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Stable Isotope Analysis (delta nitrogen-15 and delta carbon-13) and Bioenergetic Modeling of Spatial-Temporal Foraging Patterns and Consumption Dynamics in Brown and Rainbow Trout Populations Within Catch-and-Release Areas of Arkansas Tailwaters

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A dissertation submitted in partial fulfillment
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Abstract

I examined spatial and temporal consumption dynamics using an energy intake model and a bioenergetics model of rainbow trout, *Oncorhynchus mykiss*, and brown trout, *Salmo trutta*, within three catch-and-release (C-R) areas in Bull Shoals and Norfork tailwaters to determine whether trout populations were limited by food supply. I also examined the seasonal and ontogenetic shifts in the foraging patterns of brown and rainbow trout within these areas using gut content analysis (GCA) and stable isotope analysis (SIA) of $\delta^{13}C$ and $\delta^{15}N$. I examined 605 brown trout and 768 rainbow trout for GCA and SIA at Bull Shoals, Norfork, and Sylamore C-R areas. For growth analysis and abundance estimates, I tagged a total of 11,423 brown and rainbow trout. Mean rainbow trout densities were higher (47 to 342 fish·ha^{-1}) than brown trout (3 to 84 fish·ha^{-1}) at all C-R areas. The Norfork C-R area contained the highest densities of brown and rainbow trout. Benthic macroinvertebrates at Bull Shoals and Norfork were 14.0 to 18.7 times higher in biomass than at Sylamore. Biomass of sculpin was approximately 2 to 8 times higher at Norfork than Bull Shoals and Sylamore. I found a high proportion of filamentous algae, *Cladophora*, and a nuisance diatom, *Didymosphenia geminata* in the diets of rainbow trout (15-91%), despite the apparent lack of energetic value from this food source. Generally, SIA mixing model results provided broad ranges of source contributions rather than more informative narrow ranges of solutions limiting the conclusions regarding food source contributions. Large rainbow trout failed to consume sufficient food biomass to exceed maintenance ration and exhibited slow or negative seasonal growth suggesting poorer energetic conditions existed for this size class and species. In contrast, brown trout experienced high growth rates at lower densities than rainbow trout. Growth rate differences between brown and rainbow trout may be from brown trout shifting towards the incorporation of more energetically

profitable prey fish. These findings suggest rainbow trout, and not brown trout, in Arkansas tailwater C-R areas were limited by spatial-temporal fluctuations in food availability.

This dissertation is approved for
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Dedication

To my wife Peggy for her unwavering support, patience, and love.

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Introduction

In the southeastern United States rainbow trout, *Oncorhynchus mykiss*, and brown trout, *Salmo trutta*, fisheries are highly desirable and economically important in regulated rivers downstream of reservoir dams (Axon 1975). Tailwater fisheries often experience high fishing pressure and rely heavily on stocking to develop or augment a fishery (Heidinger 1993; Weiland and Hayward 1997). In Arkansas tailwaters, rainbow trout are often stocked as catchables (>228 mm TL) in put-and-take fishery. Brown trout are also stocked in Arkansas tailwaters as a put-grow-and-take fishery, but often successfully spawn (Pender and Kwak 2002). Residence times of rainbow trout stocked into tailwaters are often short due to high angler harvest with few rainbow trout reaching larger sizes (Aggus et al. 1979; Heidinger 1993; Weiland and Hayward 1997). In an effort to create and develop a fishery with higher catch rates of larger trout several special regulation catch-and-release (C-R) areas were created in Bull Shoals and Norfork tailwaters located in northcentral Arkansas with the assumption that as exploitation rates of trout decrease, residence times will increase. Implicit in the development of these special regulation C-R areas is that (*i*) trout do not move out of the special regulation areas, (*ii*) trout do not suffer high mortality rates within the special regulation areas, and (*iii*) the forage base is sufficient for growth within the special regulation areas. I evaluated the third assumption of whether food availability was sufficient to support adequate and sustained growth. If food supply is limited, intraspecific and interspecific competition may increase, leading to decreased growth. Tailwaters may be particularly food-limited for larger trout, and increasing the density and size of trout through special regulations in C-R areas in tailwaters may result in limited growth, decline in average size, and reduction in the food base (Filbert and Hawkins 1995; McKinney and Speas 2001; Weiland and Hayward 1997).

Bioenergetics models are a commonly used tool to estimate the consumption required to satisfy growth observed over a specified time interval (Kitchell et al. 1977) and may be ideal for addressing potential food limitation within C-R areas. Population level consumption rates can be compared with the abundance, biomass, or production of prey populations to determine whether prey resources provide a sustainable source of food for the predator (Ney 1990; Raborn et al. 2007) or determine potential spatial temporal bottlenecks in prey supply (Utz and Hartman 2006). When compared with independent estimates for consumption, bioenergetics models have performed well for a variety of salmonids (Beauchamp et al. 1989; Brodeur et al. 1992; Whitledge et al. 2010). I used a two pronged-bioenergetics modeling approach to assess whether the prey base was adequate to support trout production within special regulation areas on Bull Shoals and Norfork tailwaters. First, I calculated daily energy expenditure (DEE) or maintenance ration, and compared DEE to the estimated daily energy intake (DEI) ($J \cdot g^{-1} d^{-1}$) or daily ration (Eggers 1977). I compared estimates of DEI with DEE to determine if fish were obtaining sufficient energy to maintain body weight. For the second modeling approach, I constructed a time-dependent bioenergetics model to estimate seasonal and annual consumption rates of prey by brown and rainbow trout and compared this to available food resources (e.g. sculpin, benthic macroinvertebrates, and drifting macroinvertebrates) (Hanson et al. 1997).

An important and required field component in any bioenergetics modeling approach is energy intake from diet composition analysis (Ney 1993). The traditional approach for evaluating spatial and temporal diet composition has been gut contents analysis (GCA) (Bowen et al. 1996; Hyslop 1980). However, GCA only reflects individual short-term feeding by providing a "snapshot" of diet that varies temporally (Woodward and Hildrew 2002). Often prey found in GCA can be masticated or digested beyond recognition. Also, softer bodied

components that digest rapidly may be significantly underestimated in the diets (Grey 2006; Hyslop 1980). Difficulties in acquiring large sample sizes needed to describe temporal feeding patterns across a range of fish sizes is also often hindered by GCA (Bowen 1996). An alternative, and increasingly popular, complementary approach that overcomes some of the problems of GCA is the use of stable isotope analysis (SIA) using $\delta^{13}C$ and $\delta^{15}N$. This approach provides an integrated measure of assimilation over a longer-term rather than what was recently ingested (Hobson and Clark 1992; Peterson and Fry 1987). Although SIA provides a long-term advantage, SIA lacks the taxonomic resolution that GCA provides and may not reflect short-term feeding patterns due to tissue isotopic turnover rates (Johannsson et al. 2001; Persson and Hansson 1999).

Despite the popularity of using stable isotopes for dietary analysis, surprisingly little attention has been paid to the basic assumptions underlying the interpretation of stable isotope analysis (Gannes et al. 1997; Grey 2006). Assumptions of SIA often presume (*i*) little or no difference in assimilation efficiencies among diet sources, (*ii*) isotopic routing occurs equally among tissues, and (*iii*) fractionation and turnover rates of tissues are similar (Gannes et al. 1997; Post 2002). Assimilation efficiencies may depend on the amount of indigestible materials in the diet sources (Whitledge and Rabeni 1997) and consumer species (Cui and Liu 1990). Isotopic routing occurs when there is differential allocation of dietary elements to specific tissues of a consumer (Gannes et al. 1997). The extent to which isotopic routing may impact enrichment or depletion of consumer stable isotope ratios is not well understood (Gannes et al. 1997). Equal isotopic routing among tissues is an assumption that is likely often violated. Species-specific fractionation rates are often unavailable and may vary among species and diets (McCutchan et al. 2003; Vander Zanden and Rasmussen 2001). Isotopic turnover rate is the isotopic change due to

growth and metabolic tissue replacement associated with a change in diet (Hesslein et al. 1993) and is known to vary markedly among tissues (Hobson and Clark 1992; MacAvoy et al. 2001; Tieszen et al. 1983). Tissues, such as liver and mucous, typically reflect more recently assimilated diets (Church et al. 2009; Hesslein et al. 1993), whereas blood, muscle, and bone may be more appropriate for reflecting longer-term assimilated diets (MacNeil et al. 2006; Sholtodouglas et al. 1991). In fish populations exhibiting slow growth, the integrated dietary isotope ratios may be over a period of a year (Hesslein et al. 1993), compared to days in populations exhibiting fast growth rates (Herzka and Holt 2000). Examining turnover rates of a fish is critical in determining the appropriate time frame for which dietary isotopes have been integrated, particularly in the context of tailwaters where reduced growth rates may exist (McKinney and Speas 2001; Weiland and Hayward 1997). Despite the importance of understanding temporal dietary integration, estimated field turnover rates are often lacking in SIA studies due to inadequate growth rate estimates and/or laboratory or field derived species-specific metabolic tissue replacement rates.

To address a few of the assumptions in SIA, I examined the isotopic fractionation and turnover rates of $\delta^{13}C$ and $\delta^{15}N$ among different tissues of rainbow trout in a laboratory experiment. Whole blood, liver, and white muscle tissue were sampled from trout fed two natural diets, chironomids and and ozark sculpin, *Cottus hypselurus*. I examined isotopic differences among the tissues over time as rainbow trout tissue equilibrated with diet treatments and assimilation efficiency of rainbow trout fed chironomids at 10 and 25% maxiumum ration levels to assess levels of assimilated diets for stable isotope analysis of naturally ingested prey. After assessing some of the assumptions of SIA, I evaluated brown and rainbow trout spatial and temporal dietary patterns using GCA and SIA within the special regulation C-R areas in Bull

Shoals and Norfork tailwaters. Specifically, in the GCA and SIA study I attempted to: (*i*) characterize the seasonal variation in diet quantity and quality (e.g. energy) of prey, (*ii*) examine ontogenetic and trophic position shifts in $\delta^{15}N$ and GCA of brown trout, and (*iii*) compare field growth rates of brown and rainbow trout to laboratory derived metabolic turnover rates to estimate the number of days for $\delta^{13}C$ and $\delta^{15}N$ turnover (95%) to occur in white muscle tissue.

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Effects of prey and tissue type on $\delta^{13}C$ and $\delta^{15}N$ fractionation and turnover rates and assimilation efficiency of rainbow trout

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Abstract - Stable isotope analysis is increasingly used in ecological studies to examine dietary patterns of consumers. The utility of SIA studies may be limited by fundamental assumptions of the approach. Critical assumptions of stable isotope mixing models include knowledge of $\delta^{13}C$ and $\delta^{15}N$ fractionation (Δ) and turnover rates in each tissue examined along with assimilation efficiencies. We conducted laboratory experiments to examine effects of prey (sculpin and chironomid) and tissue type (blood, liver, and white muscle) on $\delta^{13}C$ and $\delta^{15}N$ fractionation and turnover rates in rainbow trout, along with determining assimilation efficiencies. Liver showed the most rapid turnover times for both $\delta^{15}N$ and $\delta^{13}C$ (T_{95} = 4-6 months), followed by blood (T_{95} = 4-7 months) and then white muscle tissue (T_{95} = 7-9 months). Turnover rates were metabolically dominated (82-93% of turnover), with the exception of $\delta^{13}C$ of blood in rainbow trout fed a chironomid diet (33%). Fractionation rates differed by tissue and diet. Based on the hatchery diet, $\Delta\delta^{15}N$ was 3.8‰ (95% CI 3.3-4.3) for white muscle, 2.9‰ (2.4-3.4) for blood and 2.5‰ (1.9-3.1) for liver, whereas $\Delta\delta^{13}C$ was 1.9‰ (1.7-2.1) for liver, 1.7‰ (1.4-2.0) for white muscle, and 1.5‰ (1.3-1.7) for blood. Assimilation efficiency averaged 55.8% (SE $\pm$ 0.90) and 64.5% (SE $\pm$ 1.98) at the 10% and 25% ration level, respectively. Based on the turnover rates we observed many food web studies using stable isotope analysis are likely to violate the assumption that $\delta^{15}N$ and $\delta^{13}C$ values of tissues are in equilibrium with a given diet. Additionally, fractionation rates of $\Delta\delta^{15}N$, and to a lesser extent $\Delta\delta^{13}C$, need to be considered in the context of inter-tissue variability. Knowledge of fractionation rates, tissue turnover rates, and assimilation efficiency can be crucial to effectively using stable isotope mixing models to assess dietary source contributions.

Key words: diet-switching, stable isotope analysis, assumptions, ration, bioenergetics

Introduction

Stable isotope analysis (SIA) has become a popular tool for ecologists in the analysis of spatial and temporal dietary patterns (Grey 2001; McIntyre et al. 2006) and trophic structure of food webs (Herwig et al. 2004; Post 2002). Stable isotope ratios of carbon and nitrogen in consumer tissues reflect the integration of dietary carbon and nitrogen assimilated by a consumer, rather than what was merely ingested (Hobson and Clark 1992; Peterson and Fry 1987). Fractionation in the tissues results in the retention of isotopically heavier ^{15}N or ^{13}C and the excretion of the isotopically lighter ^{14}N or ^{12}C (DeNiro and Epstein 1977; Minagawa and Wada 1984). Typically, nitrogen trophic fractionation ($\Delta\delta^{15}N$) is assumed to be 3.4‰ (Minagawa and Wada 1984), while carbon trophic fractionation ($\Delta\delta^{13}C$) is assumed to be <1‰ of the consumer (Peterson and Fry 1987). The $\delta^{15}N$ of a consumer can be used to evaluate the trophic level of a consumer in a food web, while $\delta^{13}C$ is more useful as an indicator of a consumers primary energy source (Post 2002).

Despite the popularity of using stable isotopes for dietary analysis and determining trophic position in aquatic food webs, surprisingly little attention has been paid to the basic assumptions underlying the interpretation of stable isotope analysis (Gannes et al. 1997; Grey 2006). SIA assumptions often presume little or no differences in assimilation efficiencies among diet sources, isotopic routing occurs equally among tissues, and fractionation and turnover rates of tissues are similar (Gannes et al. 1997; Post 2002). However, assimilation efficiencies may depend on the amount of indigestible

materials in the diet sources (Whitledge and Rabeni 1997) and consumer species (Cui and Liu 1990). For example, Elliott (1976) observed assimilation efficiency of 70-75% for brown trout, *Salmo trutta*, feeding on *Gammarus* sp., whereas Dupreez and Cockroft (1988) conducted a similar study on spotted grunter, *Pomadasys commersonni*, fed surf clams, *Donax serra*, and found much higher assimilation efficiency (average 88%). Mixing models often used to estimate the dietary patterns of a consumer using stable isotope ratios (Phillips and Gregg 2003) do not account for the possible differences in assimilation efficiencies of the diet sources.

Isotopic routing occurs when there is differential allocation of dietary elements to specific tissues of a consumer (Gannes et al. 1997). The extent to which isotopic routing may impact enrichment or depletion of consumer stable isotope ratios is not well understood (Gannes et al. 1997). However, equal isotopic routing among tissues is an assumption that is likely violated often.

Although 3.4‰ of $\Delta\delta^{15}N$ and 1.0‰ of $\Delta\delta^{13}C$ have been suggested as robust for aquatic consumers (Post 2002; Vander Zanden and Rasmussen 2001; Vanderklift and Ponsard 2003), substantial ranges of trophic fractionation rates are possible (Grey 2006). For example, Vander Zanden and Rasmussen (2001) conducted a broad-scale analysis of aquatic systems and found $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ values ranged from -0.7‰ to 9.2‰ and -2.1‰ to 2.8‰, respectively. McCutchan et al. (2003) suggested that much of the variation of trophic fractionation may be attributed to diet, and $\Delta\delta^{15}N$ varied depending on whether the consumer was sustained on an invertebrate diet (1.4‰), a plant-derived diet (2.2‰) or a high protein diet (3.3‰).

A time lag occurs before the stable isotope value in the tissue reflects the change from one food source to the new source and isotopic turnover rate is the isotopic change due to growth and metabolic tissue replacement associated with a change in diet (Hesslein et al. 1993) and is known to vary markedly among tissues (Buchheister and Latour 2010; MacAvoy et al. 2001; Tieszen et al. 1983). Metabolic turnover is expected to be higher or more important in slow-growing than in fast-growing consumers, where the contribution of growth turnover is higher. In a slow-growing population of broad whitefish, *Coregonus nasus,* white muscle tissue integrated dietary isotope ratios over a period of at least a year (Hesslein et al. 1993), while isotopic turnover was rapid in larval red drum, *Sciaenops ocellatus,* exhibiting fast growth rates, reaching isotopic equilibrium in days (Herzka and Holt 2000).

To address a few of the assumptions in SIA, we examined the isotopic fractionation and turnover rates of $\delta^{13}C$ and $\delta^{15}N$ among different tissues of rainbow trout in a laboratory experiment. Whole blood, liver, and white muscle tissue were sampled from trout fed two natural diets, chironomids and ozark sculpin, *Cottus hypselurus*. Isotopic differences were examined among the tissues over time as rainbow trout tissue equilibrated with diet treatments. We also examined assimilation efficiency of rainbow trout fed chironomids at 10 and 25% maximum ration levels to assess patterns of assimilated diets for stable isotope analysis of naturally ingested prey.

We hypothesized that fractionation rates would be similar to 3.4‰ of $\Delta\delta^{15}N$ and 1.0‰ of $\Delta\delta^{13}C$ for white muscle, but would be lower for liver and blood. We hypothesized that tissue turnover rates would be slowest for white muscle and fastest for

blood. Finally, we hypothesized that assimilation efficiencies would be in the range found by Elliott (1976) for brown trout fed *Gammarus*.

Methods

Stable isotope analysis

Hatchery-reared rainbow trout were obtained from Norfork National Fish Hatchery (NFNFH) located in Norfork, Arkansas. In the laboratory, fish were randomly assigned to one of six semi-circular tanks (440 L) equipped with a flow-through sand filtration system attached to a water chiller. Each tank received 11 fish. Temperatures were recorded daily at 15 min intervals with a digital thermometer placed in the tanks. Temperature in tanks averaged 15.2 °C (SE $\pm$ 0.003) and ranged from 14.7 to 16.0 °C throughout the experiment. The photoperiod consisted of a 12 h light:12 h dark regime. Ammonia levels were monitored on a regular basis and at least once a week 25% of the water was removed from the tanks and replaced with fresh dechlorinated water.

Fish were held for a 10-d acclimation period before the diet switching experiment began and were fed daily the same food used at the hatchery to ensure the stable isotope signal remained the same. Prior to the acclimation period each fish was anesthetized with clove oil, measured for total length (mm) and weight, and individually tagged with a visible implant (VI) alpha numeric tag in the adipose tissue behind the eye. The VI tag has been shown to have little or no effect on the mortality or growth of fish (Mourning et al. 1994; Zerrenner et al. 1997). After the acclimation period, two diets of isotopically homogenous prey chironomid (n = 3) and sculpin (n = 3), were systematically assigned to the tanks with a random starting point. These prey taxa were chosen because both are

consumed by rainbow trout in natural settings and were isotopically distinct from the hatchery signal. Fish were fed twice a day. Commercially available chironomids were frozen within small blocks of ice. A frozen cube traveled many times around the perimeter of the tank at the surface, slowly melting and releasing small pieces and individual larvae into the water column to ensure equal access to the food. Sculpin were collected in October 2007 and January 2008 from Norfork tailwater via backpack electrofishing. Upon collection sculpin were immediately placed on ice and brought back to the lab where they were frozen (-20 °C). A subsample of sculpin collected (n = 500) were weighed and measured. Sculpin averaged 76.7 mm TL (SE $\pm$ 0.48) and 7.7 g (SE $\pm$ 0.15). Sculpin were removed from the freezer, thawed and dried for 2-3 days at 50 °C in a drying oven. A pellet mill was then used to pelletize the sculpin. Prior to use, pellet mill chambers and perforated die were cleaned to remove any residual powder. Sculpin placed in the pellet mill were ground to a fine powder. The ground sculpin was then pressed through a metal perforated dye and cut to desired length. Pellets were placed in a drying oven at 50 °C for 48 h to remove any residual water from the samples. Pellets were cylindrical in shape and were 5 mm long and 1.8 mm in diameter.

Rations were determined using growth rates (100 g yr^{-1}) of smaller rainbow trout (<400 mm TL) from a mark-recapture study conducted in a catch-and-release area in Norfork tailwater (Flinders and Magoulick, unpublished data). A bioenergetics model was used to determine the ration required to sustain that growth rate (Hanson et al. 1997). We used model parameters from Rand et al. (1993) with the exception of maximum consumption and respiration, which were taken from Railsback and Rose (1999). For the simulations, caloric values used were chironomids 2,520 J g^{-1} (SE$\pm$39) Wet Weight

(WW, Flinders, unpublished data), and sculpin 5,420 J g^{-1} WW (Cummins and Wuycheck 1971). Simulations were run to estimate daily energy consumption (g WW/day) to obtain the desired growth rate in each tank at 15 °C. A dry weight:wet weight ratio of 0.21 was used to convert sculpin dry weight to wet weight (Flinders, unpublished data). Daily rations per fish ranged from 3.42 g to 6.32 g (WW of chironomids d^{-1}) and 1.59 g to 2.85 g (WW of sculpin d^{-1}), depending on fish size and experiment duration. During the experiment, the rations were adapted to the increasing fish biomass over time and accounted for any changes due to removal of fish. Bioenergetic simulation proportion of maximum ration (i.e. *P*-value) averaged 0.3088 (SE $\pm$ 0.0008) for chironomid and 0.1421 (SE $\pm$ 0.0002) for sculpin diets.

Sampling consisted of six fish per treatment (one from each tank) on days 0 (pre-diet switch), 10, 20, 30, 40, 50, 70, 90, and 110. Preliminary data with estimated specific growth rates (*k*) and metabolic turnover rate (*m*) values borrowed from the literature indicated that a minimum of 130 days would be required to achieve isotopic equilibrium (Harvey et al. 2002). Initially we planned to extend the experiment to 130 d, but a fungal outbreak near day 35 resulted in several mortalities and limited the experiment to 110 d.

Immediately after removal from the tank the fish was sacrificed and 1 cc of blood was collected with a 29-gauge, 12.7-mm hypodermic needle from the caudal vessel by puncturing the ventral midline immediately behind the anal fin (Houston 1990). The fish was then immediately frozen at –20 °C. To obtain white muscle tissue and liver samples, fish were removed from the freezer and allowed to thaw slightly. The whole liver was removed and rinsed with Millipore water and a small portion (about 1 cm^3) of white muscle tissue without skin was dissected below the dorsal fin and above the lateral line.

All samples were dried in a freeze dryer for 48 h. Liver and white muscle tissues were homogenized into a fine powder using a Wig-L-Bug (DENTSPLY Rinn Digital Wig-L-Bug Mixer/Amalgamator, Model MDS). Sculpin and hatchery pellets were further homogenized using a morter and pestle prior to analysis. Whole bodies of at least 3 individual chironomids were pooled for isotope analysis and were then freeze-dried for at least 48 h.

Carbon and nitrogen stable isotope ratios were obtained from the samples using an elemental analyzer with a continuous mass spectrometer (University of Arkansas, Stable Isotope Laboratory). Isotopic composition was expressed in δ notation:

$$\delta I = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 1000$$

where *I* is the isotope of interest (either ^{13}C or ^{15}N) and *R* is the ratio of this isotope to the lighter isotope (either ^{12}C or ^{14}N). δI is expressed as the per mil (‰) deviation of that sample from the recognized isotope standard. Standards employed were Vienna Pee Dee Belemnite for $^{13}C/^{12}C$ and atmospheric N_2 for $^{15}N/^{14}N$. Based on repeated measurements of laboratory standards, we estimated analytical errors (standard deviation) between replicates were 0.12‰ for $\delta^{13}C$ and 0.10‰ for $\delta^{15}N$.

Liver tissue typically contains higher lipid concentrations than white muscle tissue and blood (Pinnegar and Polunin 1999). Lipids usually have more negative $\delta^{13}C$ values compared to proteins and carbohydrates within an individual organism (DeNiro and Epstein 1977). Liver $\delta^{13}C$ values were mathematically corrected for lipid effects following the aquatic organism equation in Post et al. (2007):

$$\delta^{13}C_{\text{normalized}} = \delta^{13}C_{\text{untreated}} - 3.32 + 0.99 \text{ x C:N}$$

where $\delta^{13}C_{untreated}$ is the obtained value and $\delta^{13}C_{normalized}$ is an estimate of $\delta^{13}C$ normalized value.

Turnover and fractionation rates

Turnover rates were estimated using the Hesslein et al. (1993) model to estimate stable isotope turnover due to metabolism and growth at time (*t*) and can be described as:

$$\delta_{tissue(t)} = \delta_{equilibrium} + (\delta_{tissue(0)} - \delta_{equilibrium})e^{-(k+m)t}$$

where $\delta_{equilibrium}$ is the stable isotope ($\delta^{15}N$ or $\delta^{13}C$) signature of the fish at equilibrium with the new diet, $\delta_{tissue(0)}$ is the initial stable isotope value of the fish, $\delta_{tissue(t)}$ is the stable isotope value of the fish at time (*t*) of sampling, *k* is the specific growth rate constant per day, and *m* is the metabolic turnover rate constant per day. The model was used to estimate *m* and $\delta_{equilibrium}$. Specific growth rates were estimated for each treatment group (i.e. chironomids and sculpin) using the exponential growth model:

$$W_t = W_0 e^{kt}$$

where W_t is the final weight of fish on day (*t*) of sampling and W_0 is the initial weight on day 0. The estimates of turnover times to 50% (T_{50}) or half-life (HL) and 95% (T_{95}) of equilibrium with the new diet were calculated as follows (Tieszen et al. 1983):

$$T_{\alpha/100} = \frac{\ln(1 - \alpha/100)}{-(k+m)}$$

Proportion of turnover attributed to growth (P_k) and metabolism (P_m) was calculated as the relative contributions of growth (*k*) and metabolism (*m*) as a ratio of each parameter to the sum of the two parameters. Trophic fractionation ($\Delta\delta^{15}N$ and $\Delta\delta^{13}C$) was estimated for hatchery, sculpin, and chironomid diet as:

$$\Delta_{tissue} = \delta I_{consumer} - \delta I_{equilibrium}$$

where *I* is the isotope of interest (either ^{13}C or ^{15}N). Diet tissue fractionations were derived from estimates of $\delta_{equilibrium}$ in the Hesslein et al. (1993) model.

Assimilation efficiency

Hatchery-reared rainbow trout were obtained from NFNFH. In the laboratory, rainbow trout were held together in 530 L recirculating stream systems (Frigid Unit LSW-700 living stream) for a 5-d acclimation period with a 12 h light:12 h dark photoperiod regime before experiments began. Each day during the acclimation fish received a frozen pre-weighed ration of chironomids that constituted 1% body weight (dry-g-food dry-g-fish^{-1} x 100).

Assimilation efficiency rates were measured near 17 °C (range: 16.57 °C to 17.72 °C) and ration levels of maximum food consumption (C_{max}) 10 and 25% (R_{10} and R_{25}) were used. Lower ration levels were selected to compare with Elliott (1976) and also based on studies of trout in other reservoir tailwaters that suggest low daily feeding ration levels are common (Filbert and Hawkins 1995; Weiland and Hayward 1997). Maximum food consumption, C_{max}, was estimated from Railsback and Rose (1999) for rainbow trout. Maximum daily consumption (g WW of prey consumed d^{-1}) was estimated as a function of weight (g WW of trout) and temperature (T, °C) with the following equation:

$$C_{max} = aW^{(1+b)}c(T)$$

where *W* is the mean weight of the fish (g); a and b are constants; c is a constant (value; Myrick 1998). Feeding rates at each ration level were determined by estimating C_{max} and dividing the weight of food consumed (wet-g-food) by the weight of the fish (wet-g-fish^{-1}) to determine percentages.

After acclimation individual trout were randomly assigned to an experimental tank housed in a temperature controlled environmental chamber on a 12 h light:12 h dark photoperiod regime. Experiment tanks were 38 L aquaria (51 cm l x 25 cm w x 30 cm h) and filled with 20 L of water. Dissolved oxygen levels were monitored at 100% saturation using an air stone. Temperature was monitored in each tank with a submersible data logger (Hobo Water Temp Pro v2; Onset Computer Corporation, Pocasset, Massachusetts). Black polyethylene sheets covered the sides to isolate fish from visual disturbances. Nylon-mesh screening covered the tanks to prevent fish from escaping. A preliminary study indicated complete gut evacuation after 5 days. Following the gut evacuation period, fish were randomly assigned to a tank in the environmental chamber. Chironomids were weighed to nearest 0.0001 g WW and converted to DW using a DW:WW ratio of 0.137 (Flinders, unpublished data) and then frozen in small cubes of ice. Any excess chironomids were removed by pipette from the tank water after 1 h, enabling the calculation of voluntary intake of each fish. Fish were then transferred to identical experimental tanks and held for 5 d to ensure that all feces were evacuated from the gut (Elliott 1972; Elliot 1976). Feces were collected daily by pipetting the material from the tank to minimize leaching losses. Tank water was then filtered through a 1 µm Whatman GF/C glass fiber filter, 47 mm diameter, attached to a vacuum/pressure station. Filtered water was returned to the tank. Prior to use filters were placed in a combustion oven at 500ºC for 2 to 3 hours and weighed to the nearest 0.0001 g. Filters containing feces and excess chironomids collected 1 h post-feeding were dried at 60ºC for 48 h and weighed to the nearest 0.0001 g. Filters containing feces

were then bombed to determine caloric content using a Parr 6200 Calorimeter. Values for the chironomids and feces were recorded as cal g^{-1} dry mass and converted to Joules.

Ammonia and urea excretion rates from the fish were measured collecting three samples at the beginning and end of each experiment. Water samples were collected using a 50 mL sterile BD Falcon tube. Tubes were rinsed in tank water prior to collection of water sample and approximately 40 mL of tank water was collected per sample. Samples were immediately frozen (-10 °C) after collection. Total ammonia nitrogen (TAN), which is the sum of both forms of ammonia present ($NH_3 + NH_4^+$), was measured using a Shimadzu TOC-V_{CSH} coupled to a TNM-1 chemiluminescent detector (Shimadzu Scientific Instruments) and was determined colorimetrically with a Lachat QuickChem 8500. Elliott (1976) estimated the percentage of ammonia-nitrogen (NH_3) in excretory products of brown trout at 17.1 °C was $\geq$90% (Range 90% to 92%). Urea-nitrogen (NH_2) represented <10% and since urea-nitrogen was a low quantity, excretory products were converted to energy units using 24.85 J mg^{-1} for ammonia-nitrogen (Elliott 1976).

Assimilation efficiency of rainbow trout fed a low ration of chironomids was examined. Parameters estimated were amount of energy (J) egested in feces and ammonia. Absorption efficiency was calculated as:

$$ABE = \frac{W_i - W_e}{W_i} \times 100$$

where W_i and W_e are the dry weights (g) of food ingested and feces egested, respectively. Assimilation efficiency was calculated as:

$$ASE = \frac{E_i - (E_f + E_a)}{E_i} \times 100$$

where E_i is the amount of energy (J) ingested, E_f is the amount of energy (J) egested as feces, and E_a is the amount of energy (J) egested as ammonia and urea.

Statistical analysis

A *t*-test was used to compare differences in the specific growth rates of rainbow trout between diets. The parameters *m* and $\delta_{equilibrium}$ and their 95% confidence intervals for the Hesslein et al. (1993) model were estimated using the non-linear least squares (nls) routine and the *confint* method in the MASS library of program R (Overmyer et al. 2008). Differences in isotopic values ($\delta^{13}C$ and $\delta^{15}N$) between the diet sources (i.e. hatchery, sculpin, and chironomids) used in the experiments were assessed using analysis of variance (ANOVA). Prior to statistical analysis, we examined all data graphically to determine if the data met the assumptions of normality and homogeneity of variance. We also assessed the data for equality of variance using a Levene's test and examined for departure from normality using the Shapiro–Wilk test (*W*-statistic). Observed δ values of tissues were compared with predicted δ values from the Hesslien et al. (1993) model via linear regression (r^2).

To assess the differences in energy assimilated at the different ration levels, we used analysis of covariance (ANCOVA), where amount of energy (J) egested in feces and ammonia were the response variables, ration level was the predictor variable, and fish weight was the covariate (Beaupre and Dunham 1995). Prior to statistical analysis, we examined all data graphically to determine if the data met the assumptions of normality, homogeneity of variance, and homogeneity of slopes. We also screened the data for equality of variance using a Levene's test and examined for departure from normality

using the Shapiro–Wilk test (*W*-statistic). An α value of 0.05 was used to determine statistical significance for all tests. Analysis was performed using SYSTAT 13.0 (SYSTAT 2009).

Results

Stable isotope analysis

At the start of the experiment, rainbow trout in the tanks receiving the chironomid diet averaged 230 mm TL (SE $\pm$ 3.3 mm) and 115.2 g (SE $\pm$ 4.3 g). In the tanks receiving sculpin diet, rainbow trout averaged 227 mm TL (SE $\pm$ 2.9 mm) and 110.4 g (SE $\pm$ 4.7 g). During the experiment, four fish exhibited weight loss; the last such individual was sacrificed on day 70. There were no significant differences in growth between diets (*t* value = 0.383, p = 0.70) (Fig. 1). However, treatment specific growth rates (*k*) were used in the Hesslein et al. (1993) model of 2.32 x 10^{-3} d^{-1} (SE $\pm$ 5.7 x 10^{-4} d^{-1}) and 2.07 x 10^{-3} d^{-1} (SE $\pm$ 3.2 x 10^{-4} d^{-1}) for rainbow trout fed chironomids and sculpin, respectively.

Isotopic values of the diet sources (i.e. hatchery, sculpin, and chironomids) used in the experiments differed significantly for $\delta^{13}C$ (ANOVA, $F_{2,15}$ = 10,161, $P < 0.001$) and $\delta^{15}N$ (ANOVA, $F_{2,15}$ = 491, $P < 0.001$). The initial diet of hatchery food averaged -21.8‰ (SE $\pm$ 0.12) for $\delta^{13}C$ and 7.2 ‰ (SE $\pm$ 0.28) for $\delta^{15}N$. Sculpin diet averaged -32.4‰ (SE $\pm$ 0.05) for $\delta^{13}C$ and 15.4‰ (SE $\pm$ 0.03) for $\delta^{15}N$ and was depleted in $\delta^{13}C$ and highly enriched in $\delta^{15}N$ when compared to the initial diet. The chironomid diet was enriched in both $\delta^{15}N$ and $\delta^{13}C$ compared to the initial diet and averaged -15.5‰ (SE $\pm$ 0.06) for $\delta^{13}C$ and 9.1‰ (SE $\pm$ 0.17) for $\delta^{15}N$.

There were significant differences among tissues in isotopic values. Before the diet switch, liver was slightly more enriched in $\delta^{13}C$ (-19.9‰ $\pm$ 0.04) compared to white muscle tissue (-20.1‰ $\pm$ 0.07) and blood (-20.3‰ $\pm$ 0.06) (ANOVA, $F_{2,15} = 15.24$, $P < 0.001$). White muscle tissue was more enriched in $\delta^{15}N$ (11.0‰ $\pm$ 0.06) compared to blood (9.7‰ $\pm$ 0.09) and liver (9.7‰ $\pm$ 0.15) at the beginning of the experiment and all tissues differed significantly (ANOVA, $F_{2,15} = 37.27$, $P < 0.001$).

Turnover rates and fractionation

The $\delta^{13}C$ and $\delta^{15}N$ values of rainbow trout fed chironomids and sculpin exhibited turnover toward the end of the 110 d experiment, except the white muscle tissue of trout fed chironomids (Fig. 2). Non-linear regression was unable to generate an equilibrium value ($\delta_{equilibrium}$) for either $\delta^{15}N$ or $\delta^{13}C$ in white muscle tissue of rainbow trout with the chironomid diet because white muscle tissue was not able to reach $\delta^{13}C$ and $\delta^{15}N$ isotopic equilibrium.

The turnover rates differed among diet treatments, tissues, and $\delta^{13}C$ and $\delta^{15}N$ (Table 1). In general, liver had the fastest turnover rates for both $\delta^{13}C$ and $\delta^{15}N$, except for $\delta^{13}C$ in the chironomid diet, where liver (half life (HL) = 31 d) and blood (HL = 29 d) had similar turnover rates. For the sculpin diet, white muscle tissue exhibited the slowest turnover rates of $\delta^{13}C$ (HL = 61 d), while blood exhibited the slowest turnover rate of $\delta^{15}N$ (HL = 52 d). Relative to the total isotopic change ($k + m$), the Hesslein et al. (1993) model indicated that turnover rates were metabolically dominated and represented 82-93% of the turnover, with the exception of $\delta^{13}C$ of blood in rainbow trout fed the chironomid diet (33%). Inferences of $\delta^{13}C$ in blood for the chironomid diet were limited

due to poor fit with the model and large 95% confidence intervals derived for metabolic turnover constant (-0.00685 and 0.10550 d^{-1}).

Using the Hesslien et al. (1993) model there was a strong relationship between the predicted isotope change and the observed isotope change in liver for both chironomid (r^2 = 0.95 for $\delta^{13}C$ and r^2 = 0.93 for $\delta^{15}N$) and sculpin (r^2 = 0.97 for $\delta^{13}C$ and r^2 = 0.98 for $\delta^{15}N$) diets (Fig. 3). The relationship between predicted δ tissue values from model and measured δ tissue values varied among tissues and diets for $\delta^{13}C$ and $\delta^{15}N$. Liver had the best fit to the measured data for both chironomid (r^2 = 0.95 for $\delta^{13}C$ and r^2 = 0.93 for $\delta^{15}N$) and sculpin (r^2 = 0.97 for $\delta^{13}C$ and r^2 = 0.98 for $\delta^{15}N$) diets. For all tissues the sculpin diet was a better fit (i.e. higher r^2) than the chironomid diet for the model. White muscle tissue exhibited slightly weaker fit to the data (r^2 = 0.85 for $\delta^{13}C$ and r^2 = 0.76 for $\delta^{15}N$) when compared to liver and blood. The $\delta^{13}C$ of blood from the chironomid diet also had a slightly weaker fit (r^2 = 0.81). For $\delta^{13}C$ and $\delta^{15}N$ the linear relationship was positive and negative, respectively.

Fractionation values ($\Delta\delta^{15}N$ and $\Delta\delta^{13}C$) differed by tissue and diet (Fig. 4). The $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ values of fish fed the initial hatchery diet (day 0) were enriched and differed by tissue. For $\Delta\delta^{15}N$, white muscle tissue was the most enriched (3.8‰; 95% CI 3.3-4.3), followed by blood (2.9‰; 95% CI 2.4-3.4) and liver (2.5‰; 95% CI 1.9-3.1) when compared to the hatchery diet. The $\Delta\delta^{13}C$ of liver was slightly more enriched (1.9‰; 95% CI 1.7-2.1) than white muscle tissue (1.7‰; 95% CI 1.4-2.0) and blood (1.5‰; 95% CI 1.3-1.7). Differences between tissue fractionation rates among diet types were not significant for blood and white muscle tissues because of the large confidence intervals. Among the different diets, the sculpin diet liver tissue fractionation values

were the highest for $\delta^{13}C$ (3.7‰; 95% CI 2.9-4.4) and lowest for $\delta^{15}N$ (1.1‰; 95% CI 0.6-1.7).

Assimilation efficiency

Energetic values of chironomids used in the experiments averaged 21.2 kJ g^{-1} DW (SE ± 359.5). Caloric energy egested in feces was slightly higher at the 25% ration level, but was not significantly different between ration levels (ANCOVA, $F_{1,7} = 3.638$, $P = 0.098$) (Table 2). Caloric energy egested in ammonia and urea were significantly different between the ration levels (ANCOVA, $F_{1,7} = 14.506$, $P = 0.007$), with a higher amount at the 25% ration level. Assimilation efficiency averaged 55.8% (SE ± 0.90) and 64.5% (SE ± 1.98) at the 10% and 25% ration level, respectively, and were lower than ASE reported by Elliott (1976) (Table 3). Percent of energy egested in feces averaged 14.6% (SE ± 1.61) at 10% ration level and were higher than Elliott (1976), whereas at the 25% ration levels energy intake averaged 9.7% (SE ± 0.79) and were lower than Elliott (1976). Ammonia and urea excretion percentages were an order of magnitude higher than those reported by Elliott (1976) and averaged 29.6% (SE ± 2.52) and 25.8% (SE ± 2.06) at 10% and 25% ration level, respectively.

Absorption efficiency was also higher at a higher ration level. At the 10% and 25% ration levels values averaged 82.9% (SE ± 0.65) and 88.5% (SE ± 0.91), correspondingly. Assimilation efficiency of feces egested increased with a decreasing level of energy intake. However, absorption efficiency decreased with an increase in the amount of chironomids (DW g) consumed.

Discussion

Stable isotope analysis

In this study, we examined effects of prey and tissue type on $\delta^{13}C$ and $\delta^{15}N$ fractionation and tissue turnover rates in rainbow trout fed an artificial diet (hatchery pellets) and two natural diets (sculpin and chironomids). The turnover rates of $\delta^{13}C$ and $\delta^{15}N$ in rainbow trout differed among liver, blood, and white muscle tissue. Tissues hypothesized to be more metabolically active changed most rapidly (Buchheister and Latour 2010; Hobson and Clark 1993; Tieszen et al. 1983). Liver had the fastest turnover times and greatest potential to indicate a recent dietary shift in $\delta^{15}N$ and $\delta^{13}C$ (T_{95} = 4-6 months), followed by blood (T_{95} = 4-7 months) and then white muscle tissue (T_{95} = 7-9 months), which may take twice as long to reach equilibrium with a new diet compared to liver. The dietary temporal scale of interest may dictate tissue selection and further highlights the potential of using multiple tissues to assess dietary shifts over different time scales. Tissues, such as liver and mucous, may be appropriate in reflecting more recently assimilated diets (Church et al. 2009; Hesslein et al. 1993), whereas blood, muscle, and bone may be more appropriate for reflecting longer-term assimilated diets (MacNeil et al. 2006; Sholtodouglas et al. 1991). Also, based on the turnover rates we observed, many food web studies using stable isotope analysis are likely to violate the assumption that $\delta^{15}N$ and $\delta^{13}C$ values of white muscle tissue, and to a lesser extent blood and liver, are in equilibrium with a given diet (Hesslein et al. 1993; MacAvoy et al. 2001; MacNeil et al. 2006).

In addition to the consideration of turnover rates in selecting a tissue, analytical accuracy of a tissue needs to be considered (Suzuki et al. 2005). For example, Pinnegar and Polunin (1999) suggested using white muscle tissue because $\delta^{13}C$ and $\delta^{15}N$ are less variable than in the other tissues (e.g. red muscle, liver, and heart) and contain lesser amounts of lipids and inorganic carbonates. Lipids are depleted in $\delta^{13}C$ and consequently, a tissue that contains high lipid content contains a lower $\delta^{13}C$ value than tissue with low lipid content (DeNiro and Epstein 1977; DeNiro and Epstein 1978). Although liver may indicate a more recent dietary shift, liver also contains high lipids and thus a more depleted $\delta^{13}C$. Lipid extraction may cause fractionation of $\delta^{15}N$ (Pinnegar and Polunin 1999). Therefore, some researchers have opted to use tissues with lower lipid levels. However, the development of mathematical corrections for lipids may circumvent some of the problems typically associated with using livers (Post et al. 2007). Researchers should also consider whether to use lethal or non-lethal methods when selecting tissues to use for the species or population of interest. Liver and muscle typically require the fish to be sacrificed in order to sample the tissue. Several recent studies have suggested tissues such as scales and fins are non-lethal alternatives that can be used for SIA (Blanco et al. 2009; Kelly et al. 2006; Sanderson et al. 2009). Based on the results in this study, blood may also be a viable, non-lethal method for tracking longer-term assimilated diets (Hobson and Clark 1993).

Fractionation values of $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ exhibited inter-tissue variability. Such variations may lead to misinterpretation of the trophic level and primary carbon source estimates (Vander Zanden and Rasmussen 1999). The commonly applied fractionation values of $\Delta\delta^{13}C$ of 0–1‰ (DeNiro and Epstein 1978) were generally much lower than the

values we observed suggesting a value of 1.5-2‰ might be more appropriate for fish white muscle, blood, and liver (Barnes et al. 2007; Pinnegar and Polunin 1999). The $\Delta\delta^{15}N$ in white muscle tissue was consistently higher (3.8‰) than the typically reported value of 3.4‰ (Minagawa and Wada 1984). Consequently, an assumed fractionation of 3.4‰ $\Delta\delta^{15}N$ in muscle tissue may lead to overestimates in the trophic level. In contrast, blood (2.9‰) and liver (2.5‰) values were lower than the typically reported value of 3.4‰, which may underestimate the trophic level. Additionally, the commonly applied fractionation value of 1.0‰ $\Delta\delta^{13}C$ may have resulted in overestimation in primary carbon sources.

Similar to our study, Pinnegar and Polunin (1999) estimated fractionation values for juvenile rainbow trout (20 g) fed hatchery pellets of fish and prawn meal ($\delta^{13}C$ ~-19‰ and $\delta^{15}N$ ~9‰). These isotopic values were similar to the hatchery pellets used in our study ($\delta^{13}C$ -21.8‰ and $\delta^{15}N$ 7.2‰). In untreated white muscle tissue, Pinnegar and Polunin (1999) observed fractionation values of 2.54‰ for $\delta^{15}N$ and 1.85‰ for $\delta^{13}C$. We obtained similar $\Delta\delta^{13}C$ (1.74‰), but $\Delta\delta^{15}N$ was substantially higher (3.83‰) for the same species fed a similar diet. However, isotopic fractionation values of treated liver ($\Delta\delta^{15}N$ ~2.25‰ and $\Delta\delta^{13}C$ ~1.5‰) from Pinnegar and Polunin (1999) were similar to the fractionation values we obtained for liver isotopes after mathematically correcting for lipids ($\Delta\delta^{15}N$ 2.54‰ and $\Delta\delta^{13}C$ 1.94‰). Fractionation rate differences in tissues and among consumer species have been observed previously (DeNiro and Epstein 1978; Minagawa and Wada 1984; Tieszen et al. 1983), but differences in fractionation values in the same species with a similar diet have not yet been established. The difference in the $\Delta\delta^{15}N$ between our study and Pinnegar and Polunin (1999) could be due to food type

(Vander Zanden and Rasmussen 2001), isotopic composition and quality of the diets (McCutchan et al. 2003), differing assimilation efficiency (Guelinckx et al. 2007), or food rations and temperature (Barnes et al. 2007). Diets and isotopic composition were very similar between the studies and therefore it is likely that differences in assimilation efficiencies, temperature, and/or ration levels contributed to $\Delta\delta^{15}N$ differences. Pinnegar and Polunin (1999) reported a range of water temperatures (9.5-16 °C) over which the fish were reared, whereas temperature remained relatively constant throughout the duration of our experiment (15.15 °C, SE $\pm$ 0.003) and may account for some of the differences. In this study, we applied low ration levels (*P*-values 0.14 to 0.30) to mimic typical feeding conditions experienced by rainbow trout in tailwaters (Weiland and Hayward 1997). Ration levels were not reported in Pinnegar and Polunin (1999) and may be a source of differences between the studies.

Despite the observed higher growth rates in fish fed the chironomid diet (k = 0.00232 d^{-1}) compared to fish fed the sculpin diet (k = 0.00207 d^{-1}), fish fed the sculpin diet appeared to incorporate isotopes faster. This could be the result of a higher assimilation of the dietary components and/or differential isotopic routing (Gannes et al. 1997).

Metabolic turnover, rather than growth, was the dominant process and accounted for 82–93% of the isotopic changes we observed. Typically, endotherms have higher metabolic turnover rates than ectotherms (e.g. fish) (Arneson et al. 2006; Hobson and Clark 1992; MacAvoy et al. 2006; Tieszen et al. 1983). Most studies evaluating diet-switching in fish reported the majority of turnover is growth and that growth turnover generally explained 65-90% of the variation in turnover rates of $\delta^{13}C$ and $\delta^{15}N$ in fish

(Harvey et al. 2002; Herzka and Holt 2000; Hesslein et al. 1993; MacAvoy et al. 2001; MacNeil et al. 2006; Maruyama et al. 2001; Vander Zanden et al. 1998). However, the previous studies cited on isotopic changes in fish muscle were conducted with immature, rapid-growing fish. The relative contribution of metabolic turnover to isotopic changes might be higher in the case of adults or moderate to slow-growing fish (Guelinckx et al. 2007; Suzuki et al. 2005). Sakano et al. (2005) found that for sockeye salmon, *O. nerka*, the extent of metabolic contribution became increasingly more significant with age as growth rates decreased. In this study, we used adult rainbow trout (>225 mm TL) rather than faster growing juvenile fish. We also manipulated ration level to constrain growth rates (100 g/year) to those observed in the field and imitated low feeding ration levels that typically occur in tailwaters.

Only a few studies on aquatic species observed high metabolic turnover. Kaufman et al. (2008) found high metabolic turnover in an Arctic amphipod, *Onisimus litoralis*, with metabolic processes accounting for 67-89% of the turnover. Logan et al. (2006) found that in a small fish species, mummichog, *Fundulus heteroclitus*, the majority of the observed isotopic changes were the result of metabolic processes and suggested the higher metabolic turnover might have resulted from using higher water temperatures in the experiments (18 °C) than those experienced by the species in natural environments. Water temperature during our study averaged 15.15 °C (SE $\pm$ 0.003) and was similar to those experienced in normal tailwater conditions. Temperature profiles in Norfork C-R area during 2006 averaged 11.6 °C (SE $\pm$ 0.003) and ranged from 5.4 to 18.3 °C. Temperatures were near 15 °C from approximately June to December. Thus, there is little difference between the temperatures experienced by rainbow trout in the

laboratory and field for summer and fall seasons. Reported lethal and optimal growth temperatures for rainbow trout are approximately 27 °C and 17 °C, respectively (Hokanson et al. 1977; Wurtsbaugh and Davis 1977); thus temperatures of the experiments were slightly below those optimal for growth rate. Based on these results, higher metabolic turnover may not necessarily be explained by temperature effects. In tissues of slow growing adult fish, metabolic turnover is likely to be a significant, but overlooked source of isotopic changes of $\delta^{13}C$ and $\delta^{15}N$.

Assimilation efficiency

Energy losses (feces and ammonia) for rainbow trout fed chironomids ranged from 28-45% which is higher than the range (25-30%) observed by Elliott (1976) for brown trout and among the highest reported in the literature. Dupreez and Cockroft (1988) obtained a lower value of food energy lost (12%) for *Pomadasys commersonni* feeding on surf clams. Cui and Liu (1990) examined energy losses among six fish species, *Cyprinus carpio, Carassius auratus, Pseudorasbora parva, P. fulvidraco, Oreochromis mossambicus*, and *Macropodus chinensis*, and also found a lower range of values from 11-17%. Assimilation efficiencies are not affected by fish size (Dupreez and Cockroft 1988; Elliott 1976). However, temperature and ration size are thought to influence assimilation efficiencies (Elliott 1976; Solomon and Brafield 1972). Brocksen and Bugge (1974) found that assimilation efficiency in rainbow trout decreased from a high of 85% at 20 °C to 72% at 5 °C. Although temperature effects were not examined in the present study, the amount of energy egested in ammonia differed by ration level. Energy

egested in ammonia has been observed to increase with increased ration levels (Cui and Liu 1990).

We found energy egested in ammonia was twice as high as those observed in Elliott (1976) with reported values of 30 and 26% for 10 and 25% ration levels, respectively. Winberg (1956) proposed that 3-5% of energy intake was lost in excretory products and Elliott (1976) reported excretory values of 12%. Differences observed in the amount of energy egested in ammonia between the two studies may be the result of differences in methods used. Elliott (1976) determined the concentration of ammonia-nitrogen using the indophenols method whereas we used a Shimadzu TOC-V_{CSH} coupled to a TNM-1 chemiluminescent detector. We converted the amount of energy egested in ammonia using the values developed by Elliott (1976) for ammonia-nitrogen (24.85 J mg^{-1}). If ammonia values we obtained are correct then assimilation efficiency values "borrowed" from Elliott (1976) for bioenergetics models and stable isotope mixing models may be overestimated. Typically, egestion is often overlooked and is rarely considered of importance in bioenergetics modeling (Ney 1993). Bioenergetics models are deemed to be rather insensitive to percent changes in egestion parameters (Adams and Breck 1990; Kitchell et al. 1977). As a result most bioenergetics studies "borrow" the parameters from Elliott (1976) developed for brown trout (Ney 1993). Bajer (2004) suggested that inaccuracies due to errors in calculating *F* and *U* in bioenergetics models may not always be as insignificant as has typically been suggested.

For stable isotope mixing models, recently developed computer programs to estimate isotopic sources, such as SISUS (Erhardt 2008), have begun to incorporate assimilation efficiency. Since mixing models are used frequently in assessing dietary

source contributions, determining the effect of uncertainty in assimilation efficiencies on the estimation of source proportions is an area that needs further study. In the future, studies that use assimilation efficiencies in mixing models should be accompanied by discussion about how variation in assimilation efficiency may contribute to uncertainty in the calculation of source proportions. Thus, in an effort to reduce uncertainty in bioenergetics and mixing models more laboratory studies need to be conducted on species and prey specific assimilation efficiency rates.

For the assimilation efficiency experiments, we used the "single-meal procedure" which was similar to Elliott (1976). We found food needed to be withheld for five days prior to experiments to ensure complete gut evacuation at 17 °C. In contrast, Elliot (1976) only withheld food for three days prior to the experiment (Elliot 1976). The maximum rate of energy intake (i.e. assimilation efficiency) may differ at high and low food levels. At high rations a fish may be able to assimilate energy at a faster daily rate by digesting only the most-digestible portion of the food and expelling a large amount of the food through the gut at a high rate, resulting in lower total assimilation efficiency. In contrast, at low rations a fish may extract more energy from the small amount of food, resulting in higher total assimilation efficiency. Gut motility may also differ with changes in meal size, as ingested food may move through the gastrointestinal tract at a faster rate when the meal size is large compared to when the meal size is smaller. Fish that have been deprived of food for a few days may treat "single-meal procedure" as a low ration situation, whereby slowing gut motility to extract as much energy as possible, resulting in a decreased fraction of products excreted and egested which may result in a misrepresentation of the actual waste losses. Thus, the "single-meal procedure" used to

estimate assimilation efficiency may warrant further examination (James Breck, personal communication). A different approach to examine assimilation efficiency may be to feed fish at constant temperature and ration for several days and measure the average daily fecal production and nitrogen excretion over several days. The results from the "continuous-meal procedure" could be compared to the "single-meal procedure" to determine if the "single-meal procedure" maximizes assimilation efficiency.

Conclusion

The use of SIA to assess past dietary patterns has become increasingly common in ecological studies. However, understanding and testing assumptions of this approach are crucial. Our study should aid researchers by presenting fractionation and tissue turnover rates and assist in selecting appropriate tissues in rainbow trout. Additionally, we observed some of the highest reported excretion rate estimates in the literature for a species, which highlights the lack of assimilation efficiency laboratory-based evaluations. As Gannes et al. (1997) and Ney (1993) recognized over a decade ago, there is still a need for more laboratory studies to examine underlying assumptions and errors in stable isotope analysis (e.g. isotopic routing, trophic discrimination factors) and bioenergetics modeling (e.g. waste losses). It is crucial that future models incorporate species-specific assimilation efficiencies and tissue turnover and fractionation rates to enable drawing strong inferences and improve accuracy of model predictions.

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Table 1. Parameter estimates from the time-based model. Parameter estimate *k* is the specific growth rate (day^{-1}); *m* is the metabolic turnover constant (day^{-1}); T_{50} and T_{95} are the time needed to reach 50% and 95% turnover (day), respectively; P_k and P_m are the proportion of turnover attributed to growth and metabolism, respectively; $\delta_{equilibrium}$ is the estimated equilibrium isotopic value (‰) with associated 95% CI.

Isotope	Diet	Tissue	*k* (d^{-1})	95% CI	*m* (d^{-1})	95% CI	T_{50} (d)	T_{95} (d)	P_k	P_m	$\delta_{equilibrium}$	95% CI
$\delta^{13}C$	Chironomids	Blood	0.00232	0.00120 0.00345	0.02186	0.00937 0.04010	29	124	0.10	0.90	-16.83	-17.60 -15.16
		Liver			0.02030	0.01405 0.02791	31	132	0.10	0.90	-13.55	-14.33 -12.42
		Muscle			--	--	--	--	--	--	--	--
	Sculpin	Blood	0.00207	0.00144 0.00270	0.01231	0.00537 0.05088	48	208	0.14	0.86	-27.45	-31.42 -25.83
		Liver			0.02850	0.02293 0.03514	26	114	0.07	0.93	-28.73	-29.53 -28.06
		Muscle			0.00921	0.00042 0.02056	61	266	0.18	0.82	-24.30	-34.43 -22.89
$\delta^{15}N$	Chironomids	Blood	0.00232	0.00120 0.00345	0.00115	-0.00685 0.10550	200	863	0.67	0.33	16.25	16.00 --
		Liver			0.01523	0.00892 0.02274	39	171	0.13	0.87	12.94	12.39 13.90
		Muscle			--	--	--	--	--	--	--	--
	Sculpin	Blood	0.00207	0.00144 0.00270	0.01138	0.00049 0.01918	52	223	0.15	0.85	14.84	13.74 17.57
		Liver			0.02432	0.01965 0.02688	26	114	0.08	0.92	16.46	15.94 17.10
		Muscle			0.01267	0.00058 0.03109	47	203	0.14	0.86	13.44	12.63 20.86

Table 2. Dry weights (g) of food ingested (W_i) and egested (W_e), estimated absorption efficiencies (ABE, %), amount of energy (J) ingested (E_i) and egested in feces (E_f) and ammonia (E_a), and assimilation efficiencies (ASE, %) for rainbow trout fed at different ration levels (%).

Feeding ration (%)	Total length (mm)	Weight (g)	W_i (g)	W_e (g)	ABE (%)	E_i (J)	E_f (J)	E_a (J)	ASE (%)
10	295	264.7	0.338	0.060	82.2	6,201	1,006	1,681	56.7
	300	278.1	0.348	0.057	83.5	6,384	830	2,052	54.9
25	260	144.5	0.544	0.078	85.7	9,992	1,216	3,316	54.6
	267	233.8	0.774	0.078	90.0	16,455	1,430	3,608	69.4
	276	193.4	0.678	0.095	86.0	15,666	2,152	2,849	68.1
	279	230.9	0.737	0.113	84.7	13,530	1,328	2,527	71.5
	282	206.3	0.631	0.068	89.3	13,413	1,314	4,062	59.9
	290	209.4	0.706	0.063	91.1	14,833	1,130	4,076	64.9
	318	290.3	0.899	0.081	91.0	18,879	1,332	6,002	61.2
	323	281.3	0.881	0.089	89.9	18,497	1,682	4,565	66.2

Table 3. Comparison of % energy egested as feces (E_f) and ammonia (E_a) and assimilation efficiencies (ASE) from this study of rainbow trout fed chironomids to Elliott's (1976) study of brown trout fed *Gammarus* sp. at the same ration levels and temperature (17 °C).

Study	Feeding ration (%)	E_f (%)		E_a (%)		ASE (%)	
		Average	SE	Average	SE	Average	SE
Elliott (1976)	10	11.5	(0.49)	12.4	(0.82)	76.1	(0.65)
	25	13.5	(0.51)	12.2	--	74.3	(0.51)
This study	10	14.6	(1.61)	29.6	(2.52)	55.8	(0.91)
	25	9.7	(0.79)	25.8	(2.06)	64.5	(1.97)

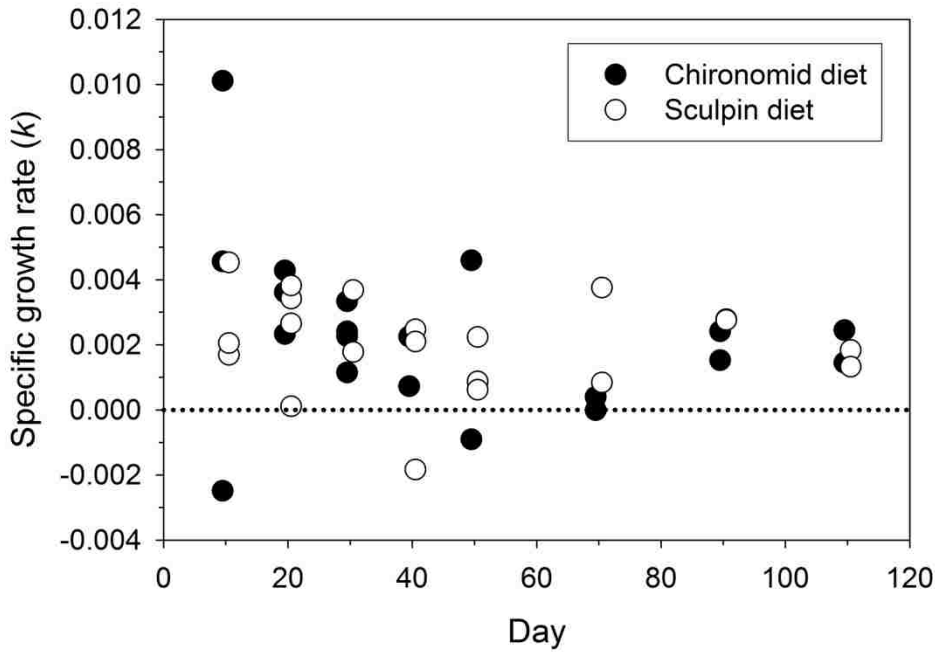

Figure 1. Specific growth rates (*k*) of rainbow trout fed chironomids or sculpin. Dots represent individuals at the time of removal from the experimental tanks.

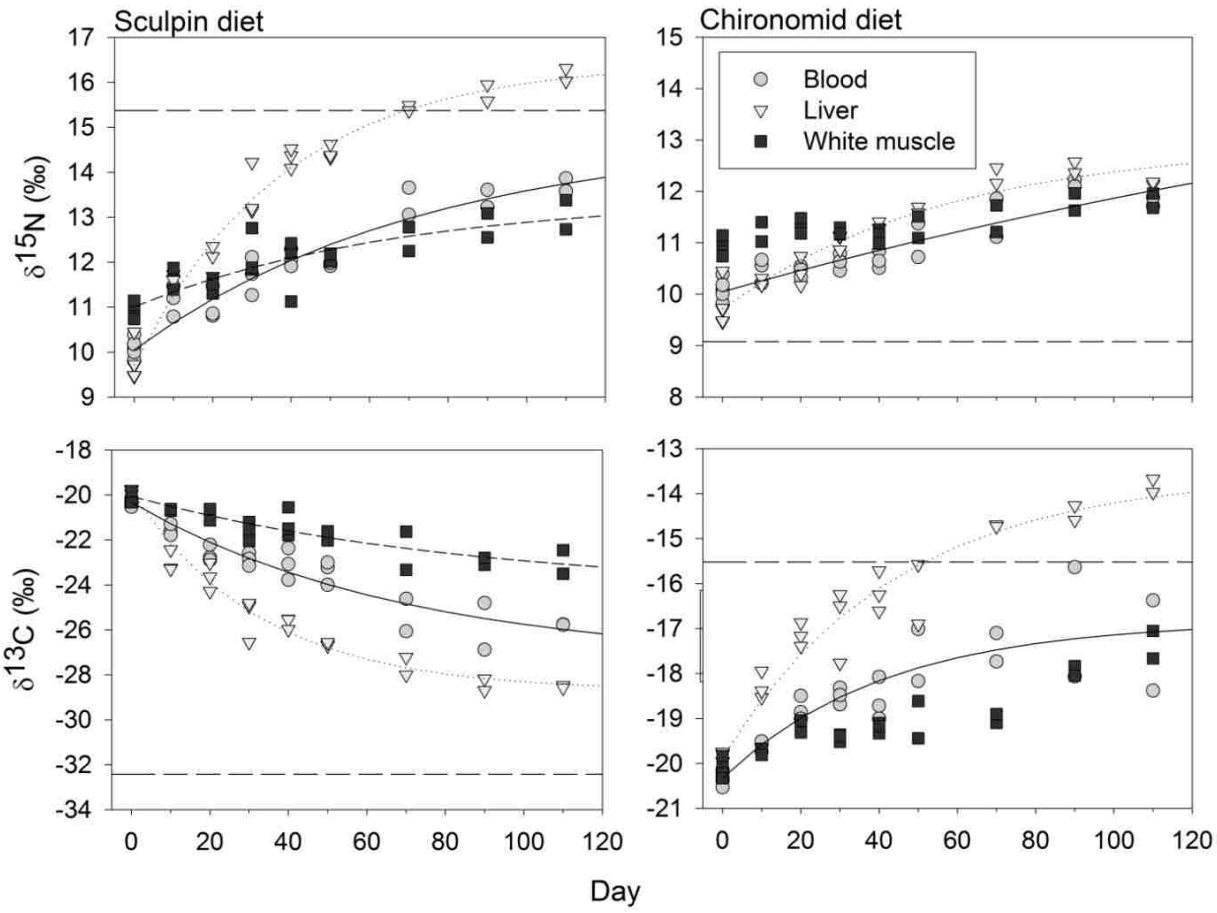

Figure 2. Tissue-specific $\delta^{13}C$ and $\delta^{15}N$ as a function of time (day) in rainbow trout on a chironomid or sculpin diet. Time based model fits are represented for blood (solid line), liver (dotted line), and white muscle (dashed line). The horizontal dashed line is the isotopic value of the diet type.

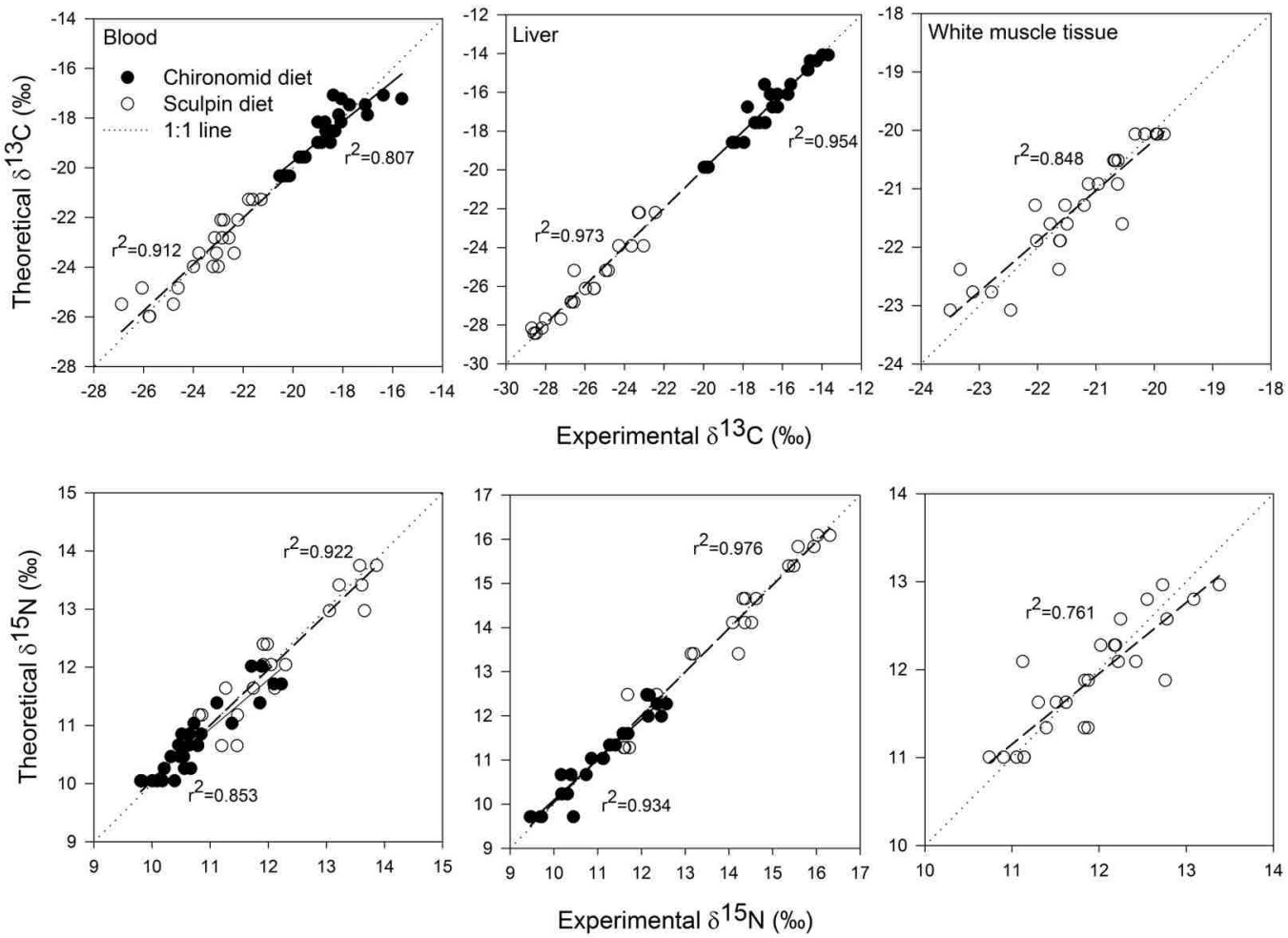

Figure 3. Comparison between observed and predicted δ tissue values derived from the time based model of Hesslein et al. 1993. Linear regression fits are represented for chironomid (solid line) and sculpin (dashed line) diet.

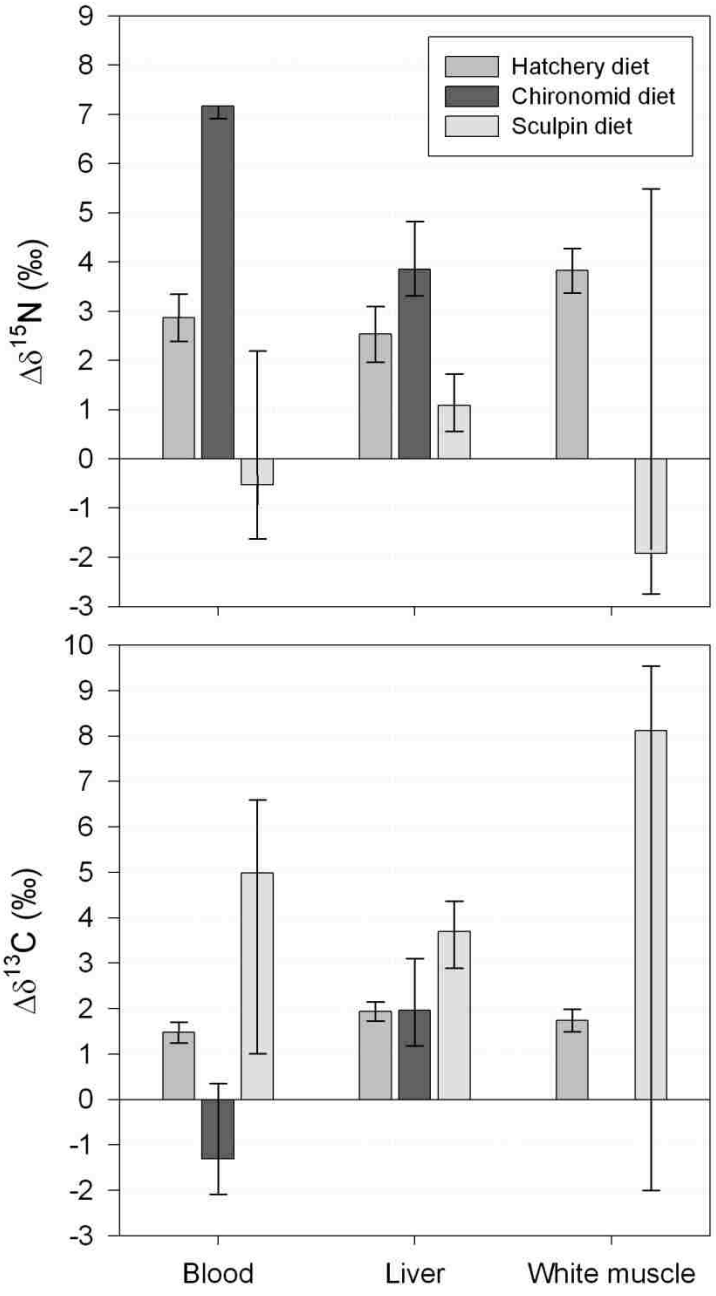

Figure 4. Fractionation values (Δ) based on $\delta_{equilibrium}$ values for sculpin and chironomid diets and their associated 95% confidence intervals for each tissue between the different diets (hatchery, chironomids, sculpin). An upper error was unsuccessfully estimated in blood for fish fed the chironomid diet.

Spatial-temporal foraging patterns of brown and rainbow trout within catch-and-release areas in Arkansas tailwaters using gut content and stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$)

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Abstract – Several special regulation catch-and-release (C-R) areas were implemented in Arkansas tailwaters with the goal of providing increased catch rates of larger brown and rainbow trout. The success of these special regulations areas is partially dependent on forage base that is sufficient to provide adequate growth for trout. We therefore initiated this study to better understand seasonal and ontogenetic shifts in the foraging patterns of brown and rainbow trout within these areas using gut content analysis (GCA) and stable isotope analysis (SIA) of $\delta^{13}C$ and $\delta^{15}N$. Growth rates estimated from mark-recapture were also examined to determine turnover times of $\delta^{13}C$ and $\delta^{15}N$ for SIA diet inferences. We examined 605 brown trout and 768 rainbow trout for GCA and SIA at Bull Shoals, Norfork, and Sylamore C-R areas. High proportions of filamentous algae, *Cladophora*, and a nuisance diatom, *Didymosphenia geminata* were observed in the diets of rainbow trout (15-91%) despite the apparent lack of energetic value from this food source. Simultaneous use of GCA and SIA of $\delta^{15}N$ proved suitable in detecting ontogenetic shifts of brown trout towards piscivory with increases in size. Both GCA and SIA of $\delta^{15}N$ indicated brown trout exhibited an ontogenetic shift from macroinvertebrates towards a more energetically profitable foraging strategy of piscivory (a greater incorporation of fish in the diets). SIA revealed distinct signatures in smaller rainbow trout that were artificially enriched with $\delta^{13}C$ and depleted in $\delta^{15}N$. SIA mixing model results for small rainbow trout indicated that they contained isotopic "memory" from hatchery food (Range 42-100%). These distinct hatchery signatures in brown trout $\delta^{13}C$ and $\delta^{15}N$ provided a suitable method to distinguish between stocked and wild fish during the winter and spring in Bull Shoals tailwater. Estimated complete turnover (95%) of white muscle tissue using growth rates from mark-recapture was estimated to require six to eleven months in the C-R areas depending on isotope ($\delta^{13}C$ and $\delta^{15}N$), species and size class. Generally, SIA mixing model results provided broad ranges of source

contributions rather than more informative narrow ranges of solutions limiting the conclusions regarding food source contributions. Our findings of rainbow trout diets high in of *Cladophora* and *D. geminata* consumption and the trout with poor growth rates suggest the C-R areas in Ozark tailwaters may often be food-limited for large rainbow trout.

Key words: food limitation, 95% turnover times, trophic position, piscivory, mixing model

Introduction

In the southeastern United States rainbow trout, *Oncorhynchus mykiss*, and brown trout, *Salmo trutta*, fisheries are highly desirable and economically important in regulated rivers downstream of reservoir dams (Axon 1975). Tailwater fisheries often experience high fishing pressure and rely heavily on stocking to develop or augment a fishery (Heidinger 1993; Weiland and Hayward 1997). In areas that receive high fishing pressure catch-and-release (C-R) regulations have been found effective at maintaining increased numbers of large trout and higher catch rates (Anderson and Nehring 1984; Carline et al. 1991; Engstrom-Heg 1981). However, the extent to which C-R regulations are effective is dependent upon an adequate forage base that is sufficient to support the growth of released fish (Muoneke and Childress 1994).

Several special regulation C-R areas were implemented in Arkansas tailwaters in 1995 with the primary goal of providing increased catch rates of larger sized trout. Growth and production of brown and rainbow trout in C-R areas depend in part on the quantity and quality of prey availability. However, tailwaters may be food-limited, particularly for larger salmonids, and increasing the density and size of trout in these C-R areas may be paralleled by food base degradation, reduced fish growth, and declining average fish size (Filbert and Hawkins 1995;

McKinney and Speas 2001; Weiland and Hayward 1997). If prey availability is limited, density dependent competition among different trout species may reduce growth rates and overall fish size. Also, C-R areas that maintain inadequate prey availability may impact the residence times of the trout as they move into areas with more abundant prey. Thus, an initial step towards understanding whether C-R areas are capable of supporting higher densities of trout is to evaluate both the quantity and quality of their diets in the framework of spatial, temporal, and ontogenetic variability.

The standard approach for evaluating spatial and temporal feeding habits and ontogenetic shifts has always been gut contents analysis (GCA) (Bowen et al. 1996; Hyslop 1980). However, GCA only reflects individual short-term feeding by providing a "snapshot" of diet that varies temporally (Woodward and Hildrew 2002). Prey found in GCA is often masticated or digested beyond recognition. Also, softer bodied components that digest rapidly may be significantly underestimated in the diets (Grey 2006; Hyslop 1980). GCA is often hindered by difficulties acquiring the large sample sizes needed to describe temporal feeding patterns across a range of fish sizes (Bowen 1996). An alternative, and increasingly popular, complementary approach that overcomes some of the problems of GCA is the use of stable isotope analysis (SIA). This approach provides a long-term integrated measure of assimilation. Tailwaters may be ideal for SIA given the relatively simple food webs compared to unregulated systems (Johnson and Harp 2005; Shaver et al. 1997).

Although SIA has some advantages over GCA, especially regarding long-term assimilated diet, SIA lacks the taxonomic resolution that GCA provides. Also, SIA may not reflect short-term feeding patterns due to differing isotopic turnover rates (Johannsson et al. 2001; Persson and Hansson 1999). Isotopic turnover rate is the isotopic change due to growth

and metabolic tissue replacement associated with a change in diet (Hesslein et al. 1993) and is known to vary markedly among tissues (Hobson and Clark 1992; MacAvoy et al. 2001; Tieszen et al. 1983). Tissues with more rapid turnover, such as liver and mucous, typically reflect more recently assimilated diets (Church et al. 2009; Hesslein et al. 1993), whereas blood, muscle, and bone with slower turnover may be more appropriate for reflecting longer-term assimilated diets (MacNeil et al. 2006; Sholtodouglas et al. 1991). In fish populations exhibiting slow growth the integrated dietary isotope ratios may be over a period of a year (Hesslein et al. 1993), compared to days in populations exhibiting fast growth rates (Herzka and Holt 2000). Thus, examining turnover rates of the fish is critical in determining the appropriate time frame for which dietary isotopes have been integrated, particularly in the context of tailwaters where reduced growth rates may exist (McKinney and Speas 2001; Weiland and Hayward 1997). Despite the importance of understanding temporal dietary integration, the field turnover rates of tissues of fish in wild natural systems are often lacking in SIA studies due to inadequate growth rate estimates and/or laboratory or field derived species-specific metabolic tissue replacement rates.

In an effort to better understand whether these C-R areas are capable of supporting restrictive special regulations, we assessed brown and rainbow trout ontogenetic shifts and spatial and temporal feeding habits using GCA and SIA. We also determined the turnover rates of two isotopes, $\delta^{13}C$ and $\delta^{15}N$, by combining laboratory derived metabolic rates with field growth rate estimates (See Chapter 1). More specifically, the primary objectives of this study were to: (*i*) characterize the seasonal variation in diet quantity and quality (e.g. energy) of prey, (ii) examine ontogenetic and trophic position shifts in $\delta^{15}N$ and GCA of brown trout and (*iii*) compare field growth rates of brown and rainbow trout to laboratory derived metabolic turnover rates to estimate $\delta^{13}C$ and $\delta^{15}N$ turnover rates.

Study site

The study was conducted on the Bull Shoals and Norfork tailwaters in the Ozark Mountains of Arkansas. Bull Shoals tailwater, below the Bull Shoals Dam, of the White River is located in Marion and Baxter Counties, Arkansas (36°21'N, 92°34'W) (Figure 1). The White River basin drains approximately 44,683 km^2. Bull Shoals Dam was created in 1952 primarily for the generation of hydroelectric power. Water releases from the dam during this study averaged 50.5 $m^3 \cdot s^{-1}$ (SE$\pm$2.84) and ranged from 1.4 to 230.4 $m^3 \cdot s^{-1}$ (US Army Corps of Engineers, unpublished data). Water temperatures during the study averaged 10.1 °C (SE$\pm$0.01; range 6.5-14.8 °C). Alternating shoal and pool areas characterize this stretch of river. Substrates were mostly gravel, with some bedrock in hydraulically scoured areas to sand and silt in pools. In the addition to filamentous algae, *Cladophora*, found attached to the substrate in the tailwater, a nuisance diatom, *Didymosphenia geminata*, was also present in high abundance and often formed thick, mucilaginous mats covering the substrate. The stream channels are stable with armoring in the upper reaches. Bull Shoals tailwater supports a trout fishery for approximately 164 km downstream from Bull Shoals Dam. Bull Shoals Dam C-R area begins 0.09 km below Bull Shoals Dam and extends downstream 1.5 km and the surface area is approximately 22.0 ha. Sylamore C-R area is located approximately 124 km downstream from Bull Shoals Dam. Sylamore C-R area is 4.1 km long and has a surface area of 60.3 ha. Water temperatures during the study experienced more fluctuation than the other areas and averaged 15.1 °C (SE$\pm$0.04) and ranged between 3.3 to 25.1 °C. Species other than trout in the fish community in the Bull Shoals C-R included Ozark sculpin, *Cottus hypselurus*, northern hog sucker, *Hypentelium nigricans*, river redhorse, *Moxostoma carinatum*, and occasionally entrained adult walleye, *Stizostedion*

vitreum. In contrast, the Sylamore C-R fish community was more diverse with greenside and rainbow darters, *Etheostoma blennioide*s and *E. caeruleum*, longear sunfish, *Lepomis megalotis*, common carp, *Cyprinus carpio*, striped and duskystrip shiner, *Notropis chrysocephanlus* and *N. pilsbryi*, northern hogsucker, river redhorse, smallmouth bass, *Micropterus dolomieu*, and Ozark sculpin.

Norfork tailwater was created in 1944 on the North Fork River, a tributary of the White River, with the completion of the Norfork Dam. Norfork tailwater is located in Baxter County, Arkansas (36°14'N, 92°14'W). The watershed of North Fork River has a drainage area of 4,683 km^2 at the Norfork Dam. Water releases from the dam averaged 28.5 $m^3 \cdot s^{-1}$ (SE$\pm$1.12) and ranged from 1.7 to 122.0 $m^3 \cdot s^{-1}$. Water temperatures during this study averaged 11.6 °C (SE$\pm$0.02; range 5.4-18.3 °C). Substrates ranged from sand to bedrock with coarse gravel being the predominant material with filamentous algae, *Cladophora*, often being attached. Norfork tailwater supports trout for approximately 7 km, from the Norfork Dam until the confluence of the tailwater with the White River. Norfork C-R area is located approximately 4 km downstream of the dam. Norfork C-R area was 1.8 km long with a surface area of 11.2 ha surface area. Species other than trout in the fish community in the Norfork C-R included Ozark sculpin, northern hog sucker, and river redhorse.

Catch-and-release trout fishing regulations were implemented by the Arkansas Game and Fish Commission (AGFC) on Jan 1, 1995 at the Bull Shoals, Norfork, and Sylamore catch-and-release (C-R) areas. All trout caught in C-R areas must be released immediately and tackle is restricted to the use of only one artificial lures with single, barbless hooking points. No trout stockings occurred in the C-R areas. However, nearby areas upriver and downriver of the C-R areas were stocked as a put-and-take fishery for rainbow trout (~279 mm total length; TL) and a

put-grow-and-take fishery for brown trout (~150 mm TL). Rainbow trout were stocked year round, whereas brown trout were only stocked in the fall and winter.

Methods

Fish Sampling

Sampling was conducted on a seasonal basis at Bull Shoals and Norfork C-R areas from May 2005 to June 2006. Sylamore C-R area was sampled seasonally from October 2005 to October 2006; however no sampling was conducted in summer of 2006 at Sylamore due to high water releases from Bull Shoals and Norfork dams. Seasons were spring (April-June), summer (July-September), fall (October-December), and winter (January-March). On each sampling date, the trout were collected at night using two crews, each consisting of an electrofishing boat and processing boat. The fiberglass electrofishing boats were equipped with Smith-Root 5.0 GPP electrofishing units and boom-mounted steel cable electrotodes. Standarized GPP unit settings were as follows: mode = DC, voltage = high range (50-1,000 volts), pulses per second = 30, percent of ≈ 30, amps ≈ 2.0-2.5. All sampling was conducted on two consecutive nights at low flows during periods of no generation. Boat electrofishing started at the upstream end of the C-R area and proceeded downstream to the lower end of C-R area. Two electrofishing boats were used with one to two dipnetters per boat. At the end of a sampling run, all trout collected were transferred from live-wells on the electrofishing boats to live-wells on the processing boat. On the first night of sampling, all brown and rainbow trout were anesthetized with a clove oil mixture (1:10 clove oil:ethanol) at 10 mL solution/20 L water (Prince and Powell 2000), measured for TL, and weighed to the nearest 0.1 g wet weight. Fish were then tagged below the dorsal fin with individually numbered yellow Hallprint TBA t-bar anchor tags (2" total length, 1-

1/4" color) and released. On the second night brown and rainbow trout collected were measured, weighed, checked for tags, and released. All trout tagged on the first night were released. A subsample of untagged trout of each species required for GCA and SIA were euthanized with a concussive blow to the cranium. Stomach contents of these fish were removed in the field and placed in a 10% buffered formalin solution. Trout were then immediately placed on ice and brought back to the laboratory and frozen (-20 °C) for SIA. Two size classes of rainbow trout and three sizes of brown trout were chosen for GCA and SIA based on size-frequency data (Stan Todd, AGFC, unpublished data). Attempts were made to collect 60 brown trout from small (<250 mm TL; n = 20), medium (250-400 mm TL; n = 20), and large (>400 mm TL; n = 20) size classes and 60 rainbow trout from small ($\leq$400 mm TL; n = 40) and large (>400 mm TL; n = 20) size classes at each site per season.

Prey collection

Potential prey sources (e.g. macroinvertebrates, zooplankton, sculpin, algae) were sampled on a seasonal basis in order to compare the $\delta^{13}C$ and $\delta^{15}N$ signatures of trout collected during those seasons with the isotopic signature of their prey and determine the caloric content (i.e. energetic value) of prey in the diets. All habitats were sampled in an effort to collect as many species as possible in the potential food web. Benthic macroinvertebrates were collected with a Hess sampler and immediately picked from the samples while still alive and immediately placed on ice. Zooplankton (Cladocera) samples were collected in a nylon drift net fitted to a PVC tube (mesh 360 μm; length, 1 m; aperture 15 cm). Benthic fish (e.g. sculpins, darters) and crayfish were sampled seasonally using a 1.0 m^2 quadrat sampler with 6-mm mesh by placing the quadrat sampler in riffles and kick-siening within the sampler to dislodge fish and crayfish and wash

them into the attached sampler bag (Peterson and Rabeni 2001). Sculpin were also captured using a backpack electrofisher (Smith Root) and crayfish were collected along the river bottom by visual observations. Filamentous green algae *Cladophora* and the diatom *D. geminata*, present only in Bull Shoals, were collected in the river bed by scraping from the substrates. All prey samples collected in the field were immediately placed on ice and transported to the laboratory and frozen (-20°C).

Gut content analysis

Prior to examination in the laboratory, stomachs were transferred from formalin solution to containers with 95% ethanol. At the time of examination, stomachs were dissected and their gut contents were placed in a Petri dish. Using a dissecting microscope prey items were identified to lowest practical taxon, counted, and measured to the nearest 0.1 mm with an ocular micrometer. Partially digested or broken macroinvertebrates were identified, counted, and measured based on head widths. Ingested fish prey that was still intact were identified and measured for TL. When prey fish were in later stages of digestion they were measured according to either vertebral length (VL; vertebral column was complete) or standard length (SL; fish missing only the caudal fin). We used the relationship between VL or SL for sculpin based on measurements of sculpin found in the stomachs which ranged in TL from 58-101 mm to determine TL from VL (TL = 1.57902[VL]; $r^2 = 0.93$) or SL (TL = 1.11903[SL]; $r^2 = 0.98$). Zooplankton (Cladocerans) were readily digested in most stomachs which made accurate length measurements difficult to obtain. In stomachs with zooplankton intact, they were measured from head to tail and an average length of 2.5 mm TL was obtained ($n = 135$; Range = 2.0-3.2 mm; SE $\pm$ 0.021). In stomachs with zooplankton not intact they were counted in a Ward counting wheel. Counts of zooplankton

were then multiplied by estimated average length from the intact zooplankton to estimate dry mass. Length-dry mass or head-width–dry mass equations from the literature were used to estimate the mass (mg) of each macroinvertebrate and fish (Benke et al. 1999; Dumont et al. 1975; Rogers et al. 1976; Sample et al. 1993; Weiland and Hayward 1997). Algae present in the stomach samples were dried in an oven at 50-60°C for 48-72 h and weighed to obtain dry weights (0.0001 mg). For GCA no distinction was made between *Cladophora* and *D. geminata* found in the trout stomachs at Bull Shoals and were combined together as algae for the analyses. Prey taxa that were consumed infrequently or in low proportions were combined. The following categories were grouped: aquatic invertebrates (e.g. Chaoboridae, Empidadae, Ephydridae, Simuliidae, Tabanidae, larval Coleoptera, larval Ephemeroptera, larval Trichoptera, Mollusca, Nematomorpha, Oligochaeta), other vertebrates (e.g. Amphibia, bigeye shiner, darters, green sunfish, northern hogsucker, rainbow trout, river redhorse, striped shiner), and terrestrial invertebrates (e.g. Coleoptera, Arachnida, Chilopoda, Dermaptera, Diplopoda, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Orthoptera, Thysanoptera).

In instances where certain taxa of macroinvertebrates were ingested in large numbers (i.e., > 125 individuals) a subsampling method was employed to randomly select prey individuals for measuring. All individuals from a taxon were placed in an Imhoff cone and total volume was increased to 1 L with water (Wrona et al. 1982). The subsample was mixed for 2-5 minutes by bubbling air with an air stone connected to the bottom of the cone. Subsamples were then removed using a 50 mL Hensen Stempel pipette and total lengths of the first 75 individuals of a taxon encountered were measured. The total counts of prey ingested were multiplied by the average length of prey measured from the subsample to estimate dry mass for the remaining macroinvertebrates in the sample.

Stomach contents were expressed as a percent weight, which is the total dry weight of each prey item expressed as percentage of the overall weight of the stomach contents of brown or rainbow trout for each season and size class. We calculated %W for each prey taxon or group as follows:

$$W_i = \frac{W_i}{\sum_{i=1}^{Q} W_i}$$

where i is the prey item, W_i is the dry weight of prey type i, and Q is the number of prey types. Only stomachs containing prey items were utilized for calculations and analyses.

Prey energy densities

In the laboratory, all prey samples were rinsed with Millipore water and inspected for any debris. Macroinvertebrates were identified to lowest practical taxon and measured using a dissecting microscope and an ocular micrometer. Sculpin were measured to the nearest TL and crayfish were measured for carapace length (CL). In order to achieve enough sample of macroinvertebrates for bombing, multiple organisms (> 3 individuals) of the same species were pooled to achieve the minimum mass (i.e. 0.2-0.02 g). Prior to bombing, prey samples were unthawed blotted dry and placed in a tared aluminum weigh boat to obtain wet weight (0.0001 mg). Samples were then dried in an oven at 50-60°C for 48-72 h and reweighed to obtain dry weights. After being dried and weighed sculpin and crayfish were homogenized whole using a Wiley Mill (40 mesh) and reground, if necessary, into a fine powder to insure homogeneity within each sample. Aquatic macroinvertebrates were homogenized using a mortar and pestle. Gastropods were extracted from their shells and organisms analyzed whole. After drying and homogenizing, the sample was added to the calorimeter vessel to get a complete firing. Prey

energy density values (cal g^{-1} dry weight) were estimated using a Parr bomb calorimeter (Parr 6200 Calorimeter). Prey energy density values (cal g^{-1} dry weight) were then converted to the appropriate units (J g^{-1} wet weight) and were based on the percent water determinations from weighed organisms. We used the energy value for the season when available. However, when no energy values were available seasonally, energy values were assumed to be constant throughout the year. The energetic values of Cladocera, rainbow trout, *Etheostoma* spp., *Notropis* spp., and terrestrial invertebrates were borrowed from the literature (Bryan et al. 1996; Cummins and Wuycheck 1971; Hanson et al. 1997; Luecke and Brandt 1993; Madon and Culver 1993).

Stable isotope analysis

In the laboratory, a small portion (about 1 cm^3) of white muscle tissue without skin was dissected from frozen trout below the dorsal fin and above the lateral line for SIA (Pinnegar and Poulin 1999) and all prey samples were rinsed with Millipore water, inspected for any debris, and refrozen at -20°C. Macroinvertebrate prey sources were identified to lowest possible taxon, counted, and measured under a dissecting scope with an ocular micrometer to the nearest mm. Fish collected were identified and measured to the nearest total length. Thawed zooplankton samples were hand-picked under a dissecting scope with 25-50 *Daphnia* per sample. Also, under a dissecting scope, *Cladophora* and *D. geminata* were inspected for any attached silt. Hatchery pellets used for trout rearing were obtained from Norfork National Fish Hatchery located in Norfork, Arkansas. Because of the small size of many macroinvertebrates, multiple organisms of the same species were pooled to obtain enough sample to achieve the minimum mass required for reliable analyses (i.e. 0.25 mg). Whole bodies of at least 3 individual macroinvertebrates

were pooled for isotope analysis. Trout tissue and prey samples were then freeze-dried for at least 48 h. Macroinvertebrates, prey fish, crayfish, and gastropoda (removed from their shells) were analyzed whole. Trout white muscle tissue was homogenized into a fine powder using a Wig-L-Bug (DENTSPLY Rinn Digital Wig-L-Bug Mixer/Amalgamator, Model MDS). Prey fish (e.g. sculpin, darters), crayfish and macroinvertebrates homogenized as described in prey energy analysis. Hatchery pellets were homogenized using mortar and pestle. Zooplankton, *Cladophora*, and *D. geminata* were analyzed without homogenization.

Carbon (^{13}C) and nitrogen (^{15}N) stable isotope ratios of trout tissue and prey sources were performed using a Finnigan Delta Plus continuous-flow isotope ratio mass spectrometer an elemental analyzer (Thermo Fisher Scientific Inc., Waltham, MA, U.S.A) at the University of Arkansas, Stable Isotope Laboratory. Samples were weighed to 0.25-0.35 mg in individual 3.5 mm x 5 mm tin capsules. Stable isotope ratios were calculated given using the standard delta notation ($\delta^{13}C$; $\delta^{15}N$) per mil (‰) according to the following formula:

$$\delta I = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where I is the isotope of interest (^{13}C or ^{15}N) and R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio in the sample and the standard. International standards employed were Vienna Pee Dee Belemnite for $^{13}C/^{12}C$ and atmospheric N_2 for $^{15}N/^{14}N$. Analytical precision (standard deviation) estimates calculated from internal standards were 0.08‰ for ^{13}C and 0.10‰ for ^{15}N.

We examined the use of SIA in brown trout tissue in distinguishing wild fish from hatchery fish. Brown trout spawning success and recruitment is known to be variable in the White River system (Pender and Kwak 2002) and we examined water releases from Bull Shoals dam ($m^3 \cdot d^{-1}$) during the study to assess the potential impacts that flow conditions may of had on the recruitment of small brown trout in spring 2005 and winter 2006 (Figure 2).

Growth and turnover times

Specific growth rates, k (d^{-1}), were estimated seasonally using the mark-recapture data for each site, species, and size class using the following growth model:

$$k = \frac{\ln(W_2 / W_1)}{t_2 - t_1}$$

where W_1 is initial weight, W_2 is final weight, t_1 is initial time, and t_2 is final time. Specific growth rates were estimated across four tagging intervals at Bull Shoals and Norfork. At Bull Shoals tagging started in May 2005 and ended in May 2006. At Norfork tagging started in June 2005 and ended in June 2006. At Sylamore specific growth rates were estimated across three tagging intervals and began in October 2005 and ended in October 2006. Fish only collected at the beginning of a seasonal tagging interval (e.g. spring-summer) were used for the specific growth rate estimates.

The estimates of turnover times to 95% (T_{95}) of equilibrium with the new diet were estimated from Tieszen et al. (1983) as follows:

$$T_{\alpha/100} = \frac{\ln(1 - \alpha/100)}{-(m + k)}$$

where m is the metabolic turnover rate constant per day, and k is the specific growth rate constant per day. The parameter m was obtained from a previous laboratory diet-switching experiment with rainbow trout fed sculpin, where m (d^{-1}) was estimated to be 0.00921 for $\delta^{13}C$ (95% CI 0.00042-0.02056) and 0.01267 for $\delta^{15}N$ (95% CI 0.00058-0.03109) (see Chapter 1; Table 1). Specific growth rate (k) was obtained by pooling across season for each C-R area and species.

Stable isotope mixing model

A multi-source stable isotope-mixing model, IsoSource (version 1.3) was used to calculate the feasible ranges of the multiple potential dietary source contributions to consumer diets (Phillips and Gregg 2003). Appropriate diet tissue fractionation values between prey and consumer were selected for the model. Prior to analysis, we applied mean fractionation values of +1.7‰ for $\Delta\delta^{13}C$ and +3.8‰ for $\Delta\delta^{15}N$ obtained from the white muscle tissue of rainbow trout fed hatchery pellets (Chapter 1). We also applied mean fractionation values of +0.8‰ for $\Delta\delta^{13}C$ and +3.4‰ for $\Delta\delta^{15}N$ based on a meta-analysis paper of aquatic systems (Vander Zanden and Rasmussen 2001). Source and tolerance increment were set at 1% and 0.1%, respectively. If no solution emerged, the tolerance parameter was increased by 0.1% until a solution was reached. Sources were selected a priori from the GCA results and the model was constrained by omitting minor dietary sources (i.e. contribution <10% across all seasons for each size class) in the consumers diet (Phillips et al. 2005). A comparison of total length against isotopic composition indicated smaller brown (<300 mm) and rainbow trout (<450 mm) exhibited isotopic compositions of a hatchery food that is highly enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$. Thus, for the mixing model hatchery food was retained as a dietary source for small brown trout and small rainbow trout. Although GCA of rainbow trout in tailwaters typically indicate that they readily ingest *Cladophora*, much of this may not necessarily be assimilated into body tissues because of lack of energetic value (Weiland and Hayward 1997). Thus, *Cladophora* and *D. geminata* were excluded from the stable isotope analysis as a dietary source. For larger (>400 mm) brown trout at Sylamore, the dietary source "other vertebrates" was considered to be Percidae and Catostomidae, while Cyprinidae was only considered for medium (250-400 mm) brown trout based on GCA. For small rainbow trout (≤400 mm) the dietary source "other vertebrates" was considered to be Cyprinidae. For the model, an average value across all the seasons was used for

the dietary sources due to slow growth rates and turnover times. Mixing model results were reported as the entire range of possible outcomes (1-99 percentile ranges) rather than focusing on the mean because many source combinations may have an equal probability of occurrence (Phillips and Gregg 2003).

Statistical analysis

We tested for differences in diets among seasons using a permutational multivariate analysis of variance (PERMANOVA), which tests the simultaneous response of one or more variables to factors in an ANOVA experimental design on the basis of a distance measure using permutation methods (Anderson 2001). The response variables were the proportion of the prey group by dry weight from the diet analysis and the predicator variable was seasons. Prey groups that represented <5% of the proportion of dry weight were excluded from the analysis. For the analysis Bray-Curtis distance measures were used with 4,999 permutations for each test (Manly 1997). PERMANOVA was performed using the packages MASS (Venables and Ripley 2002) and VEGAN (Oksanen et al. 2006) in the R-program (R Development Core Team 2007). We used an ANOVA to analyze the variation in caloric values (WW $J \cdot g^{-1}$) between the prey at Norfork and Bull Shoals.

Multivariate analyses of covariance (MANCOVA) was used to assess differences in $\delta^{13}C$ and $\delta^{15}N$ of trout tissue among seasons. The response variables were $\delta^{13}C$ and $\delta^{15}N$, predicator variable was season, and covariate was total length. Prior to statistical analysis, we examined data graphically to determine if the data met the assumptions of normality, homogeneity of variance, and homogeneity of slopes. Assumptions of normality of distributions and homogeneity of variance were verified through Shapiro–Wilk test (*W*-statistic) and Levene's test,

respectively. A general linear model was used to assess the homogeneity of slopes assumption (interaction between total length and seasons). If an interaction was significant for either $\delta^{13}C$ or $\delta^{15}N$ ($P<0.05$), then a MANOVA was performed. For MANCOVA we reported the approximate F-ratio statistic for the most robust test of multivariate statistics (Pillai's trace).

Linear regression analyses were used to determine whether the $\delta^{15}N$ values obtained from muscle tissue and/or total dry weight of fish found in GCA increased with TL of brown trout. For these analyses of $\delta^{15}N$ we only included tissue samples from brown trout that contained prey fish in their stomachs. We assumed that the predictor variable (TL) was fixed for the analysis. To prevent an isotopic hatchery signal depleted in $\delta^{15}N$ from influencing the regression models, only brown trout >300 mm TL were used in the analysis. We evaluated data distributions for normality and homogeneity of variance before tests were performed. The total dry weight of fish from GCA was $\log_{10}$ transformed to improve normality and homogeneity of variances.

We examined effect of season on specific growth rates in weight (*k*) using ANOVA. Model assumptions of normality, homogeneity of variance, and independence were evaluated graphically prior to statistical analysis. We also examined data for equality of variance using a Levene's test and departure from normality using the Shapiro–Wilk test (*W*-statistic). An α value of 0.05 was used to determine statistical significance for all tests. Analysis was performed using SYSTAT 13.0 (SYSTAT 2009).

Results

Gut content analysis

We examined the gut contents of 551, 573, and 263 trout from Bull Shoals, Norfork, and Sylamore, respectively. No large rainbow trout were collected at Sylamore during the study.

Results from the PERMANOVA indicated brown and rainbow trout diets differed significantly seasonally among each size class ($P < 0.001$), with the exception of small and large brown trout at Sylamore (Table 1).

Isopods were the dominant prey item observed in the gut contents of all sizes of brown trout collected in the summer and fall seasons at Bull Shoals, whereas amphipods were the dominant prey in the spring and winter (Figure 3). *Cladophora* and *D. geminata* were found in high proportions (29-82%) in rainbow trout stomachs year round. Large rainbow trout consumed more algae than small rainbow trout across seasons, but considerably more in the spring seasons with proportions ≥72%. Brown trout exhibited an ontogenetic shift from macroinvertebrates in smaller size class to sculpin in the medium and larger size classes. Although medium and large brown trout consumed a higher proportion of sculpin than small brown trout, a high proportion (>79%) of their diets were comprised of macroinvertebrates in most seasons. In both species and in all size classes, terrestrial invertebrates were consumed in the highest proportion in the fall, but were a relatively minor component of the overall diet (<14%).

At Norfork, small and large rainbow trout consumed high proportions of algae (≥63%) during the summer, fall, and winter season. In the fall and winter, algae accounted for 91% and 88% of the diets of small rainbow trout (Figure 4). Cladocera represented a substantial proportion of the diets of small rainbow trout during the spring season (≥20%). Large rainbow trout exhibited some piscivory during all seasons except winter. Besides algae, amphipods were dominant prey in the diets of large rainbow trout in the spring. Brown trout at Norfork exhibited little or no consumption of algae. In the fall, the diets of all sizes of brown trout were comprised almost entirely of sculpin (≥86%). Similar to Bull Shoals, smaller brown trout exhibited an ontogenetic shift from macroinvertebrates to sculpin in the medium and large size classes.

Piscivory increased with the size classes of brown trout. For large brown trout, sculpin represented the dominant prey in the diets among all seasons (46-93%). Brown trout consumed more amphipods than any other macroinvertebrate. In spring and summer 2005, amphipods accounted for 27-98% of the proportions of prey in their stomachs. Cladocera were an important prey type for small rainbow and brown trout in spring and comprised 21-24% and 9-28% of their diets.

Small rainbow trout consumed high quantities of algae in the fall and winter at Sylamore (Figure 5). Gastropods were the most commonly consumed macroinvertebrate in the diets of rainbow trout. Small rainbow trout exhibited limited piscivory in the spring when bigeye shiners were observed in the diets. Decapods were an important prey item for rainbow and brown trout in the spring and fall 2006. Small brown trout diets were comprised almost entirely by gastropods and decapods; however, they did exhibit some piscivory on sculpin in the winter. In fall 2005, the entire diet of larger brown trout was comprised of terrestrial invertebrates. The diets of medium and large brown trout reflected the increased diversity of prey fish species found at Sylamore, compared to Bull Shoals and Norfork. In winter 2005, large brown trout diets contained darters, river redhorse and northern hogsuckers. In the spring 2006 darters and striped shiners were also observed in the diets.

In general, benthic macroinvertebrates were the major prey items of small brown trout and sculpin were major prey of large brown trout, which indicated a shift to piscivory with increasing size. Based on GCA, the transition to piscivory for brown trout occurred at approximately ~200 mm TL at all sites. Large brown trout exhibited the highest seasonal diet proportions of piscivory at Norfork (Range 46-93%), Bull Shoals (Range 9-61%) and Sylamore (0-50%). Although rainbow trout at all sites exhibited some piscivory (9-15%), it was a

relatively minor component of their diets. The average TL of sculpin consumed at Bull Shoals was 63 mm TL (SE±1.53; range 34-108 mm; n = 100). The average TL of sculpin at Norfork was 72 mm (SE±1.73; range 27-110 mm; n = 89). At Sylamore, the average size and range of fish consumed was 63 mm TL (SE±2.96; range 39-110 mm; n = 31) for sculpin, 126 mm (SE±6.00; range 120-132 mm; n = 3) for Percidae, 78 mm (SE±6.08; range 52-97 mm; n = 7) for Cyprinidae, and 196 mm (SE±24.00; range 172-220 mm; n = 3) for Catostomidae. During the study, only two brown trout at Bull Shoals (542 and 557 mm) and two rainbow trout at Norfork (503 and 551 mm) exhibited cannibalism.

Prey energy densities and caloric diets

At Bull Shoals, prey caloric values (WW $J \cdot g^{-1}$) were significantly different (ANOVA, $F_{3,11}$ = 14.307, $P < 0.001$) with the lowest caloric values were found in Gastropods (Pleuroceridae) and the highest caloric values in sculpin (Table 2). We also found significant differences in the caloric values of prey at Norfork (ANOVA, $F_{4,15}$ = 29.861, $P < 0.001$). At Norfork the lowest caloric values were found in Decapods and the highest in sculpin. As sculpin increased in TL their caloric values decreased at Norfork (Linear regression, $F_{1,8}$ = 15.145, P = 0.005, r^2 = 0.654), while sculpin at Bull Shoals exhibited no relationship between TL with caloric values (Linear regression, $F_{1,6}$ = 0.763, P = 0.416, r^2 = 0.113).

Sculpin was the most important prey calorically in brown and rainbow trout diets at Bull Shoals, owing to their higher caloric content compared to macroinvertebrates (Figure 6 and 7). When only a few sculpin were in the diets of trout at Bull Shoals the majority of their calories were obtained from isopods and amphipods. Similar to Bull Shoals, brown and rainbow trout at Norfork that contained sculpin in the diets exhibited high caloric intake. Amphipods were the

major macroinvertebrate caloric source in the diets of trout at Norfork. At Sylamore, prey fish in the diets, and to lesser extent sculpin, were of primary importance calorically in brown and rainbow trout, but varied depending on size class and season. Although gastropods were found in high proportions of the diets of trout in Sylamore they contributed very little from an energetic standpoint. At Sylamore, decapods were most important in the winter and spring of 2006 in rainbow trout diets. Macroinvertebrates (e.g. Ephmeroptera, Plecoptera, etc.) were of particular importance calorically to small brown trout.

In comparing caloric intake across sites by species, the lowest caloric intake occurred in small rainbow trout at Sylamore in the winter 2006 with an average of 481 J (SE$\pm$136.6) consumed. In contrast, the highest level of caloric intake in rainbow trout occurred in the large size class at Norfork when an average of 44,685 J (SE$\pm$17,963.2) was consumed in spring 2005 due to the high piscivory rate. In brown trout across all sites both the lowest and highest caloric intake occurred in large size class at Sylamore. Large brown trout caloric intake at Sylamore was lowest in fall 2005 when only terrestrial invertebrates (Average = 20 J SE$\pm$12.3) and highest in winter 2006 when the diets were comprised of prey fish (Average = 131,238 J SE$\pm$70,936.3).

Stable isotope analysis

We examined stable isotopes in white muscle tissues in 243 brown and 305 rainbow trout from Bull Shoals, 262 brown and 305 rainbow trout from Norfork, and 100 brown and 158 rainbow trout from Sylamore. Similar to the GCA, MANCOVA results indicated that isotopic signatures of brown and rainbow trout differed seasonally among each size class. Only small and large brown trout at Sylamore did not differ among seasons (Table 1). In rainbow trout, $\delta^{13}C$ and $\delta^{15}N$ ranged from -32.53 to -19.13‰ and 9.36 to 19.68‰ at Bull Shoals, -33.91 to -19.04‰ and 9.36

to 17.97‰ at Norfork, and -27.93 to -18.52‰ and 9.38 to 15.12‰ at Sylamore, respectively (Figure 8). In general, rainbow trout became progressively more depleted in $\delta^{13}C$ and enriched in $\delta^{15}N$ as TL increased at Bull Shoals and Norfork. The isotopic signatures of rainbow trout at Sylamore varied little over the range of fish lengths, with exception of three fish containing a more depleted $\delta^{13}C$ and enriched $\delta^{15}N$ signature, because no large rainbow trout were collected.

Carbon and nitrogen stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) in brown trout ranged from -34.52 to -22.05‰ and 12.59 to 21.53‰ at Bull Shoals, -34.48 to -19.32‰ and 10.39 to 17.71‰ at Norfork, and -30.04 to -18.95‰ and 10.24 to 16.69‰ at Sylamore, respectively (Figure 9). With the exception of 20 fish collected in spring 2005 at Bull Shoals, small brown trout stable isotope signatures typically reflected the hatchery isotopic "memory", being enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$. These small brown trout had divergent isotope signatures from similar sized brown trout in winter 2006, suggesting that these were wild brown trout. In general, brown trout became gradually more depleted in $\delta^{13}C$ and enriched in $\delta^{15}N$ as length increased and typically lost their hatchery signal around 300 mm TL.

Total number of prey samples collected for SIA was 185 at Bull Shoals, 186 at Norfork, and 101 at Sylamore (Table 3, 4, and 5). The number of taxonomically different prey sources including algae was 10 at Bull Shoals and 8 at Norfork. We collected a higher number of of potential prey sources at Sylamore, which included 1 algae, 11 macroinvertebrate, 11 vertebrate species.

Potential prey sources were generally more enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$ than trout white muscle tissue, with the major exception being small rainbow trout (Figure 10, 11, and 12). Brown trout (>300 mm TL) were more enriched in $\delta^{15}N$ than rainbow trout. Carbon and nitrogen isotopes provided some discrimination among sculpin, zooplankton, and

macroinvertebrates (Amphipods, Chironomids, Isopods) sources based on the biplot axes at Bull Shoals and Norfork. However, stable isotope signatures of primary macroinvertebrates sources (Amphipods, Chironomids, Isopods) at both sites were functionally consistent and isotopically similar exhibiting little separation between taxa with mean δ values < 2‰ different. Sculpin exhibited the highest $\delta^{15}N$ and trophic position of all prey species. Zooplankton were intermediate of sculpin and macroinvertebrates in $\delta^{15}N$. Isotopic signal of hatchery food was highly enriched in $\delta^{13}C$ (-21.0 SE±1.6; range -19.3 to -22.6; *n* = 2) and depleted in $\delta^{15}N$ (6.7 SE±0.1; range 6.6 to 6.8) when compared to the other sources. *D. geminata* collected at Bull Shoals was more enriched in $\delta^{13}C$ (Range -21.2 to -22.32‰) when compared to *Cladophora* (Range -35.3 to -36.2).

All macroinvertebrates, with the exception of Isopods, were more enriched in $\delta^{15}N$ than *Cladophora* at Sylamore. The stable isotope signatures of taxonomic groups of macroinvertebrates ranged from -25.49 to -34.76‰ for $\delta^{13}C$ and from 7.22 to 11.48‰ for $\delta^{15}N$ at Sylamore. Stable isotope signatures were isotopically similar within *Isonychia*, Hydropsychidae, *Gammarus*, and Heptageniidae. Chironomidae and *Pteronarchys* also exhibited little isotopic separation. The macroinvertebrate occupying the highest trophic position was Ephemeroptera of the family Oligoneuriidae. Sculpin and darters had similar isotopic signatures and were enriched in approximately 4-5‰ of $\delta^{15}N$ above the majority of macroinvertebrates. Crayfish contained similar $\delta^{15}N$ to macroinvertebrates, but a more enriched $\delta^{13}C$ signature. Prey fish occupying the highest trophic positions were *Pomoxis* and *E. blenniodes* with $\delta^{15}N$ signatures of 14.57‰ and 14.60‰, respectively. Across all the seasons, rainbow trout were enriched in $\delta^{13}C$ compared to macroinvertebrates and fish. Large brown trout likely occupied the highest trophic

position in the food web given their enriched in $\delta^{15}N$ was higher than any prey fishes and macroinvertebrates.

The increase in $\delta^{15}N$ of brown trout indicated ontogenetic shifts in trophic position. Assuming an average shift in $\delta^{15}N$ of 3.4‰ between trophic levels (Vander Zanden and Rasmussen 2001) for brown trout, $\delta^{15}N$ values increased by an average of 0.7 trophic levels at Bull Shoals ($\delta^{15}N$ = 17.3-19.6‰), 0.5 trophic levels at Norfork ($\delta^{15}N$ = 14.9-16.7‰), and 0.5 trophic levels at Sylamore ($\delta^{15}N$ = 14.0-15.6‰). At all three sites, brown trout increased in the trophic level with increasing length indicating a shift towards more piscivory.

When we compared $\delta^{15}N$ and total dry weight of fish in GCA from the same fish (Figure 13), brown trout signatures became progressively more $\delta^{15}N$ enriched as fish length increased at Bull Shoals (Linear regression, $F_{1,51} = 26.068$, $P < 0.001$, $r^2 = 0.338$) and Sylamore (Linear regression, $F_{1,32} = 11.790$, $P = 0.002$, $r^2 = 0.269$), but not at Norfork (Linear regression, $F_{1,80} = 1.090$, $P = 0.300$, $r^2 = 0.013$). We found that total dry weight of fish in GCA increased linearly with total length at Sylamore (Linear regression, $F_{1,47} = 18.333$, $P < 0.001$, $r^2 = 0.281$) where a more diverse fish assemblage existed. In contrast, there was no clear relationship between total dry weight of fish and total length at Bull Shoals (Linear regression, $F_{1,56} = 1.747$, $P = 0.192$, $r^2 = 0.030$) and Norfork (Linear regression, $F_{1,87} = 2.175$, $P = 0.144$, $r^2 = 0.024$) where sculpin were the predominant prey fish.

Growth and turnover times

The total number of brown and rainbow trout tagged and released during the study was 1,525 and 3,350 at Bull Shoals, 1,434 and 3,579 at Norfork, and 157 and 1,378 at Sylamore, respectively. On average, 30%, 24%, and 18% of the brown trout that were captured at the start

of a seasonal sampling interval were also captured at the end of a seasonal sampling interval at Bull Shoals, Norfork, and Sylamore, respectively. Average recapture rate was lower for rainbow trout when compared to brown trout and was 13% at Bull Shoals, 15% at Norfork, and 5% at Sylamore.

Specific growth rates were decidedly seasonal for small rainbow trout at Bull Shoals (ANOVA, $F_{3,329} = 30.759$, $P < 0.001$), Norfork (ANOVA, $F_{3,344} = 42.111$, $P < 0.001$), and Sylamore (ANOVA, $F_{1,65} = 4.062$, $P = 0.048$) , with the fast growth period from spring to fall and negative growth during winter at Bull Shoals and Norfork (Figure 14). All observed growth rates for rainbow trout at Sylamore were negative. Seasonal differences were observed in large rainbow trout at Norfork (ANOVA, $F_{3,45} = 3.731$, $P = 0.018$), but not in those collected at Bull Shoals (ANOVA, $F_{3,78} = 2.697$, $P = 0.052$). For larger rainbow trout at Norfork the major growth period was in spring. At Bull Shoals, large rainbow trout exhibited an opposite pattern with no growth or negative growth across the seasons, with a particular depression during the spring.

There were no significant differences in specific growth rates across seasons for small brown trout at Bull Shoals (ANOVA, $F_{2,10} = 0.620$, $P = 0.557$) and Norfork (ANOVA, $F_{1,5} = 4.653$, $P = 0.083$). However, these fish exhibited rapid growth across the intervals. Only one small brown trout was recaptured at Sylamore, thus no growth rates comparison across seasons was possible for this size class. Growth was high and not seasonal for medium brown trout at Bull Shoals (ANOVA, $F_{3,112} = 1.558$, $P = 0.204$), Norfork (ANOVA, $F_{3,128} = 2.008$, $P = 0.116$), and Sylamore (ANOVA, $F_{2,19} = 1.725$, $P = 0.205$). Growth was seasonal for large brown trout at Bull Shoals (ANOVA, $F_{3,273} = 5.107$, $P = 0.002$) and Norfork (ANOVA, $F_{1,184} = 32.980$, $P < 0.001$) exhibiting negative growth in winter season, during and shortly after the spawning period.

At Sylamore, large brown trout growth displayed minimal changes in growth seasonally (ANOVA, $F_{2,13} = 3.219$, $P = 0.179$) and approached no net growth during the seasons.

Turnover times to 95% (T_{95}) of isotopic equilibrium were estimated to be slower in $\delta^{13}C$ than $\delta^{15}N$ among the sites, size classes, and species (Figure 15). Small brown trout at Norfork exhibited the quickest turnover times of $\delta^{13}C$ and $\delta^{15}N$ in 209 d (SE$\pm$12.8) and 168 d (SE$\pm$8.4), respectively. In contrast, small rainbow trout at Sylamore exhibited the slowest turnover times of $\delta^{13}C$ and $\delta^{15}N$ in 323 d (SE$\pm$1.9) and 235 d (SE$\pm$1.1), respectively. In general, across the size classes and species fish at Norfork had quicker turnover times than fish at Bull Shoals and Sylamore. The species and size class exhibiting the fastest turnover times at all sites was small brown trout owing to their observed higher growth rates. The proportion of isotopic turnover rate due to growth and metabolic tissue replacement was dominated by metaboblic turnover at all sites and size classes, which averaged 86% and 95% for brown and rainbow trout, respectively. Small rainbow trout at Sylamore exhibited the highest proportion of metabolic turnover (100%), whereas small brown trout at Norfork exhibited the lowest proportion of metabolic turnover (64%). The majority of the larger rainbow trout at Bull Shoals and Norfork had sufficient turnover rates to replace the isotopic hatchery signal at approximately 425 to 450 mm TL.

Stable isotope mixing model

Mixing model results indicated that at all sites, smaller rainbow trout contained isotopic "memory" from hatchery food (Range 42-100%), particularly at Sylamore (Range 95-100%) (Tables 6, 7, and 8). Smaller brown trout also contained some isotopic hatchery "memory" in the fall, winter and spring at all the sites (Range 41-99%), the only exception was in the fall at

Bull Shoals. For large rainbow trout at Bull Shoals the major dietary source was isopods whereas at Norfork the major dietary source was amphipods.

Sculpin was a source contribution in the mixing model in small and large brown trout at Bull Shoals. However, in medium brown trout the model indicated that sculpin was not a source in the diets. At Norfork, sculpin became increasingly more important as a source in the diets of the brown trout as they increased in size, and contributed up to as much as 59-61% of the diet in large brown trout. At Sylamore fish prey species such as Cyprinidae, Percidae, Catostomidae contributed to the bulk of the diets in brown trout with sculpin being less utilized. Also, at Sylamore mixing models indicated decapoda was an important prey source in the diets of brown trout in the fall and winter.

Dominant macroinvertebrates contributing to the diets based on mixing models differed between the areas. At Norfork, the major macroinvertebrate prey source estimated from the mixing models across species and size classes was amphipods. In contrast, the major macroinvertebrate dietary source contribution at Bull Shoals was chironomids for brown trout and isopoda for rainbow trout. The mixing model indicated macroinvertebrates contributed little to the diets of both species at Sylamore.

Generally results from the mixing models exhibited little alterations in response to changes in the field and laboratory derivied fractionation values used (Δ_a and Δ_b). In a few instances the ranges of feasible solutions for the sources differed depending on the fractionation value used (Δ_a and Δ_b). This discrepancy was apparent in small rainbow trout at Bull Shoals, where the dietary sources, amphipods and chironomids, were constrained differently by the model. Amphipods were an important source in the diet with a fractionation value of Δ_a with a

range of 3-44%, whereas Δ_b indicated chironomids were an important source comprising from 29-56% of the assimilated diet.

Discussion

The low benthic macroinvertebrate diversity in the tailwaters was reflected in the low diversity of prey encountered in the stomachs of trout which were largely comprised of amphipods, chironomids, isopods, and gastropods, a finding similar with Pender and Kwak (2002) for brown trout. At Bull Shoals, diets of trout alternated between isopods and amphipods seasonally as the dominant macroinvertebrate prey. These foraging shifts may have resulted from temporal fluctuations in the abundances of these macroinvertebrates in the drift and benthos. In response to reductions in one macroinvertebrate, trout might possibly depend on other macroinvertebrates to maintain sufficient growth. Amphipods were the only dominant macroinvertebrate prey in the diets of trout at Norfork likely due to the low abundance of isopods at this area. Amphipods provided a slightly higher energetic value than isopods possibly contributing to the higher observed growth rates of trout at Norfork. Gastropods were the major macroinvertebrate prey in the diets of trout at Sylamore. This low nutritional quality prey contributed very little energetically. The reliance of trout on terrestrial macroinvertebrates was only a relatively minor component of their diets in all the areas and reflects the low terrestrial input in typically found in Arkansas tailwaters (Johnson et al. 2006).

Benthic macroinvertebrate taxa abundant in the tailwaters that are not prone to actively drift (e.g. isopods, amphipods, gastropods) were commonly observed in the diets from GCA of brown and rainbow trout which implies a foraging strategy on the benthos. Also, despite the lack of energetic value, *Cladophora* and *D. geminata* were found in high proportions in rainbow

trout diets which further suggests frequent epibenthic feeding (Tippets and Moyle 1978; Weiland and Hayward 1997). Brown trout exhibited limited algae consumption despite evident epibenthic foraging. Drifting macroinvertebrate taxa only occupying the water column and prone to drift (e.g. chironomidae pupae, *Daphnia*) were regularly observed in the diets of rainbow trout. This suggests rainbow trout exhibited alternating foraging strategies between the drift and benthos. Alternating foraging shifts may be in response to spatial or temporal changes in food availability (McKinney and Speas 2001). A diet of poor energetic quality comprised principally of *Cladophora* and *D. geminata* in other systems has been suggested to occur during periods of low food availability (McKinney and Speas 2001; Weiland and Hayward 1997). Large rainbow trout that experienced slower or negative growth also tended to consume higher proportions of *Cladophora* and *D. geminata* signifying epibenthic foraging as an energetically ineffective strategy. Hatchery-reared salmonids released into streams can experience lower feeding efficiencies and consume less or few types of natural prey than wild salmonids (Bachman 1984). Foraging inefficiencies in recently stocked smaller rainbow trout may partly explain the high algal consumption. However, more resident, large rainbow trout (>400 mm), which have typically been in the tailwater for at least a year, also consumed high proportions of algae and employ this as a foraging strategy. Diets that constitute high proportions of algae tend to be poor nutritionally and energetically with a resultant decrease in trout growth (McKinney and Speas 2001; Weiland and Hayward 1997). Distinct seasonal differences in growth rates further suggest food availability fluctuates temporally (Railsback and Rose 1999). The goal of C-R areas is to provide increased catch rates of larger fish and is in part dependent on a fish growing to larger sizes. Our findings of rainbow trout diets high in algae consumption and poor growth rates are similar to other findings that tailwaters may often be food-limited for large

rainbow trout (Filbert and Hawkins 1995; McKinney and Speas 2001; Weiland and Hayward 1997). Brown trout exhibited an ontogenetic shift towards the addition of prey fish into their diets at ~200 mm. The caloric content of prey fish (i.e. sculpin) was greater than aquatic macroinvertebrates in the tailwaters and this incorporation of piscivory into their diets allowed them to consume more prey biomass and calories compared to those feeding solely on macroinvertebrates (Elliott and Hurley 2000; Foresth and Jonsson 1994). Johnson et al. (2006) found a growth bottleneck in brown trout populations in the regulated Little Red River, Arkansas due to the lack of available suitably sized prey fish (e.g. sculpin) present in the tailwater. Brown trout at Norfork exhibited a higher degree of piscivory than at Bull Shoals and Sylamore likely due to higher densities and biomass of sculpin available in this area. Generally brown trout experienced positive seasonal growth rates at all the areas from the higher caloric fish intake. This suggests brown trout may not experience food limitation in the tailwater C-R areas owing to their shift towards more piscivory. Benthic macroinvertebrate production may be insufficient to support adequate large rainbow trout.

Relatively few stable isotope studies have focused on tailwaters, which typically contain simple food webs and may be ideal for using SIA (Johnson and Harp 2005; Quinn and Kwak 2003; Shaver et al 1997). Despite a simple food web the taxonomic precision afforded from GCA enhanced isotopic inferences by limiting the number of food sources required in the mixing model simulations as opposed to relying solely on isotopic data. A major benefit with SIA is that it provides time-integrated assimilated dietary information when compared to the traditional temporally limited "snapshot" GCA method for dietary studies. In this study GCA indicated trout foraged extensively on filamentous algae, *Cladophora,* and at Bull Shoals a nuisance diatom, *D. geminata*. *Cladophora* and *D. geminata* are not readily assimilated by trout (Weiland

and Hayward 1997) and if only SIA was performed the role of *Cladophora* and *D. geminata* in the dietary dynamics of trout would not have been detected. This epibenthic foraging strategy was important in understanding possible bottlenecks in spatial and temporal food availability in the C-R areas (Filbert and Hawkins 1995; McKinney and Speas 2001; Weiland and Hayward 1997) and highlights an advantage of using SIA and GCA in tandem. In contrast, SIA may be more effective in detecting the importance and incorporation of zooplankton into diets owing to their small size and high surface to volume ratios which facilitates a quick digestion, evacuation, and assimilation (Hylsop 1980). For example, GCA only indicated the importance of zooplankton during the spring for small rainbow trout at Norfork which represented approximately 20% of their diets. Although the majority of SIA mixing model results indicated a residual hatchery signal as the primary food source in small rainbow trout at Norfork the simulations also indicated zooplankton was of secondary importance and represented almost all of the new production in white muscle tissue. This suggests, that based on SIA, zooplankton was highly assimilated and of primary importance in the diets and production of new tissue. Entrained zooplankton from reservoir hypolimnetic releases can be the principal component in drift and an important food resource in tailwaters (Jackson et al. 1991; Ward 1974). Entrained zooplankton likely provides a readily available alternative food resource in the drift with presumably high capture success rates and low foraging costs. Consequently, feeding on temporally abundant zooplankton may represent an energetically profitable foraging strategy for rainbow trout. SIA may be an ideal tool to detect zooplankton given the discrepancy between methodologies which could result in an underrepresentation of zooplankton in GCA due to differences in assimilation efficiency, digestibility, and evacuation rates (Hyslop 1980). Pros and cons between the methodologies also need to be considered in the context of estimating dietary

proportions for various bioenergetics modeling applications (Chipps and Wahl 2008; Ney 1993). Bioenergetics models estimating short-term consumption (e.g. daily) such as the Eggers (1977) model only provide a means to estimate consumption utilizing GCA. In contrast, long-term diet proportions estimated from SIA may be more comparable and appropriate for seasonal modeling in daily summed "Wisconsin" bioenergetics based consumption estimates than GCA (Hanson et al. 1997).

The isotopic signature of small rainbow trout were considerably enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$ indicating that they contained isotopic "memory" from hatchery food, which is also highly enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$. Subsequently there was a substantial shift in isotopic signatures with increasing fish length towards a more depleted $\delta^{13}C$ and enriched $\delta^{15}N$. Source contributions from the mixing model indicated that a significant portion of the diet in small rainbow trout was also comprised of hatchery food. Christensen and Moore (2009) found interpreting informative SIA with hatchery stocked brook trout in Washington lakes was unfeasible. Similarly, the artificially induced diet in rainbow trout prohibited any meaningful SIA estimates until sufficient time had passed for adequate tissue turnover. Tissue turnover rate is the isotopic change due to growth and metabolic tissue replacement associated with a change in diet (Hesslein et al. 1993). Growth turnover can be attributed to a "dilution" of the previous ratio by added tissue of differing isotopic composition. Metabolic turnover involves the replacement of old tissue with new, and occurs despite no net growth. Rainbow trout at Norfork generally grew at faster rates, and as expected appeared to lose the hatchery signal slightly faster in response to more rapid tissue turnover from growth. At Bull Shoals large rainbow trout exhibited almost no net growth throughout the year and as a result isotopic change was likely driven by metabolic rather than growth turnover. Similarly, rainbow trout at Sylamore

experienced no net growth, with metabolic turnover being required to replace the hatchery signal. Generally, the isotopic hatchery signal in rainbow trout was lost at approximately 400-450 mm when adequate time had lapsed to replace the tissue. With the observed growth rates in the specific C-R area, rainbow trout may require 292 to 302 days for $\delta^{13}C$ and 218 to 234 days for $\delta^{15}N$ to almost completely lose the hatchery signal and equilibrated (95% turnover) with a new diet after stocking. In cold tailwaters, using white muscle tissue for SIA in rainbow trout may provide limited dietary insights until sufficient turnover has occurred due to the highly augmented slow growing trout populations containing hatchery "memory".

Periods of higher growth for rainbow trout at Bull Shoals and Norfork occurred in spring and summer providing greater tissue production and a more rapid change in isotopic composition (Perga and Gerdeaux 2005). Generally, brown trout maintained much more seasonally stable growth patterns with expected constant changes in isotopic composition over time. Larger more mature brown trout did experience a decrease in growth in the fall and winter likely due to spawning limiting growth turnover during this time period. Slower growing larger older fish of both species encompassed longer temporal scales of dietary information and are less responsive to changes in diet than smaller fish. Depending on growth, turnover times to isotopic equilibrium (95%) were estimated to require between six to eleven months. Although growth rate partly determine the length of the time for which the isotopic value of fish represents the diet, in our study the majority of the turnover was dominated by metabolic rather than growth. Given the slow growth rates of trout in tailwaters, a tissue with faster turnover, such as liver may be more responsive to diets shifts over much shorter periods of time (Hesslein et al. 1993). Liver is regulatory tissue with continuous protein turnover and reveals dietary shifts of fish with a much higher temporal resolution than white muscle tissue, which has a much slower isotopic

turnover. Selection of the appropriate tissue should depend on the length of time for the specific SIA study because various tissues reflect dietary signatures over varying time periods. Dietary information over several temporal scales can be obtained by measuring several tissues of a fish depending on specific tissue turnover rates (Buchheister and Latour 2010). Coupling growth rates along with SIA studies provides an investigator the ability to infer the time period reflected in the dietary signatures since different sized fish may have different growth rates with usually older fish growing slower.

We found SIA broadly supported GCA with limited insights into the dietary patterns of trout within the tailwaters. A study conducted on the diet of ruffe also found that the SIA model was unsuccessful in providing any objective additional knowledge (Tarvainen et al. 2008). Wide ranges of feasible food source solutions rather than narrow ranges in the SIA model output may be due to a food source not sampled and incorporated into the model, food sources sampled yet isotopically different when consumed, or incorrect fractionation values (Caut et al. 2009; Hesslein et al. 1993). However, in this study these issues seem highly unlikely. With the relatively simple food webs and high number of stomachs processed for GCA (n = 1,387) the likelihood that a food source was missing from the model seems doubtful. In an effort to overcome the disequilibrium of consumers with their food sources and reduce this confounding temporal variation and obtain truer time integrated isotopic values we ran food sources from across several time periods for inclusion into the SIA model. Fractionation values for $\delta^{13}C$ and $\delta^{15}N$ were empirically estimated for the same species with a similar body size using the same tissue as suggested in Gannes et al. (1997) for rainbow trout (Chapter 1). Additionally, we used a fractionation value developed from a meta-analysis field-derived value, which tends to be smaller than laboratory-derived values (Vander Zanden and Rasmussen 2001). Thus, errors in

the applied fractionation values in affecting mixing model estimates should be minimal (Caut et al. 2009). Alternating fractionation values between the laboratory and field-derived values in the mixing model typically did not improve or alter the results.

Mixing models of SIA perform best when the overlap in isotopic compositions of food sources is small (Phillips and Gregg 2003). A strong overlap of many macroinvertebrate food sources $\delta^{13}C$ and $\delta^{15}N$ may have restricted the use of mixing models in the tailwaters. This overlap often results in broad ranges of feasible solutions rather than more informative narrow ranges of solutions which provide significant conclusions regarding food source contributions. Similar isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of macroinvertebrates suggest they occupy related niches and the high degree of overlap in $\delta^{13}C$ values across species implies that the macroinvertebrates are reliant on similar organic matter. There was a distinct separation between sculpin and macroinvertebrates, with sculpin occupying the expected trophic level enrichment of ~3‰ of $\delta^{15}N$ above macroinvertebrates. However, entrained zooplankton (e.g.*Daphnia*) contained a similarly enriched $\delta^{15}N$ with sculpin and may have restricted the model in distinguishing between the two food sources when used in conjunction for simulations. To overcome the overlap, aggregating food sources is considered reasonable if they are functionally similar (Phillips et al. 2005). Aggregating all macroinvertebrate food sources into one 'macroinvertebrate' food category could have been considered reasonable given they occupy similar trophic guilds. Although aggregating may have resulted in a more constrained model with feasible solutions the ability to determine taxon specific source contributions into the tissue would have been lost. Ultimately this pooling of macroinvertebrates would have only provided broad conclusions about the importance of macroinvertebrates and fish in the tailwaters with limited utility.

In the White River system, wild, self-sustaining populations of brown trout are known to exist, but reproductive success can be variable among years and within tailwaters (Pender and Kwak 2002). Given adequate isotopic separation of $\delta^{13}C$ and $\delta^{15}N$ food sources, stable isotope analysis offers a method to distinguish recently stocked fish from wild fish (Dempson and Power 2004). Stocked juvenile brown trout contained hatchery signal enriched in $\delta^{13}C$ and depleted in $\delta^{15}N$. This isotopic separation in $\delta^{15}N$ and $\delta^{13}C$ of small brown trout signatures at Bull Shoals in the spring stocking seasons (2005 versus 2006), suggests a successful recruitment of wild brown trout occurred in 2005. Based on this finding SIA may be useful tool in tailwaters that reliably distinguishes hatchery-produced from wild spawned fish due to the highly enriched and depleted isotopic hatchery "memory." Using SIA would allow managers the ability estimate the relative contributions of each stock to the reproductive population. Estimating the proportion of hatchery to wild fish within a tailwater could reduce the need for costly hatchery stocking in areas or year's when high numbers of wild fish successfully recruit. Stocking of hatchery brown trout along with wild brown trout may affect wild populations negatively through density dependence interactions and decreased growth (Bohlin et al. 2002; Grant and Kramer 1990). Otolith microchemistry has also been found to be an effective method in discriminating hatchery-reared salmonids to tributary spawned salmonids in Arkansas tailwaters (Coghlan et al. 2007). However, this method may be more expensive and labor intensive than SIA in assessing relative contributions of hatchery versus wild populations. Otolith microchemistry was also found to be an ineffective method in the Bull Shoals and Norfork tailwaters in differentiating between origins of fish collected in the C-R areas (Cushing 2007). Although we used a lethal method to assess SIA non-lethal methods such as scales or fins could be used to assess wild to hatchery proportions (Kelly et al. 2006; Sanderson et al. 2009). A critical first step in any study

attempting to use SIA to assess hatchery versus wild is to determine the amount of time a fish retains their characteristic hatchery signature. Fish experiencing fast growth rates may limit the utility of SIA as a tool owing to the rapid turnover rate. In my study, small brown trout exhibited the highest growth rates. Based on growth rates, a complete loss (95% turnover) of the hatchery signal would have occurred within 206-265 days for $\delta^{13}C$ and 166-203 days for $\delta^{15}N$, whereas half-life (i.e. amount of time to reach a midpoint value) of the hatchery signal would have occurred within 48-61 days for $\delta^{13}C$ and 38-47 days for $\delta^{15}N$. Fish would likely need to be sampled in close proximity to the half-life to ensure the signal is still apparent enough to effectively distinguish hatchery from wild brown trout in the tailwaters.

Decreased flows in 2005 may have improved recruitment in the tailwater. Flow conditions in White River affect brown trout adult spawning timing and juvenile survival (Pender and Kwak 2002). Flow patterns were similar during spawning between years (2003 and 2004). However, at juvenile emergence flow was generally lower in 2004 as compared to 2005 from the end of February to beginning of June. In the White River when higher water flows persisted, brown trout sought spawning habitat near the water margins and redds constructed near the water margins in high water were abandoned and left dry when water levels ebbed (Pender and Kwak 2002). Flow regimes during spawning time periods (2004 vs. 2005) were similarly low indicating abandonment of redds in either year unlikely as a cause for reproductive failure. At the time of fry emergence flow conditions were higher in 2005, which may have negatively affected their survival due to inadequate habitat or inadequate food base for metabolic energy requirements.

Conclusions

In general, our findings suggest SIA of $\delta^{13}C$ and $\delta^{15}N$ appear to be complementary and not necessarily a substitute to GCA in detecting spatial and temporal dietary patterns of brown and rainbow trout in Ozark tailwaters. The "artificial" enrichment of $\delta^{13}C$ and depletion of $\delta^{15}N$ in rainbow trout tissue from the hatchery food coupled with the slow growth rates prevented informative interpretation from mixing model simulations. In systems such as tailwaters that contain highly augmented stocked populations GCA may be the only method of detecting dietary patterns, until adequate growth or metabolic tissue turnover occurs. With the observed growth rates, complete turnover (95%) of white muscle tissue was estimated to require six to eleven months depending on isotope ($\delta^{13}C$ and $\delta^{15}N$), species and size class. A tissue with a faster turnover (e.g. liver) may assist in providing a finer temporal resolution for detecting SIA dietary patterns in tailwaters. However, selection of the appropriate tissue should depend on the length of time for the pertinent SIA study because various tissues reflect dietary signatures over varying time periods. Concurrent use of GCA and SIA of $\delta^{15}N$ proved suitable in detecting ontogenetic shifts of brown trout to piscivory. SIA also provided a method to distinguish hatchery versus wild brown trout given the wide isotopic separation of $\delta^{13}C$ and $\delta^{15}N$ between isotopic hatchery "memory" and food sources. This isotopic separation provides useful tool for managers in detecting wild recruitment of brown trout in tailwater C-R areas. Our findings of rainbow trout diets high in of *Cladophora* and *D. geminata* consumption and poor growth rates suggest the C-R areas in tailwaters may often be food-limited for large rainbow trout. As growth is reduced from food limitation fewer fish will be reaching desirable sizes for anglers and ultimately decreases the probability that the C-R areas will meet the goal of an increased density of large rainbow trout.

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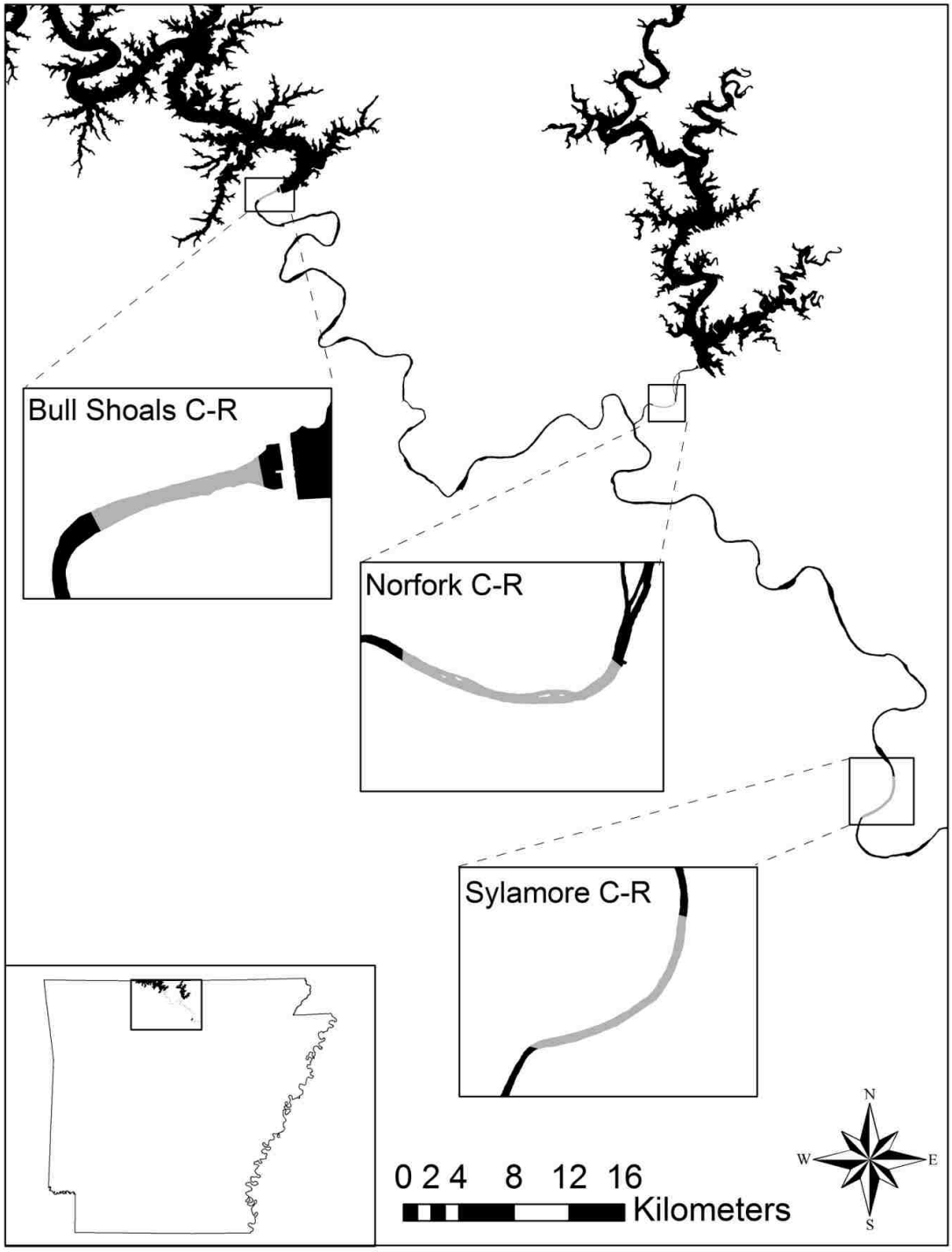

Figure 1. Map depicting the three special regulation catch-and-release (C-R) areas sampled during this study on the White and North Fork of the White Rivers, Arkansas.

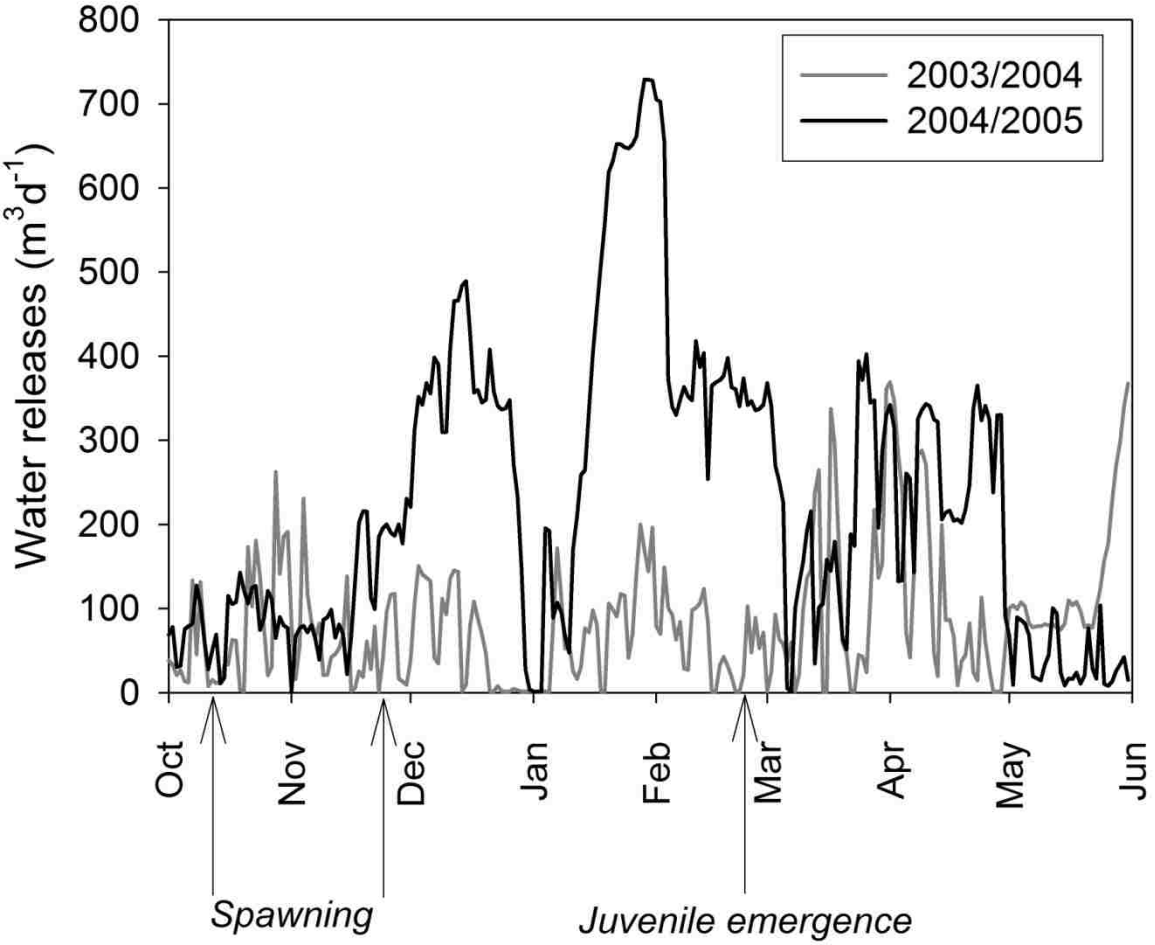

Figure 2. Monthly dam water releases ($m^3 \cdot d^{-1}$) from Bull Shoals tailwater from October 1 2003 and 2004 to May 31 in 2004 and 2005. Arrows indicate typical brown trout spawning and juvenile emergence timing in White River system (Pender and Kwak 2002).

Table 1. MANCOVA results for stable isotopes analysis (SIA) of δ13C and δ15N and PERMANOVA results for gut content analysis (GCA) by site, species and size class. Pillai Trace is represented by PT.

			SIA				GCA		
Site	Species	Size class	PT	df	*F*	*P*	df	*F*	*P*
Bull Shoals	Rainbow trout	Small	0.303	8, 400	8.925	<0.001	4, 194	6.22	<0.01
		Large	0.234	8, 186	3.077	0.003	4, 92	3.51	<0.01
	Brown trout	Small	1.116*	8, 76	11.992	<0.001	4, 35	2.83	<0.01
		Medium	0.338	8, 192	4.874	<0.001	4, 91	5.82	<0.01
		Large	0.339	8, 184	4.701	<0.001	4, 81	5.07	<0.01
Norfork	Rainbow trout	Small	0.181	8, 404	5.02	<0.001	4, 201	20.48	<0.01
		Large	0.291	8, 182	3.881	<0.001	4, 89	3.45	<0.01
	Brown trout	Small	1.263*	8, 96	20.386	<0.001	4, 37	4.32	<0.01
		Medium	0.469	8, 198	7.584	<0.001	4, 86	5.81	<0.01
		Large	0.312	8, 196	4.521	<0.001	4, 78	2.75	<0.01
Sylamore	Rainbow trout	Small	0.111	6, 306	3.009	0.007	3, 146	15.07	<0.01
	Brown trout	Small	0.525	4, 20	1.781	0.172	2, 6	0.63	0.84
		Medium	0.209	6, 128	2.494	0.026	3, 54	18.57	<0.01
		Large	0.481*	6, 26	1.374	0.262	2, 9	1.84	0.08

*Indicates MANOVA results instead of MANCOVA.

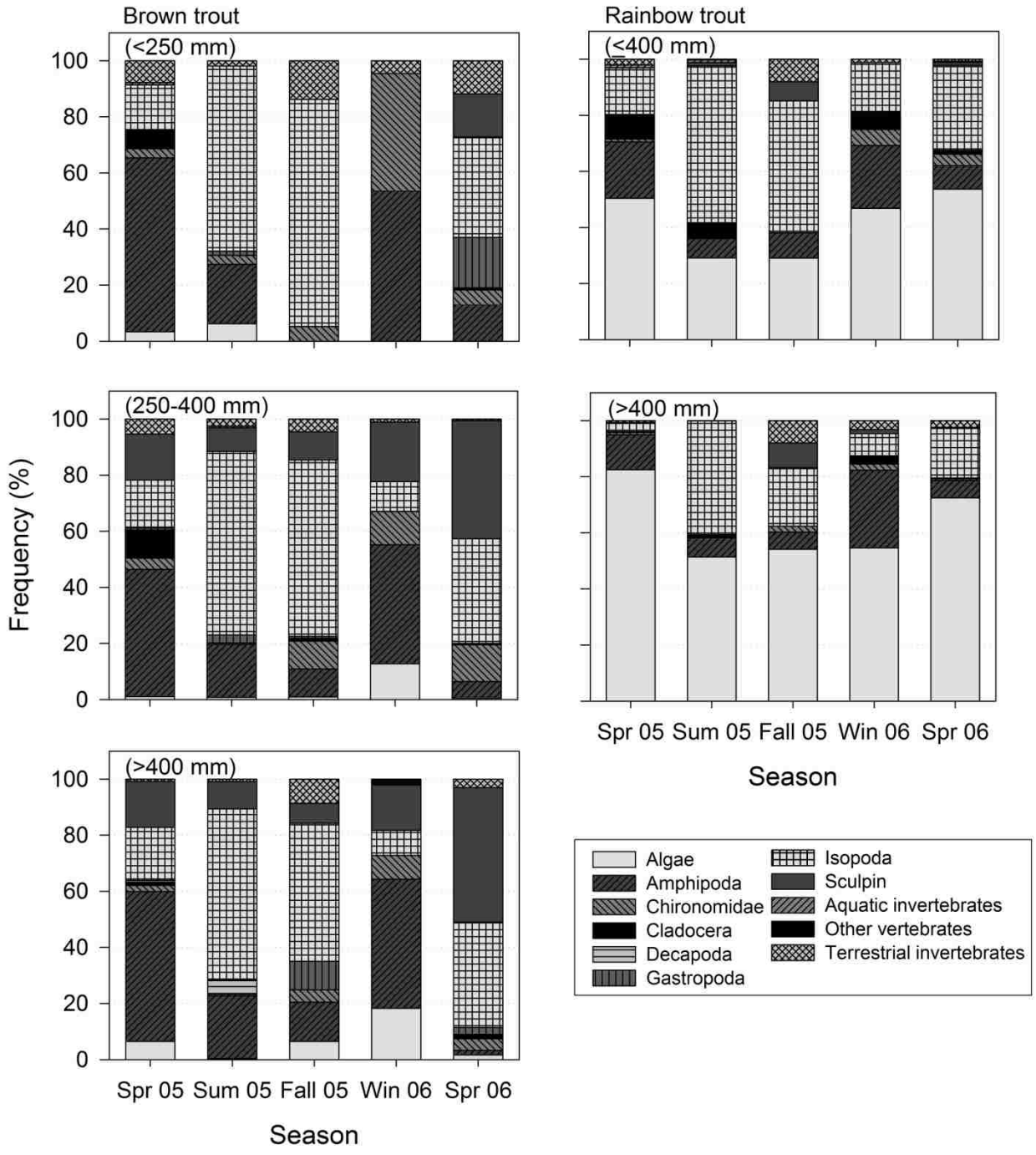

Figure 3. Diet compositions based on percent frequency of occurrence in three size classes of brown trout and two size classes of rainbow trout collected at Bull Shoals C-R area from May 2005 to May 2006.

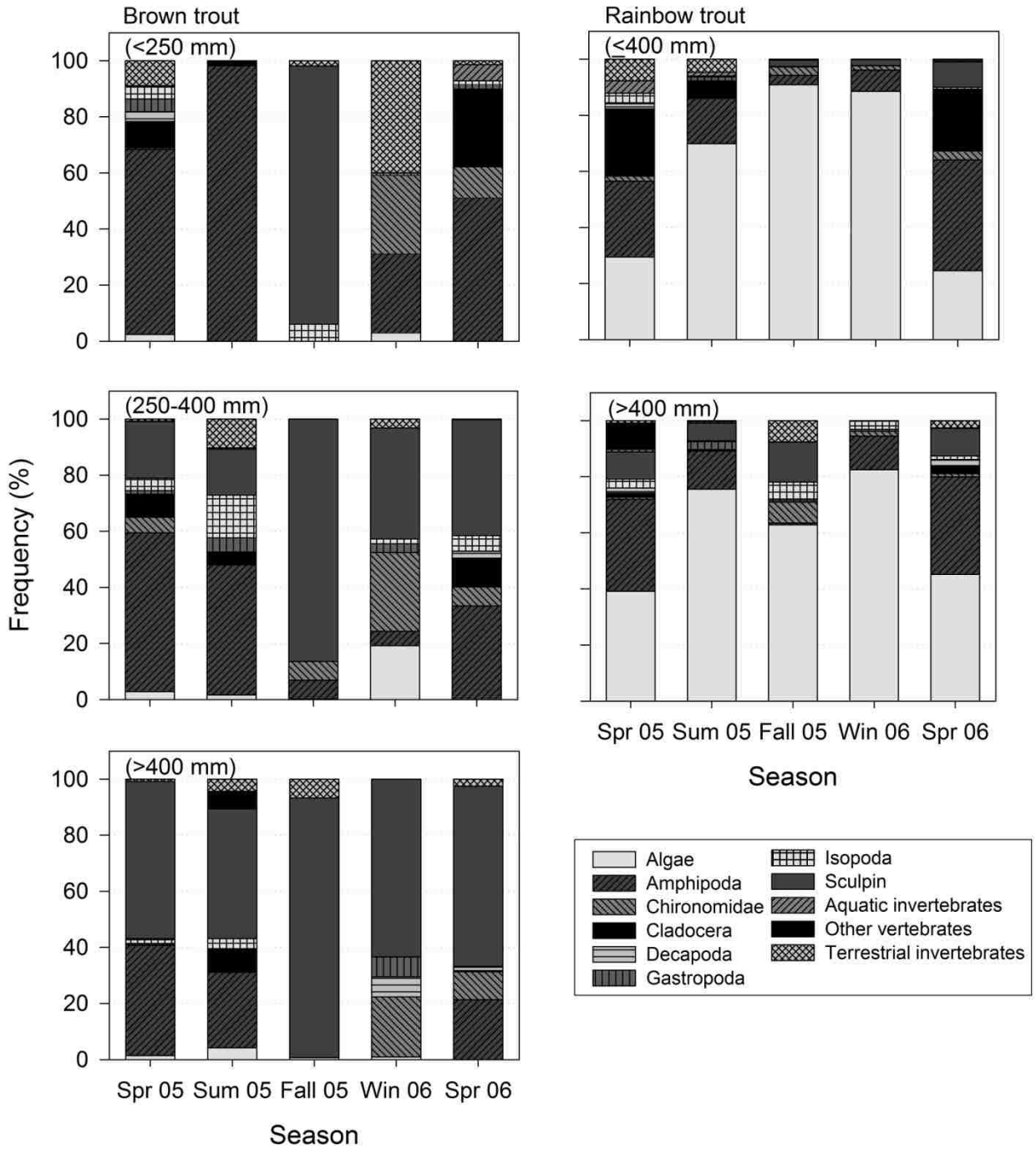

Figure 4. Diet compositions based on percent frequency of occurrence in three size classes of brown trout and two size classes of rainbow trout collected at Norfork C-R area from June 2005 to June 2006.

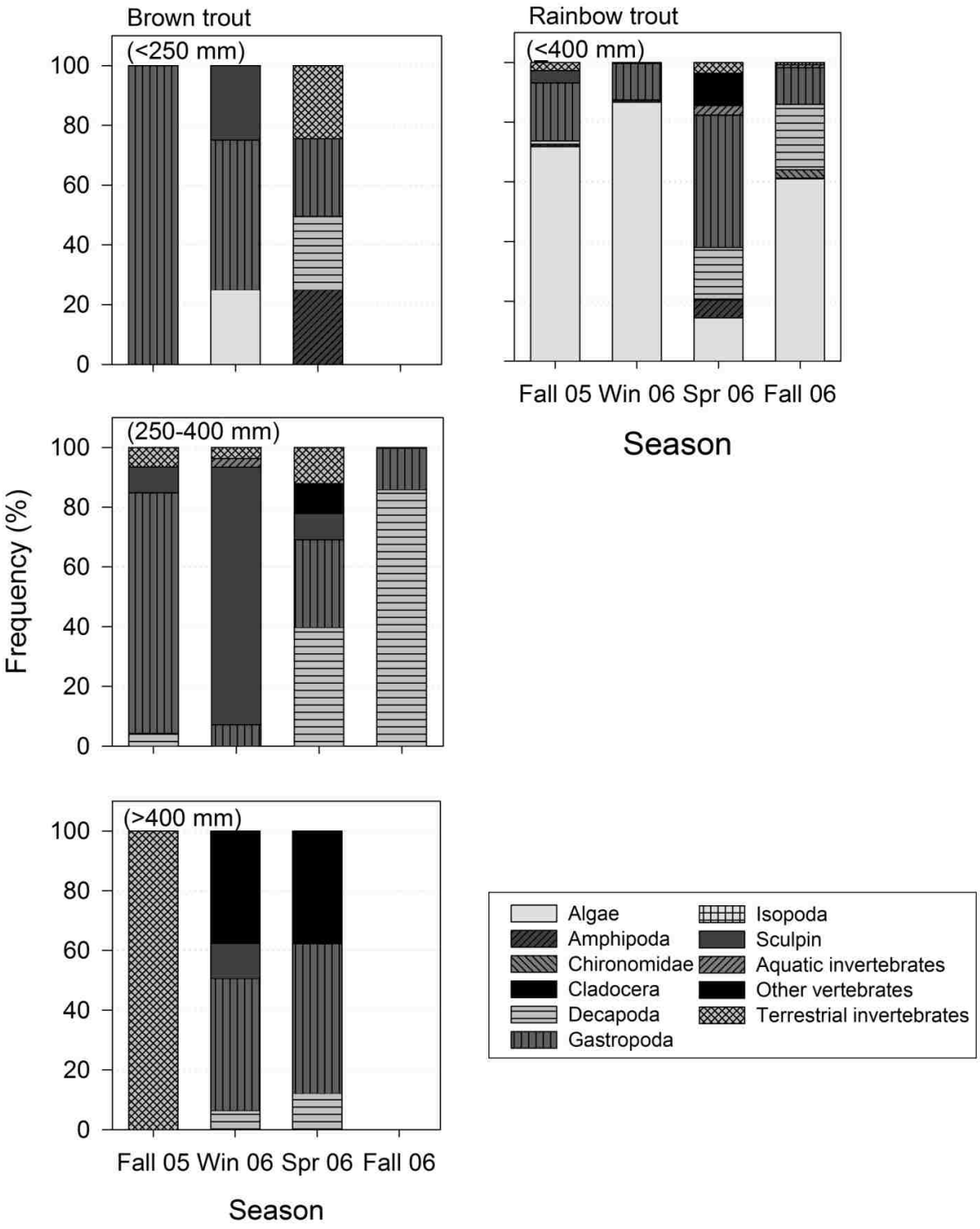

Figure 5. Diet compositions based on percent frequency of occurrence in three size classes of brown trout and two size classes of rainbow trout collected at Sylamore C-R area from October 2005 to October 2006.

Table 2. Energy densities ($J \cdot g^{-1}$) estimates of dry weight (DW) and wet weight (WW) of prey categories used in diets.

Prey	Site	Season	*N*	% DW	$J \cdot g^{-1}$ DW (±SE)	$J \cdot g^{-1}$ WW (±SE)	Sources
Amphipoda							
Gammarus spp.	Norfork	Spr 06	2	23.12	14,259 (213)	3,297 (49)	
Aquatic invertebrates						3,815[a]	Cummins and Wuycheck (1971)
Chironomidae[b]			3	13.56	23,117 (290)	3,134 (39)	
Cladocera							
Daphnia spp.						3,812	Luecke and Brandt (1993)
Decapoda							
Orconectes neglectus	Bull Shoals	Fall 05	3	23.29	13,073 (561)	3,044 (131)	
	Norfork	Spr 05	3	23.29	11,061 (289)	2,575 (67)	
Gastropoda							
Pleuroceridae	Bull Shoals	Spr 06	2	16.62	15,102 (10)	2,510 (2)	
Physidae	Norfork	Spr 06	3	20.08	13,532 (62)	2,717 (12)	
Isopoda							
Lirceus spp.	Bull Shoals	Spr 06	2	22.28	13,270 (19)	2,956 (4)	
	Norfork	Spr 06	2	21.58	13,629 (90)	2,942 (19)	
Other vertebrates							
Oncorhynchus mykiss						5,764	Hanson et al. (1997)
Etheostoma spp.						3,345	Madon and Culver (1993)
Notropis spp.						4,995	Bryan et al. (1996)
Hypentelium nigricans						4,657[c]	
Moxostoma carinatium						4,657[c]	
Sculpin							
Cottus hypselurus	Bull Shoals	Spr 05	2	24.36	21,648 (682)	5,273 (166)	
		Sum 05	2	24.36	19,997 (1,546)	4,871 (377)	
		Fall 05	2	24.36	18,342 (1,072)	4,468 (261)	
		Win 06	2	24.36	16,686 (598)	4,064 (146)	
		Spr 06	2	24.36	16,652 (1,180)	4,056 (287)	
	Norfork	Spr 05	2	24.36	17,236 (1,010)	4,198 (246)	
		Sum 05	2	24.36	19,820 (2,046)	4,828 (498)	
		Fall 05	2	24.36	20,039 (61)	4,881 (15)	
		Spr 06	2	24.36	16,813 (943)	4,095 (230)	
		Win 06	2	24.36	18,437 (659)	4,491 (161)	
Terrestrial invertebrates						3,170[d]	Cummins and Wuycheck (1971)

[a] Average of aquatic invertebrates (e.g. Ephemeroptera, Tricoptera)
[b] Commercially available chironomids
[c] Average of other fish
[d] Average of terrestrial invertebrates

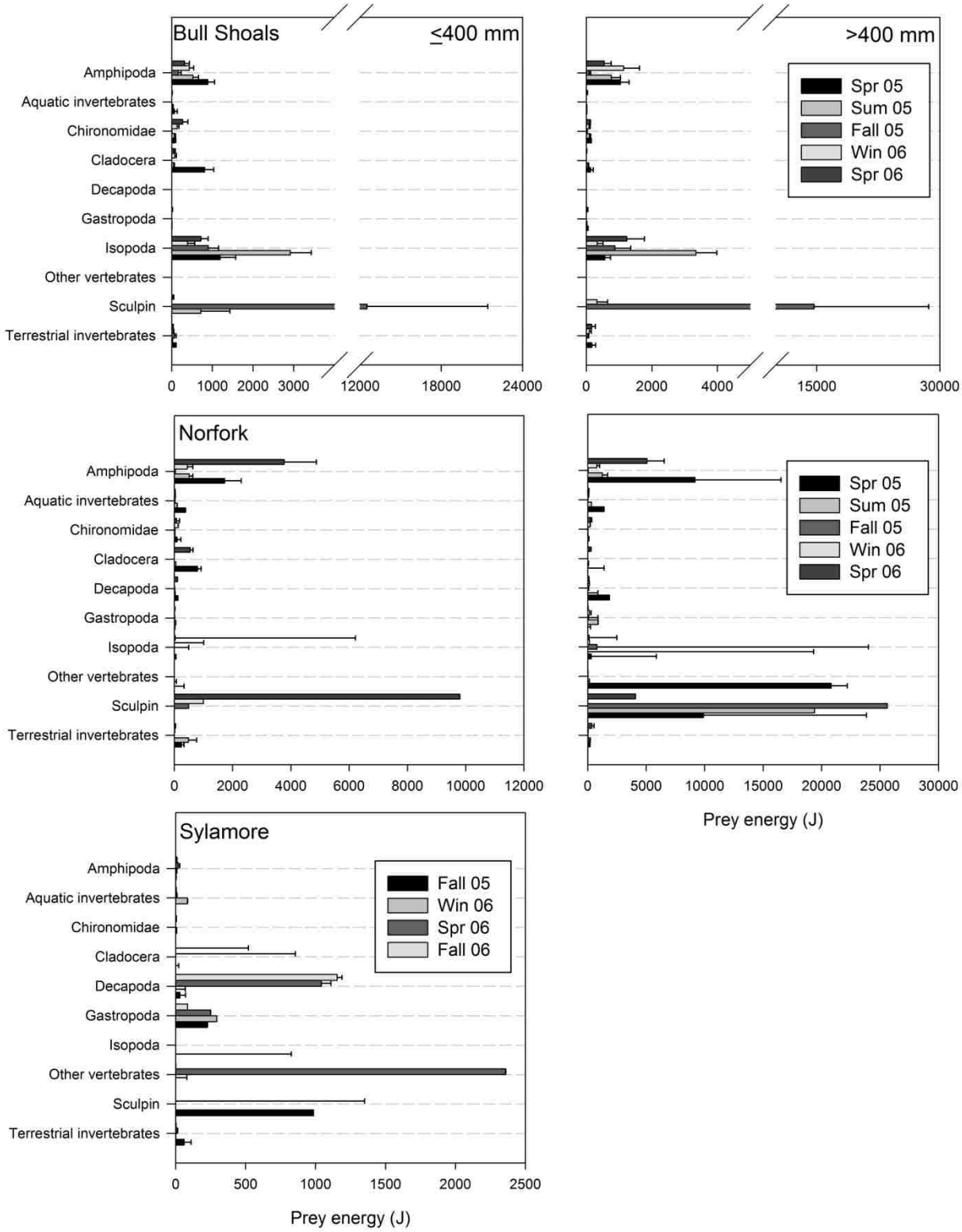

Figure 6. Energy (J) of prey items found in GCA (mean ± S.E.) of rainbow trout across by season among the C-R areas.

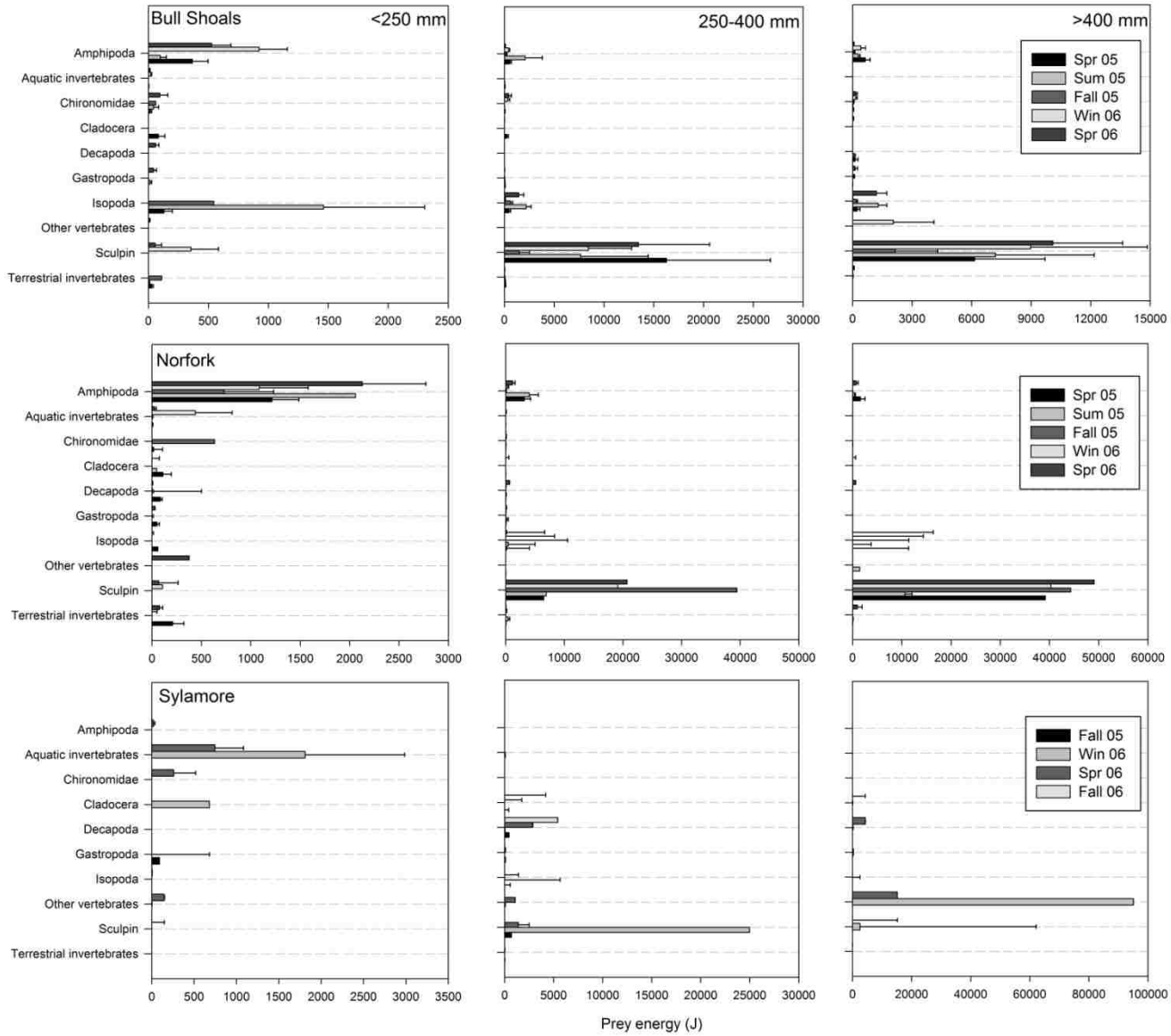

Figure 7. Energy (J) of prey items found in GCA (mean ± S.E.) of brown trout across by season among the C-R areas.

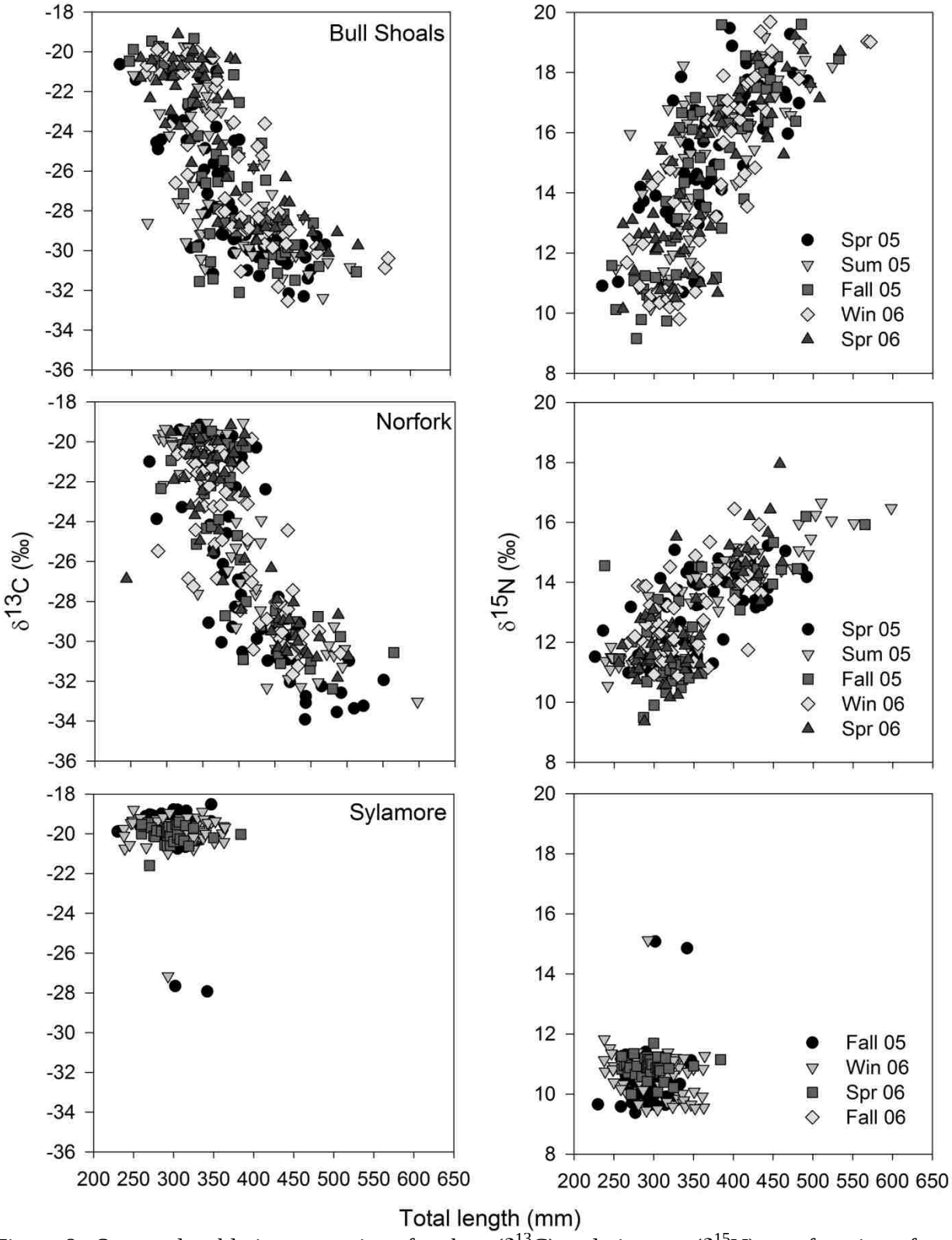

Figure 8. Seasonal stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) as a function of total length in rainbow trout at Bull Shoals, Norfork, and Sylamore C-R areas.

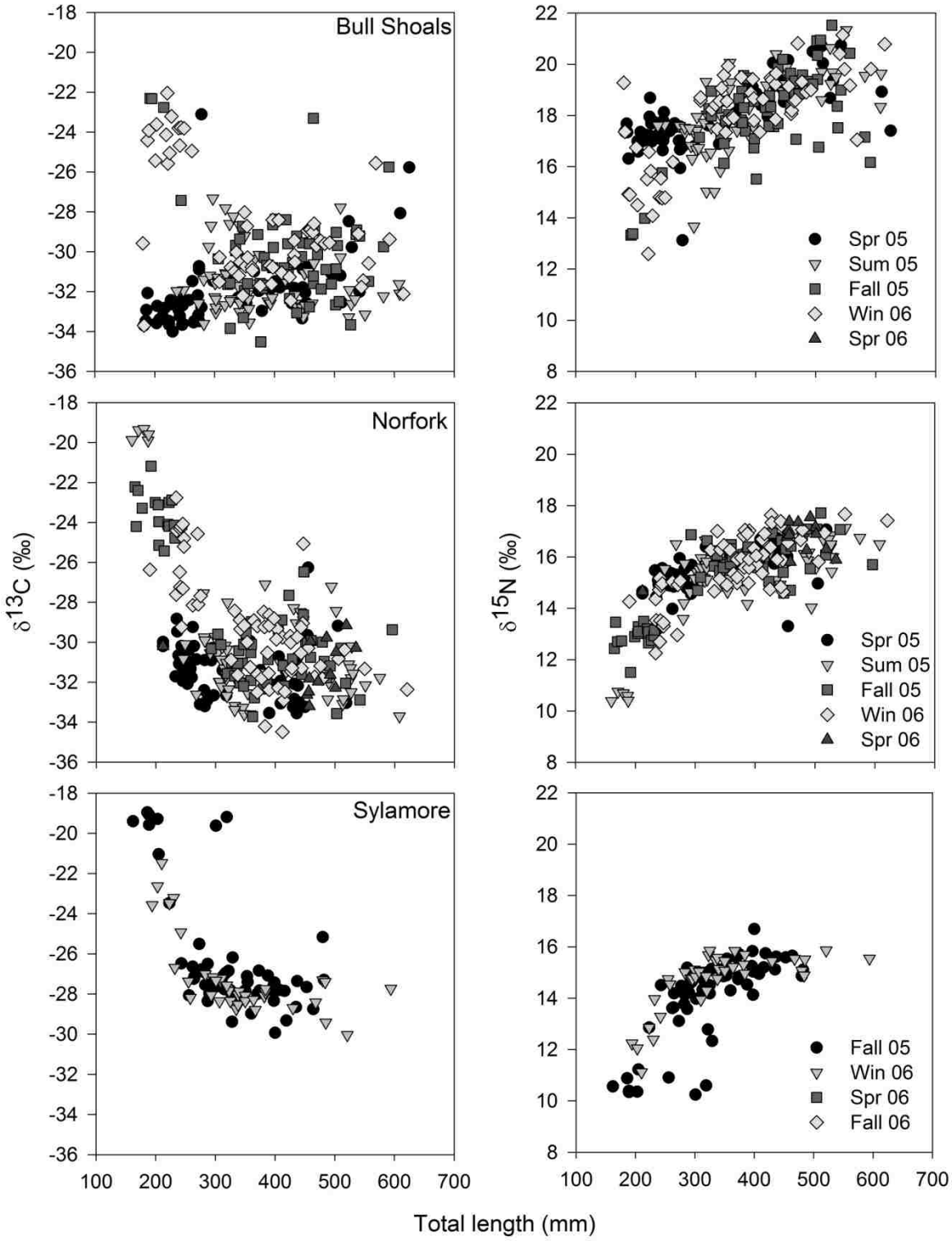

Figure 9. Seasonal stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) as a function of total length in brown trout at Bull Shoals, Norfork, and Sylamore C-R areas.

Table 3. Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) and size (TL/CL/SL) of prey collected at Bull Shoals by season and species and subsequently used in the mixing model.

					$\delta^{13}C$ (‰)				$\delta^{15}N$ (‰)					TL/CL/SL			
Season	**Order**	**Family**	**Species**	***N***	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	***N***	**Mean**	**SE**	**Min**	**Max**
Spr 05	Amphipoda	Gammaridae	*Gammarus* spp.	5	-33.7	0.5	-34.9	-32.7	20.2	0.2	19.5	20.7	25	5.7	0.21	4	7.8
	Cladophorales	Cladophoraceae	*Cladophora* spp.	3	-35.3	0.5	-36.0	-34.3	28.9	0.2	28.5	29.2					
	Cymbellales	Gomphonemataceae	*Didymosphenia geminata*	3	-21.2	0.1	-21.4	-21.0	14.1	0.4	13.4	14.8					
	Decapoda	Cambaridae	*Orconectes neglectus*	1	-31.3		-31.3	-31.3	14.7		14.7	14.7	1	51.0		51	51
	Diptera	Chironomidae		5	-32.5	0.9	-35.0	-30.4	22.1	0.8	20.3	24.8	25	4.2	0.18	2	5.8
	Isopoda	Asellidae	*Lirceus* spp.	4	-30.3	0.2	-30.7	-29.7	18.1	0.2	17.6	18.5	25	6.2	0.25	4	8.5
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	15	-31.2	0.8	-35.8	-26.4	18.6	0.2	16.6	19.7	15	61.1	2.99	44	80
Sum 05	Amphipoda	Gammaridae	*Gammarus* spp.	7	-31.6	0.2	-32.0	-30.8	14.3	0.2	13.7	15.2	25	6.0	0.23	4	8
	Cladophorales	Cladophoraceae	*Cladophora* spp.	5	-36.2	0.2	-36.6	-35.4	13.5	0.2	12.7	14.2					
	Diptera	Chironomidae		8	-36.5	0.3	-37.4	-34.7	12.1	0.5	10.5	14.1	25	7.6	0.25	5.5	10.3
	Gastropoda[1]	Physidae		1	-34.0				11.1				5	6.4	0.22	3.3	9.5
	Gastropoda[1]	Pleuroceridae		1	-26.3				11.4				6	7.5	0.18	4.5	8.3
	Isopoda	Asellidae	*Lirceus* spp.	8	-31.9	0.5	-33.8	-30.3	13.1	0.3	12.0	14.2	25	5.8	0.35	2.2	10.2
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	6	-34.0	0.4	-35.5	-32.4	20.3	1.0	17.5	24.0	6	65.3	8.28	38	91
Fall 05	Amphipoda	Gammaridae	*Gammarus* spp.	5	-29.0	0.5	-30.6	-28.1	12.2	0.2	11.7	12.6	25	6.5	0.17	4.9	8.2
	Decapoda	Cambaridae	*Orconectes neglectus*	7	-30.0	0.3	-30.9	-28.5	13.4	0.2	12.7	14.3	7	34.4	3.51	24.1	49.8
	Diptera	Chironomidae		3	-28.7	0.4	-29.4	-28.0	12.9	0.7	11.7	14.1	15	5.6	0.57	3.8	7.5
	Gastropoda[1]	Physidae		5	-31.2	0.3	-32.2	-30.5	12.3	0.2	11.6	13.1	15	2.5	0.12	1.7	3.5
	Isopoda	Asellidae	*Lirceus* spp.	5	-27.9	0.2	-28.2	-27.1	11.1	0.1	10.7	11.4	25	6.9	0.31	3	9.2
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	9	-32.3	0.3	-33.4	-30.4	15.9	0.3	14.8	18.4	9	28.6	3.54	20	54
Win 06	Amphipoda	Gammaridae	*Gammarus* spp.	5	-28.5	0.2	-28.9	-28.1	15.5	0.1	15.2	16.1	25	6.7	0.20	5	8.4
	Cladocera	Daphniidae	*Daphnia* spp.	5	-34.9	0.1	-35.0	-34.7	19.1	0.0	19.1	19.2	105	1.9	0.02	1.5	2.5
	Diptera	Chironomidae		5	-28.2	1.0	-31.1	-25.0	14.6	0.5	12.8	15.3	25	5.5	0.25	3.1	8.8
	Gastropoda[1]	Physidae		3	-30.6	0.4	-31.5	-30.2	13.9	0.5	13.3	14.8	9	3.5	0.62	2	5.9
	Isopoda	Asellidae	*Lirceus* spp.	5	-27.2	0.1	-27.4	-26.8	14.6	0.3	14.0	15.3	25	7.4	0.35	4.8	10.5
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	8	-31.6	0.6	-33.8	-29.8	18.6	0.3	17.6	19.7	8	50.1	8.80	19	87

					δ^{13}C (‰)				δ^{15}N (‰)					TL/CL/SL			
Season	**Order**	**Family**	**Species**	***N***	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	***N***	**Mean**	**SE**	**Min**	**Max**
Spr 06	Amphipoda	Gammaridae	*Gammarus* spp.	5	-28.8	0.6	-31.1	-28.1	15.7	0.4	15.0	17.3	25	4.7	0.19	3.5	6.9
	Cladocera	Daphniidae	*Daphnia* spp.	5	-32.1	0.1	-32.5	-31.9	15.5	0.1	15.1	15.8	106	2.2	0.04	1.2	3.3
	Cladophorales	Cladophoraceae	*Cladophora* spp.	5	-35.4	0.3	-36.1	-34.5	8.1	0.1	7.6	8.4					
	Cymbellales	Gomphonemataceae	*Didymosphenia geminata*	5	-22.3	0.2	-22.8	-21.7	11.7	0.1	11.5	12.0					
	Diptera	Chironomidae		10	-28.4	0.5	-30.5	-26.1	12.7	0.5	10.4	14.5	46	4.9	0.19	3.3	8.1
	Gastropoda[1]	Pleuroceridae		5	-27.3	0.2	-28.0	-26.7	12.3	0.3	11.3	12.8	25	3.3	0.06	2.4	3.9
	Isopoda	Asellidae	*Lirceus* spp.	5	-28.6	0.2	-29.3	-27.9	14.5	0.2	14.0	15.1	25	6.2	0.18	4.7	9
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	8	-30.1	0.6	-33.0	-27.7	18.8	0.3	17.4	20.4	8	64.0	6.20	37	87

[1]Represents Class

Table 4. Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) and size (TL/CL/SL) of prey collected at Norfork by season and species and subsequently used in the mixing model.

					$\delta^{13}C$ (‰)				$\delta^{15}N$ (‰)					TL/CL/SL			
Season	**Order**	**Family**	**Species**	***N***	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	***N***	**Mean**	**SE**	**Min**	**Max**
Spr 05	Amphipoda	Gammaridae	*Gammarus* spp.	5	-31.6	0.2	-32.1	-30.9	9.7	0.4	8.7	11.0	25	7.7	0.27	5.3	10.2
	Cladocera	Daphniidae	*Daphnia* spp.	8	-34.9	0.1	-35.3	-34.6	12.7	0.1	12.3	13.2	159	2.6	0.05	1.5	3.5
	Cladophorales	Cladophoraceae	*Cladophora* spp.	5	-32.0	1.7	-35.2	-25.7	9.7	0.6	8.1	11.1					
	Decapoda	Cambaridae	*Orconectes neglectus*	3	-29.2	0.5	-29.8	-28.2	10.0	0.5	9.2	10.9	3	36.7	4.63	29	45
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	14	-33.7	0.4	-36.4	-31.3	15.2	0.2	14.3	16.4	14	69.8	4.56	49	103
Sum 05	Amphipoda	Gammaridae	*Gammarus* spp.	7	-29.2	0.2	-29.9	-28.4	9.6	0.1	9.4	10.1	25	5.7	0.22	4.1	8
	Diptera	Chironomidae		9	-31.1	0.6	-33.7	-28.6	10.1	0.2	9.3	11.0	45	5.8	0.20	3.5	7.6
	Gastropoda[1]	Physidae		5	-32.7	0.4	-33.8	-31.6	10.4	0.0	10.2	10.5	24	6.2	0.23	4.3	7.6
	Isopoda	Asellidae	*Lirceus* spp.	8	-29.7	0.4	-31.4	-28.0	10.2	0.3	8.7	10.9	26	6.7	0.35	3.8	9
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	9	-32.9	0.4	-34.0	-29.9	13.9	0.3	12.8	15.2	9	58.1	7.82	25	86
Fall 05	Amphipoda	Gammaridae	*Gammarus* spp.	5	-36.5	0.6	-38.1	-34.8	9.3	0.3	8.7	10.0	25	7.5	0.22	5.2	10.4
	Diptera	Chironomidae		5	-34.1	0.9	-36.2	-31.4	6.6	0.5	5.0	8.2	25	4.6	0.26	2.7	7.8
	Gastropoda[1]	Physidae		5	-39.7	0.8	-41.9	-37.5	6.8	0.5	5.2	8.3	20	4.3	0.31	1.8	7
	Isopoda	Asellidae	*Lirceus* spp.	5	-40.1	1.2	-42.8	-36.9	6.1	0.4	4.9	7.1	25	6.9	0.45	4.3	12.2
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	8	-32.3	0.2	-34.0	-31.7	13.8	0.2	13.2	14.5	8	57.8	5.26	34	77
Win 06	Amphipoda	Gammaridae	*Gammarus* spp.	5	-32.5	0.2	-33.0	-31.9	11.4	0.2	11.1	12.0	25	7.6	0.22	5.5	9.8
	Cladocera	Daphniidae	*Daphnia* spp.	5	-32.7	0.1	-33.1	-32.5	15.7	0.2	15.5	16.3	98	2.9	0.04	2.1	3.9
	Cladophorales	Cladophoraceae	*Cladophora* spp.	5	-34.5	0.1	-34.8	-34.1	8.1	0.5	6.9	9.3					
	Diptera	Chironomidae		5	-34.4	0.5	-36.0	-32.7	12.0	0.7	9.5	13.5	25	4.2	0.18	3	6.7
	Gastropoda[1]	Physidae		5	-33.2	0.5	-34.3	-31.6	9.9	0.5	8.7	11.5	25	5.4	0.32	2.2	8.8
	Isopoda	Asellidae	*Lirceus* spp.	5	-32.1	0.5	-33.4	-30.5	9.5	0.2	9.1	10.1	25	6.8	0.49	3	12.5
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	9	-33.4	0.3	-35.1	-32.3	14.9	0.1	14.4	15.4	9	72.1	8.91	37	128
Spr 06	Amphipoda	Gammaridae	*Gammarus* spp.	5	-30.7	0.2	-31.2	-30.2	12.3	0.1	12.0	12.6	25	7.2	0.23	5.3	9.1
	Cladocera	Daphniidae	*Daphnia* spp.	5	-34.0	0.1	-34.2	-33.8	13.4	0.2	12.9	13.8	105	2.5	0.06	1.5	3.9
	Diptera	Chironomidae		10	-34.2	0.5	-37.1	-30.7	9.8	0.1	9.1	10.3	52	4.7	0.15	2	6.6

					δ^{13}C (‰)				δ^{15}N (‰)					TL/CL/SL			
Season	**Order**	**Family**	**Species**	***N***	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	***N***	**Mean**	**SE**	**Min**	**Max**
	Gastropoda[1]	Physidae		5	-30.4	0.2	-30.8	-30.0	9.5	0.1	9.3	9.7	15	4.3	0.24	2.9	6.1
	Isopoda	Asellidae	*Lirceus* spp.	4	-29.0	0.4	-29.9	-28.1	10.0	0.1	9.6	10.3	20	8.4	0.31	4.5	11.8
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	9	-31.5	0.2	-32.2	-30.3	15.4	0.2	14.6	16.1	9	67.8	4.02	52	86

[1]Represents Class

Table 5. Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) and size (TL/CL/SL) of prey collected at Sylamore by season and species and subsequently used in the mixing model.

					$\delta^{13}C$ (‰)				$\delta^{15}N$ (‰)					TL/CL/SL			
Season	**Order**	**Family**	**Species**	***N***	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	***N***	**Mean**	**SE**	**Min**	**Max**
Win 06	Decapoda	Cambaridae	*Orconectes neglectus*	3	-28.3	1.4	-31.1	-26.9	9.4	0.6	8.6	10.4	3	22.3	0.88	21	24
	Diptera	Chironomidae		3	-34.7	0.7	-35.5	-33.3	9.0	0.7	7.8	10.1	15	4.8	0.17	3.5	5.6
	Ephemeroptera	Ephemeridae		1	-34.8				9.3				3	8.1	0.12	7.9	8.3
	Ephemeroptera	Heptageniidae		1	-31.8				10.4				4	5.3	0.56	3.8	6.3
	Ephemeroptera	Oligoneuriidae		1	-32.8				11.5				3	11.6			
	Perciformes	Percidae	*Etheostoma blennioides*	1	-30.9				14.1				1	64			
	Perciformes	Percidae	*Etheostoma caeruleum*	2	-30.3	1.1	-31.4	-29.2	13.9	0.2	13.8	14.1	2	44.5	7.50	37	52
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	4	-31.0	0.1	-31.2	-30.7	13.5	0.1	13.4	13.6	4	46.0	2.35	42	51
Spr 06	Amphipoda	Gammaridae	*Gammarus* spp.	5	-30.8	0.3	-31.8	-30.3	9.3	0.2	8.8	9.8	25	6.7	0.12	5.8	8
	Cypriniformes	Cyprinidae	*Notropis pilsbryi*	1	-28.5				12.3				1	101			
	Cypriniformes	Catostomidae	*Moxostoma carinatum*	1	-29.3				11.9				1	200			
	Cypriniformes	Cyprinidae	*Notropis chrysocephalus*	3	-28.5	0.4	-29.4	-28.0	11.9	0.4	11.1	12.4	3	141.0	6.03	134	153
	Diptera	Chironomidae		5	-32.6	0.9	-35.9	-31.3	7.4	0.7	6.4	10.1	25	5.1	0.38	3	10.4
	Ephemeroptera	Heptageniidae		4	-30.0	0.2	-30.3	-29.4	7.3	0.2	6.8	7.6	12	5.9	0.24	4.5	7.3
	Ephemeroptera	Isonychiidae	*Isonychia* spp.	4	-30.1	0.4	-31.2	-29.6	8.3	0.2	8.0	8.8	5	6.6	0.34	5.9	7.6
	Gastropoda[1]	Pleuroceridae		5	-31.9	0.2	-32.6	-31.5	10.2	0.3	9.1	10.6	25	5.0	0.36	3	9.2
	Isopoda	Asellidae	*Lirceus* spp.	2	-25.5	0.5	-26.0	-25.0	7.2	1.1	6.1	8.4	6	4.7	0.15	4.5	4.8
	Perciformes	Centrarchidae	*Pomoxis nigromaculatus*	1	-27.8				14.6				1	106			
	Perciformes	Centrarchidae	*Lepomis macrochirus*	1	-27.8				11.9				1	113			
	Plecoptera	Pteronarcyidae	*Pteronarcys* spp.	5	-32.7	0.1	-33.0	-32.4	7.7	0.1	7.5	8.0	20	15.3	0.41	10.2	18.2
	Trichoptera	Brachycentridae	*Brachycentrus* spp.	3	-33.2	0.2	-33.6	-32.8	7.9	0.0	7.8	8.0	9	4.2	0.22	3.8	5.2
	Trichoptera	Hydropsychidae		3	-30.9	0.0	-30.9	-30.9	8.7	0.1	8.5	8.8	10	7.9	0.50	6.2	9.5
Fall 06	Amphipoda	Gammaridae	*Gammarus* spp.	5	-32.3	0.3	-33.1	-31.8	8.7	0.1	8.5	9.1	25	6.6	0.18	4.7	8.1
	Cladophorales	Cladophoraceae	*Cladophora* spp.	6	-30.8	0.2	-31.7	-30.0	7.4	0.1	7.1	7.7					
	Cypriniformes	Cyprinidae	*Cyprinus carpio*	1	-30.3				9.3				1	175			

					δ^{13}C (‰)				δ^{15}N (‰)					TL/CL/SL			
Season	**Order**	**Family**	**Species**	***N***	**Mean**	**SE**	**Min**	**Max**	**Mean**	**SE**	**Min**	**Max**	***N***	**Mean**	**SE**	**Min**	**Max**
	Cypriniformes	Cyprinidae	*Notropis pilsbryi*	1	-28.4				11.2				1	100			
	Cypriniformes	Catostomidae	*Hypentelium nigricans*	1	-28.2				11.7				1	153			
	Cypriniformes	Catostomidae	*Moxostoma carinatum*	2	-28.3	0.4	-28.8	-27.9	12.4	0.3	12.1	12.7	2	143.5	1.50	142	145
	Cypriniformes	Cyprinidae	*Notropis chrysocephalus*	3	-28.1	0.2	-28.2	-27.9	10.8	0.4	10.1	11.4	3	123.7	3.84	118	131
	Decapoda	Cambaridae	*Orconectes neglectus*	3	-26.8	0.8	-28.2	-25.3	8.4	0.2	7.9	8.7	3	29.3	5.46	22	40
	Gastropoda[1]	Pleuroceridae		5	-31.0	0.3	-31.6	-30.2	10.6	0.2	9.9	11.1	25	6.3	0.21	4.2	8.2
	Perciformes	Percidae	*Etheostoma blennioides*	2	-28.0	0.1	-28.1	-27.9	15.1	0.3	14.8	15.4	2	111.5	14.50	97	126
	Perciformes	Centrarchidae	*Lepomis megalotis*	1	-28.0				11.3				1	105			
	Perciformes	Percidae	*Etheostoma caeruleum*	2	-29.5	0.5	-30.0	-29.0	13.4	0.1	13.2	13.6	3	59.0	1.53	57	62
	Plecoptera	Pteronarcyidae	*Pteronarcys* spp.	5	-33.7	0.2	-34.2	-32.9	8.1	0.1	7.8	8.3	15	24.0	0.67	20.1	28.2
	Scorpaeniformes	Cottidae	*Cottus hypselurus*	4	-30.5	0.5	-31.5	-29.4	13.5	0.1	13.2	13.8	15	81.5	6.30	69	99

[1]Represents Class

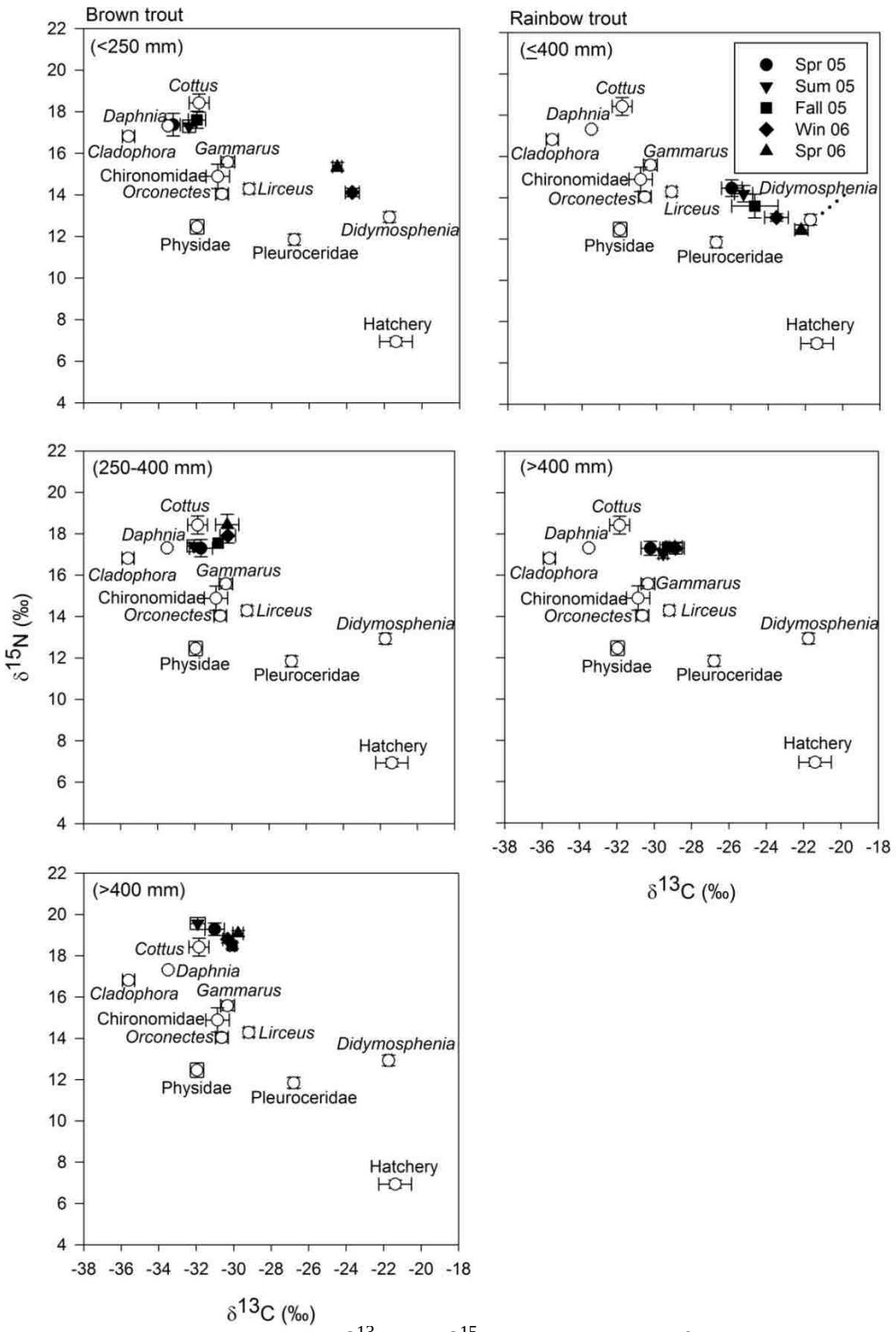

Figure 10. Isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$ compositions) of trout and potential prey sources in Bull Shoals C-R area.

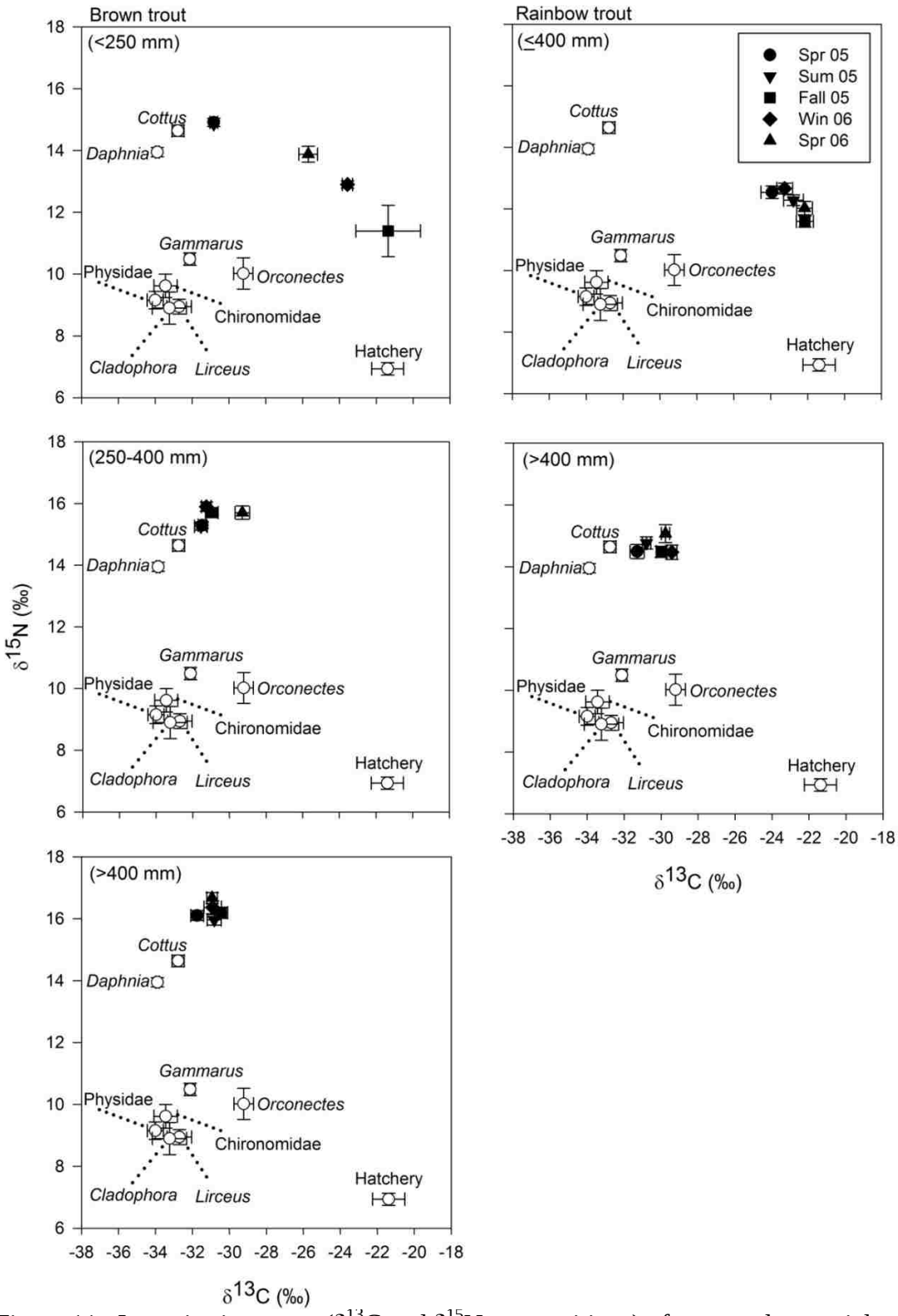

Figure 11. Isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$ compositions) of trout and potential prey sources in Norfork C-R area.

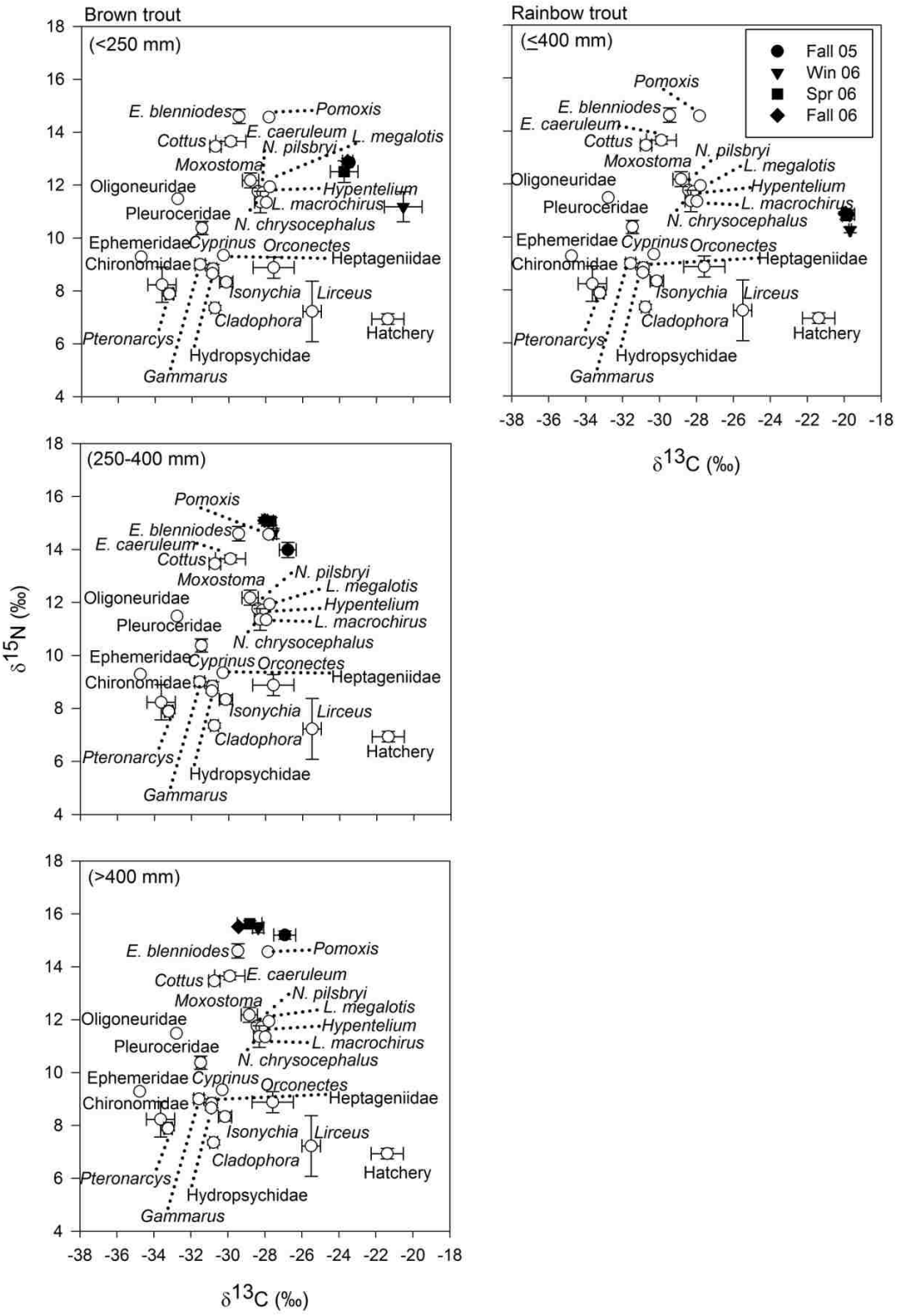

Figure 12. Isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$ compositions) of trout and potential prey sources in Sylamore C-R area.

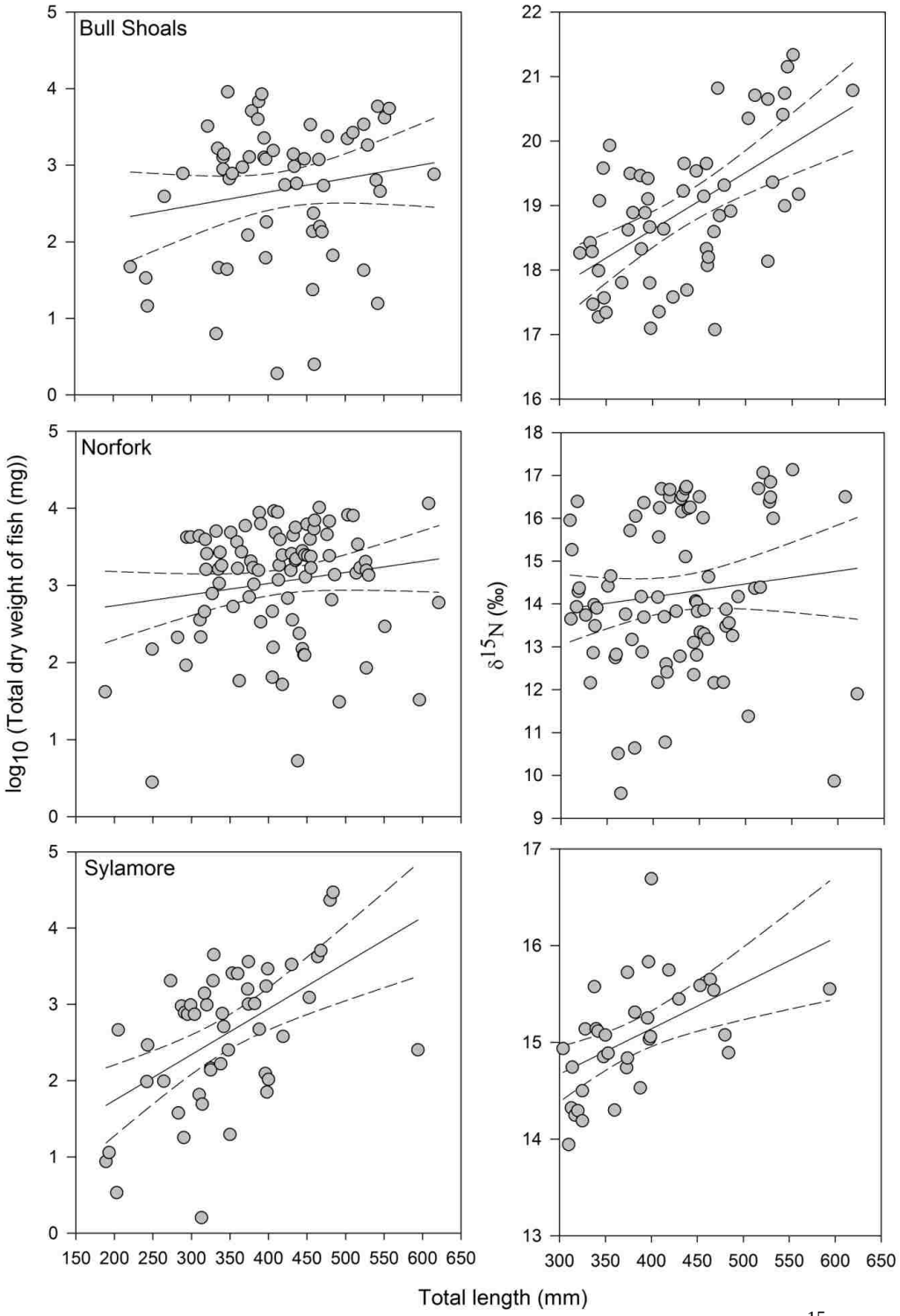

Figure 13. The $\log_{10}$ of dry weight of fish (mg) found in the GCA and $\delta^{15}N$ against the total length (mm) of brown trout by site. Linear regression fits are represented (solid line) along with 95% confidence intervals (dashed line).

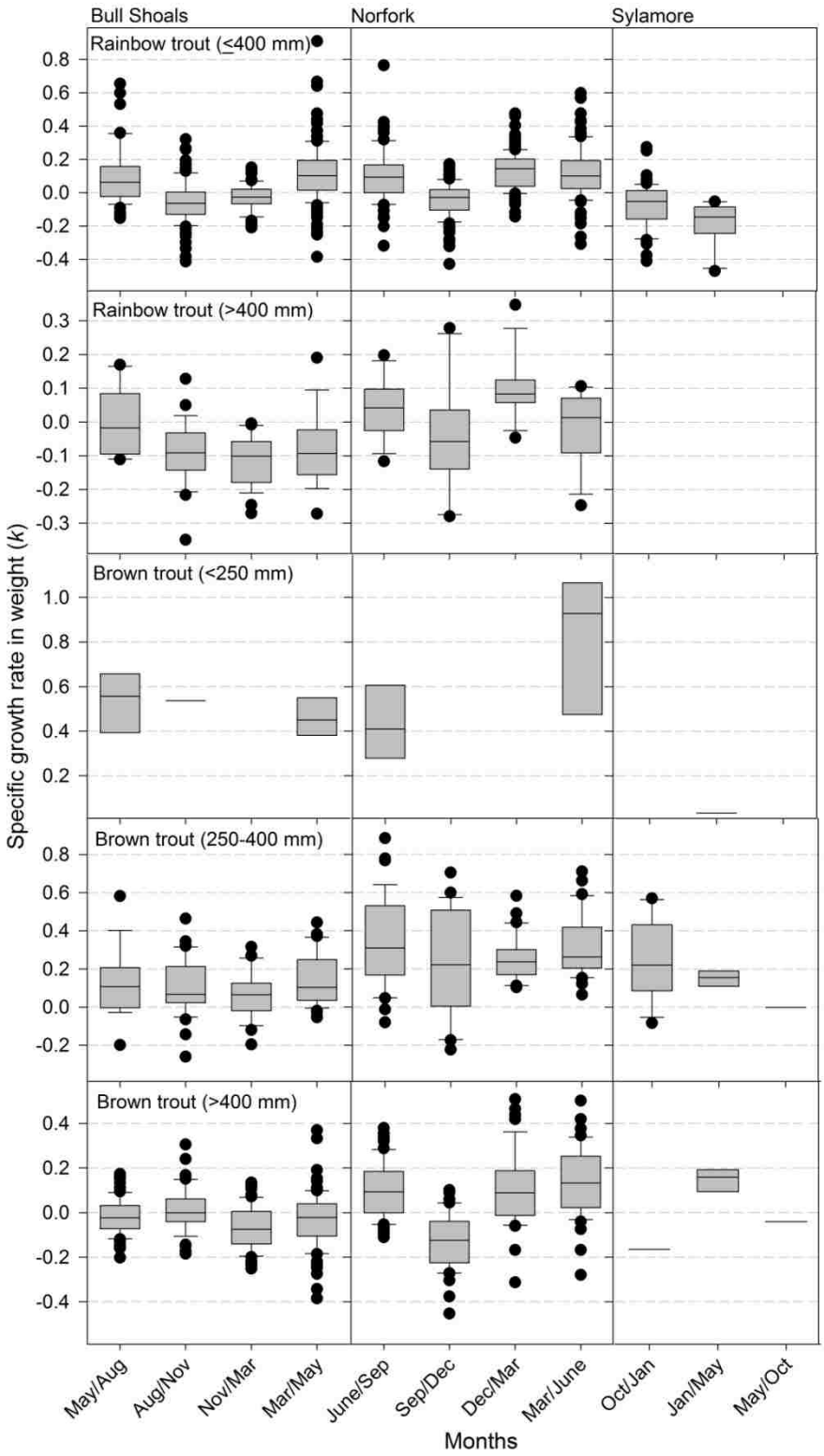

Figure 14. Specific growth rate in weight (*k*) (±SE) of brown and rainbow trout by monthly mark-recapture intervals for Bull Shoals, Norfork, and Sylmaore C-R area.

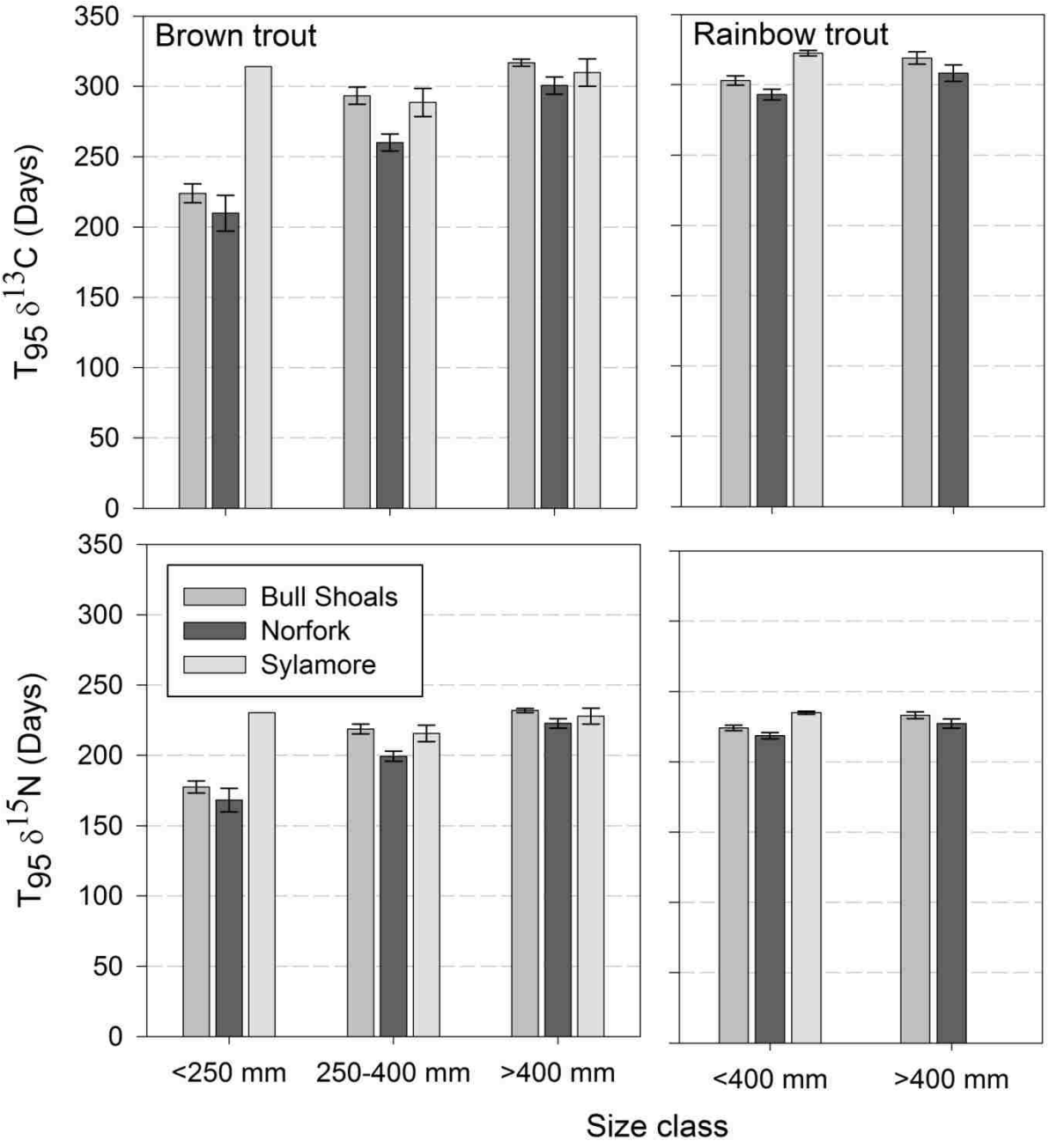

Figure 15. Estimated turnover times (days) to 95% (T_{95}) of equilibrium with the new diet (±SE) based on mark-recapture estimates of specific growth rate, *k* (day^{-1}).

Table 6. Percentage contribution (1-99 percentile ranges) of prey sources for each trout species in Bull Shoals C-R area by size class and season. The percent contributions were estimated using two different fractionation values (Δ) in the mixing model. Δ_a and Δ_b represent $\Delta\delta^{15}N$ of 3.4‰ and $\Delta\delta^{13}C$ of 0.8‰ and $\Delta\delta^{15}N$ of 3.8‰ and $\Delta\delta^{13}C$ of 1.8‰, respectively. The major prey sources (potentially ≥10% of assimilated prey source) are shown in bold.

			Spr 05		Sum 05		Fall 05		Win 06		Spr 06	
Trout	Size class	Prey	Δ_a	Δ_b	Δ_a	Δ_b	Δ_a	Δ_b	Δ_a	Δ_b	Δ_a	Δ_b
Rainbow	Small	Amphipoda	0-29	0	**12-44**	0-1	3-36	0	**26-27**	0	**18-20**	0-12
		Chironomidae	0-25	**50-56**	0-6	**43-52**	0-7	**40-43**	0-1	**29**	0-1	0-22
		Cladocera	0-22	0-6	0-5	0-7	0-6	1-4	0	5	0	0-18
		Hatchery	**45-56**	**42-44**	**50-56**	**48-50**	**57-63**	**55-56**	**72**	**66**	**80**	**71-78**
		Isopoda	0-42	0-2	0-37	0-1	0-38	0-1	1	0	0-1	0-17
	Large	Amphipoda	0	0	0	0	0	0	0	0	0	0
		Chironomidae	**30-31**	**83**	0	**39-40**	**0**	**43-45**	0	**26**	0	13
		Isopoda	**69-70**	**17**	**100**	**60-61**	**100**	**55-57**	**100**	**74**	**100**	**87**
Brown	Small	Amphipoda	0	0	0	0	0	0	0-4	0-24	0-7	0-44
		Chironomidae	**65-67**	**40**	**85-87**	**60**	**89**	**55-63**	0-1	0-35	0-3	0-23
		Gastropoda	0-1	0	0-1	0	0	0-4	0	2-22	0-2	0-14
		Hatchery	0	0	0	0	0	0	**71-72**	**51-58**	**61-63**	**41-51**
		Isopoda	0	0	0	0	0	0	0-3	0-30	0-5	0-48
		Sculpin	**33-34**	**60**	**13-14**	**40**	**11**	**37-41**	**25-28**	0-15	**31-37**	0-28
	Medium	Amphipoda	0	0	0	0	0	0	0	0	0-35	0
		Chironomidae	**96**	**78**	**94**	**70**	**61**	**94**	**83**	**84**	8-50	**84**
		Cladocera	0	**22**	6	**30**	0	6	0	**16**	0-21	16
		Isopoda	4	0	0	0	**39**	0	**17**	0	**24-68**	0
		Sculpin	0	0	0	0	0	0	0	0	0-10	0
	Large	Amphipoda	0-14	0	0-5	0	0-78	0	0-80	0	0	0
		Chironomidae	1-66	**45-47**	7-49	**20**	0-36	**79-85**	0-36	**68-74**	0	**76-78**
		Gastropoda	0-38	0-1	0-21	0	0-22	0-3	0-22	0-3	0	0-1
		Isopoda	0-7	0	0-2	0	6-50	0	0-42	0	**69**	0
		Sculpin	**27-58**	**53-54**	**50-70**	**80**	0-29	**15-18**	1-36	**26-29**	**31**	**22-23**

Table 7. Percentage contribution (1-99 percentile ranges) of prey sources for each trout species in Norfork C-R area by size class and season. The percent contributions were estimated using two different fractionation values (Δ) in the mixing model. Δ_a and Δ_b represent $\Delta\delta^{15}N$ of 3.4‰ and $\Delta\delta^{13}C$ of 0.8‰ and $\Delta\delta^{15}N$ of 3.8‰ and $\Delta\delta^{13}C$ of 1.8‰, respectively. The major prey sources (potentially ≥10% of assimilated prey source) are shown in bold.

			Spr 05		Sum 05		Fall 05		Win 06		Spr 06	
Trout	Size class	Prey	Δ_a	Δ_b	Δ_a	Δ_b	Δ_a	Δ_b	Δ_a	Δ_b	Δ_a	Δ_b
Rainbow	Small	Amphipoda	1	0-24	0	0-7	1	1-22	0	0	0-1	0-6
		Chironomidae	0	0-14	0	0-4	0	0-13	0	0	0	0-3
		Cladocera	**24**	**13-21**	**18**	**19-22**	**10**	1-8	**22**	**28**	**12-13**	**15-18**
		Hatchery	**75**	**63-66**	**82**	**74-75**	**89**	**77-79**	**78**	**72**	**87**	**78-80**
	Large	Amphipoda	**100**	**19-26**	**100**	**58-65**	**100**	**100**	**100**	**100**	**100**	**95-96**
		Chironomidae	0	**56-63**	0	**18-25**	0	0	0	0	0	0
		Sculpin	0	**17-19**	0	**16-18**	0	0	0	0	0	4-5
Brown	Small	Amphipoda	**100**	0-75	**100**	0-75	1	0-14	0	0-12	0	0-23
		Chironomidae	0	6-59	0	6-59	0	0-8	0	0-8	0	0-15
		Cladocera	0	0-38	0	0-38	0	0-8	0	0-28	0	0-43
		Hatchery	0	0-9	0	0-9	**94**	**84-86**	**75**	**65-68**	**58**	**46-52**
		Sculpin	0	0-31	0	0-31	5	0-6	0	2-25	**42**	0-35
	Medium	Amphipoda	**80-81**	0-28	**80-81**	0-22	**85**	8-58	**75**	0-46	**100**	**93**
		Chironomidae	0	0-58	0	2-57	0	0-24	0	0-41	0	0
		Cladocera	0	5-47	0	**14-50**	0	0-28	0	0-47	0	0
		Isopoda	0-1	0-46	0-1	0-45	0	0-40	0	0-38	0	0
		Sculpin	**19-20**	0-34	**19-20**	0-26	**15**	**11-49**	**25**	2-50	0	7
	Large	Amphipoda	**60**	0	**80-81**	**46-53**	**85**	**60**	**70**	**33-41**	**63-64**	**30-38**
		Chironomidae	0	**50-52**	0	4-11	0	0	0	7-13	0	3-10
		Sculpin	**40**	**48-50**	**19-20**	**42-44**	**15**	**40**	**30**	**52-55**	**36-37**	**59-61**

Table 8. Percentage contribution (1-99 percentile ranges) of prey sources for each trout species in Sylamore C-R area by size class and season. The percent contributions were estimated using two different fractionation values (Δ) in the mixing model. Δ_a and Δ_b represent $\Delta\delta^{15}N$ of 3.4‰ and $\Delta\delta^{13}C$ of 0.8‰ and $\Delta\delta^{15}N$ of 3.8‰ and $\Delta\delta^{13}C$ of 1.8‰, respectively. The major prey sources (potentially ≥10% of assimilated prey source) are shown in bold. No small brown trout were collected in fall 2006 (--).

			Fall 05		Win 06		Spr 06		Fall 06	
Trout	Size class	Prey	Δ_a	Δ_b	Δ_a	Δ_b	Δ_a	Δ_b	Δ_a	Δ_b
Rainbow	Small	Chironomidae	0	0	0	0	0	0-1	0	0-1
		Decapoda	0	0	0	0	0	0-4	0	0-3
		Gastropoda	0	0	0	0	0	0-2	0	0-2
		Hatchery	**100**	**97-98**	**100**	**100**	**100**	**96-98**	**100**	**95-96**
		Other vertebrates	0	2-3	0	0	0	0-3	0	2-5
Brown	Small	Amphipoda	0	0-9	0	0-2	0-78	0-19	--	--
		Decapoda	0	0-21	1	0-6	0-90	0-41	--	--
		Gastropoda	0	0-13	0	0-3	0-31	0-26	--	--
		Hatchery	**70**	**52-62**	**99**	**89-92**	2-14	**43-59**	--	--
		Sculpin	**30**	**25-30**	0	5-8	0-6	**12-20**	--	--
	Medium	Decapoda	**70-71**	**44-71**	**30-31**	**14-49**	**14**	0-43	5	0-34
		Gastropoda	0	0-16	0	0-53	0	6-31	0	**19-39**
		Sculpin	0	0-28	0	**14-34**	0	2-50	0	8-46
		Other vertebrates	**29-30**	0-41	**69-70**	0-37	**86**	0-67	**95**	0-53
	Large	Decapoda	**41-42**	**14-50**	0	0-24	0-34	0-14	0-31	0-2
		Gastropoda	0	0-7	0	**23-44**	0-6	**34-54**	0-23	**54-62**
		Sculpin	0	0-15	0	0-50	0-18	0-38	0-53	**25-43**
		Other vertebrates	**58-59**	2-61	**100**	0-39	4-70	0-31	0-55	0-9

Food availability and consumption dynamics of brown and rainbow trout populations within catch-and-release areas in Arkansas tailwaters: a bioenergetics modeling approach

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Abstract – We examined spatial and temporal consumption dynamics using an energy intake model and a bioenergetics model of rainbow trout, *Oncorhynchus mykiss*, and brown trout, *Salmo trutta*, within three catch-and-release (C-R) areas in Bull Shoals and Norfork tailwaters to determine whether trout populations were limited by food supply. We combined field data on seasonal growth rates, diet composition, abundance, and thermal experience with species-specific bioenergetics models to quantify seasonal consumption of benthic fish, macroinvertebrates, and *Daphnia* from reservoir releases. In 2005 and 2006, we tagged a total of 11,423 brown and rainbow trout for growth analysis and abundance estimates. Mean rainbow trout densities were higher (47 to 342 fish·ha^{-1}) than brown trout (3 to 84 fish·ha^{-1}) at all C-R areas. Norfork contained 2.0 to 7.2 times higher rainbow trout densities and 1.6 to 27.5 times higher brown trout densities than Bull Shoals and Sylamore C-R areas. Benthic macroinvertebrates at Bull Shoals and Norfork were 14.0 to 18.7 times higher in biomass than at Sylamore. Biomass of sculpin was approximately 2 to 8 times higher at Norfork than Bull Shoals and Sylamore. Food supply of drifting macroinvertebrates in the tailwaters peaked in spring and steadily decreased from spring through fall. Despite the lack of energetic value to rainbow trout, *Cladophora*, filamentous algae, and a nuisance diatom *Didymosphenia geminata* were found in high proportions in their stomachs and ranged seasonally from 15-91% in the diets. In contrast to rainbow trout foraging patterns, brown trout exhibited limited algae consumption in their diets. Bioenergetic simulations indicated bottlenecks in macroinvertebrate food supply emerged for trout. If trout only had access to drifting macroinvertebrates, the seasonal consumption by trout would have exceeded the biomass of macroinvertebrates available, particularly in relation to amphipods, chironomids, and isopods. At all sites rainbow trout daily ration was significantly below the minimum maintenance ration in the winter despite

reduced metabolic costs from the lower water temperatures and suggests a metabolic deficiency and bottleneck in food availability during this time period. Large rainbow trout failed to consume sufficient energy to exceed maintenance ration and exhibited slow or negative seasonal growth suggesting that poorer energetic conditions existed for this size class. In contrast, brown trout experienced high growth rates at lower densities than rainbow trout. Growth rate differences between brown and rainbow trout may result from brown trout shifting towards the incorporation of more energetically profitable prey fish. We found that the forage base may severely limit the numbers of large rainbow trout in the C-R areas. Brown trout experienced limited temporal bottlenecks in food availability and this species may be more suited for C-R areas from a forage base perspective.

Key words: consumption, prey availability, diets, bioenergetics simulations

Introduction

Catch-and-release (C-R) regulations have been readily adopted in many waters as a fisheries management tool for a diverse array of fishes (Muoneke and Childress 1994) and establish a zero-creel limit regulation and no fish of any size can be harvested. If properly applied, C-R regulations provide a fishery management response to potential angling-induced impacts on fish populations by reducing angling mortality leading to increased residence times of fish and higher densities of larger fish (Anderson and Nehring 1984; Carline et al. 1991; Lucy and Studholme 2002). Implicit in C-R regulations is the assumption that the released fish will survive and grow, and that fish in river systems will remain within the section of designated C-R restrictions (i.e. limited movement) (Schill et al. 1986; Wydoski 1977).

Despite the rapid incorporation of C-R regulations into many salmonid fisheries management programs, limited data exist to predict the success of such regulations (Cooke and Schramm 2007; Matlock 2002). Typically, C-R studies address factors that affect immediate or delayed mortality rates in fish populations and to a lesser extent sub-lethal effects (Meka and Margraf 2007; Pollock and Pine 2007). A component lacking in many C-R studies is the evaluation of growth and production of fish populations in response to increased density-dependent factors from a food availability perspective (Arlinghaus et al. 2007; Cooke and Schramm 2007). If food supply is limited, intraspecific and interspecific competition may increase, leading to decreased growth. Growth is a function of food availability (i.e. proportion of potential prey detected, captured, and consumed), metabolic costs including those of obtaining and processing food, and the assimilation efficiency of the food (Fausch 1984). Thus, a decrease in food availability affects growth, and therefore, population size structure. Food limitation has been found to occur in both regulated rivers (Filbert and Hawkins 1995; Weiland and Hayward 1997) and unregulated streams (Cada et al. 1987; Ensign et al. 1990; Huryn 1996). Food availability for salmonids is generally described as the abundance or biomass of benthic macroinvertebrates (Jowett 1995). However, abundance and biomass of benthic macroinvertebrates or 'invertebrate production' may not necessarily constitute the total amount of food available or 'prey production' (Poff and Huryn 1998). Allen (1951) found the estimated production of benthic macroinvertebrates was insufficient to support trout production in a New Zealand stream while still providing a surplus of macroinvertebrates (i.e., "Allen paradox"). An inherent complexity in studies assessing food-limitation is determining what constitutes available prey for salmonids. Salmonids typically feed opportunistically from the drift (Bachman 1984; Filbert and Hawkins 1995; Rader 1997); however, some salmonids have been found to exhibit an

epibenthic foraging strategy and/or have shifted ontogenetically to piscivory (Tippets and Moyle 1978; Weiland and Hayward 1997; Yard et al. 2011). Also, the vulnerability of drifting and benthic macroinvertebrates to trout predation varies depending on taxon, size, mobility, and drift behavior (Rader 1997).

In Arkansas tailwaters, nonnative rainbow trout, *Oncorhynchus mykiss*, and brown trout, *Salmo trutta* are highly desirable and economically important fisheries and often experience high fishing pressure (>1,000 angler-hours per hectare annually) (Bowman et al. 1996). The use of C-R regulations in rivers and streams that receive high fishing pressure have been effective in sustaining high numbers of large trout and higher catch rates (Anderson and Nehring 1984; Carline et al. 1991; Engstrom-Heg 1981). Several C-R areas were implemented in Arkansas tailwaters in 1995 with the goal of providing increased catch rates of larger trout. Implicit in the development of these special regulation C-R areas was that (*i*) trout do not move out of the special regulation areas, (*ii*) trout do not suffer high mortality rates within the special regulation areas, and (*iii*) the forage base is sufficient for growth within the special regulation areas. Prior to implementation little data existed on forage base within these special regulation areas and it was unknown whether higher densities of large trout could be maintained from a food availability perspective. Tailwaters may be particularly food-limited for larger trout, and increasing the density and size of trout in tailwaters may result in limited growth, decline in average size, and a reduction in the forage base (Filbert and Hawkins 1995; McKinney and Speas 2001; Weiland and Hayward 1997). Carrying capacities of trout in the C-R areas may depend in large part on the amount of food available. If the C-R areas contain a high amount of food available, there may be little lost foraging opportunities or energetic losses to the trout even at higher densities. Conversely, if food limitation occurs, a large net loss of energy available to

trout and a decrease in production is possible in the C-R areas. Therefore, an examination of food availability in Arkansas C-R areas may provide a means to assess if C-R regulations were compatible with the C-R objectives of higher densities of large trout.

Bioenergetics models are a commonly used tool to estimate the consumption required to satisfy growth observed over a specified time interval (Kitchell et al. 1977) and may be ideal for addressing potential food limitation within special regulation C-R areas. Population level consumption rates can be compared with the abundance, biomass, or production of prey populations to determine whether prey resources provide a sustainable source of food for the predator (Ney 1990; Raborn et al. 2007) or determine potential spatial-temporal bottlenecks in prey supply (Utz and Hartman 2006). Evaluations of bioenergetics modeling have performed well for a variety of salmonids when compared with independent estimates for consumptions (Beauchamp et al. 1989; Brodeur et al. 1992; Whitledge et al. 2010). Herein, we used a bioenergetics model to quantify the seasonal trends in consumption dynamics of brown and rainbow trout populations and compared these results to relative abundances of sculpin in three C-R areas. More specifically, the objectives of this study were to: (*i*) estimate the size-class abundances of brown and rainbow trout; (*ii*) describe and quantify the seasonal and size-specific diets of brown and rainbow trout; (*iii*) relate diet and consumption rates to the seasonal availability of prey in the forage base (e.g. macroinvertebrates, sculpin); (*iv*) determine whether food supply limited the growth of any sizes-classes of brown and rainbow trout; and (*v*) determine whether estimated levels of consumption in the size-classes of brown and rainbow trout were sufficient to meet their metabolic demands.

Study site

The study was conducted on the Bull Shoals and Norfork tailwaters in the Ozark Mountains of Arkansas. Bull Shoals tailwater, below the Bull Shoals Dam, of the White River is located in Marion and Baxter Counties, Arkansas (36°21'N, 92°34'W) (Figure 1). The White River basin drains approximately 44,683 km^2. Bull Shoals Dam was created in 1952 primarily for the generation of hydroelectric power. Water discharges from the dam during the study averaged 50.5 $m^3 \cdot s^{-1}$ (SE$\pm$2.84). The amount of discharge was lowest in the winter, while the highest discharge occurred in the spring (Figure 2). Yearly water discharge at Bull Shoals dam in 2006 was the lowest reported in 25 years (Figure 3). The mean discharge across 25 years was 171 $m^3 \cdot d^{-1}$ (SE$\pm$14.5). The percent below the mean discharge was 13% in 2005 and 78% in 2006. Water releases from the dam during this study averaged 50.5 $m^3 \cdot s^{-1}$ (SE$\pm$2.84) and ranged from 1.4 to 230.4 $m^3 \cdot s^{-1}$ (US Army Corps of Engineers, unpublished data). Alternating shoal and pool areas characterize this stretch of river. Substrates were mostly gravel, with some bedrock in hydraulically scoured areas to sand and silt in pools. In the addition to filamentous algae, *Cladophora*, found attached to the substrate in the tailwater, a nuisance diatom, *Didymosphenia geminata*, was also present in high abundance and often formed thick, mucilaginous mats covering the substrate. The stream channels are stable with armoring in the upper reaches. Bull Shoals tailwater supports a trout fishery for approximately 164 km downstream from Bull Shoals Dam. Bull Shoals Dam C-R area begins 0.09 km below Bull Shoals Dam extending downstream 1.5 km and the surface area is approximately 22.0 ha. Sylamore C-R area is located approximately 124 km downstream from Bull Shoals Dam. Sylamore C-R area is 4.1 km long and has a surface area of 60.3 ha. Species other than trout in the fish community in the Bull Shoals C-R included Ozark sculpin, *Cottus hypselurus*, northern hog sucker, *Hypentelium nigricans*, river redhorse, *Moxostoma carinatum*, and occasionally entrained adult walleye,

Stizostedion vitreum. In contrast, the Sylamore C-R fish community was more diverse with greenside and rainbow darters, *Etheostoma blenniode*s and *E. caeruleum*, longear sunfish, *Lepomis megalotis*, common carp, *Cyprinus carpio*, striped and duskystrip shiner, *Notropis chrysocephanlus* and *N. pilsbryi*, northern hogsucker, river redhorse, smallmouth bass, *Micropterus dolomieu*, and Ozark sculpin.

Norfork tailwater was created in 1944 on the North Fork River, a tributary of the White River, with the completion of the Norfork Dam. Norfork tailwater is located in Baxter County, Arkansas (36°14'N, 92°14'W). The watershed of North Fork River has a drainage area of 4,683 km^2 at the Norfork Dam. Water releases from the dam averaged 28.5 $m^3 \cdot s^{-1}$ (SE$\pm$1.12) and ranged from 1.7 to 122.0 $m^3 \cdot s^{-1}$. The amount of discharge was lowest in the winter, while the highest discharge occurred in the spring. The mean yearly water discharge across 25 years was 54 $m^3 \cdot d^{-1}$ (SE$\pm$4.6). In 2005 water discharge was slightly below the 25 year mean by 7%. In 2006 water discharge was 38% below the 25 year mean, but was not the lowest reported in 25 years. Water releases from the dam averaged 28.5 $m^3 \cdot s^{-1}$ (SE$\pm$1.12) and ranged from 1.7 to 122.0 $m^3 \cdot s^{-1}$. Substrates ranged from sand to bedrock with coarse gravel being the predominant material with filamentous algae, *Cladophora*, often being attached. Norfork tailwater supports trout for approximately 7 km, from the Norfork Dam until the confluence of the tailwater with the White River. Norfork C-R area is located approximately 4 km downstream of the dam. Norfork C-R area was 1.8 km long with a surface area of 11.2 ha surface area. Species other than trout in the fish community in the Norfork C-R included Ozark sculpin, northern hog sucker, and river redhorse.

Catch-and-release trout fishing regulations were implemented by the Arkansas Game and Fish Commission (AGFC) on Jan 1, 1995 at the Bull Shoals, Norfork, and Sylamore catch-and-

release (C-R) areas. All trout caught in C-R areas must be released immediately and tackle is restricted to the use of only an artificial lure with a single, barbless hook. While the C-R areas were not directly stocked the surrounding areas were highly augmented by a put-and-take fishery for rainbow trout (~279 mm total length; TL) and a put-grow-and-take fishery for brown trout (~150 mm TL). Rainbow trout were stocked year round, whereas brown trout were only stocked in the fall and winter. Approximately 1.18 million and 92,000 rainbow trout were stocked annually at Bull Shoals and Norfork tailwaters, respectively (AGFC, unpublished data). Cutthroat trout, *O. clarkii*, and brook trout, *Salvelinus fontinalus*, were also stocked in low numbers within both tailwaters.

Methods

Bioenergetics approach

We used two bioenergetics modeling approaches to assess spatial and temporal energy demands by each size class of brown and rainbow trout. For the first modeling approach, we calculated daily energy expenditure (DEE) or maintenance ration, which is the amount of energy required to obtain zero growth over the course of a day ($J \cdot g^{-1} d^{-1}$), and compared DEE to the estimated daily energy intake (DEI) ($J \cdot g^{-1} d^{-1}$) or daily ration. We compared estimates of DEI with DEE to determine if fish were obtaining sufficient energy to maintain body weight. This approach provides insight into seasonal bottlenecks in food availability compared to consumption. For the second modeling approach, we constructed a time-dependent bioenergetics model to estimate seasonal and annual consumption rates by brown and rainbow trout on sculpin, macroinvertebrates, and other major prey. This modeling approach provides a useful method for quantifying consumption at various temporal and spatial scales for individuals or populations of

predators. For both modeling approaches, field sampling was used to obtain data for the models for trout and prey abundances, trout growth rates, trout diets, prey energy, and thermal experience of trout.

Fish Sampling

Sampling was conducted on a seasonal basis at Bull Shoals and Norfork C-R areas from May 2005 to June 2006. Sylamore C-R area was sampled seasonally from October 2005 to October 2006; however no sampling was conducted in summer of 2006 at Sylamore due to high water releases from Bull Shoals and Norfork dams. Seasons were spring (April-June), summer (July-September), fall (October-December), and winter (January-March). On each sampling date, the trout were collected at night using two crews, each consisting of an electrofishing boat and processing boat. The fiberglass electrofishing boats were equipped with Smith-Root 5.0 GPP electrofishing units and boom-mounted steel cable electrotodes. Standarized GPP unit settings were as follows: mode = DC, voltage = high range (50-1,000 volts), pulses per second = 30, percent of ≈ 30, amps ≈ 2.0-2.5. All sampling was conducted on two consecutive nights at low flows during periods of no power generation. Boat electrofishing started at the upstream end of the C-R area and proceeded downstream to the lower end of C-R area. At the end of a sampling run, all trout collected were transferred from live-wells on the electrofishing boats to live-wells on the processing boat. On the first night of sampling, all brown and rainbow trout were anesthetized with a clove oil mixture (1:10 clove oil:ethanol) at 10 mL solution/20 L water (Prince and Powell 2000), measured for TL, and weighed to the nearest 0.1 g wet weight. Fish were then tagged below the dorsal fin with individually numbered yellow Hallprint TBA t-bar anchor tags (2" total length, 1-1/4" color) and released. On the second night brown and rainbow

trout collected were measured, weighed, checked for tags, and released. All trout tagged on the first night were released. Subsamples of untagged trout from each species for GCA were euthanized with a concussive blow to the cranium. Stomach contents of these fish were removed in the field and placed in a 10% buffered formalin solution. Two size classes of rainbow trout and three sizes of brown trout were chosen for GCA based on size-frequency data (Stan Todd, AGFC, unpublished data). Attempts were made to collect 60 brown trout from small (<250 mm TL; n = 20), medium (250-400 mm TL; n = 20), and large (>400 mm TL; n = 20) size classes and 60 rainbow trout from small (≤400 mm TL; n = 40) and large (>400 mm TL; n = 20) size classes at each site per season.

Trout abundance

A Peterson single mark-recapture population estimate with the Chapman modification was used to estimate trout abundance in the catch-and-release areas (Ricker 1975):

$$\hat{N} = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1,$$

where n_1 = number caught and marked in first sampling period; n_2 = number caught in second sampling period; and m_2 = number of marked animals in second sampling period. Confidence intervals were calculated using the table provided in Chapman (1948).

Biomass was estimated as the following:

$$\hat{B} = \hat{N}\overline{w},$$

where $\hat{B}$ = estimated biomass (g), $\hat{N}$ = estimated abundance, and $\overline{w}$ = mean weight of fish in the population (g). We converted abundance estimates to standard area units by dividing the estimates by wetted area (ha) at baseflow per site for biomass and density estimates. Boat

electrofishing sampling below the second downstream island in the C-R area at Norfork was not possible due to an inability to maneuver the boat in shallow waters. Thus, surface area was assumed to be 11.2 ha at Norfork for the estimates. All reported measures for biomass and density were for wet weight. Length-frequency distributions of brown and rainbow trout were developed to evaluate the population size structure.

Growth rates

We calculated growth from the change in length of tagged individuals recaptured from seasonal population estimate surveys. Fish had to be captured at both the beginning and ending dates of a seasonal time period to be included in the analysis of growth for that time period. Growth rates were estimated for each season and an average of the seasonal changes in lengths was used to estimate growth rates per year for each size class. Instantaneous daily rate of growth and annual growth rates were estimated across four tagging intervals at Bull Shoals from May 2005 to May 2006 and at Norfork from June 2005 to June 2006. At Sylamore, instantaneous daily rate of growth and annual growth rates were estimated across three tagging intervals from October 2005 to October 2006. Only fish collected at the beginning of a seasonal tagging interval (e.g. spring-summer) were used for instantaneous daily rate of growth estimates. The instantaneous daily rate of growth in weight (G) was estimated using:

$$G = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

where W_1 is initial weight, W_2 is final weight, t_1 is initial time, and t_2 is final time.

Relative weight (W_R), which may be an indicator of food availability, were calculated to assess fish condition (Anderson and Neumann 1996). Relative weights (W_R) were based on length-specific standard weights (W_s) equations proposed by Milewski and Brown (1994) for

brown trout at least 140 mm TL ($\log_{10}(W_s) = -5.023 + 3.024\log_{10}(TL)$) and Simpkins and Hubert (1996) for rainbow trout at least 120 mm TL ($\log_{10}(W_s) = -4.867 + 2.96\log_{10}(TL)$). We calculated W_r ($W_r = [W/W_s] \times 100$) for each fish, where W was the wet weight (g) of the fish and W_s was the standard weight for a fish of the same TL.

Gut content analysis

Prior to examination in the laboratory, stomachs were transferred from formalin solution to containers with 95% ethanol. At the time of examination, stomachs were dissected and their gut contents were placed in a Petri dish. Using a dissecting microscope prey items were identified to lowest practical taxon, counted, and measured to the nearest 0.1 mm with an ocular micrometer. Partially digested or broken macroinvertebrates were identified, counted, and measured based on head widths. Ingested fish prey still intact were identified and measured for TL. When prey fish were in later stages of digestion they were measured according to either vertebral length (VL; vertebral column was complete) or standard length (SL; fish missing only the caudal fin). We used the relationship between VL or SL for sculpin based on measurements of sculpin found in the stomachs which ranged in TL from 58-101 mm to determine TL from VL (TL = 1.57902[VL]; $r^2 = 0.93$) or SL (TL = 1.11903[SL]; $r^2 = 0.98$). Zooplankton (Cladocerans) were readily digested in most stomachs which made accurate length measurements difficult to obtain. In stomachs with zooplankton intact, they were measured from head to tail and an average length of 2.5 mm TL was obtained ($n = 135$; Range = 2.0-3.2 mm; SE $\pm$ 0.021). In stomachs where zooplankton were not intact they were counted in a Ward counting wheel. Counts of zooplankton were then multiplied by estimated average length from the intact zooplankton to estimate dry mass. Length-dry mass or head-width–dry mass equations from the literature were

used to estimate the mass (mg) of each macroinvertebrate and fish (Benke et al. 1999; Dumont et al. 1975; Rogers et al. 1976; Sample et al. 1993; Weiland and Hayward 1997). Algae present in the stomach samples were dried in an oven at 50-60°C for 48-72 h and weighed to obtain dry weights (0.0001 mg). For GCA no distinction was made between *Cladophora* and *D. geminata* found in the trout stomachs at Bull Shoals and were combined together as algae for the analyses. Prey taxa that were consumed infrequently or in low proportions were combined. The following categories were grouped: aquatic invertebrates (e.g. Chaoboridae, Empidadae, Ephydridae, Simuliidae, Tabanidae, larval Coleoptera, larval Ephemeroptera, larval Trichoptera, Mollusca, Nematomorpha, Oligochaeta), other vertebrates (e.g. Amphibia, bigeye shiner, darters, green sunfish, northern hogsucker, rainbow trout, river redhorse, striped shiner), and terrestrial invertebrates (e.g. Coleoptera, Arachnida, Chilopoda, Dermaptera, Diplopoda, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Orthoptera, Thysanoptera).

In instances where certain taxa of macroinvertebrates were ingested in large numbers (i.e., > 125 individuals) a subsampling method was employed to randomly select prey individuals for measuring. All individuals from a taxon were placed in an Imhoff cone and total volume was increased to 1 L with water (Wrona et al. 1982). The subsample was mixed for 2-5 minutes by bubbling air with an air stone connected to the bottom of the cone. Subsamples were then removed using a 50 mL Hensen Stempel pipette and total lengths of the first 75 individuals of a taxon encountered were measured. The total counts of prey ingested were multiplied by the average length of prey measured from the subsample to estimate dry mass for the remaining macroinvertebrates in the sample.

Stomach contents were expressed as a percent weight, which is the total dry weight of each prey item expressed as percentage of the overall weight of the stomach contents of brown or

rainbow trout for each season and size class. We calculated %W for each prey taxon or group as follows:

$$W_i = \frac{W_i}{\sum_{i=1}^{Q} W_i}$$

where i is the prey item, W_i is the dry weight of prey type i, and Q is the number of prey types. Only stomachs containing prey items were utilized for calculations and analyses.

Prey collection

We sampled drifting and benthic macroinvertebrates within each C-R area seasonally to assess differences in macroinvertebrate prey availability. Two sites were randomly selected for drifting macroinvertebrate within each C-R area and sampled subsequently. Drift samples were collected with a nylon drift net fitted to a PVC tube (mesh 360 μm; length, 1 m; aperture 15 cm). During each sampling event, sites were sampled for drifting macroinvertebrates during daylight hours at dawn, around midday (1200-1300 hours), and at dusk. No attempts were made to collect drift samples at night since previous studies have found that nocturnal feeding by salmonids in streams is limited (Angradi and Griffin 1990; Tippets and Moyle 1978). At each time of day, three samples with three consecutive replicates were collected at 15 min intervals and taken at evenly spaced intervals across the river at baseflows. However, when high flow conditions existed due to increased generation, samples were collected with the aid of a boat. In those instances, drift nets were attached to 3 m steel rods placed in cement bucket that were dropped over the side of the boat and the boat was held stationary. Due to the increased velocities during generation, samples were collected during three, one minute intervals to prevent nets from clogging. We measured water depth and velocity to the nearest 0.01 m s^{-1} (Marsh-McBirney

Flowmate Model 2000) in the center of each net at the beginning and end and used the averages to calculate the catch of drifting macroinvertebrates per unit volume of water. Samples were taken at approximately 0.6 of total depth (Platts et al. 1983). Drift samples were preserved in 95% ethanol. Drift densities (numbers m^{-3}) and biomass (dry weight mg m^{-3}) were calculated by dividing the number or biomass of organisms in the net by the volume of water filtered ($m^{-3} \cdot hr$) and were used to quantify macroinvertebrate biovolume per C-R area.

Benthic macroinvertebrates were collected using a vacuum benthos sampler with an area of 0.1 m^2 (Brown et al. 1987). The substrate within the sampling pipe was disturbed/agitated for 5 minutes using a hand rake; macroinvertebrates were filtered into a 360 μm mesh bag and then preserved in a jar with 95% ethanol. At each C-R area, 10-12 randomly selected sites using a stratified sampling design based on habitat types (e.g. riffle, run, backwater) were sampled seasonally. Habitat types were estimated qualitatively using flow rate and depth. Riffles were shallower, faster flowing water with visible surface turbulence. Runs were fast to moderate flow in deeper water with little visible surface turbulence. Backwaters were areas with no turbulence and velocity. Benthic densities (numbers m^{-2}) and biomass (dry weight mg m^{-2}) were calculated by dividing by the area sampled.

We processed prey items in the drift and benthic samples using the same methods described above for GCA. Macroinvertebrates in benthic and drift samples were separated from organic material in the laboratory. In drift samples, prey taxa collected in low numbers were grouped, which were: aquatic macroinvertebrates (e.g. Chaoboridae, Empidadae, Ephydridae, Simuliidae, Tabanidae, larval Coleoptera, larval Ephemeroptera, larval Trichoptera) and terrestrial invertebrates (e.g. Coleoptera, Arachnida, Chilopoda, Dermaptera, Diplopoda, Hemiptera, Homoptera, Hymenoptera, Lepidoptera, Orthoptera, Thysanoptera). Benthic samples

were grouped according to macroinvertebrate order, with exception of Chironomidae. Based on minimum size of zooplankton observed in diets only zooplankton >2.0 mm TL were included in the analysis and enumerated in a Ward counting wheel. Only macroinvertebrates observed in the diet were included in the benthic and drift analysis. Previous studies and my own data indicate that smaller prey (< 1 mm) are rarely consumed by salmonids (Keeley and Grant 2001); thus, we only analyzed organisms > 1 mm in the drift and benthic samples.

Benthic fish (e.g. sculpins, darters) and crayfish were sampled seasonally using a 1.0 m^2 quadrat sampler with 6-mm mesh (Rabeni 1985) to determine benthic prey fish and crayfish abundances. Samples were collected by placing the quadrat sampler in riffles and kick-siening within the sampler to dislodge fish and crayfish and wash them into the attached sampler bag (Peterson and Rabeni 2001). Fish and crayfish were identified, measured (TL or CL), and weighed (g). At each C-R area, 20 randomly selected sites were sampled seasonally. Peterson and Rabeni (1995) found that 20 samples were adequate to ensure estimates for their sites were within $\pm$ 20% precision. Sites were sampled using a stratified sampling design based on habitat types (e.g. riffle, run, backwater).

Prey energy densities

In the laboratory, all prey samples were rinsed with Millipore water and inspected for any debris. Macroinvertebrates were identified to lowest practical taxa and measured using a dissecting microscope and an ocular micrometer. Sculpin were measured to the nearest TL and crayfish were measured for carapace length (CL). In order to achieve enough sample of macroinvertebrates for bombing, multiple organisms (> 3 individuals) of the same species were pooled to achieve the minimum mass (i.e. 0.2-0.02 g). Prior to bombing, prey samples were

thawed blotted dry and placed in a tared aluminum weigh boat to obtain wet weight to the nearest 0.0001 mg. Samples were then dried in an oven at 50-60°C for 48-72 h and reweighed to obtain dry weights. After being dried and weighed sculpin and crayfish were homogenized whole using a Wiley Mill (40 mesh) and reground, if necessary, into a fine powder to insure homogeneity within each sample. Aquatic macroinvertebrates were homogenized using a mortar and pestle. Gastropods were extracted from their shells and organisms analyzed whole. After drying and homogenizing, the sample was added to the calorimeter vessel to get a complete firing. Prey energy density values (cal g^{-1} dry weight) were estimated using a Parr bomb calorimeter (Parr 6200 Calorimeter). Prey energy density values (cal g^{-1} dry weight) were then converted to the appropriate units (J g^{-1} wet weight) and were based on the percent water determinations from weighed organisms. We used the energy value for the season when available. However, when no energy values were available seasonally, energy values were assumed to be constant throughout the year. The energetic values of Cladocera, rainbow trout, *Etheostoma* spp., *Notropis* spp., and terrestrial invertebrates were borrowed from the literature (Bryan et al. 1996; Cummins and Wuycheck 1971; Hanson et al. 1997; Luecke and Brandt 1993; Madon and Culver 1993).

Thermal experience

Water temperatures in the three C-R areas were monitored throughout the study period with HOBO data loggers (Onset, Pocaset, Massachusetts). Temperature loggers were anchored to the bottom of the substrate and placed at an upper, middle, and lower location within each C-R area. The mean water temperature for 1 d was calculated from data collected at 15-min intervals for

each data logger. Temperatures were then averaged daily across the three data loggers to generate the average temperature.

Daily energy intake and expenditure

Estimates of consumption to determine DEI ($J \cdot g^{-1} \cdot d^{-1}$) were derived using the Eggers (1977) model:

$$C_{24} = E_{24} \cdot R$$

where C_{24} is consumption (i.e. DEI) over 24 hrs, E_{24} is the energy in stomach contents over 24 hrs and R is the instantaneous gastric evacuation rate. Taxon-specific length-dry mass regressions of prey observed in the diets were used to convert to energy (J). We assumed no energy was obtained from *Cladophora* and *D. geminata* (Weiland and Hayward 1997). For each sampling event, gastric evacuation rates were calculated for different water temperatures (T °C) using the equation of Elliott (1972) for brown trout ($R = 0.053e^{0.112T}$) and Hayward and Weiland (1998) for rainbow trout ($R = 0.0405e^{0.067T}$). We used stomachs collected from night sampling as opposed to day sampling. Weiland and Hayward (1997) found no differences between mean food weight of rainbow trout in day and night samples collected at baseflows in the White River system. Fish with empty stomachs were included in the DEI estimates.

We estimated DEE ($J \cdot g^{-1} \cdot d^{-1}$) using the "Wisconsin" bioenergetics model which is based on the balanced energy equation (Hanson et al. 1997):

$$G = C - (M + F + U),$$

where G = growth, C = consumption, M = metabolic rate (includes specific dynamic action, standard metabolism, and active metabolism), F = egestion, and U = excretion. We calculated daily energy required to obtain zero growth using the model. The model required specific inputs

on temperature occupied by the fish, fish weight, and fish energy density. Physiological variables used in the model for rainbow trout were from Rand et al. (1993) with the exception of maximum consumption and respiration, which were taken from Railsback and Rose (1999). Brown trout physiological variables were from Dieterman et al. (2004), which has been shown to provide accurate predictions under various fish sizes, water temperatures, and ration levels (Whitledge et al. 2010). Fish energy densities were estimated using the dry weight to energy density equation for Salmonidae (Hartman and Brandt 1995). Average temperature from the date of sampling was used for the simulations.

Consumption bioenergetics model

The seasonal demands by different size-classes of brown and rainbow trout in each C-R area were simulated for each relevant prey category by means of a bioenergetics model (Hanson et al. 1997). The same physiological variables used to estimate DEE were used to estimate consumption (Dieterman et al. 2004; Railsback and Rose 1999; Rand et al. 1993). Site-specific parameters included observed growth rates, diet composition, abundances, and thermal history. The model interpolated values for growth, diet composition, and thermal experience between dates. Growth during the study period was determined from changes in the weight of tagged individuals recaptured seasonally and interpolated between sampling events. Energy values for prey were obtained from the literature and our own data. Average water temperature for each day was used in the simulations.

Population-level consumption rates were estimated seasonally for each size class of brown and rainbow trout. Simulations began on 1 April (simulation day 1) and ended on 30 June the following year (simulation day 456) at Bull Shoals and Norfork. At Sylamore, simulations

began on 1 October (simulation day 1) and ended on 31 December the following year (simulation day 457).

Food availability

To provide an approximation of predation impacts by brown and rainbow trout on sculpin populations and determine prey fish availability, we translated the sculpin predation by each size class of rainbow and brown trout back into actual numbers of sculpin consumed per season. Sculpin consumption estimates (g WW·d^{-1}) for individual brown and rainbow trout from bioenergetics modeling were divided by the mean body mass of sculpin collected in diets (g WW) from each size class of trout seasonally. Individual consumption was multiplied by size-class structured population estimates (95% CI) of brown and rainbow trout to estimate the total sculpin biomass consumed by the entire brown and rainbow trout populations during each season. Because no abundance or biomass estimates were available for cyprinids, catostomids, and centrachids at Sylamore, the effects of brown trout predation on these species was not assessed.

We determined macroinvertebrate availability using biomass estimates of macroinvertebrates from benthic and drift sampling. We converted macroinvertebrate biomass in drift and benthos (mg DW) to the appropriate units for bioenergetics modeling consumption estimates (g WW). We then compared macroinvertebrate biomass to bioenergetic simulations of seasonal consumption (g WW) by brown and rainbow trout. For drift we obtained water discharges (m^{-3}·hr) from Bull Shoals and Norfork dams (US Army Corps of Engineers, unpublished data) and USGS Calico Rock water gauging station for Sylamore. For each season we multiplied the mean seasonal drift biomass with the amount of water released in the daylight

hours only (i.e. dawn to dusk). We conducted a small scale foraging behavioral observation study via snorkeling at Norfork tailwater in 2006 and found that both brown and rainbow trout exhibited epibenthic foraging from 0-40% of the time, but varied depending on habitat, time of day, and size of fish (Flinders, unpublished data). Thus, benthic macroinvertebrates were included in assessing food availability. We constrained benthic macroinvertebrate availability to only the areas occupied by trout. To estimate the amount of area occupied for benthic foraging we used seasonal linear home ranges (LHR) determined from a telemetry companion study that examined rainbow trout (>314 mm TL) movements implanted with radiotransmitters within each C-R area (Cushing 2007). In that study, fish were tagged from July 2005 to October 2006 and monitored weekly for a year. Linear home range (LHR) is defined as the distance between the most upstream and farthest downstream relocations of an individual fish (Vokoun 2003). A study conducted at Beaver tailwater C-R area found that brown and rainbow trout movement distributions were not significantly different (Quinn and Kwak 2011) and brown trout were assumed to have similar LHR as rainbow trout. For benthic macroinvertebrate availability, we multiplied the seasonal benthic biomass by the surface area (m^2) of each site that fish occupied based on LHR.

Statistical analysis

We tested for differences in diets among seasons using a permutational multivariate analysis of variance (PERMANOVA), which tests the simultaneous response of one or more variables to factors in an ANOVA experimental design on the basis of a distance measure using permutation methods (Anderson 2001). The response variables were the proportion of the prey group by dry weight from the diet analysis and the predictor variable was seasons. Prey groups that

represented <5% of the proportion of dry weight were excluded from the analysis. For the analysis, Bray-Curtis distance measures were used with 4,999 permutations for each test (Manly 1997). PERMANOVA was performed using the packages MASS (Venables and Ripley 2002) and VEGAN (Oksanen et al. 2006) in the R-program (R Development Core Team 2007).

To assess the differences in relative weights seasonally, we used analysis of covariance (ANCOVA), where relative weights was the response variable, season was the predictor variable, and fish length was the covariate. Prior to statistical analysis, we examined all data graphically to determine if the data met the assumptions of normality, homogeneity of variance, and homogeneity of slopes. We also screened the data for equality of variance using a Levene's test and examined for departure from normality using the Shapiro–Wilk test (*W*-statistic). If the homogeneity of slope assumption was not met an ANOVA was performed. A Tukey's post hoc test was used for pairwise comparisons. We examined the effect of season on instantaneous daily rate of growth in weight (*G*) using ANOVA. Model assumptions of normality, homogeneity of variance, and independence were evaluated graphically prior to statistical analysis. We also examined data for equality of variance using a Levene's test and departure from normality using the Shapiro–Wilk test (*W*-statistic).

Differences in the temporal patterns of drifting and benthic macroinvertebrate densities and biomass among seasons were assessed at Bull Shoals and Norfork with an ANOVA. A *t*-test was used at Sylamore. Macroinvertebrate densities and biomass were log(x+1) transformed when necessary after checking the data for normality and residuals for homogeneity of variance. An α value of 0.05 was used to determine statistical significance for all tests. Analyses were performed using SYSTAT 13.0 (SYSTAT 2009).

Results

Abundance, density, and biomass of trout

In 2005 and 2006, the total numbers of brown and rainbow trout tagged were 11,423, with 4,875 at Bull Shoals, 5,013 at Norfork, and 1,535 at Sylamore. Of the fish tagged on the first night of a marking event, the total number of marked fish recaptured on second sampling events (i.e. recapture) was 925, 1,025, and 250 for Bull Shoals, Norfork, and Sylamore respectively (Table 1). Average percent of recaptured tagged fish at Bull Shoals, Norfork, and Sylamore was 19.0%, 21.1%, and 16.2%, respectively. At all sites brown trout were recaptured at a higher rate than rainbow trout. Average rainbow trout abundances were higher than brown trout at all sites. Average abundance of rainbow trout across the seasons at Bull Shoals, Norfork, and Sylamore was 3,736 (95% CI 3,045-4,555), 3,860 (95% CI 3,250-4,566), and 2,857 (95% CI 1,860-4,977), correspondingly. Brown trout average abundance across the seasons was 1,113 (95% CI) at Bull Shoals, 937 (95% CI 772-1,118) at Norfork, and 218 (95% CI 74-916) at Sylamore.

Densities and biomass of small rainbow trout were considerably lower at Bull Shoals and Sylamore than at Norfork during all seasons (Figure 4). Average densities of small rainbow trout were 169 fish/ha at Bull Shoals, 342 fish/ha at Norfork, and 47 fish/ha at Sylmore. Average density of small rainbow trout was 2.4 and 6.6-fold higher at Norfork than at Bull Shoals and Sylamore, respectively. Densities of large rainbow trout in the spring seasons were similar at Bull Shoals and Norfork; however, densities were higher in 2005 than 2006. In spring 2005 and 2006 large rainbow trout densities were 52.8 (95% CI 35.0-136.0) and 20.9 (95% CI 8.7-14.6) fish/ha and 43.5 (95% CI 23.3-87.5) and 15.5 (95% CI 9.3-24.4) fish/ha for Bull Shoals and Norfork, respectively. Densities and biomass of brown trout were lower at Sylamore across all size classes and seasons compared to Bull Shoals and Norfork. Population estimates of brown

trout at Sylamore contained large confidence intervals given that only 268 brown trout were collected there across the seasons.

Proportionally, rainbow trout at Bull Shoals represented 68-80% of the relative density seasonally when compared to brown trout. Rainbow trout comprised a slightly lower relative biomass proportionally (52-75%) due to the larger biomass of the brown trout population. At Norfork, rainbow trout proportionately represented 76-84% of the relative density seasonally compared to brown trout. Similar to Bull Shoals rainbow trout at Norfork comprised a slightly lower relative biomass 62-70% due to the larger biomass of brown trout population compared to relative density. At Sylamore rainbow trout dominated the relative density and biomass compared to brown trout, which ranged seasonally from 93-95% and 7-12%, respectively.

Length-frequency

Rainbow trout length-frequency distributions at all sites contained the highest proportion of fish near the size at which they were stocked (~279 mm TL) (Figure 5). In contrast, brown trout distributions generally exhibited several size classes and contained a higher proportion of larger fish, with the exception of seasons when brown trout stocked in fall where abundant (Figure 6). At Bull Shoals, rainbow trout and brown trout lengths ranged from 197 to 645 mm TL and 164 to 735 mm TL, respectively. The peak of the distribution of rainbow trout occurred at approximately 300-350. Brown trout size structure was dominated with larger individuals with the highest proportion ranging from 420-460 mm across all seasons. In the fall, a higher proportion of larger brown trout (>550 mm) were observed. At Norfork, rainbow trout and brown trout lengths ranged from 164 to 643 mm TL and 159 to 732 mm TL, respectively. The highest proportion of fish distribution seasonally ranged from 290-310 mm, slightly higher than

the average rainbow trout size at stocking. Brown trout likely stocked (~150 mm TL) previously in the spring of 2005 represented a size class with the highest proportion in the distribution throughout the seasons starting at 250 mm TL in spring 2005, 290 mm TL in summer 2006, 320 mm TL in fall 2005, and 400 mm TL in winter and spring 2006. In Sylamore, rainbow trout and brown trout lengths ranged from 180 to 399 mm TL and 162 to 594 mm TL, respectively. Rainbow trout distribution at Sylamore was narrow (Range 280-300 mm TL) across all of the seasons. The highest proportion of brown trout was more variable seasonally and ranged from 280-370 mm TL.

Growth rates

Growth was decidedly seasonal for small rainbow trout at Bull Shoals (ANOVA, $F_{3,329} = 30.759$, $P < 0.001$), Norfork (ANOVA, $F_{3,344} = 42.111$, $P < 0.001$), and Sylamore (ANOVA, $F_{1,65} = 4.062$, $P = 0.048$) , with the fast growth period from spring to fall and negative growth during winter at Bull Shoals and Norfork (Figure 7). All observed growth rates for rainbow trout at Sylamore were negative. Seasonal differences were observed in large rainbow trout at Norfork (ANOVA, $F_{3,45} = 3.731$, $P = 0.018$), but not in those collected at Bull Shoals (ANOVA, $F_{3,78} = 2.697$, $P = 0.052$). For large rainbow trout at Norfork the major growth period was in spring. At Bull Shoals, large rainbow trout exhibited an opposite pattern with no growth or negative growth across the seasons, with a particular depression during the spring.

There were no significant differences in growth across seasons for small brown trout at Bull Shoals (ANOVA, $F_{2,10} = 0.620$, $P = 0.557$) and Norfork (ANOVA, $F_{1,5} = 4.653$, $P = 0.083$). However, these fish exhibited rapid growth across the intervals. Growth was not highly seasonal for medium brown trout at Bull Shoals (ANOVA, $F_{3,112} = 1.558$, $P = 0.204$), Norfork (ANOVA,

$F_{3,128}$ = 2.008, P = 0.116), and Sylamore (ANOVA, $F_{2,19}$ = 1.725, P = 0.205). Growth of medium brown trout remained positive or no net gain across all the seasons and sites. Growth was seasonal for large brown trout at Bull Shoals (ANOVA, $F_{3,273}$ = 5.107, P = 0.002) and Norfork (ANOVA, $F_{1,184}$ = 32.980, P < 0.001) exhibiting negative growth in winter season, during and shortly after the spawning period. At Sylamore, large brown trout growth displayed minimal changes in growth seasonally (ANOVA, $F_{2,13}$ = 3.219, P = 0.179) and approached no net growth across the seasons.

All size classes of brown and rainbow trout at Norfork exhibited faster annual growth rates than trout at Bull Shoals and Sylamore. While fish tagging was conducted from October 2005 to 2006 at Sylamore, after May 2006 no rainbow trout and only one medium and large brown trout were recaptured; therefore annual estimates were not possible for rainbow trout and were limited for brown trout. Small brown trout experienced the highest annual growth of both species and was 162 mm TL (SE±25.9) and 378 g (SE±83.8) at Norfork and 157 mm TL (SE±19.9) and 265 g (SE±39.4) at Bull Shoals. Annual growth for medium brown trout was 105 mm TL (SE±11.0) and 510 g (SE±67.4) at Norfork, 50 mm TL (SE±8.7) and 132 g (SE±38.0) at Bull Shoals, and 43 mm TL (SE±8.3) and 138 g (SE±30.7) at Sylamore. Annual growth decreased in large brown trout to 40 mm TL (SE±6.5) and 176 g (SE±106.1) at Norfork. At Bull Shoals and Sylamore large brown trout experienced negative growth at 8 mm TL (SE±3.4) and -116 g (SE±46.2) and 19 mm TL (SE±17.3) and -27 g (SE±192.6). For small rainbow trout, annual estimates were 44 mm TL (SE±4.2) and 94 g (SE±17.1) at Norfork and 29 mm TL (SE±4.3) and 14 g (SE±20.8) at Bull Shoals. Large rainbow trout at Norfork exhibited some growth, 23 TL (SE±11.2) and 89 g (SE±110.0), whereas at Bull Shoals only negative growth occurred, -1 mm TL (SE±6.5) and -228 g (SE±64.7).

Condition

The relative weights of brown and rainbow trout varied seasonally across all size classes, with the exception of larger brown trout at Sylamore (Table 2). Rainbow trout at Bull Shoals exhibited a sharp decline in condition between spring 2005 and winter 2006, and then increased slightly in spring 2006. However, the seasonal decline in rainbow trout condition was more negative in larger (78.0) than smaller fish (87.2), when the lowest W_R occurred in the winter. Similarly at Bull Shoals, brown trout of all sizes had their lowest relative weights in winter 2006. Both size classes of rainbow trout at Norfork demonstrated a decline in condition from spring 2005 to a low in fall 2005, then a gradual increase through winter and spring 2006. Rainbow trout conditions were significantly lower in spring 2005 compared to spring 2006 (P<0.001) at both Bull Shoals and Norfork. In general, condition of rainbow trout at Sylamore was poor.

Diets

A total of 1,387 trout stomachs were collected for GCA from the C-R areas. At Bull Shoals, Norfork, and Sylamore we examined 551, 573, and 263 stomachs, respectively. Empty stomachs were observed in both brown and rainbow trout (Table 3). Brown trout stomachs were proportionately empty more often than rainbow trout. Brown and rainbow trout diets differed seasonally among each size class, with the exception of small and large brown trout at Sylamore (Table 4).

Isopods were the dominant macroinvertebrate prey item in the summer and fall seasons at Bull Shoals, whereas in the spring and winter amphipods were the dominant prey. Despite the lack of energetic value to rainbow trout, *Cladophora*, filamentous algae, and *D. geminata* were

found in high proportions in their stomachs. Large rainbow trout consumed higher quantities of algae than small rainbow trout across all seasons, but considerably more in the spring seasons (72-82%). Brown trout exhibited an ontogenetic shift from macroinvertebrates in small size class to the inclusion of sculpin into the diets of medium and large size classes. However, for medium and large brown trout, the percentage of piscivory was similar among the size classes and across the seasons, suggesting that piscivory was not increasing with size and a high portion of the diet was comprised of macroinvertebrates (>79%), with the exception of spring 2006. In both species and in all size classes, terrestrial invertebrates were consumed in the highest proportion in the fall, but were a relatively minor overall component of the diet (<14%).

At Norfork small and large rainbow trout consumed high amounts of algae (>63%) during summer, fall, and winter, particularly in the small rainbow trout in the fall and winter when algae represented 91% and 88% of the diet, respectively. Cladocera represented a significant portion of the diet in small rainbow trout during the spring (>20%). Larger rainbow trout exhibited some piscivory during all seasons, with the exception of winter. Besides algae, amphipods were dominant prey in the diets of the rainbow trout in the spring. Brown trout exhibited little or no consumption of algae. Brown trout exhibited high piscivory in the fall for all size classes where sculpin represented >86% of the diet. Similar to Bull Shoals, smaller brown trout exhibited an ontogenetic shift from macroinvertebrates to sculpin in the medium and large size classes. Piscivory increased with the size classes of brown trout. For large brown trout, sculpin represented the dominant prey in the diets among all seasons (46-93%). Amphipods were the most commonly consumed macroinvertebrate in the diets of brown trout, particularly in spring and summer. Cladocera were important in the diet of small rainbow and brown trout in spring and comprised 21-24% and 9-28%, respectively, of the diet.

Small rainbow trout consumed high quantities of algae in the fall and winter at Sylamore. Gastropoda were the most commonly consumed macroinvertebrate in the diets of rainbow trout. Smaller rainbow trout exhibited piscivory in the spring when bigeye shiners were observed in the diets. Decapoda were an important prey for rainbow and brown trout in the spring and fall 2006. Smaller brown trout diets were dominated by gastropod and decapoda, but did exhibit some piscivory in the winter when sculpin were consumed. In the fall, the entire diet of larger brown trout was terrestrial macroinvertebrates. Diets of medium and large brown trout comprised various fish species, not found at Bull Shoals and Norfork. In the winter, large brown trout diets contained darters, river redhorse and northern hogsuckers. In the spring darters and striped shiners were observed in the diets.

In general, benthic macroinvertebrates were the major prey items of smaller brown trout, whereas larger brown trout increased consumption of sculpin with size, indicating a shift to piscivory with size. Based on diets, the transition to piscivory for brown trout occurred at approximately 200-250 mm TL at all sites. Large brown trout exhibited the highest seasonal range of piscivory at Norfork (46-93%) followed by Bull Shoals (9-61%) and Sylamore (0-50%). Rainbow trout exhibited some piscivory at the all the sites (9-15%), but varied markedly among size classes and seasons. The average size (TL) of sculpin consumed at Bull Shoals was 63 mm (SE$\pm$1.53) with a range of 34-108 mm (N = 100). At Norfork, the average size of sculpin consumed was slightly longer than at Bull Shoals and was 72 mm (SE$\pm$1.73) with a range of 27-110 mm (N = 89). At Sylamore, the average size and range of fish consumed was 63 mm (SE$\pm$2.96; 39-110 mm; N = 31) for sculpin, 126 mm (SE$\pm$6.00; 120-132 mm; N = 3) for Percidae, 78 mm (SE$\pm$6.08; 52-97 mm; N = 7) for Cyprinidae, and 196 mm (SE$\pm$24.00; 172-220 mm; N = 3) for Catostomidae. Consumption of rainbow trout by brown trout was limited and

was observed at Bull Shoals with two larger brown trout, 542 and 557 mm TL, with the rainbow trout 182 and 147 mm, respectively. Also, two larger rainbow trout, 503 and 551 mm TL, exhibited some cannibalism in spring 2005 at Norfork.

Prey abundance

A total of 507 drift samples were collected across five seasons at Bull Shoals and Norfork and four seasons at Sylamore. The number of samples collected at Bull Shoals, Norfork, and Sylamore was 223 (*N* = 36-53 season), 238 (*N* = 43-52 season), and 46 (*N* = 22-24 season), respectively. Approximately 26,496 macroinvertebrates were collected, measured, and identified from drift samples. Although drift samples collected contained 12 aquatic and 5 terrestrial taxa, the dominant drift taxa were chironomids at all sites and *Daphnia* at Bull Shoals and Norfork. Frequently collected terrestrial drift taxa included beetles (Coleoptera), flies (Diptera), cicadas (Hemiptera), and bees and ants (Hymenoptera).

Mean drift density (numbers m^{-3}) across the seasons was highest at Norfork at 5.3 individuals m^{-3} (SE$\pm$1.1), followed by Bull Shoals at 3.2 individuals m^{-3} (SE$\pm$0.6) and then Sylamore at 0.7 individuals m^{-3} (SE$\pm$0.1) (Figure 8). However, Bull Shoals and Norfork had similar mean drifting biomass (mg DW m^{-3}) with 0.4 mg DW m^{-3} (SE$\pm$0.1) and 0.5 mg DW m^{-3} (SE$\pm$0.1), respectively, due to the higher densities of larger terrestrial invertebrates drifting at Bull Shoals. At Sylamore, drifting biomass was low with an average of 0.05 mg DW m^{-3} (SE$\pm$0.01). Average biomass of drifting macroinvertebrates was 8.0 and 9.1-fold higher at Bull Shoals and Norfork, respectively, than Sylamore.

Mean drift density (numbers m^{-3}) and biomass (mg DW m^{-3}) estimates were generally highest in spring seasons at Bull Shoals and Norfork followed by summer then fall. Significant

differences in drift densities and biomass were detected between seasons at Bull Shoals (density $F_{4,218}$ = 25.443 P<0.001; biomass $F_{4,218}$ = 9.612 P<0.001) , Norfork (density $F_{4,233}$ = 10.758 P<0.000; biomass $F_{4,233}$ = 8.342 P<0.001) and Sylamore (density t-test = -2.205, df = 44, P=0.033; biomass t-test = -2.754, df = 44, P=0.009). At Bull Shoals and Norfork, drift densities and biomass were highest in the spring 2005 (BS, density P<0.001; biomass P=0.003; NF, density P= 0.046; biomass P=0.013) and lowest in the fall 2005 (BS, density P<0.001; biomass P<0.001; NF density P<0.001; biomass P<0.001). Despite drift density being dominated by *Daphnia* (Cladocera) at Bull Shoals and Norfork, their overall contribution to biomass was low due to their small size (~2.5 mm). *Daphnia* densities peaked in spring at Bull Shoals and Norfork and then steadily declined during summer and were the lowest in the fall. Densities increased from the fall through the spring. Terrestrial taxa were an abundant group, particularly at Bull Shoals, and since many of the taxa were large their overall input to biomass was significant. Aquatic macroinvertebrates (e.g. Ephemeroptera, Plecoptera) became more pronounced in the drift as species diversity increased at Sylamore.

A total of 121 benthic samples were collected at Bull Shoals (N=52), Norfork (N=52), and Sylamore (N=17). We only collected benthic samples at Sylamore in fall 2005 and winter 2006 due to high flows. Approximately of 113,045 macroinvertebrates were collected, measured, and identified. These collections represented 12 orders, 22 families, and 15 genera (Table 5). A few macroinvertebrate taxa dominated the benthic samples in density (numbers m^{-2}) and biomass (mg DW m^{-2}), but the dominant taxa varied by site (Figure 9). At Bull Shoals, chironomids (57,153 m^{-2} SE$\pm$17,700), isopods (51,815 m^{-2} SE$\pm$18,212), and amphipods (21,120 m^{-2} SE$\pm$5,273) were found in the highest average densities. However, due to the small size of chironomids, biomass was dominated by isopods and amphipods. Chironomids and amphipod

densities were the highest observed at Norfork. Amphipods dominated the biomass at Norfork. In fall 2005 at Sylamore gastropods comprised the majority of macroinvertebrates in terms of both density and biomass; however, in winter 2006 chironomids were most abundant.

Mean benthic density (numbers m^{-2}) and biomass (mg DW m^{-2}) across seasons was highest at Bull Shoals at 6,513 (SE±1,207) and 1,264 (SE±266), respectively. Mean benthic density and biomass was slightly lower at Norfork at 4,002 (SE±1,034) and 953 (SE±268). At Sylamore, benthic densities and biomass were extremely low. Bull Shoals and Norfork samples generally had 18.7 and 14.0 higher biomass of benthic macroinvertebrates than Sylamore, respectively. Mean benthic density and biomass was 191 (SE±48) and 68 (SE±36) at Sylamore.

Significant differences in benthic densities and biomass were detected between seasons at Bull Shoals (density $F_{4,47} = 6.112$ $P<0.000$; biomass $F_{4,47} = 7.14$ $P<0.000$). At Norfork benthic density differed significantly seasonally ($F_{4,47} = 4.261$ $P=0.005$), whereas biomass did not ($F_{4,47} = 1.707$ $P=0.164$). There were no significant seasonal differences detected between density (t value = -0.084, $df = 15$ $P=0.934$) and biomass (t value = 0.405, $df = 15$ $P=0.691$) at Sylamore. Benthic density in spring 2005 at Bull Shoals was significantly lower than in summer 2005 ($P=0.003$) and fall 2005 ($P=0.001$). In summer 2005 benthic biomass at Bull Shoals was higher than in spring 2006 ($P=0.003$) and benthic density was significantly higher in spring 2006 than winter 2006 ($P=0.011$).

The dominant macroinvertebrate taxa in benthic samples collected from Bull Shoals were isopods and amphipods, which comprised between 23 to 64% and 22 to 48% of the total biomass of benthic macroinvertebrates collected (Table 6). Despite being the dominant taxa in the benthos, isopods and amphipods occurred less frequently in the drift across the seasons (<30%). Similarly at Norfork, amphipods were a dominant taxon numerically in the benthos, which

comprised between 42 and 88% of the samples. Also at Norfork, chironomids represented an abundant taxon in the drift and benthos, particularly in the drift, where drifting individuals were between 29 to 60% seasonally. Abundant drift taxa that were absent in the benthic samples were Cladocera and terrestrial invertebrates. Cladocera was the principal taxon in the drift at Bull Shoals. At Sylamore, amphipods and isopods became much less abundant as gastropods became much more abundant (33 to 64%). Chironomids were also important taxon numerically in the drift samples (37 to 54%) at Sylamore, even though their abundance was relatively low in the benthos (3 to 20%).

A total of 237 sites were sampled using a quadrat sampler at Bull Shoals (*N*=98), Norfork (*N*=99), and Sylamore (*N*=40). The total number of sculpin collected across the five seasons at Bull Shoals was 72 (AVE TL=46 mm and WT=2.0 g). The length and weight of sculpin collected in the quadrat sampler at Bull Shoals ranged from 16-87 mm and 0.04-8.6 g. At Norfork, the total number of sculpin collected across the five seasons was 159 (AVE TL=53 mm and WT=2.9 g). The length and weight of sculpin collected in the quadrat sampler at Norfork ranged from 16-103 mm and 0.04-15.4 g. Only one crayfish was collected in the quadrat sampler at Norfork whereas none were collected at Bull Shoals; thus abundance estimates were unfeasible. We only conducted quadrat sampling at Sylamore in fall 2005 and winter 2006 due to high flows during the other seasons. At Sylamore, the total number of sculpin, darters, and crayfish collected was 37 (AVE TL=37 mm and WT=0.6 g), 18 (AVE TL=37 mm and WT=0.6 g), and 33 (AVE CL=16 and WT=2.1), respectively. Length and weight ranged from 30-51 mm and 0.3-1.6 g in sculpin, 29-64 mm and 0.1-2.0 g in darters, and 9-37 mm and 0.7-17.1 g in crayfish at Sylamore. At Sylamore, the density and biomass of crayfish was 1.0 crayfish$\cdot m^{-2}$ (SE$\pm$0.39) and 2.2 g$\cdot m^{-2}$ (SE$\pm$0.86) in fall 2005 and 0.7 crayfish$\cdot m^{-2}$ (SE$\pm$0.22) and 1.3 g$\cdot m^{-2}$

(SE±0.44) in winter 2006. The density and biomass of darters at Sylamore was 0.2 fish·m^{-2} (SE±0.09) and 0.1 g·m^{-2} (SE±0.03) in fall 2005 and 0.7 crayfish·m^{-2} (SE±0.29) and 0.4 g·m^{-2} (SE±0.16) in winter 2006. Densities and biomass of sculpin were considerably lower at Bull Shoals and Sylamore than at Norfork during all seasons. Average biomass of sculpin was 1.43 g·m^{-2} (SE±0.73) at Bull Shoals, 4.70 g·m^{-2} (SE±1.67) at Norfork, and 0.57 g·m^{-2} (SE±0.21) at Sylamore.

Prey energy

Fish (e.g. sculpin) had greater prey energy density (J·g^{-1}) than macroinvertebrates (e.g. Amphipoda, Isopoda, Gastropoda) and crayfish at Bull Shoals and Norfork (Table 7). Amphipods had slightly greater energy density than isopods, and gastropods were the lowest energy density. At Bull Shoals, prey caloric values (WW J·g^{-1}) were significantly different (ANOVA, $F_{3,11} = 14.307$, $P < 0.001$) with the lowest caloric values in Gastropods (Pleuroceridae) and the highest in sculpin. We also found significant differences in the caloric values of prey at Norfork (ANOVA, $F_{4,15} = 29.861$, $P < 0.001$). At Norfork the lowest caloric values were found in Decapods and the highest in sculpin. As sculpin increased in TL their caloric values decreased at Norfork (Linear regression, $F_{1,8} = 15.145$, $P = 0.005$, $r^2 = 0.654$), while sculpin at Bull Shoals exhibited no relationship between TL with caloric values (Linear regression, $F_{1,6} = 0.763$, $P = 0.416$, $r^2 = 0.113$).

Temperature

Temperature profiles at Bull Shoals and Norfork were relatively stable and exhibited similar seasonal patterns (Figure 10). The highest water temperatures occurred in the fall during

November 2005 with maximum temperatures reaching 13.8 °C at Bull Shoals and 14.7 °C at Norfork. The lowest water temperatures occurred in February with Norfork exhibiting a slightly lower minimum temperature at 6.1 °C compared to Bull Shoals at 7.4 °C. Sylamore temperature patterns were the most variable with a maximum of 23.2 °C in May and a minimum of 4.3 °C in February. The lowest water temperature occurred in winter, which was similar to Bull Shoals and Norfork. However, the highest water temperature at Sylamore occurred in the spring rather than the fall. Water temperatures for the bioenergetics model simulations averaged 9.9 °C (SE±0.06), 11.5 °C (SE±0.09), and 14.5 °C (SE±0.21) for Bull Shoals, Norfork, and Sylamore, respectively.

Daily energy expenditure and intake

We used the diets of 1,387 stomachs to determine the spatial and temporal DEI estimates. Brown and rainbow trout DEI varied between seasons and sites (Figure 11). DEE was highest at Sylamore, except in the winter, compared to the other sites due to the elevated water temperatures. We generally estimated much higher DEI in brown trout than in rainbow trout. Brown trout DEI at Norfork exceeded DEE more frequently than at Bull Shoals and Sylamore. Larger brown trout at Bull Shoals during the fall spawning season only had 5% of fish with DEI exceeding DEE. Also, larger brown trout at Sylamore had no fish with DEI in the fall seasons due to a high percent of empty stomachs.

DEI results for rainbow trout suggest that submaintenance feeding conditions were common for both size classes throughout most of the seasons. For small rainbow trout the percentage of fish that exceeded DEE (i.e., metabolic demands) averaged across the seasons was generally low with 14% (range 5-22%), 13% (range 2-32%), and 9% (range 0-20%) at Bull

Shoals, Norfork, and Sylamore, respectively. Similarly for large rainbow trout the percentage of fish DEI that exceeded DEE averaged across the seasons was also low with 10% (range 0-20%) at Bull Shoals and 22% (range 0-45%) at Norfork. For small brown trout the percentage DEI that exceeded DEE averaged across the seasons was generally high with 51% (range 21-100%) at Bull Shoals and 59% (range 25-100%) at Norfork. However, at Sylamore on average across the seasons only 19% (range 0-33%) of small brown trout had DEI that exceeded DEE. Similar to the small brown trout, the percentage of DEI that exceeded DEE in medium brown trout averaged across the seasons was generally high with 56% (range 33-80%) at Bull Shoals, 66% (range 52-76%) at Norfork, and 43% (range 12-89%) at Sylamore. For large brown trout the percentage DEI that exceeded DEE averaged across the seasons was generally moderate with 31% (range 5-65%) at Bull Shoals, 55% (range 43-68%) at Norfork, and 25% (range 0-67%) at Sylamore.

Bioenergetic model estimates of consumption

The total biomass of all prey consumed by brown and rainbow trout during the simulations varied markedly among size classes (23-8,876 kg) and sites (5,980-14,791 kg) (Figure 12). Total consumption was highest for both brown (4,344 kg) and rainbow trout (10,446 kg) simulations at Norfork, and included much higher consumption rates on sculpin. Simulations indicated that total consumption by brown (3,307 kg) and rainbow trout (8,749) was slightly lower at Bull Shoals, but exhibited extremely high consumption rates of isopods compared to the other sites. Due to the low abundance of brown trout at Sylamore, our estimates of total consumption by brown trout were low (657 kg). Although total consumption by rainbow trout at Sylamore was

lower (5,980 kg) than the other sites, the amount consumed was still relatively high considering no larger rainbow trout were collected at the site.

Model simulations of estimates of consumption by rainbow trout, expressed as a proportion (*P*-values) of maximum consumption (C_{max}) of the daily ration, indicated that all rainbow trout fed at relatively low consumption rates (*P*-values range = 0.14–0.30) (Table 8). In contrast, brown trout differed in *P*-values among the size classes and for small brown trout *P*-values were high at Bull Shoals and Norfork (*P*-values range = 0.45–0.82) as a result of rapid growth, whereas medium and large size classes of brown trout experienced moderate to low *P*-values (*P*-values range = 0.13–0.46). Brown trout at Sylamore experienced a drastic difference in *P*-values, with extremely high *P*-values in the summer when temperatures approached upper lethal temperatures.

At all sites, rainbow trout were responsible for the majority of consumption of macroinvertebrates, whereas brown trout were responsible for the bulk of consumption of sculpin. Total predation by individual fish increased with body size, but the size class effects of small rainbow trout exceeded that of other size classes due to the higher abundance of fish in this size class. The total daily consumption of sculpin by individual brown trout increased with size, but cumulatively, large brown trout had the highest impact on sculpin due to their high relative abundances. Sculpin represented only 0–9% of total rainbow trout consumption at Bull Shoals. Total rainbow trout consumption of sculpin represented 0-16% at Norfork and was particularly high in the fall for larger rainbow trout. Small brown trout imposed the least overall consumptive demand on prey resources.

Food availability

Density and biomass of sculpin was approximately 2-3 and 2-8 times higher at Norfork than Bull Shoals and Sylamore, respectively (Figure 13). Consumption to biomass (C/B) by brown and rainbow trout at Bull Shoals indicated that only a minor porortion of sculpin were removed (5–27%) during spring, summer, and winter (Table 9). A more considerable portion of sculpin (*C/B*) was consumed the in fall (65%) at Bull Shoals. At Norfork, consumption of sculpin by rainbow and brown trout (*C/B*) attained the total amount available (100%) in spring of 2006 when seasonal sculpin biomass was lowest. Brown trout consumption of sculpin (*C/B*) removed only minor proportions (3-4%) of available at Sylamore. Based on GCA, the total length of sculpin consumed by brown and rainbow trout ranged from 59-84 mm (2.9-8.4 g), 68-76 mm (5.2-7.3 g) and 51-66 mm (1.8-4.6 g) at Bull Shoals, Norfork, and Sylamore, respectively. When predation rates were converted from biomass to size-specific numerical losses, model simulations indicated that brown trout seasonally consumed an estimated 7,791 to 56,642 sculpin at Bull Shoals, 39,148 to 109,598 sculpin at Norfork, and 27 to 21,365 sculpin at Sylamore.

In the simulations, seasonal population level consumption of drifting macroinvertebrate biomass (*C/B*) by brown and rainbow trout was exceeded by 1.4 to 24.1 fold at Bull Shoals, 2.3 to 39.5 fold at Norfork, and 15.5 to 22.2 fold at Sylamore (Table 10). In contrast, consumption of available benthic macroinvertebrate biomass (*C/B*) was never exceeded (<18%) in all the simulations. At Bull Shoals, consumption demand on the available prey biomass (*C*/*B*) was highest during winter and corresponded with the lowest abundance of macroinvertebrates and lowest mean temperatures (8.7°C). At Norfork, the fraction of the available prey biomass consumed by brown and rainbow trout (*C*/*B*) was highest in the summer when abundance of amphipods declined and mean temperatures were highest (13.4°C), and then *C/B* declined

dramatically in the fall as amphipod abundance increased and outpaced consumption. After the fall at Sylamore, *C*/*B* increased drastically as macroinvertebrate biomass decreased considerably.

Discussion

Differences in trout densities and forage base were observed among the C-R areas suggesting some areas and species were more tailored for C-R management than others. At Bull Shoals and Norfork the biomass of macroinvertebrate forage base was generally similar. However, the biomass of available benthic fish (e.g. sculpin) was approximately 2-8 times higher at Norfork than Bull Shoals and Sylamore. Brown trout densities were also 2-3 times higher at Norfork compared to Bull Shoals, excluding the fall spawning season. The higher brown trout densities were likely supported by the increased abundance and availability of prey fish (e.g. sculpin). Ozark sculpin prefer shallow, gravel-bottomed riffles with strong currents (Robins and Robison 1985). Qualitative evaluation of habitat indicated that the Norfork C-R area contained the most riffle habitat (~25%) compared to only ~10% at Bull Shoals. An increase in the amount of available riffle habitat at Norfork may have contributed to the higher sculpin densities. The macroinvertebrate and benthic fish forage base available to trout was least abundant at Sylamore. An insufficient forage base coupled with elevated water temperatures (>19 °C) at Sylamore made it difficult for rainbow trout to meet their metabolic demands, contributing to negative growth rates. Brown trout net energy intake typically met or exceeded required maintenance ration at Sylamore. Despite postive or no net growth in brown trout at Sylamore, their densities remained extremely low (~3 fish/ha). The inability to collect any large rainbow trout and low densities of brown trout suggests this area is marginal trout habitat. In general, brown trout growth was positive and daily ration was above or at minimum for maintenance ration across the

seasons at all three C-R areas. Temporal bottlenecks in food availability were limited for brown trout, which suggests they may be more suited for C-R areas than rainbow trout from a forage base perspective. However, in this study and a companion study (Cushing 2007), we did not evaluate the other two implicit assumptions in C-R areas for brown trout which are: they do not suffer high mortality rates and do not move out of special regulation areas.

Rainbow trout densities in the three C-R areas at Bull Shoals and Norfork tailwaters were substantially lower during this study than in another Ozark tailwater. Densities of rainbow trout stocked in Taneycomo tailwater were approximately 1,400 fish·ha^{-1} (Weiland and Hayward 1997). Mean densities of rainbow trout in Bull Shoals and Norfork tailwaters during this study ranged from 47 to 342 fish·ha^{-1}, which translates into a 4 to 30 fold decrease in densities. Inversely, benthic macroinvertebrate densities during this study were 4 to 15 times higher than in Taneycomo tailwater. The higher density of macroinvertebrates is likely due to the lower trout densities and subsequent decreased consumption of macroinvertebrates in the food base relative to Taneycomo tailwater. Despite lower densities of rainbow trout and high numbers of drifting macroinvertebrates, food availability still appeared to limit growth of rainbow trout. Lower densities in some of the C-R areas may be necessary to increase food availability and allow for high growth rates, particularly for large rainbow trout. Although no trout were directly stocked into the C-R areas, hatchery stockings of trout nearby (~1 km) move into the C-R areas (Cushing 2007) influencing trout densities in the C-R areas. Rainbow trout experience limited to no reproductive success based on stable isotope analysis (See Chapter 2). Since rainbow trout have limited success in recruiting in the tailwaters, densities in the C-R areas are largely dependent on stockings outside C-R areas. As stocking densities are increased or decreased in nearby areas rainbow trout densities in the C-R areas should respond accordingly. If the C-R areas exceed

carrying capacity through recruitment of wild fish or stocking strategies, then growth and survival of trout populations will suffer. Improving the growth of resident rainbow trout may be achievable by decreasing the stocking densities upriver and/or downriver of the C-R areas. However, put-and-take anglers may not be willing to allow decreased stocking rates (e.g. lower catch rates) of rainbow trout in areas outside the C-R areas in an effort to improve growth rates of rainbow trout within C-R areas. Another possible option for reducing rainbow trout densities in the C-R areas would be allow harvest of small rainbow trout, suggest as a minimum size limit, to help counter age and size truncations under selective angling mortality. Harvest of small, recently stocked rainbow trout (<300 mm) would reduce their population levels, thus increasing food availability to surviving fish and potentially increasing their growth rates. Obviously with either option, reducing stockings nearby or a minimum size limit, managers must consider the social implications of such a decision for anglers fishing within and outside the C-R areas and weigh those against any possible biological gains that might be achieved in the trout populations within C-R areas.

Daily ration (i.e. energy intake) provides a measure of the ability of fish to meet energy requirements for growth after allocating energy towards metabolism (Elliott 1976). Despite reduced metabolic costs in the winter from lower temperatures, rainbow trout daily ration was significantly below the minimum for maintenance ration. Seasonal changes in rainbow trout DEI indicated an early winter metabolic deficiency, with a particular bottleneck in food availability during this time period. Generally the observed growth rates from mark-recapture and DEI results were in agreement. Brown and rainbow trout at Norfork exhibited higher yearly growth rates and DEI than at Bull Shoals and Sylamore. The exception to this observation was with rainbow trout at Norfork. Large rainbow trout at Norfork had slightly higher DEI's than small

rainbow trout. However, growth rates for small rainbow trout were higher than the large size class. This discrepancy may be the result of assumption of no energy intake from algae or missing available prey. Similar to other tailwaters, larger rainbow trout appeared to experience poorer energetic conditions than smaller rainbow trout (McKinney and Speas 2001; Weiland and Hayward 1997). Food availability is considered a function of drifting macroinvertebrate density and drift rate likely exerts a more significant influence on growth than the effects of temperature on metabolism (Railsback and Rose 1999). Macroinvertebrate drift rates decreased considerably during winter. Filbert and Hawkins (1995) also found trout condition and densities of drifting macroinvertebrates lowest in the winter (February) in the tailwater of Green River below Flaming Gorge Dam. Food limitation for salmonids in unregulated Appalachian streams has been observed in the summer (Cada et al. 1987; Ensign et al. 1990) and winter (Utz and Hartman 2006) due to inadequate energy intake. In other regulated tailwaters, food supply increased in the summer and steadily decreased through fall and winter (Filbert and Hawkins 1995; McKinney and Speas 2001; Weiland and Hayward 1997). We found a similarly high food supply in drifting macroinvertebrates in spring followed by a steady decrease through the fall.

In this study we also quantified consumption dynamics using a Wisconsin bioenergetics model at the population level of brown and rainbow trout within a spatial-temporal framework to identify possible bottlenecks in growth and food availability. Model simulations indicated bottlenecks in macroinvertebrate food supply only emerged under the drifting feeding scenarios of consumption to available prey biomass (*C/B*). If trout only had access to drifting macroinvertebrates, the seasonal consumption by trout would have exceeded the biomass for most available macroinvertebrates, particularly in relation to amphipods, chironomids, and isopods. The fraction of available macroinvertebrate biomass consumed declined dramatically

when foraging scenarios included macroinvertebrates in the benthos as available prey. A simplifying assumption in our modeling was the availability of prey. We assumed all fish had equal access to benthic and drifting macroinvertebrates and fish prey. Salmonids are territorial and select feeding locations that provide 'optimal foraging' (Fausch 1984). Therefore, salmonids not holding feeding territories would be expected to occupy the less profitable foraging areas with reductions in macroinvertebrate drift rates, benthic macroinvertebrates, and/or prey fish (Chapman 1966; Elliott 1990). Another complexity was in determining what constitutes available prey in a lotic system with trout that alternated between benthic and drifting feeding modes. Given the opportunistic nature of salmonid feeding, foraging patterns are likely to shift spatially and temporally in response to abiotic (e.g. temperature, flow) and biotic (e.g. competition, predation) processes (Allan 1981; Angradi and Griffith 1990; Dill 1983). We simply lacked data to realistically model these contingencies.

Salmonids, especially rainbow trout, are known to feed predominantly on drifting macroinvertebrates (Bachman 1984; Brittain and Eikeland 1988; McIntosh and Townsend 1995). Despite the lack of energetic value to trout, *Cladophora* and *D. geminata* at Bull Shoals, were found in high proportions in stomachs of rainbow trout, indicating a high amount of epibenthic foraging. Disproportionately high numbers of rarely drifting prey taxa (e.g. amphipods, isopods, gastropods) in the diets further suggested epibenthic foraging as a feeding mode (Rader 1997). Shifting feeding modes from drift to epibenthic foraging may allow rainbow trout to exploit benthos in an effort to increase prey availability (Angradi and Griffith 1990; Bisson 1978). In other regulated systems, where algae constituted a large proportion of trout diets, the relative conditions of the trout were poor (Filbert and Hawkins 1995; McKinney and Speas 2001; Weiland and Hayward 1997). In those instances, researchers attributed the poor conditions to an

inability by the trout to extract energy from algal and diatom resources (Weiland and Hayward 1997). Relative biomass of algal consumption may provide an indicator of spatial and temporal changes in food availability. Algal consumption by small and large rainbow trout, increased in some seasons and size classes. The highest algae consumption by both size classes of rainbow trout occurred in the spring at Bull Shoals, with large rainbow trout consuming higher proportions than small rainbow trout. Inversely, high algae consumption at Norfork occurred in the fall and winter when the abundances of drifting macroinvertebrates were lowest. Despite high algal consumption in rainbow trout at Sylamore their foraging shifts of algae in the diets across the seasons were minimal (61-87%), an exception was in spring when gastropods dominated their diets. A similar high level of algal consumption (40-50%) by trout in other regulated systems has been observed (McKinney and Speas 2001; Weiland and Hayward 1997).

In contrast to rainbow trout foraging patterns, brown trout exhibited limited algae consumption despite evident epibenthic foraging. Macroinvertebrates, such as amphipods, isopods, and gastropods, were not commonly collected in the drift, but were abundant in the diets of brown trout. Epibenthic foraging effectiveness that limits algal consumption may be due to a more wild foraging behavior of brown trout than rainbow trout. Brown trout were stocked at a much smaller size (~178 mm) than rainbow trout (~279 mm). Also, wild, self-sustaining populations of brown trout occur in the White River (Pender and Kwak 2002). As a result brown trout foraging behavior in the tailwaters may be more similar to wild fish than hatchery fish. Field and laboratory studies suggest hatchery fish were not able to forage effectively compared to their wild counterparts causing slower growth for hatchery fish (Olla et al. 1998). Hatcheries typically rear fish in environments with lower current velocities and at much higher densities than encountered in natural aquatic environments. Fish are also fed artificial foods at high

maintenance rations. Due to the rearing environment, hatchery released fish may be less energetically efficient than wild fish (Weber and Fausch 2003).

Growth rate differences between brown and rainbow trout may be from differences in the feeding strategies of brown trout which more often exploited prey fish. Although some rainbow trout exhibited piscivory this was limited and was only found to occur in a few fish, particularly larger fish. A dietary study in Lee's Ferry tailwater found rainbow trout were drastically less piscivorous than brown trout (Yard et al. 2011). Faster growth rates by piscivorous brown trout compared to non-piscivorous brown trout have been demonstrated in laboratory and field settings (Elliott and Hurley 2000; Grey 2001). Also, caloric content of prey fish (i.e. sculpin) was greater than aquatic macroinvertebrates in the tailwaters. Brown trout shifted ontogenetically towards the incorporation of piscivory into their diets at ~200 mm. The incorporation of fish into their diets allowed them to consume more prey biomass and calories compared to those feeding solely on macroinvertebrates (Elliott and Hurley 2000; Foresth and Jonsson 1994). Johnson et al. (2006) found a growth bottleneck in brown trout populations in the regulated Little Red River, Arkansas due to the lack of available suitably sized prey fish (e.g. sculpin). Brown trout at Norfork exhibited a higher degree of piscivory than at Bull Shoals and Sylamore likely due to higher densities and biomass of sculpin available in the benthos. An increase in caloric content from prey fish at Norfork likely allowed brown trout (>250 mm) to grow at faster rates and support a higher biomass.

In addition to diets and food availability influencing trout growth, handling practices from C-R and/or the number of times a fish is recaptured throughout a season may also impact growth. Cutthroat trout in the Yellowstone River were estimated to be captured 9.7 times per season (Schill et al. 1986) and fish captured numerous times may experience reduced growth

(Clapp and Clark Jr. 1989; Diodati and Richards 1996). Stress from capture and handling can cause feeding cessation to last from several hours to days (Pickering et al. 1982) and may cause growth reduction as feeding intake decreases (Clapp and Clark Jr. 1989; Diodati and Richards 1996; Meka and Margraf 2007). If feeding cessation is known to occur after capture and a high proportion of the population are captured multiple times throughout the season, managers may consider evaluating these sub-lethal impacts on growth to understand and predict fishery effects from recreational angling.

The maximum water temperatures observed in Bull Shoals (13.8°C) and Norfork (14.8°C) were well below the upper lethal temperatures and near the optimal range for trout growth throughout the summer and fall (10-14 °C). The optimal reported range for growth in brown trout is 12-13°C and 17-18°C in rainbow trout (Elliott and Hurley 1998; Hokanson et al. 1977; Jobling 1991). Upper lethal temperatures for brown trout are slightly higher (29-30°C) than those reported for rainbow trout (25-27°C) (Bear et al. 2007; Elliott 1995; Hokanson et al. 1977). Spring water temperatures at Sylamore approached lethal limits for brown and rainbow trout (23.2°C). Temperature directly affects the metabolic costs and feeding efficiencies of fish (Elliott 1976; Wurtsbaugh and Davis 1977). Despite the high temperatures at the time of sampling in the spring (18 °C) the amount of energy ingested by rainbow trout approached the maintenance ration due to decreased algae consumption. The observed negative growth rates and poor condition in rainbow trout at Sylamore suggest higher maintenance energy from elevated water temperatures plays a large role in regulating their growth. Cushing (2007) observed weekly rainbow trout movements were positively related to water temperature at Sylamore. As temperature increased average net weekly movement increased and by the end of May when water temperatures exceeded 20 °C all radio tagged rainbow trout moved outside of

the Sylamore C-R area. Brown trout at Sylamore generally maintained their growth and condition during throughout the year and during periods of higher water temperatures.

Dams with hypoliminial releases act as discontinuities within the river continuum and cause changes in both abiotic (i.e. flow, temperature, substrate) and biotic (i.e. predation, competition) processes (Ward and Stanford 1983). Food web dynamics typical of unregulated rivers are altered in tailwaters, resulting in reduced macroinvertebrate diversity and shifts in the macroinvertebrate functional groups (i.e. shredders, collectors, scrapers) present (Vannote et al. 1980). Autochthonous energy in tailwaters within close proximity to the dams typically includes filamentous algae with associated epiphyton. In contrast, unregulated rivers receive autochthonous energy from coarse particulate carbon, such as leaves. These shifts in food resources alter the trophic structure of the food webs in the tailwater with a trend towards macroinvertebrate grazers (e.g. Amphipods, Isopods) as opposed to shredders, collectors, and detritivores (Blinn et al. 1998). Macroinvertebrate assemblages at Bull Shoals and Norfork exhibited a low diversity of macroinvertebrates which is consistent with other findings on southeastern tailwaters (Johnson and Harp 2005; Weiland and Hayward 1997) and western tailwaters (Filbert and Hawkins 1995; McKinney and Speas 2001). Few Ephemeroptera, Plectopera, and Tricoptera (EPTs) were collected during this study. Daily water level fluctuations and chronic cold temperatures near the dams constrain the life cycles of EPT which limit their abundance within these environments (Johnson and Harp 2005). Macroinvertebrate diversity and EPT increased downriver at Sylamore, as ecological conditions reset toward natural conditions and temperatures increased, which typically occurs (Ward and Stanford 1995). At Bull Shoals, isopods and amphipods dominated the benthic samples, whereas only amphipods dominated at Norfork.

In 2006, tailwater discharge from Bull Shoals dam was the lowest reported in twenty-five years. Flow reductions from hypolimion releases can alter abundances of biotic assemblages (McKinney et al. 1999). The extremely low water discharge and/or drought conditions at Bull Shoals in 2006 allowed for visibly noticeable extensive, mucilaginous mats of *D. geminata* attached to the substrate. Bull Shoals was the only C-R area in 2005-2006 to contain any noticeable presence of *D. geminata* attached to the substrate. In other systems with high production of *D. geminata* macroinvertebrate abundances increased and diversity shifted from large taxa (Ephemeroptera, Plecoptera, and Tricoptera) towards smaller Diptera taxa (chironomidae) (Gills and Chalifour 2010; James et al. 2010a; Kilroy et al. 2009). James et al. (2010) found that brown trout conditions (W_r) remained high (>100) despite thick diatom mats of *D. geminata* and suggested that the amount of food available was adequate. Despite the presence of *D. geminata*, the low flow conditions possibly reduced prey production by decreasing the production of *Daphnia* and amount of lateral habitat available. Drift dynamics in the tailwater are likely influenced by season and dam operations (McKinney et al. 1999). Water velocity and discharge are major abiotic measures often correlated with drift density and some studies have observed a positive correlation between drift density and discharge (Allan 1987; Williams and Williams, 1993). Increased water velocities during peak flows may improve the availability of food resources by displacing macroinvertebrates into the water column (e.g. drift) and increase drifting zooplankton from hypolimnetic releases (Lagarrigue et al. 2002; Lauters et al. 1996; Simpkins and Hubert 2000). The low water releases in 2006 at Bull Shoals may have decreased the availability of food resources and negatively impacted trout growth. However, it is unknown whether brown and rainbow trout are able to forage with equal effort during peak and base flows. Declines in biomass of salmonids have also been documented in periods of drought as habitat

availability and food resources are altered (Hakala and Hartman 2004; James et al. 2010b). We found a decrease in the biomass in both brown and rainbow trout at Bull Shoals from spring 2005 to 2006 even though stocking levels of rainbow trout in nearby areas were similar in the spring between years (2005 = 39,280 rainbow trout vs. 2006 = 44,949 rainbow trout). Brown trout biomass decreased 27% and rainbow trout decreased 49% between years and implies a reduction in flows decreased fish production at Bull Shoals.

Entrained zooplankton from reservoir releases can be the principal component in drift and an important food resource in tailwaters (Jackson et al. 1991; Ward 1974). At Bull Shoals and Norfork the amount of drifting zooplankton contributed significantly to the overall density of drifting macroinvertebrates and was a temporally important prey for the trout. Zooplankton constituted a higher percent of the diets of brown and rainbow trout in the spring seasons. Increased generation from the dams in the spring likely resulted in higher densities of entrained zooplankton in drift at both Bull Shoals and Norfork. In the White River, zooplankton were observed in the area directly below the dam (Bull Shoals C-R area), but were not observed at Sylamore which is 124 rkm below the dam. Drifting distances of zooplankton often vary longitudinally in tailwaters as individuals damaged through the entrainment process settle out and/or are removed by fish predators (Jackson et al. 1991). Despite the Norfork C-R area being 4 rkm below the dam, it contained the highest observed zooplankton densities of all the C-R areas. Zooplankton densities at Bull Shoals and Norfork (1.8 and 3.9 number/m^3) were comparatively low to a Wyoming tailwater where mean zooplankton densities ranged from 125 to 275 (number/m^3) during the winter (Simpkins and Hubert 2000). However, we only reported the amount of zooplankton in the drift that was utilized by trout (> 2.0 mm TL) which comprised a relatively small proportion of the total number of zooplankton collected (range 11-24%).

A potential prey source that was noticeably absent during the course of the study was threadfin shad, *Dorosoma petenense*, which can be a high-caloric winter fish prey. As reservoir water temperatures decrease in the winter (to less than 7°C) the entrainment of threadfin shad, a species intolerant of cold temperatures, begins to occur below Bull Shoals and Norfork dams (Jeff Williams, AGFC, personal communication). In Taneycomo tailwater, threadfin shad were found to be an important source of calories in the diets of rainbow trout in the winter (Weiland and Hayward 1997). Elevated winter reservoir temperatures during this study likely prevented threadfin shad from being entrained in the tailwaters. In winters when high abundances of threadfin shad are available for trout consumption at Bull Shoals C-R area food limitation may not occur during this critical time period. It is less likely that trout in Norfork C-R area benefit from entrained threadfin due the distance of this area downriver from the dam (4 rkm). Predators upriver of the C-R area likely consume the majority of the shad before they reach the C-R area.

In summary, bioenergetics modeling simulations suggested rainbow trout, and not brown trout, in Arkansas tailwaters were limited by spatial-temporal fluctuations in food availability. The extent of population level impacts from C-R regulations may depend on species composition and carrying capacity of the populations (Shuter 1990). Estimating the carrying capacity of trout in C-R areas is an important management objective. By monitoring abundance, diets, growth of trout and benthic prey simultaneously, we can evaluate seasonal bottlenecks in resource supply. If trout populations expand, through increased stockings in surrounding areas or increased recruitment, seasonal bottlenecks in the food supply may become more pronounced. Continued monitoring of trout populations will be necessary to understand how C-R restrictions will affect the long-term success and stability of the fisheries in these areas.

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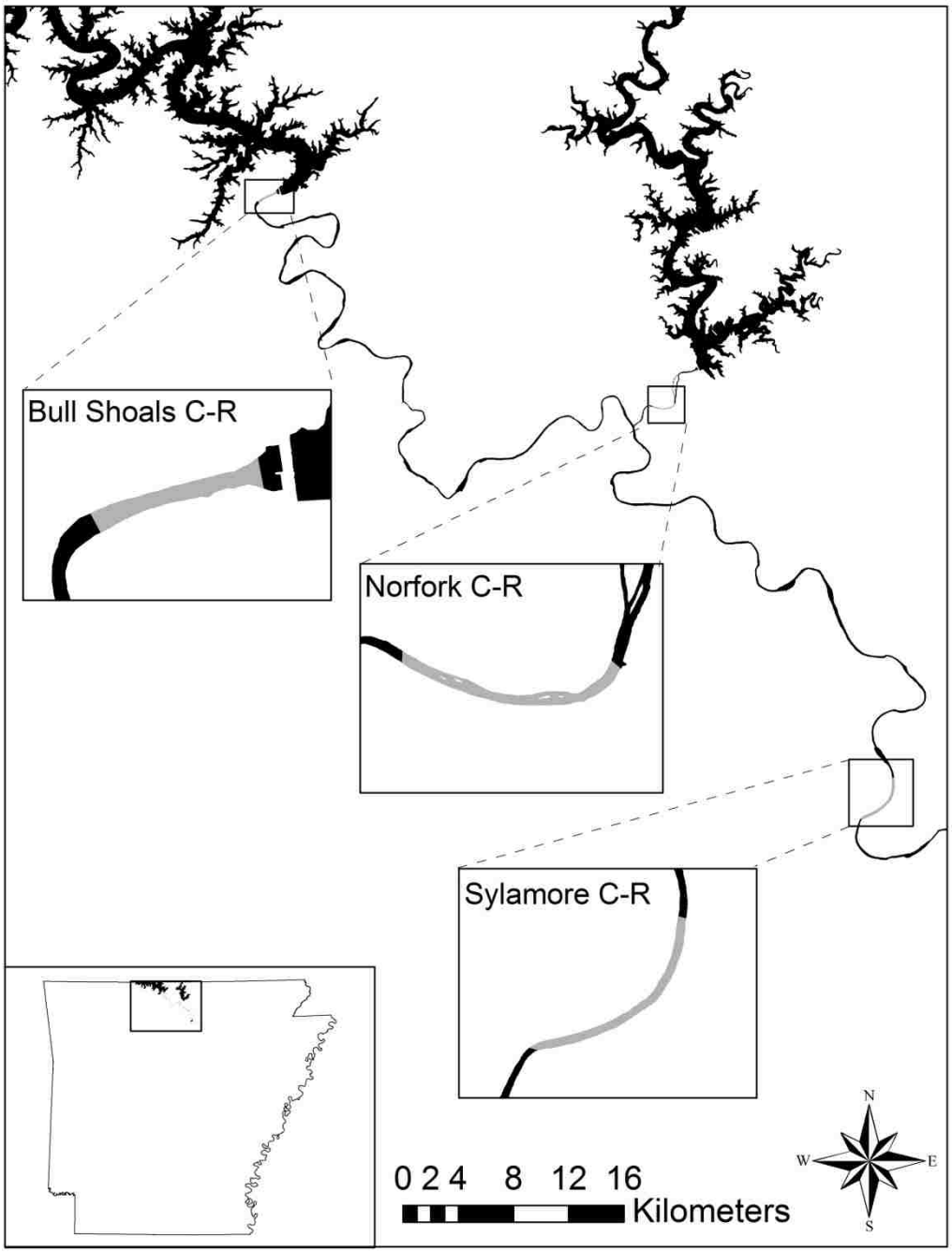


Figure 1. Map of the tailwater catch-and-release (C-R) areas below Bull Shoals and Norfork reservoirs, Arkansas.

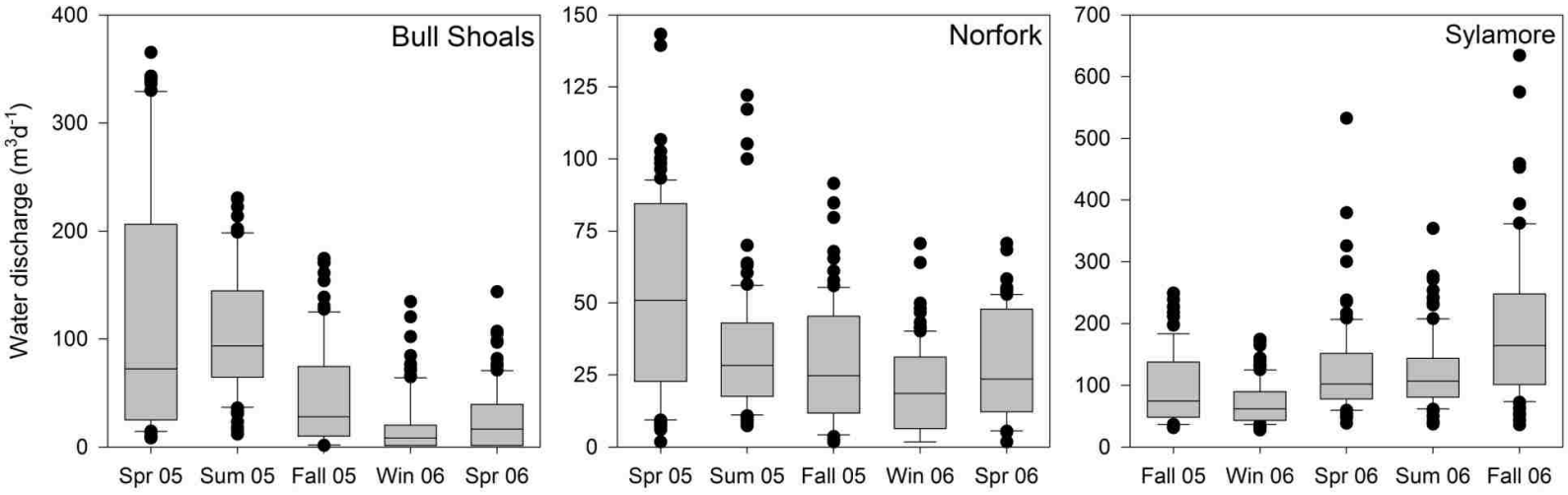


Figure 2. Boxplots of water discharge ($m^3 \cdot d^{-1}$) from Bull Shoals and Norfork tailwaters from April 1, 2005 to June 30, 2006. Water discharge ($m^3 \cdot d^{-1}$) for Sylamore were obtained from a USGS gauging station at Calico Rock from October 1, 2005 to December 31, 2006.

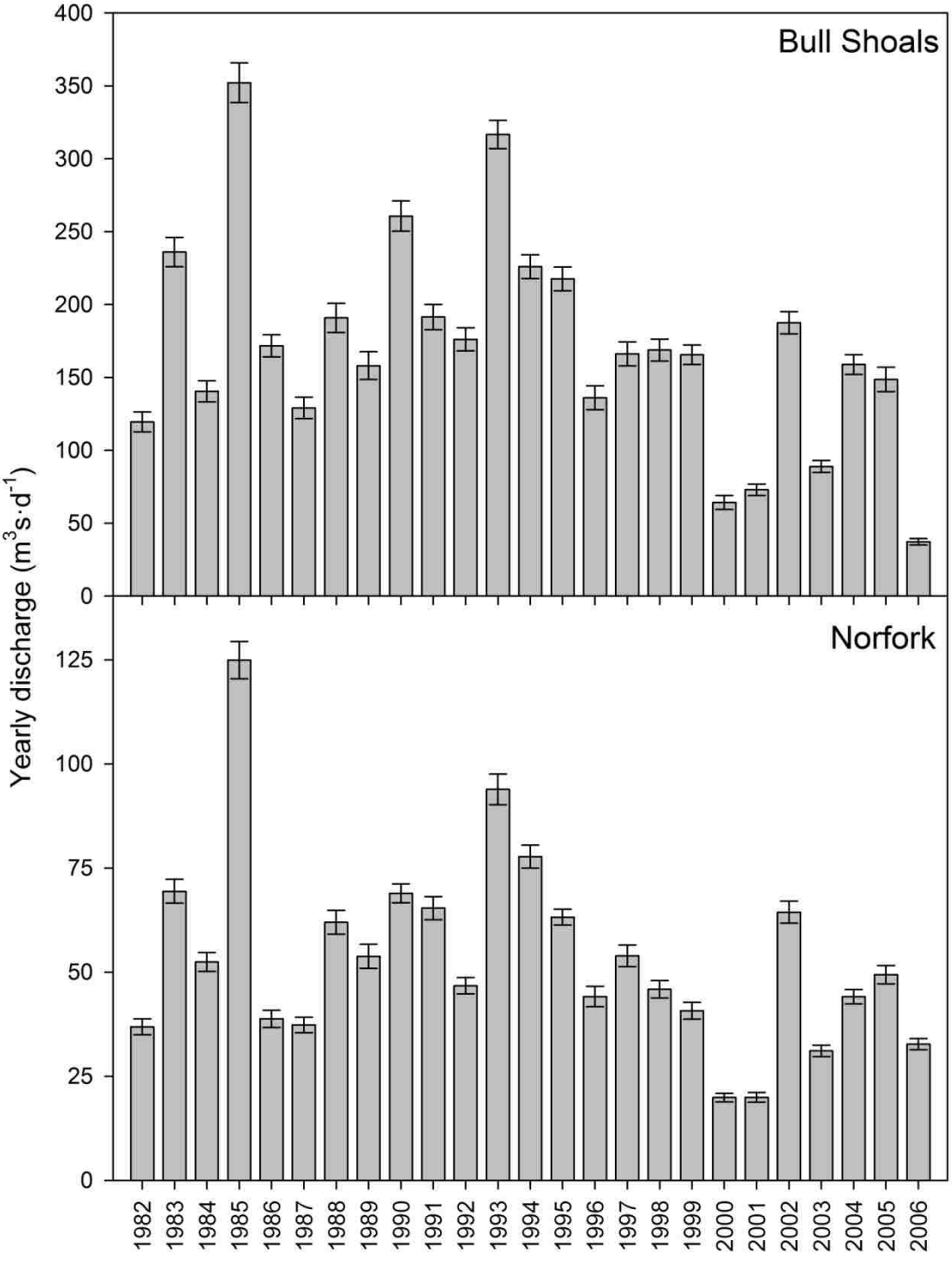


Figure 3. Historical mean yearly discharge ($m^3 \cdot d^{-1}$) at Bull Shoals and Norfork dams.

Table 1. The numbers of fish tagged during the first sampling event (n_1), numbers of fish during the second sampling event (n_2), and numbers of tagged fish captured during the second sampling event (m_2) of the mark-recapture. Abundance estimates with 95% confidence intervals by size class for brown and rainbow trout are provided seasonally for each of the C-R areas in 2005 and 2006.

				Mark-recapture			Abundance	
Site	Season	Species	Size class	n_1	n_2	m_2	$\hat{N}$	95% CI
Bull Shoals	Spr 05	Brown trout	Small	26	31	5	143	(52-413)
			Medium	74	75	21	258	(161-405)
			Large	142	99	16	840	(492-1,434)
		Rainbow trout	Small	355	296	29	3,523	(2,395-5,201)
			Large	96	59	4	1,163	(391-4,180)
	Sum 05	Brown trout	Small	10	9	4	21	(6-66)
			Medium	111	100	37	297	(209-413)
			Large	184	180	60	548	(457-639)
		Rainbow trout	Small	507	397	67	2,972	(2,378-3,567)
			Large	151	152	20	1,106	(689-1,774)
	Fall 05	Brown trout	Small	1	2	1	2	(1-39)
			Medium	85	84	13	521	(286-950)
			Large	237	213	43	1,157	(842-1,577)
		Rainbow trout	Small	456	456	81	2,546	(2,096-2,996)
			Large	186	153	28	992	(666-1,468)
	Win 06	Brown trout	Small	12	10	6	19	(7-47)
			Medium	128	86	36	302	(212-423)
			Large	233	173	54	739	(599-880)
		Rainbow trout	Small	693	543	142	2,639	(2,309-2,969)
			Large	122	95	28	406	(271-598)
	Spr 06	Brown trout	Small	11	20	6	35	(13-85)
			Medium	92	67	21	286	(179-449)
			Large	179	143	52	488	(401-575)
		Rainbow trout	Small	688	542	135	2,750	(2,393-3,107)
			Large	96	80	16	461	(269-783)
Norfork	Spr 05	Brown trout	Small	24	24	7	77	(41-1,226)
			Medium	170	109	30	606	(473-1095)
			Large	191	127	49	491	(363-653)
		Rainbow trout	Small	397	225	27	3,211	(2,151-4,815)
			Large	79	48	7	489	(228-1,471)
	Sum 05	Brown trout	Small	2	1	0	5	(1-9)
			Medium	154	114	38	456	(324-632)
			Large	202	126	54	468	(389-547)
		Rainbow trout	Small	593	838	120	4,118	(3,514-4,721)
			Large	103	91	15	597	(342-1,040)
	Fall 05	Brown trout	Small	1	7	1	7	(1-136)
			Medium	80	86	15	439	(251-764)
			Large	95	73	21	322	(201-506)
		Rainbow trout	Small	636	717	142	3,197	(2,786-3,609)
			Large	38	47	10	169	(84-336)

				Mark-recapture			Abundance	
Site	Season	Species	Size class	n_1	n_2	m_2	$\hat{N}$	95% CI
	Win 06	Brown trout	Small	25	22	6	84	(33-213)
			Medium	106	92	26	368	(242-549)
			Large	107	115	37	329	(232-458)
		Rainbow trout	Small	869	814	220	3,207	(2,896-3,519)
			Large	73	74	23	230	(147-353)
	Spr 06	Brown trout	Small	12	14	1	97	(12-3,274)
			Medium	113	112	25	494	(323-748)
			Large	152	163	51	482	(394-569)
		Rainbow trout	Small	756	662	131	3,801	(3,276-4,327)
			Large	35	33	6	174	(69-448)
Sylamore	Fall 05	Brown trout	Small	1	1	0	3	(1-5)
			Medium	35	31	6	164	(65-421)
			Large	9	7	2	26	(6-178)
		Rainbow trout	Small	285	258	30	2,388	(1,633-3,493)
	Win 06	Brown trout	Small	10	11	2	43	(8-310)
			Medium	54	45	15	157	(89-270)
			Large	9	11	2	39	(8-279)
		Rainbow trout	Small	910	955	179	4,837	(4,269-5,406)
	Spr 06	Brown trout	Small	8	7	1	35	(4-1,091)
			Medium	14	14	1	112	(14-3,820)
			Large	6	3	0	27	--
		Rainbow trout	Small	139	211	11	2,472	(1,224-3,721)
	Fall 06	Brown trout	Small	1	0	0	1	--
			Medium	8	13	0	125	(0-284)
			Large	2	1	0	5	(0-9)
		Rainbow trout	Small	44	76	1	1,732	(241-6,171)

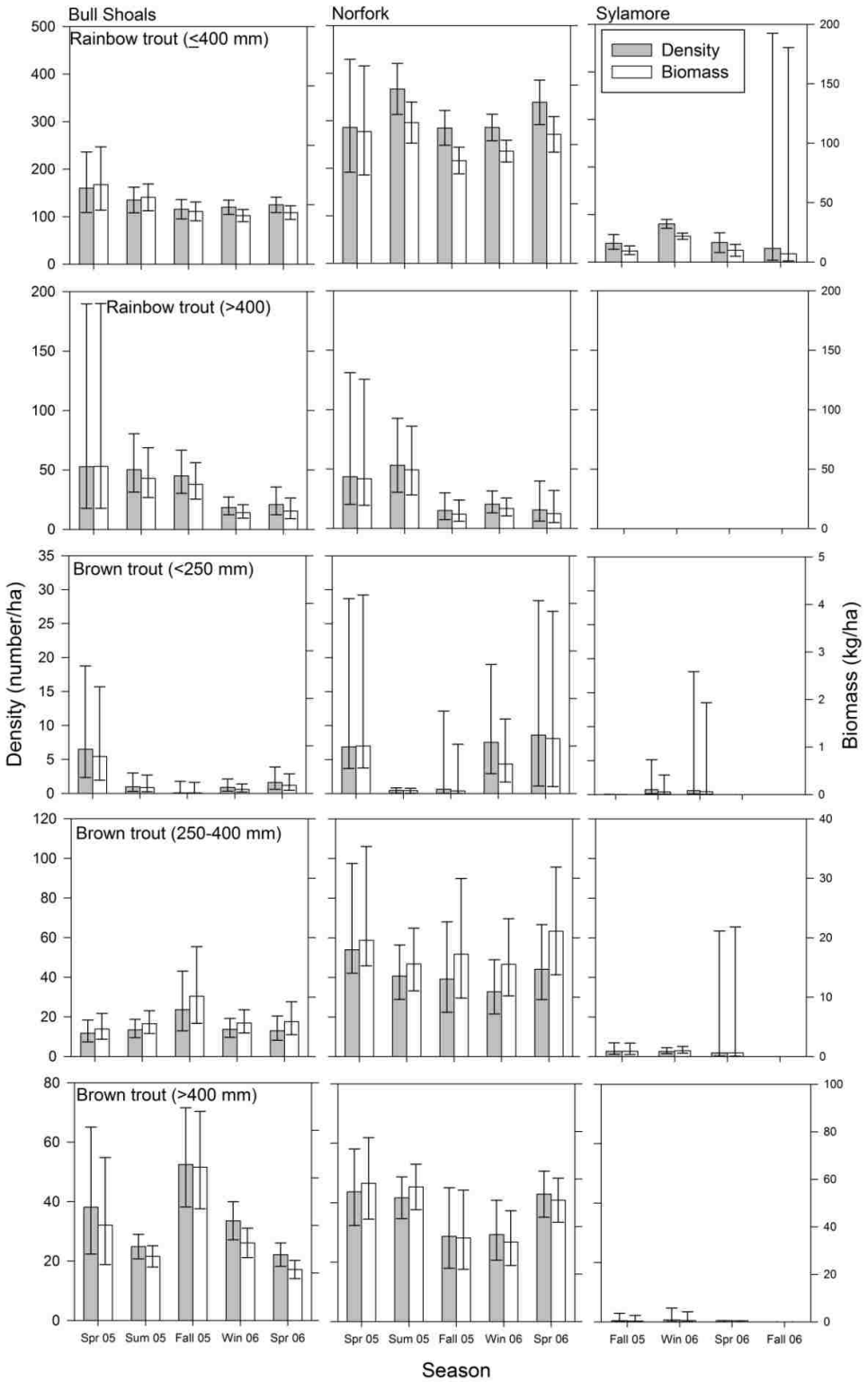


Figure 4. Seasonal density (number/ha) and biomass (kg/ha) estimates with 95% confidence intervals by size class for brown and rainbow trout in each of the C-R areas in 2005 and 2006.

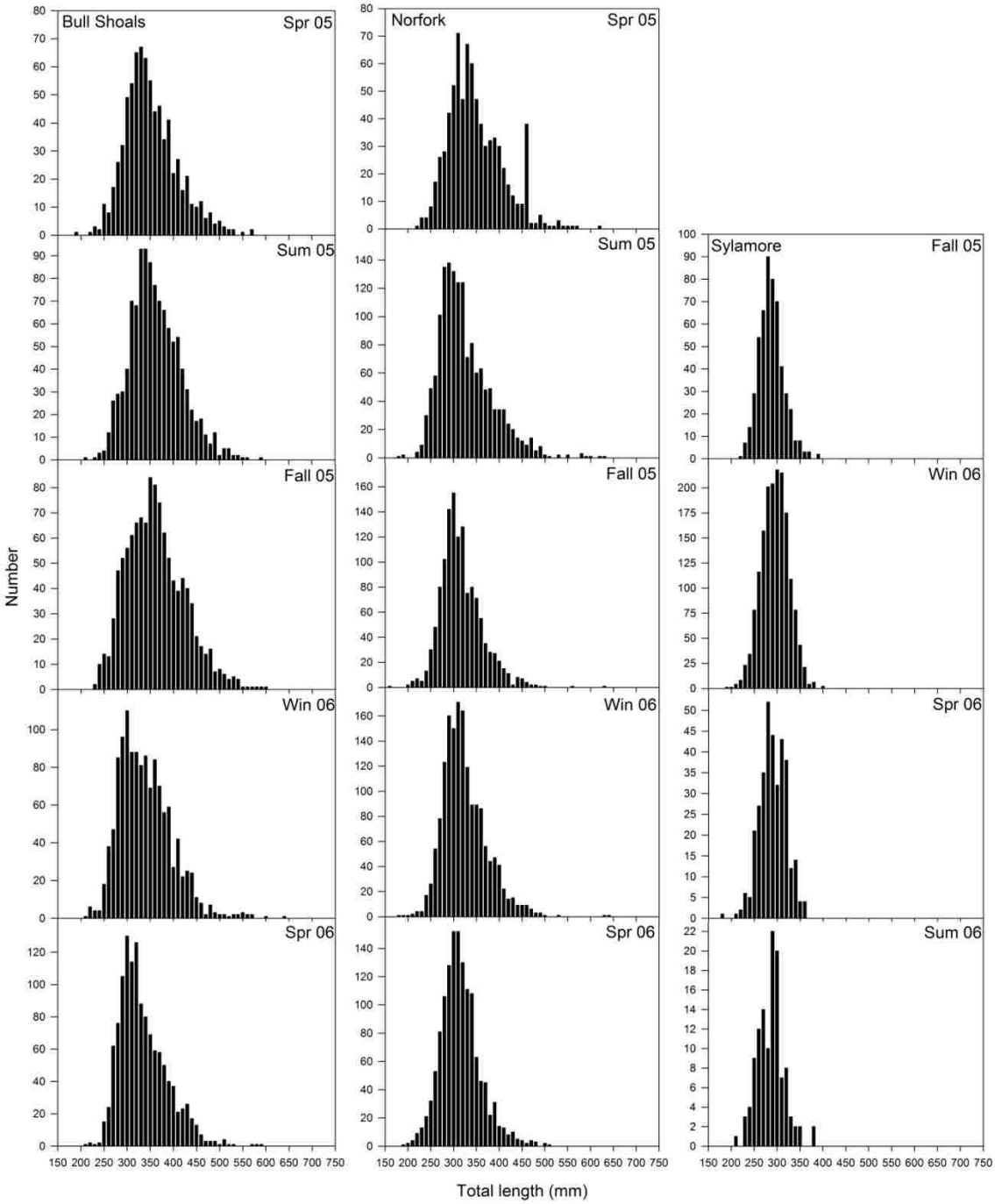


Figure 5. Length-frequency distribution of rainbow trout in Bull Shoals, Norfork, and Sylamore by season.

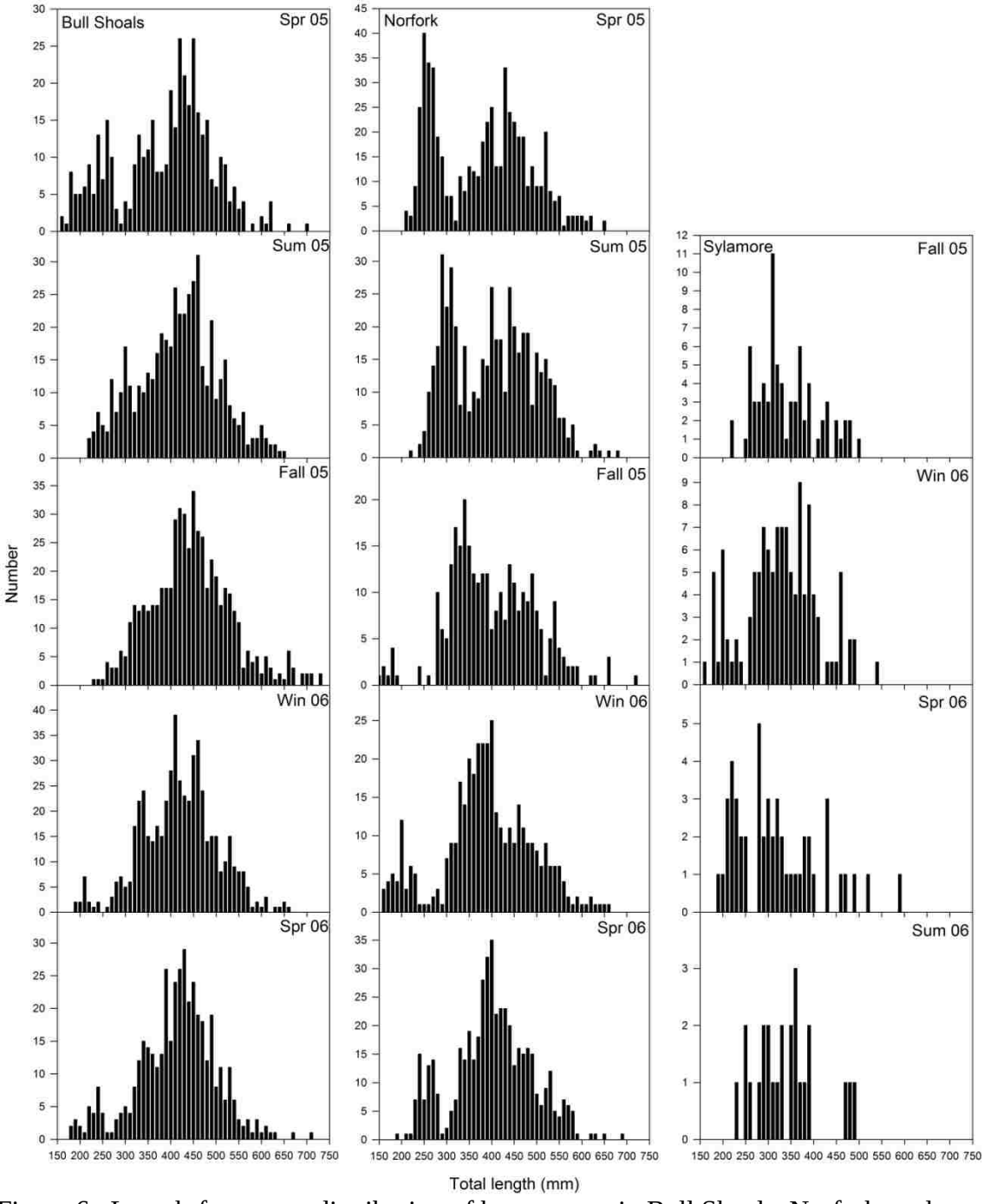


Figure 6. Length-frequency distribution of brown trout in Bull Shoals, Norfork, and Sylamore seasonally.

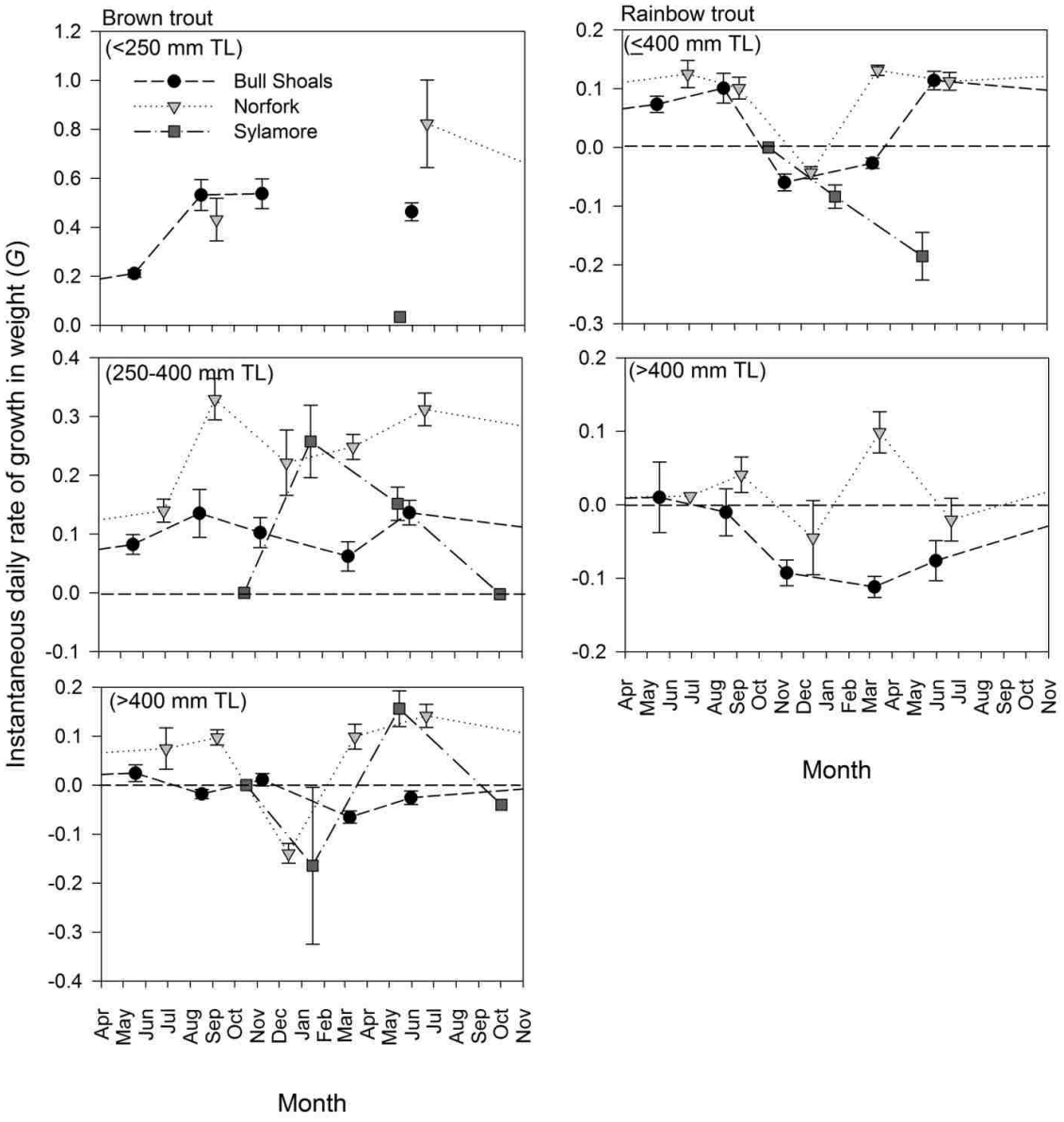


Figure 7. Instantaneous daily rate of growth in weight (*G*) with standard error of brown and rainbow trout by size class in the C-R areas from May 2005 to November 2006.

Table 2. Mean (±SE) relative weights (W_R) by site, species size class, season, and ANCOVA and ANOVA results from May 2005 to November 2006.

			Season								
Site	Trout	Size class	Spr 05	Sum 05	Fall 05	Win 06	Spr 06	Fall 06	df	*F*	*P*
Bull Shoals	Rainbow	Small	98.7 (0.48)	93.5 (0.33)	89.2 (0.35)	87.2 (0.35)	90.8 (0.31)	--	4, 4,465	132.10	<0.01
		Large	99.0 (1.16)	89.6 (0.60)	83.8 (0.54)	78.0 (0.71)	80.2 (0.88)	--	4, 1,080	104.36	<0.01
	Brown	Small	92.1 (1.19)	86.5 (1.74)	88.2 (16.60)	81.4 (1.62)	84.8 (1.23)	--	4, 106	7.52	<0.01
		Medium	94.4 (1.04)	94.1 (1.03)	92.4 (0.80)	86.8 (0.71)	92.9 (0.99)	--	4, 762	13.22	<0.01
		Large	92.8 (0.76)	90.8 (0.73)	92.4 (0.60)	83.9 (0.63)	85.3 (0.71)	--	4, 1,523	37.95	<0.01
Norfork	Rainbow	Small	97.2 (0.46)	92.9 (0.24)	86.0 (0.26)	90.2 (0.28)	92.9 (0.30)	--	4, 5,914	157.81	<0.01
		Large	96.9 (0.93)	91.6 (0.82)	84.6 (1.22)	88.2 (0.85)	89.4 (1.39)	--	4, 574	19.36	<0.01
	Brown	Small	98.1 (1.13)	89.5 (5.08)	96.3 (3.14)	84.9 (0.99)	92.3 (1.80)	--	4, 117	12.74	<0.01
		Medium	102.8 (0.70)	100.6 (0.71)	96.2 (0.85)	95.0 (0.83)	101.8 (0.91)	--	4, 999	25.69	<0.01
		Large	111.3 (0.90)	110.4 (0.83)	96.9 (1.09)	96.6 (0.88)	104.7 (0.91)	--	4, 1,096	51.85	<0.01
Sylamore	Rainbow	Small	--	--	86.7 (0.52)	89.7 (0.28)	83.9 (0.55)	89.3 (1.17)	3, 2,670	28.73	<0.01
	Brown	Small	--	--	72.1 (1.24)	83.5 (1.61)	87.2 (2.71)	102.7	2, 32	3.64	0.02
		Medium	--	--	84.2 (1.21)	90.4 (1.07)	91.4 (1.28)	90.4 (1.80)	3, 187	6.74	<0.01
		Large	--	--	89.4 (3.15)	87.4 (2.78)	95.6 (3.84)	98.1 (5.84)	2, 39	0.86	0.47

Table 3. Percent frequency of occurrence of prey items in the diets with algae (%F[a]) and without algae for bioenergetic simulations (%F) of brown and rainbow trout by size classes in Bull Shoals, Norfork, and Sylamore C-R area collected from May 2005 to November 2006. The number of full (*N*) and empty stomach (N^E) were also reported.

						Algae		Amphipoda		Chironomidae		Cladocera		Decapoda		Gastropoda		Isopoda		Sculpin		Aquatic Inverts.		Other Verts.		Terrestrial Inverts.	
Site	Trout	Size class	Season	*N*	N^E	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F
Bull Shoals	Rainbow	Small	Spr 05	40	2	50	--	20	37	1	4	8	22	0	0	0	0	17	32	0	0	1	1	0	0	2	3
			Sum 05	46	0	29	--	7	11	0	5	5	5	0	0	0	0	56	75	1	1	1	2	0	0	0	1
			Fall 05	41	1	29	--	9	13	0	1	0	0	0	0	0	0	47	70	7	7	0	0	0	0	8	9
			Win 06	40	0	47	--	22	47	6	13	6	11	0	0	0	0	17	24	0	0	0	0	0	0	1	3
			Spr 06	41	3	54	--	8	23	4	12	1	4	0	0	0	2	30	53	1	2	0	3	0	0	1	3
		Large	Spr 05	20	1	82	--	12	49	1	13	0	5	0	0	0	1	3	28	0	0	0	0	0	0	1	3
			Sum 05	20	0	51	--	7	21	0	7	1	1	0	0	0	0	41	70	0	0	0	0	0	0	0	0
			Fall 05	20	0	54	--	6	16	2	8	0	0	0	0	0	0	21	55	9	9	0	0	0	0	8	11
			Win 06	20	1	55	--	28	59	2	12	3	3	0	0	0	0	8	16	1	4	0	0	0	0	3	6
			Spr 06	19	0	72	--	6	25	1	22	0	2	0	0	0	0	18	39	0	0	0	3	0	0	2	9
	Brown	Small	Spr 05	19	0	3	--	62	65	3	3	7	7	0	0	0	0	16	16	0	0	1	1	0	0	8	8
			Sum 05	5	0	6	--	21	21	3	4	0	0	0	0	2	2	66	71	0	0	0	0	0	0	2	2
			Fall 05	1	0	0	--	0	0	5	5	0	0	0	0	0	0	81	81	0	0	0	0	0	0	14	14
			Win 06	4	0	0	--	54	54	42	42	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	5
			Spr 06	14	1	0	--	13	13	5	5	1	1	0	0	18	18	36	36	15	15	0	0	0	0	12	12
		Medium	Spr 05	21	0	1	--	45	46	4	4	10	10	0	0	1	1	17	18	16	16	0	0	0	0	5	5
			Sum 05	20	1	1	--	19	19	1	1	0	0	0	0	3	3	65	66	9	9	1	1	0	0	3	3
			Fall 05	21	0	1	--	10	10	10	10	1	1	0	0	1	1	63	64	10	10	0	0	0	0	5	5
			Win 06	20	1	13	--	42	47	12	18	0	0	0	0	0	0	11	11	21	23	0	0	0	0	1	1
			Spr 06	20	2	0	--	6	6	13	13	0	0	0	0	0	0	37	38	42	42	0	0	0	0	0	0
		Large	Spr 05	20	2	6	--	53	60	2	2	1	1	1	1	1	1	18	18	16	16	0	0	0	0	1	1
			Sum 05	21	0	0	--	22	22	1	1	0	0	5	5	0	0	61	61	10	10	0	0	0	0	1	1
			Fall 05	19	5	6	--	14	16	4	4	0	0	0	0	10	10	49	52	7	7	0	0	0	0	9	10
			Win 06	19	3	18	--	46	51	8	10	0	0	0	0	0	0	9	19	16	18	0	0	2	2	0	0
			Spr 06	20	0	2	--	2	2	4	4	2	2	0	0	2	2	38	38	48	50	0	0	0	0	3	3
Norfork	Rainbow	Small	Spr 05	41	0	29	--	27	40	2	5	24	33	2	2	0	0	4	5	0	0	4	5	0	0	8	10
			Sum 05	43	0	70	--	16	44	0	4	6	33	0	0	1	3	0	2	0	0	1	5	0	0	5	10
			Fall 05	42	1	91	--	3	26	3	62	0	0	0	0	0	3	0	3	2	3	0	1	0	0	0	3

						Algae		Amphipoda		Chironomidae		Cladocera		Decapoda		Gastropoda		Isopoda		Sculpin		Aquatic Inverts.		Other Verts.		Terrestrial Inverts.	
Site	Trout	Size class	Season	*N*	N^E	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F
			Win 06	44	0	88	--	8	40	2	50	0	1	0	0	0	0	0	3	2	2	0	0	0	0	0	4
			Spr 06	41	1	25	--	39	52	3	7	21	29	0	0	0	0	1	1	9	9	1	1	0	0	0	1
		Large	Spr 05	23	1	39	--	33	56	1	9	1	5	2	2	0	0	3	5	10	10	1	1	9	10	1	3
			Sum 05	18	0	76	--	14	73	0	0	0	8	0	0	3	4	0	2	6	8	1	4	0	0	0	1
			Fall 05	19	3	63	--	1	18	7	30	0	3	0	0	1	5	6	9	14	15	0	0	0	0	8	20
			Win 06	20	0	82	--	12	68	2	17	0	0	0	0	1	4	3	5	0	0	0	3	0	0	0	2
			Spr 06	20	0	45	--	35	57	1	7	3	7	2	3	0	0	1	6	10	14	0	0	0	0	3	6
	Brown	Small	Spr 05	17	0	2	--	66	68	1	1	9	9	4	4	5	5	5	5	0	0	0	0	0	0	9	9
			Sum 05	1	0	0	--	98	98	0	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
			Fall 05	6	2	0	--	0	0	0	0	0	0	0	0	0	0	6	6	92	92	0	0	0	0	2	2
			Win 06	16	5	3	--	28	29	28	30	0	0	0	0	1	1	0	0	0	0	0	0	0	0	40	40
			Spr 06	13	1	0	--	51	51	11	11	28	28	0	0	2	2	1	1	0	0	6	6	0	0	1	1
		Medium	Spr 05	25	2	3	--	57	59	6	6	8	8	0	0	1	1	4	4	20	20	0	0	0	0	1	1
			Sum 05	20	2	2	--	46	48	0	0	5	5	0	0	5	5	15	15	16	16	1	1	0	0	10	10
			Fall 05	20	5	0	--	7	7	7	7	0	0	0	0	0	0	0	0	86	87	0	0	0	0	0	0
			Win 06	19	2	19	--	5	5	28	47	0	0	0	0	3	3	2	2	40	40	0	0	0	0	3	3
			Spr 06	21	1	0	--	33	33	7	7	10	10	2	2	0	0	6	6	41	41	0	0	0	0	0	0
		Large	Spr 05	24	1	1	--	39	40	0	0	0	0	0	0	0	0	2	2	56	56	0	0	0	0	1	1
			Sum 05	21	5	4	--	27	31	0	0	8	8	0	0	0	0	4	4	46	47	0	0	6	6	4	4
			Fall 05	22	5	1	--	0	0	0	0	0	0	0	0	0	0	0	0	93	93	0	0	0	0	7	7
			Win 06	18	3	1	--	0	0	21	21	0	0	7	7	7	7	0	0	63	64	0	0	0	0	0	0
			Spr 06	19	3	0	--	21	21	10	10	0	0	1	1	0	0	0	0	64	64	0	0	0	0	2	2
Sylamore	Rainbow	Small	Fall 05	40	1	72	--	1	1	0	10	0	0	1	5	19	67	0	1	4	6	0	0	0	0	3	10
			Win 06	40	1	87	--	1	4	0	14	0	0	0	0	12	76	0	0	0	0	0	6	0	0	0	0
			Spr 06	40	3	15	--	6	6	0	0	0	0	17	21	44	51	0	0	0	0	3	7	11	11	4	4
			Fall 06	40	0	61	--	0	3	3	29	0	0	22	35	12	27	0	0	0	0	1	3	0	0	1	3
	Brown	Small	Fall 05	1	0	0	--	0	0	0	0	0	0	0	0	100	100	0	0	0	0	0	0	0	0	0	0
			Win 06	8	2	25	--	0	0	0	0	0	0	0	0	50	67	0	0	25	33	0	0	0	0	0	0
			Spr 06	6	2	0	--	25	25	0	0	0	0	25	25	26	26	0	0	0	0	0	0	0	0	24	24
		Medium	Fall 05	25	1	0	--	0	0	0	0	0	0	4	4	81	81	0	0	9	9	0	0	0	0	7	7
			Win 06	19	0	0	--	0	0	0	0	0	0	0	0	7	7	0	0	86	86	3	3	0	0	4	4
			Spr 06	13	1	0	--	0	0	0	0	0	0	40	40	29	29	0	0	9	9	0	0	10	10	12	12
			Fall 06	13	3	0	--	0	0	0	0	0	0	86	86	14	14	0	0	0	0	0	0	0	0	0	0
		Large	Fall 05	5	3	0	--	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	100
			Win 06	9	0	0	--	0	0	0	0	0	0	6	6	44	44	0	0	12	12	0	0	38	38	0	0

						Algae		Amphipoda		Chironomidae		Cladocera		Decapoda		Gastropoda		Isopoda		Sculpin		Aquatic Inverts.		Other Verts.		Terrestrial Inverts.	
Site	Trout	Size class	Season	*N*	N^E	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F	%F[a]	%F
			Spr 06	3	1	0	--	0	0	0	0	0	0	12	12	50	50	0	0	0	0	0	0	38	38	0	0
			Fall 06	1	1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--

Table 4. PERMANOVA results for gut content analysis (GCA) by site, species and size class.

			GCA		
Site	Species	Size class	df	*F*	*P*
Bull Shoals	Rainbow trout	Small	4, 194	6.22	<0.01
		Large	4, 92	3.51	<0.01
	Brown trout	Small	4, 35	2.83	<0.01
		Medium	4, 91	5.82	<0.01
		Large	4, 81	5.07	<0.01
Norfork	Rainbow trout	Small	4, 201	20.48	<0.01
		Large	4, 89	3.45	<0.01
	Brown trout	Small	4, 37	4.32	<0.01
		Medium	4, 86	5.81	<0.01
		Large	4, 78	2.75	<0.01
Sylamore	Rainbow trout	Small	3, 146	15.07	<0.01
		Large	--	--	--
	Brown trout	Small	2, 6	0.63	0.84
		Medium	3, 54	18.57	<0.01
		Large	2, 9	1.84	0.08

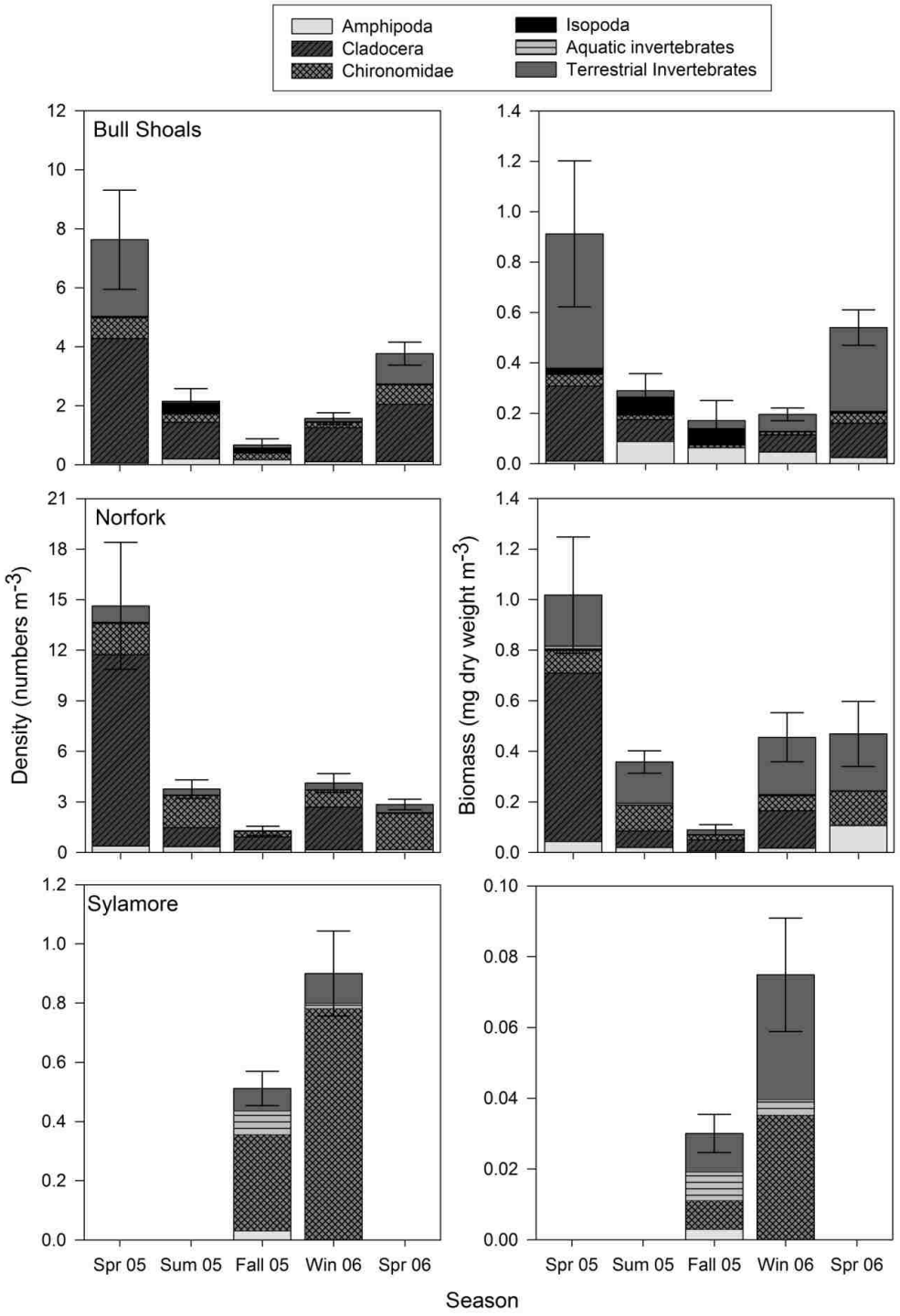


Figure 8. Mean (SE) invertebrate drift density of total individuals (numbers m^{-3}) and biomass (mg dry weight m^{-3}) in Bull Shoals, Norfork, and Sylamore C-R areas collected from May 2005 to November 2006.

Table 5. Taxa collected in the Bull Shoals and Norfork tailwaters. Sites are coded as BS, NF, and SY for Bull Shoals, Norfork, and Sylamore C-R areas, respectively.

Order	Family	Genera	Site
Amphipoda	Gammaridae	*Gammarus*	BS, SY
Coleoptera	Elmidae		SY
	Curculionidae		NF
Diptera	Chironomidae		BS, SY
	Empedidae	*Chelifera*	BS, SY
		Hemerodramia	BS, SY
	Epididae		SY
	Simuliidae	*Simulium*	NF, SY
	Tipulidae		NF
Ephemeroptera	Ephemerellidae	*Ephemerella*	BS, NF, SY
	Heptageniidae	*Stenonema*	NF, SY
	Heptaseneidae		SY
Gastropoda	Physidae	*Physa*	BS, NF, SY
	Pleurocidae	*Pleurocera*	BS, NF, SY
Hydracarina			BS, NF, SY
Isopoda	Asellidae	*Lirceus*	BS, NF, SY
Nematomorpha			BS, NF, SY
Oligochaeta			BS, NF, SY
Plecoptera	Perlidae	*Neoperla*	SY
	Pteronarcydidae	*Pteronarcys*	SY
Tricoptera	Brachycentridae		NF
	Hydropsychidae	*Hydropsyche*	NF, SY
	Hydroptilidae	*Hydroptila*	NF, SY
	Psychomyiidae		NF, SY
	Polycentropodidae	*Cyrnellus*	NF, SY
Turbellaria	Planariidae	*Dugesia*	BS, SY

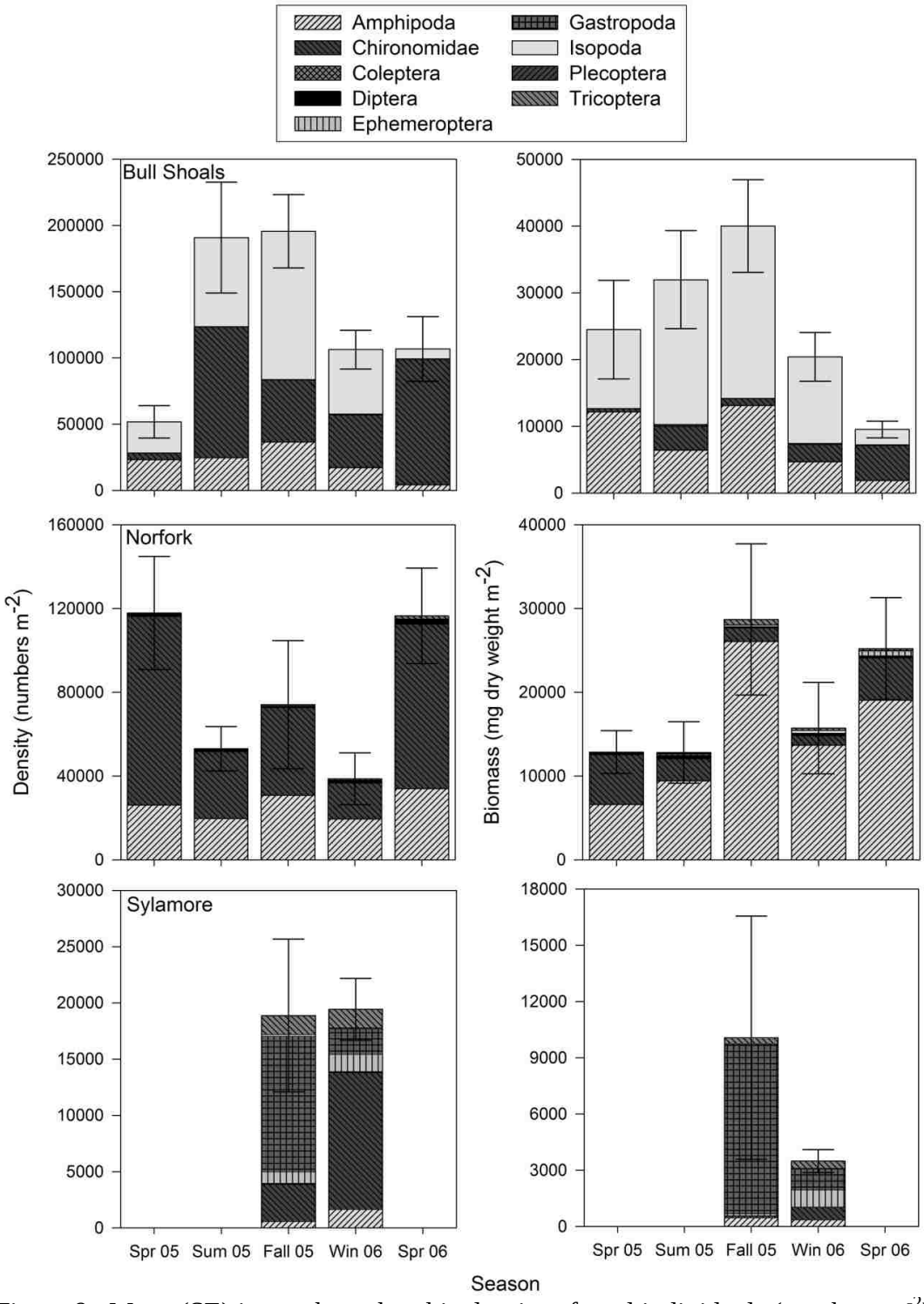


Figure 9. Mean (SE) invertebrate benthic density of total individuals (numbers m^{-2}) and biomass (mg dry weight m^{-2}) in Bull Shoals, Norfork, and Sylamore C-R areas collected from May 2005 to November 2006.

Table 6. Mean relative abundance (±SE) of invertebrate taxa in the drift (%) and benthos (%) for each season and site. Values were percent of total invertebrate biomass (mg DW). 'NA' is not available in the samples due to sampling method.

		Spr 05		Sum 05		Fall 05		Win 06		Spr 06	
Site	Invertebrate category	Drift	Benthic	Drift	Benthic	Drift	Benthic	Drift	Benthic	Drift	Benthic
Bull Shoals	Amphipoda	5.4 (2.2)	47.6 (3.3)	11.9 (3.3)	24.7 (4.2)	29.7 (6.4)	32.4 (5.2)	25.0 (4.0)	25.6 (4.8)	5.3 (1.6)	21.7 (5.2)
	Chironomidae	20.2 (3.6)	2.6 (0.8)	20.2 (4.3)	19.2 (6.5)	17.0 (4.5)	3.9 (1.6)	8.2 (1.1)	19.5 (6.0)	10.9 (1.7)	55.1 (7.0)
	Cladocera	54.2 (5.6)	NA	32.6 (5.6)	NA	0	NA	44.2 (4.9)	NA	33.4 (4.6)	NA
	Gastropoda	NA	0	NA	0.6 (0.4)	NA	0	NA	0	NA	0.4 (0.3)
	Isopoda	3.5 (1.3)	49.8 (3.2)	18.7 (4.3)	55.4 (9.0)	19.9 (5.3)	63.7 (6.0)	2.2 (1.0)	53.6 (8.1)	2.0 (0.7)	22.7 (5.7)
	Aquatic invertebrates	0.1 (0.1)	0	0	0.1 (0.1)	0	0.1 (0.1)	0	1.3 (0.8)	0	0.1 (0.1)
	Terrestrial Invertebrates	16.6 (4.4)	NA	16.6 (4.4)	NA	33.4 (6.0)	NA	20.5 (4.1)	NA	48.2 (4.6)	NA
Norfork	Amphipoda	3.6 (1.3)	42.1 (7.4)	4.9 (1.6)	64.1 (7.1)	5.5 (1.7)	88.3 (3.6)	7.5 (1.8)	80.7 (5.0)	7.3 (2.8)	63.6 (9.1)
	Chironomidae	28.9 (3.7)	55.7 (7.4)	41.9 (4.0)	25.9 (5.5)	53.3 (6.0)	6.7 (2.4)	38.4 (4.7)	8.9 (2.2)	59.8 (4.8)	30.0 (7.6)
	Cladocera	18.8 (4.6)	NA	9.2 (3.0)	NA	30.5 (5.0)	NA	32.6 (4.5)	NA	0	NA
	Gastropoda	NA	0	NA	0.8 (0.8)	NA	0	NA	0.7 (0.7)	NA	0
	Isopoda	0.1 (0.1)	0.8 (0.2)	0.2 (0.2)	6.6 (5.5)	0.1 (0.1)	1.4 (0.7)	0.1 (0.1)	2.3 (1.3)	0	0.2 (0.1)
	Aquatic invertebrates	1.7 (0.7)	1.4 (0.7)	1.0 (0.5)	2.6 (0.8)	2.1 (1.7)	3.6 (2.5)	1.0 (0.5)	7.5 (3.5)	0.4 (0.1)	6.2 (2.2)
	Terrestrial Invertebrates	47.0 (4.8)	NA	42.7 (4.1)	NA	8.6 (3.1)	NA	20.5 (4.2)	NA	32.4 (4.7)	NA
Sylamore	Amphipoda					5.3 (2.4)	19.1 (8.4)	1	8.5 (4.2)		
	Chironomidae					37.0 (4.8)	2.5 (1.3)	57.4 (8.4)	20.3 (3.6)		
	Cladocera					0	NA	0	NA		
	Gastropoda					NA	64.0 (9.2)	NA	33.4 (8.8)		
	Isopoda					0	1.9 (1.1)	0	0		
	Aquatic invertebrates					27.2 (4.4)	12.5 (3.8)	3.4 (1.2)	37.7 (6.3)		
	Terrestrial Invertebrates					30.5 (5.7)	NA	38.2 (7.9)	NA		

Table 7. Prey energy densities ($J \cdot g^{-1}$ wet weight) determined by bomb calorimetry, expect where otherwise indicated, and used in the bioenergetics model and caloric diets.

Prey category	Species/Family	Site	Season	Surrogate	*N*	DW (%)	$J \cdot g^{-1}$ (±SE)
Amphipoda	*Gammarus* spp.	Norfork	Spr 06		2	23.12	3,297 (49)
Aquatic invertebrates							3,815[a]
Chironomidae							3,134 (39)[b]
Cladocera	*Daphnia* spp.						3,812[c]
Decapoda	*Orconectes neglectus*	Bull Shoals	Fall 05		3	23.29	3,044 (131)
		Norfork	Spr 05		3	23.18	2,575 (67)
Gastropoda	Pleuroceridae	Bull Shoals	Spr 06		3	16.62	2,510 (2)
	Physidae	Norfork	Spr 06		3	20.08	2,717 (12)
Isopoda	*Lirceus* spp.	Bull Shoals	Spr 06		2	22.28	2,956 (4)
		Norfork	Spr 06		2	21.58	2,942 (19)
Other vertebrates	*Oncorhynchus mykiss*						5,764[d]
	Etheostoma spp.			*E. nigrum*			3,345[e]
	Notropis spp.			*Cyprinella lutrensis*			4,995[f]
	Hypentelium nigricans						4,657[g]
	Moxostoma carinatium						4,657[g]
Sculpin	*Cottus hypselurus*	Bull Shoals	Spr 05		2	24.15	5,273 (166)
			Sum 05		2	24.15	4,871 (377)
			Fall 05		2	24.15	4,468 (261)
			Win 06		2	24.15	4,064 (146)
			Spr 06		2	24.15	4,056 (287)
		Norfork	Spr 05		2	24.36	4,198 (246)
			Sum 05		2	24.36	4,828 (498)
			Fall 05		2	24.36	4,881 (15)
			Spr 06		2	24.36	4,095 (230)
			Win 06		2	24.36	4,491 (161)
Terrestrial invertebrates							3,170[h]

[a] Average of aquatic invertebrates (e.g. Ephemeroptera, Tricoptera) from Cummins and Wuycheck (1971)
[b] Commercially available chironomids
[c] Luecke and Brandt (1993)
[d] Hanson et al. (1997)
[e] Madon and Culver (1993)
[f] Bryan et al. (1996)
[g] Average of other fish
[h] Average of terrestrial invertebrates from Cummins and Wuycheck (1971)

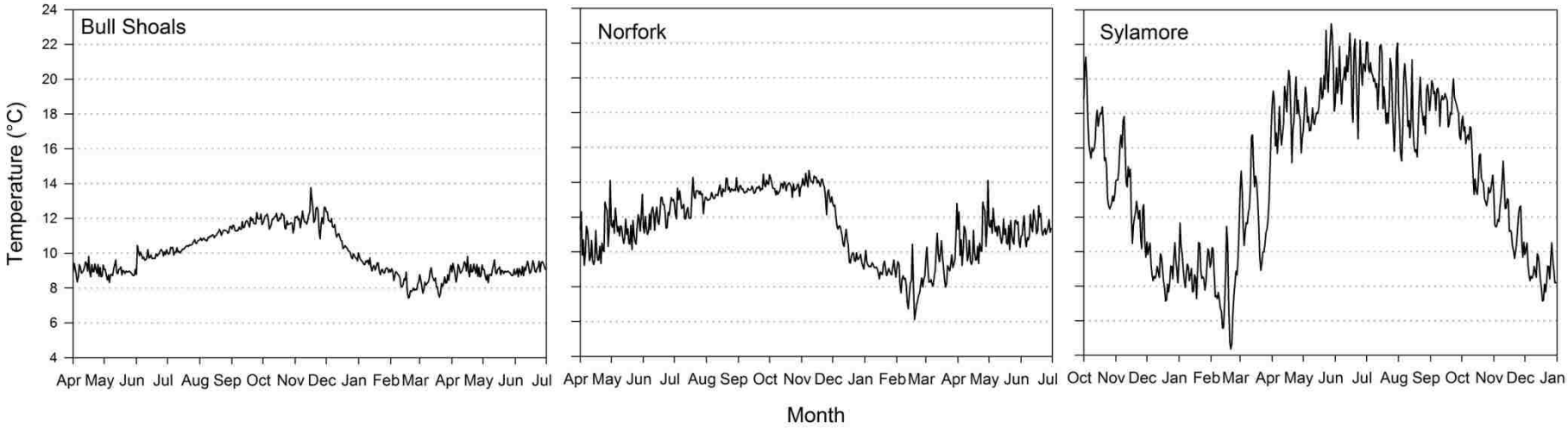


Figure 10. Temperature profiles used in the bioenergetics model at Bull Shoals and Norfork from April 2005 to July 2006, and at Sylamore from October 2005 to January 2007.

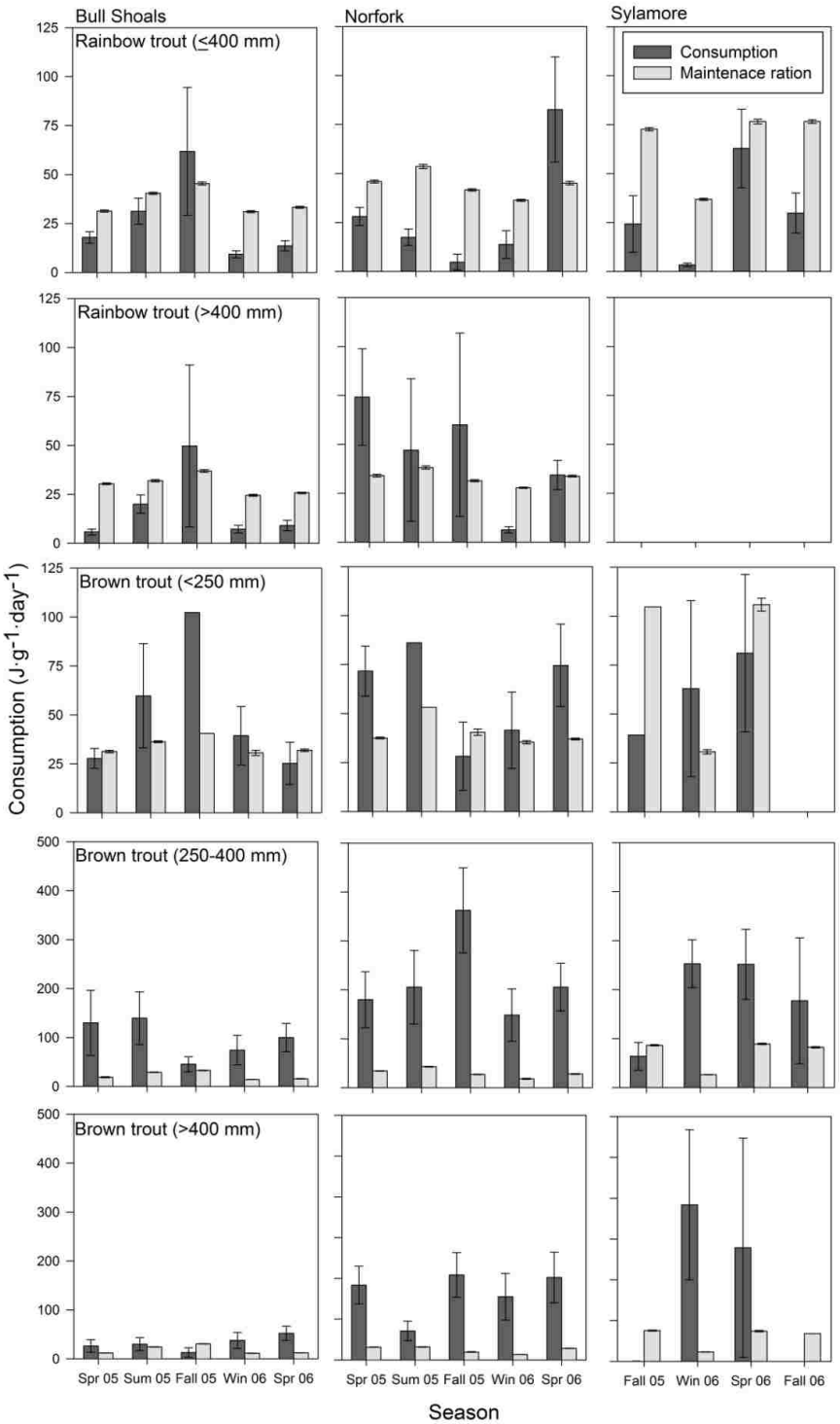


Figure 11. Seasonally observed daily energy intake or consumption ($J \cdot g^{-1} \cdot day^{-1}$) compared to daily energy expenditure or maintenance ration ($J \cdot g^{-1} \cdot day^{-1}$) with 95% confidence intervals by size class for brown and rainbow trout in each C-R area.

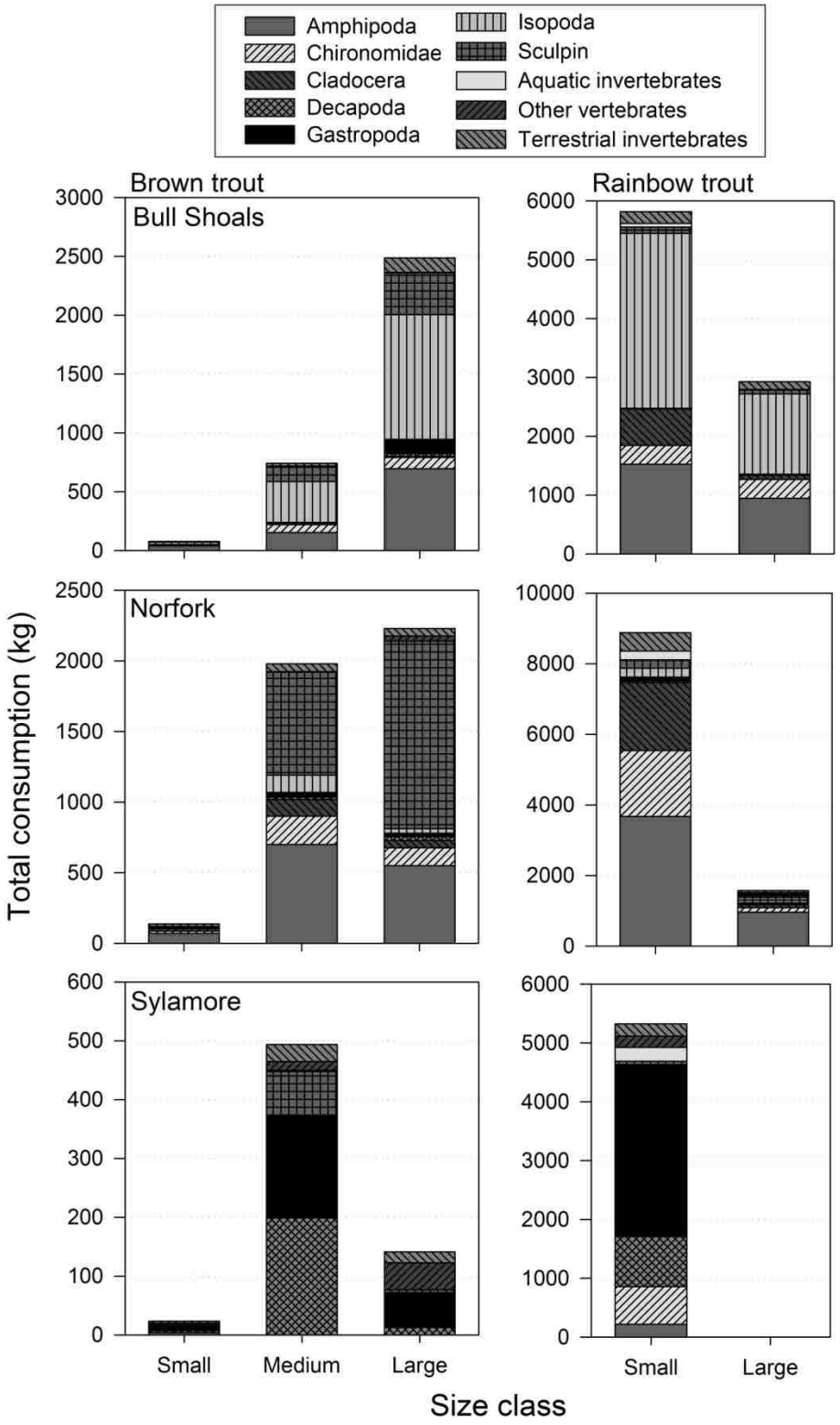


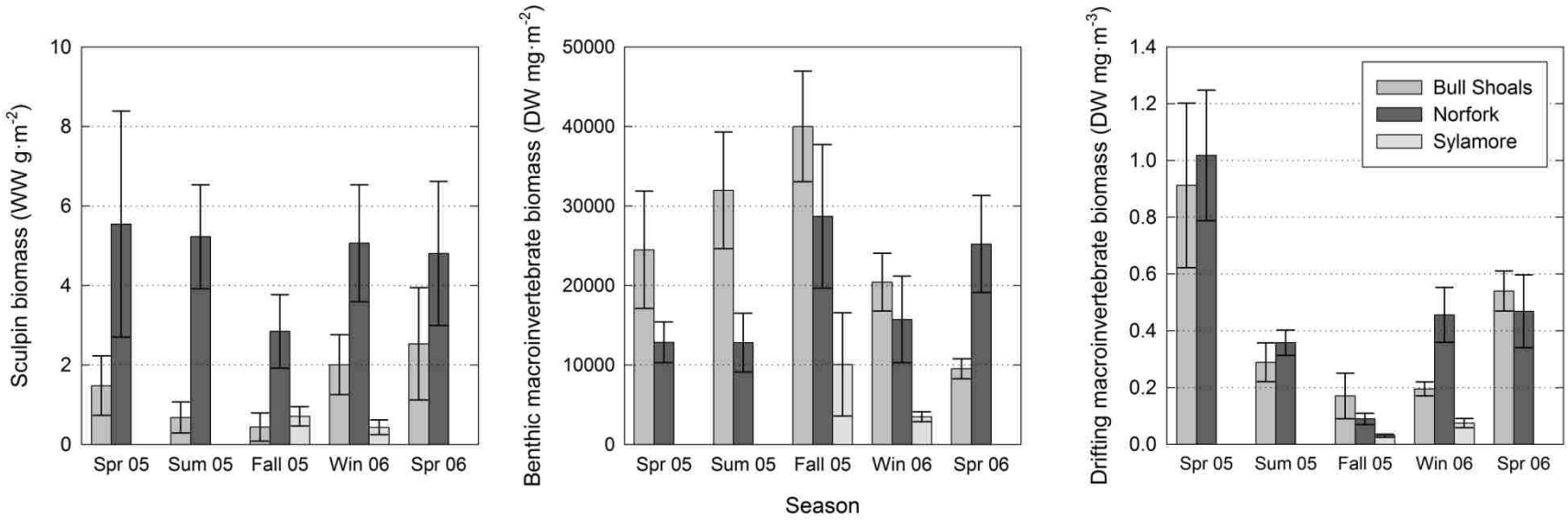
Figure 12. Wisconsin bioenergetics model estimates of total consumption (kg) of prey by size class and site from 2005 and 2006.

Table 8. Bioenergetics model estimates of total biomass (kg) consumed by season by each size class of rainbow and brown trout in Bull Shoals, Norfork, and Sylamore. The proportion (*P*-value) of maximum consumption as predicted by the bioenergetics model is provided for each size class and season. Abbrevations for prey are the following: AM = Amphipoda; CH = Chironomidae; CL = Cladocera; DE = Decapoda; GA = Gastropoda; IS = Isopoda; SC = Sculpin; AI = Aquatic invertebrates; OV = Other vertebrates; TI = Terrestrial invertebrates.

					Prey										
Site	Trout	Size class	Season	*P*-value	AM	CH	CL	DE	GA	IS	SC	AI	OV	TI	Total
Bull Shoals	Rainbow	Small	Spr 05	0.26	698	72	418	0	6	603	0	22	0	52	1869
			Sum 05	0.21	171	77	82	0	1	1153	17	25	0	10	1536
			Fall 05	0.18	139	7	0	0	1	763	80	0	0	97	1086
			Win 06	0.21	411	116	98	0	0	213	0	0	0	30	868
			Spr 06	0.28	104	53	17	0	8	242	10	14	0	12	459
		Large	Spr 05	0.24	502	136	55	0	14	289	0	3	0	29	1028
			Sum 05	0.20	184	64	7	0	2	608	0	2	0	0	866
			Fall 05	0.15	100	47	0	0	0	338	57	0	0	70	612
			Win 06	0.14	92	19	5	0	0	25	6	0	0	10	156
			Spr 06	0.21	67	58	6	0	1	104	0	8	0	25	268
	Brown	Small	Spr 05	0.56	34	2	3	0	0	9	0	0	0	4	52
			Sum 05	0.54	2	0	0	0	0	6	0	0	0	0	9
			Fall 05	0.53	0	0	0	0	0	1	0	0	0	0	1
			Win 06	0.58	3	2	0	0	0	0	0	0	0	0	6
			Spr 06	0.50	1	1	0	0	2	4	2	0	0	1	10
		Medium	Spr 05	0.27	45	4	10	0	1	17	16	0	0	5	98
			Sum 05	0.31	29	1	0	0	4	103	13	1	0	4	155
			Fall 05	0.29	27	27	3	0	2	170	27	0	0	13	268
			Win 06	0.25	46	18	0	0	0	11	22	0	0	1	99

					Prey										
Site	Trout	Size class	Season	*P*-value	AM	CH	CL	DE	GA	IS	SC	AI	OV	TI	Total
			Spr 06	0.28	7	16	0	0	0	46	51	0	0	1	122
		Large	Spr 05	0.21	295	11	6	3	3	91	81	0	0	4	493
			Sum 05	0.24	101	3	0	22	1	276	45	0	0	4	452
			Fall 05	0.24	171	48	0	0	110	564	77	0	0	108	1077
			Win 06	0.14	124	25	0	0	0	46	44	0	5	1	244
			Spr 06	0.18	4	9	4	0	5	84	110	0	0	7	222
Norfork	Rainbow	Small	Spr 05	0.27	858	99	699	39	2	105	0	114	0	208	2123
			Sum 05	0.21	934	83	700	0	68	43	0	111	0	204	2142
			Fall 05	0.20	346	832	0	0	39	38	38	8	0	39	1340
			Win 06	0.28	592	733	10	0	2	46	34	7	0	53	1478
			Spr 06	0.23	941	117	516	7	3	20	166	12	0	11	1793
		Large	Spr 05	0.20	241	39	22	8	0	21	43	4	42	11	432
			Sum 05	0.21	475	0	51	0	29	14	53	26	0	6	653
			Fall 05	0.20	26	43	4	0	7	13	23	0	0	30	147
			Win 06	0.30	141	36	1	0	8	11	0	6	0	5	207
			Spr 06	0.20	75	9	9	4	0	8	19	0	0	8	133
	Brown	Small	Spr 05	0.63	31	0	4	2	2	2	0	0	0	4	45
			Sum 05	0.50	2	0	0	0	0	0	0	0	0	0	2
			Fall 05	0.45	0	0	0	0	0	0	2	0	0	0	2
			Win 06	0.82	10	11	0	0	0	0	0	0	0	14	35
			Spr 06	0.60	26	6	14	0	1	1	0	3	0	1	52
		Medium	Spr 05	0.45	267	26	37	1	6	20	93	1	0	5	455
			Sum 05	0.46	195	0	18	0	21	62	67	2	0	42	407
			Fall 05	0.29	17	17	0	0	0	0	217	0	0	0	251
			Win 06	0.42	13	115	0	0	7	4	96	0	0	8	243
			Spr 06	0.36	208	42	64	16	0	35	258	0	0	1	623
		Large	Spr 05	0.30	247	3	1	0	0	12	343	0	0	5	611
			Sum 05	0.26	173	0	48	0	0	20	262	0	36	24	562
			Fall 05	0.13	0	0	0	0	0	0	144	0	0	10	154

					Prey										
Site	Trout	Size class	Season	*P*-value	AM	CH	CL	DE	GA	IS	SC	AI	OV	TI	Total
			Win 06	0.31	0	64	0	21	21	0	191	0	0	0	297
			Spr 06	0.33	129	60	2	7	1	0	389	0	0	15	605
Sylamore	Rainbow	Small	Fall 05	0.25	14	103	0	51	690	14	58	0	0	104	1035
			Win 06	0.19	57	185	0	0	1007	0	0	80	0	2	1331
			Spr 06	0.22	74	4	0	257	614	3	0	79	137	45	1214
			Sum 06	0.22	48	152	0	297	405	1	0	50	59	35	1048
			Fall 06	0.24	22	199	0	247	185	0	0	22	0	21	696
	Brown	Small	Fall 05	0.38	0	0	0	0	1	0	0	0	0	0	1
			Win 06	0.24	0	0	0	0	3	0	1	0	0	0	4
			Spr 06	0.28	2	0	0	2	3	0	0	0	0	2	10
			Sum 06	0.88	1	0	0	1	5	0	0	0	0	1	8
			Fall 06	0.33	0	0	0	0	0	0	0	0	0	0	0
		Medium	Fall 05	0.57	0	0	0	6	105	0	11	0	0	9	131
			Win 06	0.27	0	0	0	0	4	0	50	2	0	2	58
			Spr 06	0.81	0	0	0	35	26	0	8	0	9	11	89
			Sum 06	0.89	0	0	0	74	26	0	5	0	6	7	119
			Fall 06	0.49	0	0	0	83	13	0	0	0	0	0	97
		Large	Fall 05	0.17	0	0	0	0	0	0	0	0	0	12	12
			Win 06	0.32	0	0	0	2	15	0	4	0	12	0	33
			Spr 06	0.38	0	0	0	7	29	0	0	0	22	0	58
			Sum 06	0.80	0	0	0	3	15	0	1	0	11	6	36
			Fall 06	0.13	0	0	0	0	1	0	0	0	1	1	2



210 Figure 13. Seasonal biomass (±SE) of sculpin (WW g·m^2), benthic macroinvertebrates (DW mg·m^2), and drifting macroinvertebrates (DW mg·m^3) at Bull Shoals, Norfork, and Sylamore.

Table 9. The number of sculpin consumed based on bioenergetics simulations by site, season, and trout species. Average sculpin total length (mm) was collected from sculpin observed in GCA. Sculpin weight (g) was estimated based on length-weight relationships. Population estimates of sculpin within the C-R areas were from quadrat sampling. Standard errors are reported in parentheses.

Site	Season	Trout	Consumption (g)	TL (mm)	Weight (g)	Consumption (#)	Population estimate	Consumed (%)
Bull Shoals	Spr 05	Brown	96,805	63 (2.9)	3.6 (0.5)	27,062	99,120 (37,391)	27
		Rainbow	--	--	--	--		
	Sum 05	Brown	58,398	66 (6.1)	4.7 (1.4)	12,326	66,080 (28,135)	27
		Rainbow	17,247	60 (14.0)	3.1 (2.0)	5,498		
	Fall 05	Brown	103,649	75 (5.7)	6.6 (1.5)	15,721	116,612 (90,814)	65
		Rainbow	136,757	55 (8.1)	2.3 (3.2)	60,131		
	Win 06	Brown	65,821	84 (5.3)	8.4 (1.5)	7,791	253,307 (73,707)	5
		Rainbow	5,676	49	1.4	4,020		
	Spr 06	Brown	162,708	59 (1.7)	2.9 (0.2)	56,642	278,232 (87,269)	21
		Rainbow	9,509	68	4	2,391		
Norfork	Spr 05	Brown	436,250	68 (4.4)	5.2 (0.8)	84,251	166,648 (61,778)	55
		Rainbow	42,960	75 (6.9)	6.4 (1.7)	6,718		
	Sum 05	Brown	328,708	73 (3.4)	5.8 (0.7)	56,537	431,237 (96,690)	14
		Rainbow	52,726	92	11.5	4,578		
	Fall 05	Brown	362,882	68 (3.8)	5.4 (0.9)	66,878	175,419 (44,858)	41
		Rainbow	60,311	92	11.2	5,380		
	Win 06	Brown	287,194	76 (6.0)	7.3 (1.8)	39,148	222,197 (59,944)	20
		Rainbow	34,088	74	5.6	6,096		
	Spr 06	Brown	646,231	72 (3.8)	5.9 (1.1)	109,598	138,873 (43,787)	100

Site	Season	Trout	Consumption (g)	TL (mm)	Weight (g)	Consumption (#)	Population estimate	Consumed (%)
		Rainbow	184,768	76 (4.7)	6.3 (1.3)	29,418		
Sylamore	Fall 05	Brown	11,314	51 (9.7)	1.8 (0.7)	6,267	843,931 (284,764)	3
		Rainbow	58,463	59 (6.5)	2.7 (0.6)	21,365		
	Win 06	Brown	55,337	66 (4.1)	4.6 (0.2)	12,099	285,541 (125,132)	4
		Rainbow	--	--	--	--		
	Spr 06	Brown	7,859	51 (9.6)	1.9 (0.8)	4,240	--	--
		Rainbow	--	--	--	--		
	Sum 06	Brown	5,925	55	2.5	2,159	--	--
		Rainbow	--	--	--	--		
	Fall 06	Brown	86	58 (6.9)	3.2 (0.5)	27	--	--
		Rainbow	--	--	--	--		

Table 10. The amount of invertebrate type consumed by brown and rainbow trout (g WW) based on bioenergetics simulations compared to the amount (g WW) and weight (g) and percentage (%) of available drifting and benthic macroinvertebrates estimated by sampling forage base by site and season. 'NA' is not available in the samples due to sampling method.

			Macroinvertebrates (g)			Consumption (g)			Consumed (%)		
Site	Season	Invertebrates	Drift	Benthic	Total	Brown	Rainbow	Total	Drift	Benthic	Total
Bull Shoals	Spr 05	Amphipoda	26,687	5,067,137	5,093,824	374,622	1,199,789	1,574,411	5,900	31	31
		Chironomidae	121,385	211,544	332,929	16,462	207,464	223,926	184	106	67
		Cladocera	798,050	NA	798,050	18,942	472,998	491,940	62	NA	62
		Gastropoda	NA	0	0	3,543	19,876	23,420	NA	0	0
		Isopoda	63,922	4,922,319	4,986,241	116,815	891,913	1,008,727	1,578	20	20
		Aquatic	1,841	0	1,841	482	24,181	24,663	1,340	0	1,340
		Terrestrial	1,427,548	NA	1,427,548	13,247	81,278	94,526	7	NA	7
		Total	2,439,433	10,201,000	12,640,433	544,114	2,897,499	3,418,193	140	34	27
	Sum 05	Amphipoda	231,234	2,368,463	2,599,697	132,450	355,019	487,469	211	21	19
		Chironomidae	46,803	1,321,769	1,368,572	3,750	140,612	144,362	308	11	11
		Cladocera	231,342	NA	231,342	0	88,179	88,179	38	NA	38
		Gastropoda	NA	80,184	80,184	5,332	2,543	7,875	NA	10	10
		Isopoda	188,255	7,983,715	8,171,970	385,790	1,760,942	2,146,732	1,140	27	26
		Aquatic	0	15,355	15,355	795	27,611	28,407	0	185	185
		Terrestrial	66,646	NA	66,646	8,166	10,193	18,359	28	NA	28
		Total	764,279	11,769,486	12,533,765	536,283	2,385,100	2,913,508	381	25	23
	Fall 05	Amphipoda	41,295	3,235,463	3,276,758	197,738	239,042	436,780	1,058	13	13
		Chironomidae	7,146	254,427	261,573	74,576	54,005	128,581	1,799	51	49
		Cladocera	0	NA	0	2,565	0	2,565	0	NA	0
		Gastropoda	NA	3,127	3,127	111,725	914	112,639	NA	3,602	3,602
		Isopoda	42,423	6,361,986	6,404,409	734,623	1,100,800	1,835,423	4,326	29	29
		Aquatic	0	2,956	2,956	35	12	46	0	2	2
		Terrestrial	20,937	NA	20,937	120,631	166,807	287,438	1,373	NA	1,373
		Total	111,802	9,857,958	9,969,760	1,241,892	1,561,580	2,690,833	2,407	27	27
	Win 06	Amphipoda	14,449	788,480	802,929	173,466	503,131	676,597	4,683	86	84
		Chironomidae	3,485	435,565	439,050	45,170	134,298	179,468	5,150	41	41
		Cladocera	22,042	NA	22,042	0	102,766	102,766	466	NA	466
		Gastropoda	NA	0	0	90	0	90	NA	0	0
		Isopoda	1,028	2,174,912	2,175,940	56,806	237,795	294,600	28,658	14	14
		Aquatic	0	21,474	21,474	0	245	245	0	1	1
		Terrestrial	21,470	NA	21,470	1,884	40,244	42,128	196	NA	196
		Total	62,474	3,420,431	3,482,905	277,415	1,018,478	1,295,804	2,074	38	37
	Spr 06	Amphipoda	16,050	782,139	798,189	12,104	170,976	183,080	1,141	23	23
		Chironomidae	26,229	2,201,867	2,228,096	25,655	110,671	136,326	520	6	6
		Cladocera	92,741	NA	92,741	3,907	22,417	26,323	28	NA	28
		Gastropoda	NA	19,918	19,918	7,473	8,667	16,140	NA	81	81
		Isopoda	5,122	961,488	966,610	133,222	346,699	479,920	9,370	50	50
		Aquatic	256	3,873	4,129	52	21,806	21,858	8,538	564	529
		Terrestrial	225,579	NA	225,579	8,320	36,260	44,580	20	NA	20
		Total	365,977	3,969,284	4,335,261	190,733	717,495	892,088	244	22	21
Norfork	Spr 05	Amphipoda	56,131	2,043,595	2,099,726	544,691	1,098,424	1,643,114	2,927	80	78
		Chironomidae	115,388	1,841,730	1,957,118	29,531	137,734	167,265	145	9	9
		Cladocera	865,387	NA	865,387	42,230	720,670	762,901	88	NA	88
		Gastropoda	NA	0	0	8,144	2,167	10,312	NA	0	0
		Isopoda	7,192	32,376	39,568	34,200	125,944	160,144	2,227	495	405
		Aquatic	14,616	57,028	71,644	648	118,132	118,780	813	208	166

			Macroinvertebrates (g)			Consumption (g)			Consumed (%)		
Site	Season	Invertebrates	Drift	Benthic	Total	Brown	Rainbow	Total	Drift	Benthic	Total
		Terrestrial	263,446	NA	263,446	13,475	219,411	232,886	88	NA	88
		Total	1,322,160	3,974,731	5,296,891	672,919	2,422,483	3,085,090	233	78	58
	Sum 05	Amphipoda	16,129	1,383,520	1,399,649	370,516	1,408,848	1,779,364	11,032	129	127
		Chironomidae	86,915	820,385	907,300	198	82,886	83,084	96	10	9
		Cladocera	56,456	NA	56,456	66,038	750,323	816,361	1,446	NA	1,446
		Gastropoda	NA	112,368	112,368	20,510	96,964	117,474	NA	105	105
		Isopoda	304	42,857	43,161	81,951	56,615	138,566	45,581	323	321
		Aquatic	5,337	76,326	81,663	2,263	136,989	139,252	2,609	182	171
		Terrestrial	139,937	NA	139,937	65,637	209,579	275,217	197	NA	197
		Total	305,078	3,962,636	4,267,714	607,113	2,742,205	3,231,844	1,059	82	76
	Fall 05	Amphipoda	1,906	6,623,336	6,625,242	16,752	372,479	389,231	20,421	6	6
		Chironomidae	7,884	421,630	429,514	16,724	875,589	892,313	11,318	212	208
		Cladocera	18,074	NA	18,074	0	4,153	4,153	23	NA	23
		Gastropoda	NA	0	0	0	46,064	46,064	NA	0	0
		Isopoda	42	54,434	54,476	151	51,333	51,484	122,581	95	95
		Aquatic	530	197,184	197,714	0	8,474	8,474	1,599	4	4
		Terrestrial	7,628	NA	7,628	10,301	68,267	78,568	1,030	NA	1,030
		Total	36,064	7,296,585	7,332,649	43,928	1,426,360	1,424,224	3,949	20	19
	Win 06	Amphipoda	5,064	2,676,397	2,681,461	22,750	733,417	756,167	14,932	28	28
		Chironomidae	17,951	223,002	240,953	189,108	768,724	957,832	5,336	430	398
		Cladocera	45,381	NA	45,381	0	10,065	10,065	22	NA	22
		Gastropoda	NA	9,704	9,704	29,015	9,712	38,727	NA	399	399
		Isopoda	65	71,155	71,220	4,325	56,943	61,268	94,258	86	86
		Aquatic	1,383	98,952	100,335	33	13,117	13,150	951	13	13
		Terrestrial	69,186	NA	69,186	21,753	58,411	80,164	116	NA	116
		Total	139,031	3,079,211	3,218,242	266,984	1,650,389	1,878,646	1,351	61	58
	Spr 06	Amphipoda	69,022	5,892,065	5,961,087	363,443	1,016,356	1,379,800	1,999	23	23
		Chironomidae	88,624	1,571,390	1,660,014	107,770	126,430	234,200	264	15	14
		Cladocera	0	NA	0	80,838	525,278	606,116	0	NA	0
		Gastropoda	NA	0	0	2,459	2,973	5,432	NA	0	0
		Isopoda	0	17,332	17,332	35,711	27,540	63,251	0	365	365
		Aquatic	897	319,915	320,812	2,988	12,759	15,748	1,756	5	5
		Terrestrial	146,350	NA	146,350	16,802	18,574	35,375	24	NA	24
		Total	304,894	7,800,703	8,105,597	610,011	1,729,910	2,334,489	766	30	29
Sylamore	Fall 05	Amphipoda	4,664	282,447	287,111	0	13,590	13,590	291	5	5
		Chironomidae	0	61,183	61,183	2	102,825	102,827	0	168	168
		Cladocera	12,985	NA	12,985	0	0	0	0	NA	0
		Gastropoda	NA	5,482,217	5,482,217	105,790	689,643	795,433	NA	15	15
		Isopoda	0	23,266	23,266	0	14,391	14,391	0	62	62
		Aquatic	12,598	248,856	261,454	0	430	430	3	0	0
		Terrestrial	17,078	NA	17,078	20,210	104,181	124,391	728	NA	728
		Total	47,326	6,097,969	6,145,295	126,001	925,061	255,629	540	4	4
	Win 06	Amphipoda	190	193,698	193,888	0	57,068	57,068	30,036	29	29
		Chironomidae	0	357,085	357,085	0	185,406	185,406	0	52	52
		Cladocera	42,581	NA	42,581	0	0	0	0	NA	0
		Gastropoda	NA	602,747	602,747	21,414	1,006,777	1,028,191	NA	171	171
		Isopoda	0	597	597	0	0	0	0	0	0
		Aquatic	5,263	696,605	701,868	1,720	80,377	82,097	1,560	12	12
		Terrestrial	42,667	NA	42,667	2,169	1,699	3,868	9	NA	9
		Total	90,700	1,850,732	1,941,432	25,303	1,331,328	328,440	362	18	17

Conclusion

In this study, I examined effects of prey and tissue type on $\delta^{13}C$ and $\delta^{15}N$ fractionation and tissue turnover rates in rainbow trout fed an artificial diet (hatchery pellets) and two natural diets (sculpin and chironomids) in a laboratory study. The turnover rates of $\delta^{13}C$ and $\delta^{15}N$ in rainbow trout differed among liver, blood, and white muscle tissue. Tissues hypothesized to be more metabolically active changed most rapidly (Buchheister and Latour 2010; Hobson and Clark 1993; Tieszen et al. 1983). Liver had the fastest turnover times and greatest potential to indicate a recent dietary shift in $\delta^{15}N$ and $\delta^{13}C$ (T_{95} = 4-6 months), followed by blood (T_{95} = 4-7 months) and then white muscle tissue (T_{95} = 7-9 months), which may take twice as long to reach equilibrium with a new diet compared to liver. The dietary temporal scale of interest may dictate tissue selection and further highlights the potential of using multiple tissues to assess dietary shifts over different time scales. Tissues, such as liver and mucous, may be appropriate in reflecting more recently assimilated diets (Church et al. 2009; Hesslein et al. 1993), whereas blood, muscle, and bone may be more appropriate for reflecting longer-term assimilated diets (MacNeil et al. 2006; Sholtodouglas et al. 1991). Also, based on the turnover rates I observed, many food web studies using stable isotope analysis are likely to violate the assumption that $\delta^{15}N$ and $\delta^{13}C$ values of white muscle tissue, and to a lesser extent blood and liver, are in equilibrium with a given diet (Hesslein et al. 1993; MacAvoy et al. 2001; MacNeil et al. 2006).

I also found that fractionation values of $\Delta\delta^{15}N$ and $\Delta\delta^{13}C$ exhibited inter-tissue variability. Such variations may lead to misinterpretation of the trophic level and primary carbon source estimates (Vander Zanden and Rasmussen 1999). The commonly applied fractionation values of $\Delta\delta^{13}C$ of 0–1‰ (DeNiro and Epstein 1978) were generally much lower than the values I observed, which suggests a value of 1.5-2‰ might be more appropriate for fish white muscle,

blood, and liver (Barnes et al. 2007; Pinnegar and Polunin 1999). The $\Delta\delta^{15}N$ in white muscle tissue was consistently higher (3.8‰) than the typically reported value of 3.4‰ (Minagawa and Wada 1984). Consequently, an assumed fractionation of 3.4‰ $\Delta\delta^{15}N$ in muscle tissue may lead to overestimates in the trophic level. In contrast, blood (2.9‰) and liver (2.5‰) values were lower than the typically reported value of 3.4‰, which may underestimate the trophic level. Additionally, the commonly applied fractionation value of 1.0‰ $\Delta\delta^{13}C$ may have resulted in overestimation in primary carbon sources.

Relatively few stable isotope studies have focused on tailwaters, which typically contain simple food webs and may be ideal for using SIA in estimating source contributions (Johnson and Harp 2005; Quinn and Kwak 2003; Shaver et al 1997). I found that despite a simple food web the taxonomic precision afforded from GCA enhanced isotopic inferences by limiting the number of food sources required in the mixing model simulations as opposed to relying solely on isotopic data. A major benefit with SIA is that it provides time-integrated assimilated dietary information when compared to the traditional temporally limited "snapshot" GCA method for dietary studies. In this study GCA indicated trout foraged extensively on filamentous algae, *Cladophora*, and at Bull Shoals a nuisance diatom, *D. geminata*. *Cladophora* and *D. geminata* are not readily assimilated by trout (Weiland and Hayward 1997) and if only SIA was performed the role of *Cladophora* and *D. geminata* in the dietary dynamics of trout would not have been detected. This epibenthic foraging strategy was important in understanding possible bottlenecks in spatial and temporal food availability in the tailwater catch-and-release (C-R) areas (Filbert and Hawkins 1995; McKinney and Speas 2001; Weiland and Hayward 1997) and highlights an advantage of using SIA and GCA in tandem. In contrast, SIA may be more effective in detecting the importance and incorporation of zooplankton into diets owing to their small size and high

surface to volume ratios which facilitates a quick digestion, evacuation, and assimilation (Hylsop 1980). For example, GCA only indicated the importance of zooplankton during the spring for small rainbow trout at Norfork which represented approximately 20% of their diets. Although the majority of SIA mixing model results indicated a residual hatchery signal as the primary food source in small rainbow trout at Norfork the simulations also indicated zooplankton was of secondary importance and represented almost all of the new production in white muscle tissue. This suggests, that based on SIA, zooplankton was highly assimilated and of primary importance in the diets and production of new tissue. Entrained zooplankton from reservoir hypolimnetic releases can be the principal component in drift and an important food resource in tailwaters (Jackson et al. 1991; Ward 1974). Entrained zooplankton likely provides a readily available alternative food resource in the drift with presumably high capture success rates and low foraging costs. Consequently, feeding on temporally abundant zooplankton may represent an energetically profitable foraging strategy for rainbow trout. SIA may be an ideal tool to detect zooplankton given the discrepancy between methodologies which could result in an underrepresentation of zooplankton in GCA due to differences in assimilation efficiency, digestibility, and evacuation rates (Hyslop 1980). Pros and cons between the methods also need to be considered in the context of estimating dietary proportions for various bioenergetics modeling applications (Chipps and Wahl 2008; Ney 1993).

Finally, I evaluated the spatial-temporal consumption dynamics using an energy intake model and a bioenergetics model of rainbow trout and brown trout within three catch-and-release (C-R) areas in Bull Shoals and Norfork tailwaters to determine whether trout populations were limited by food supply. I combined field data on seasonal growth rates, diet composition, abundance, and thermal experience with species-specific bioenergetics models to quantify

seasonal consumption of benthic fish, macroinvertebrates, and *Daphnia* from reservoir releases. Similar to other tailwaters, larger rainbow trout appeared to experience poorer energetic conditions than smaller rainbow trout (McKinney and Speas 2001; Weiland and Hayward 1997). Bioenergetics modeling simulations suggested rainbow trout, and not brown trout, in Arkansas tailwaters were limited by spatial-temporal fluctuations in food availability.

Food availability is considered a function of drifting macroinvertebrate density and drift rate likely exerts a more significant influence on growth than the effects of temperature on metabolism (Railsback and Rose 1999). Macroinvertebrate drift rates decreased considerably during winter. Food limitation for salmonids in unregulated Appalachian streams has been observed in the summer (Cada et al. 1987; Ensign et al. 1990) and winter (Utz and Hartman 2006) due to inadequate energy intake. In other regulated tailwaters, food supply increased in the summer and steadily decreased through fall and winter (Filbert and Hawkins 1995; McKinney and Speas 2001; Weiland and Hayward 1997). I found a similarly high food supply in drifting macroinvertebrates in spring followed by a steady decrease through the fall.

The extent of population level impacts from C-R regulations may depend on species composition and carrying capacity of the populations (Shuter 1990). Estimating the carrying capacity of trout in C-R areas is an important management objective. By monitoring abundance, diets, growth of trout and benthic prey simultaneously, researchers can evaluate seasonal bottlenecks in resource supply. If trout populations expand, through increased stockings in surrounding areas or increased recruitment, seasonal bottlenecks in the food supply may become more pronounced. Continued monitoring of trout populations will be necessary to understand how C-R restrictions will affect the long-term success and stability of the fisheries in these areas.

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