population. Both local population size and relative competition levels are not known for each foraging position. It is possible that through diurnal drift foraging, fish can obtain sufficient food through shorter active foraging bouts, which could potentially impact future foraging models. However, despite these
findings, nocturnal and benthic foraging behavior were found across all fish populations in moderate levels.

Drift foraging appears common in riverine fishes, ranging from cyprinids to perciforms, but this behavior is particularly modeled for salmonid fishes (Piccolo et al. 2014). Drift foraging in streams is an effective strategy for salmonids, with salmonid like fish-occurring 88 MYA (Macqueen and Johnston 2014), and salmonids long persisting in western North American rivers (Behnke et al. 2002; Trotter et al. 2018). With predictable drifting food sources moving through water systems, salmonid fishes, including cutthroat trout, can take advantage of riverine habitats despite heavy pressures in space, temperature, and ranges in seasonal resources (Chapman 1966; Thurow et al. 1997). However, selective pressures seem to have supported some degree of foraging plasticity in salmonids under certain environmental conditions, sustaining benthic and nocturnal foraging (Tippets and Moyle 1978; Fausch et al. 1997). Despite this, salmonid fishes appear to have physiological limits, which re-enforce the dominance of diel drift foraging behavior (Fraser and Metcalfe 1997; Rader 1997).

Cutthroat trout are understood to be drift foraging predators. However, with documented departures from this behavior, uncertainty exists in quantifying the foraging requirements of salmonid fishes (Grant 1987; Rosenfeld et al. 2005; Hayes et al. 2018). My findings highlight the importance of drift foraging behavior and provide insight into alternative foraging strategies. Using videography, salmonid foraging ecology was able to be captured over a broad seasonal scale. With many native fish species threatened throughout the American west, accurate foraging models are needed to inform wildlife management and to restore native fish populations.
CONCLUSIONS

Drift foraging behavior has long been established as the primary mechanism by which salmonid fishes acquire food. However, it can sometimes be difficult to quantify food availability for individuals in natural environments and to understand all resources used in foraging activity. In this study, videography supported the dominance of drift foraging behavior for cutthroat trout; however, moderate levels of benthic and nocturnal foraging were found to occur at 15.6% and 24% of total foraging activity, respectively. Environmental effects had a strong influence on foraging rate and intake location, including diel period, season, size class, and fish position. In terms of energy content, nocturnal and benthic behavior were less effective than diurnal drift foraging behavior. Energy intake was found to be significantly larger for diurnal drift foraging behavior throughout the study season, exceeding the modeled metabolic limit for fish in October and November. Observations of foraging behavior support the use of videography in stream settings. Significantly, foraging behavior was found to be more complex than previously modeled, with many multifaceted relationships between cutthroat trout and their food sources.
LITERATURE CITED


Hughes, N. F., and L. M. Dill. 1990. Position choice by drift-feeding salmonids: model and test for arctic grayling (Thymallus arcticus) in subarctic mountain streams,


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Figure 1. Map of three first-order streams in Southeastern Idaho where cutthroat trout were observed in order to quantify foraging behavior. Invertebrate sampling and video segments were captured at Inman Creek (latitude: 42.8213044, longitude: -112.2202474), Goodenough Creek (latitude: 42.6543057, longitude: -112.28583213) and Harkness Creek (latitude: 42.6579718, longitude: -112.1924671), in Bannock County, Idaho.
Figure 2. Mean proportion of video with cutthroat trout present (+1 SE) during diurnal (open bar) and nocturnal (solid bar) periods, over four months (n=452).
Foraging rate (mean number \cdot minute^{-1})

Figure 3. Mean foraging rate (+ 1 SE) of cutthroat trout during diurnal (open bar) and nocturnal (solid bar) periods (n=97).
Figure 4. Mean foraging rate (+ 1 SE) of cutthroat trout during diurnal (open bars) periods or nocturnal (solid bars), and according to foraging location in the stream (n=452).
Figure 5. (a) Mean foraging distance (body lengths) (+ 1 SE), and (b) mean rejection rate of foraging behavior (+ 1 SE), measured diurnally (open bars) and nocturnally (solid bars) in a subset of video segments (n=10).
Figure 6. Mean no. foraging attempts (+ 1 SE) during diurnal (open bar) and nocturnal (solid bar) periods, in a subset of video segments (n=10).
Figure 7. Mean monthly foraging rate (± 1 SE) of cutthroat trout observed during (a) diurnal periods or (b) nocturnal periods, and according to foraging intake location, (square = benthic, circles = water column, triangle = surface) (n = 107).
Figure 8. Mean foraging rate (+ 1 SE) of cutthroat trout during (a) diurnal and (b) nocturnal periods, partitioned by fish size and according to foraging intake location (solid bars = benthic, open = water column, hatched = surface) (8a: n=270, 8b: n=171).
Figure 9. Mean foraging rate (+ 1 SE) of cutthroat trout during (a) diurnal and (b) nocturnal periods, partitioned by fish position in group and according to foraging intake location (solid bars = benthic, open = water column, hatched = surface) (9a: n=324, 9b: n=168).
Figure 10. Mean invertebrate abundance (± 1 SE) from (a) drifting and (b) benthic invertebrate measures, across summer and fall months. Right-hand vertical axis was provided as a reference for conversion to untransformed values of drifting and benthic invertebrates, (solid circles = nocturnal concentrations, open circles = diurnal concentrations) (10a: n=68, 10b: n=71).
Figure 11. Mean monthly stream temperatures (°C) (±1 SE), (diurnal periods = dashed line, nocturnal periods = solid line) (n=145).
Figure 12. Mean monthly diurnal stream light levels (lumens x m$^{-2}$) (±1 SE) in first-order Idaho streams, (dashed lines = minimum and maximum light levels) (n=145).
Figure 13. Mean estimated energy intake (±1 SE) of cutthroat trout by month, from the drift (solid lines) or benthos (dashed lines), (diurnal periods = open circles, nocturnal periods = solid circles) (n=456).
Figure 14. The comparison of the mean maximum daily ration of a 10 cm fish with mean monthly energy intake estimates for fish in this study (±1 SE), from the drift (solid lines) or benthos (dashed lines), (diurnal periods = open circles, nocturnal periods = solid circles). Monthly averaged maximum daily ration is shown by the dotted line (n=456).