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Tracking Trophic Interactions in Coldwater Reservoirs Using Naturally Occurring Stable Isotopes

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Abstract.—We measured signatures of naturally occurring stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) in important invertebrate and fish taxa in two coldwater reservoirs in Colorado that had different food webs. One reservoir, Lake Granby, contained a large population of an opossum shrimp, *Mysis relicta*, and the other, Blue Mesa Reservoir, did not. We compared temporal dynamics of isotopic signatures of all taxa between lakes to quantify sources of variability in consumer signatures and to assess potential turnover rates of isotopic signatures in the top predator. Stable isotope signatures varied little across season or body size within most taxa, but large differences across reservoirs were observed. Nitrogen signatures of lake trout *Salvelinus namaycush* were enriched in larger individuals in both reservoirs, indicating increasing trophic position with body size. Carbon signatures in lake trout livers were consistently lower than those in muscle samples but did not change more rapidly than muscle signatures, suggesting that either lake trout diet was relatively invariant during the study or that liver signatures change at the same rate as muscle signatures in these fish. Inferences about diets from carbon and nitrogen signatures were corroborated by information from stomach analysis. Food web structure derived from stable isotope analysis indicated large differences in energy and materials pathways between the reservoirs with and without *M. relicta*. Rather than diversifying trophic structure by providing an alternative food source for planktivorous sport fish, as the introduction originally intended, *M. relicta* in Lake Granby short-circuited a major energy conduit, the zooplankton, from channeling pelagic primary production into sport fish biomass.

Because of the central ecological role fish play as consumers in aquatic ecosystems, an understanding of trophic structure is often essential to ecological studies and to fishery assessment and management. Sport fish are typically the apical aquatic predators in fisheries, so knowledge of their diet is needed to predict top-down consequences of various fishery management actions, such as stocking and harvest regulations (Johnson et al. 1992; Johnson and Martinez 1995, 2000; Kitchell et al. 1997). Predicting and understanding the bottom-up effects of natural and anthropogenic disturbances like climate, water management, and eutrophication on aquatic ecosystems also require information on food web structure (Saito et al. 2001). Knowledge of ontogenetic shifts in food resource use is needed in complex ''middle-out'' systems where prey species may compete with or prey upon early life stages of their ultimate predators (DeVries and Stein 1992; Johnson and Goettl 1999). Furthermore, comprehensive trophic information is needed to parameterize exciting developments in the modeling of exploited ecosystems (e.g., Walters et al. 1997; Kitchell et al. 2000).

Intensive field sampling and characterization of predator stomach contents has historically been the primary method for documenting predator diet composition (Bowen 1996). Problems with this approach include regurgitation of stomach contents

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during the sampling process; difficulty in identifying digested prey remains; fine-scale temporal dimension necessitating repeated sampling; a high fraction of empty stomachs in piscivores, necessitating an even greater sample size; and sampling mortality among many large, valuable fish. Additionally, some coldwater fishes maintain relatively high consumption rates in winter when sampling can be problematic. Identifying trophic linkages in an entire food web with traditional approaches is a daunting task.

Recently, analysis of naturally occurring stable isotopes has emerged as a powerful tool for studying trophic relationships in terrestrial, aquatic, and linked terrestrial–aquatic food webs (Peterson and Fry 1987; Lajtha and Michener 1994; vander Zanden et al. 1997). Stable isotope signatures of organic materials change from food to consumer in a highly predictable fashion because of selective uptake and metabolic fractionation of isotopes. Carbon isotope signature is typically only enriched by about 1‰ during trophic transfer from prey to predator, mainly due to selective loss of ^{12}C during respiration (Peterson and Fry 1987). Therefore, the carbon signature of the food web's primary producers is preserved through several trophic levels (Michener and Schell 1994) and the carbon isotope signature is often used as a dietary tracer. The nitrogen isotope signature of a consumer is typically enriched by 3–4‰ relative to its prey, due to the preferential loss of 14N in nitrogenous wastes. Thus, nitrogen isotopes are usually used as an indicator of trophic position (vander Zanden and Rasmussen 1996; vander Zanden et al. 1997). An advantage of stable isotope analysis over traditional approaches is that stable isotopes are temporally integrative (Gearing 1991; Lajtha and Michener 1994), so much less field sampling and potentially fewer predator mortalities are required to estimate seasonal diet composition. Because naturally occurring stable isotopes are not radioactive and are ubiquitous, they are superior to radioactive isotope tracers for many kinds of studies.

The stable isotope approach has proven useful for understanding nutrient dynamics associated with salmon and their natal streams (Schuldt and Hershey 1995; Doucett et al. 1997), tracking fish migration patterns (Hansson et al. 1997), following contaminant flow through food webs (Cabana and Rasmussen 1994), studying terrestrial versus aquatic producer inputs to aquatic food webs (Angradi 1994; Hecky and Hesslein 1995; France 1997), and mapping food web structure (Yoshioka et al.1994; Bootsma et al. 1996; Gu et al. 1996).

Few studies have evaluated the application of stable isotope analysis for studying predator–prey relationships in coldwater reservoirs, and yet, strong isotopic distinctions between terrestrial, benthic, and pelagic carbon sources coupled with relatively simple food webs in these systems suggest that the approach may have considerable utility. In this study we assessed various factors affecting isotopic signatures of important invertebrate and fish taxa in two coldwater reservoirs with differing food webs. We also compared temporal dynamics of isotopic signatures of all taxa between lakes to quantify sources of variability in consumer signatures and to assess potential turnover rates of isotopic signatures in the top predator. Ultimately, we sought to characterize nitrogen and carbon isotope signatures of lake trout *Salvelinus namaycush* and their potential prey organisms to determine if stable isotopes can be used to identify differences in trophic relationships in two reservoir ecosystems, one where a nonnative opossum shrimp *Mysis relicta* was present and the other where it was not.

Methods

Samples were collected from May to October 1997 from two coldwater reservoirs in Colorado: Blue Mesa Reservoir (13S 296839 4258870), Gunnison County, and Lake Granby (13T 426164 4444683), Grand County. These large (>2,800 ha surface area), high-elevation (2,286 and 2,524 m, respectively) storage impoundments have hypolimnetic outlets and are of similar trophic state (Johnson and Martinez 2000). Lake Granby was constructed in 1949 and Blue Mesa Reservoir in 1965. Annual water-level fluctuations limit littoral production and both systems are managed for a pelagic fish assemblage (Johnson and Martinez 2000). Sport fisheries in each reservoir primarily target kokanee *Oncorhynchus nerka*, rainbow trout *O. mykiss*, and lake trout (B. M. Johnson and J. D. Stockwell, unpublished; P. J. Martinez, unpublished). Kokanee and rainbow trout populations are sustained by stocking; lake trout and catostomids are naturally reproducing in each lake. Kokanee are stocked as fry (about 50 mm total length [TL]) and rainbow trout are stocked as subcatchables (about 100 mm TL) or catchables (about 250 mm TL). *Mysis relicta* were introduced into Lake Granby in 1971 and they became abundant by 1978 (Martinez 1986). During the 1990s *M. relicta* density in Lake Granby averaged 488 mysids/m^2 or about 1.9 g dry/m^2 (Martinez, unpublished). *Mysis*

relicta were never stocked in, nor have they invaded, Blue Mesa Reservoir.

Zooplankton in the top 10 m of the water column were sampled with a 500-μm plankton net in summer in both reservoirs. This net was highly selective for daphnia *Daphnia* sp. longer than 1.0 mm (Johnson and Stockwell, unpublished), the size fraction preferred by planktivorous fish (O'Brien 1979). *Mysis relicta* were collected from Lake Granby with a benthic sled (Bergersen et al. 1993) during May 1997. All invertebrate samples were frozen in the field and stored frozen until they could be dried and processed. No samples of terrestrial insects were available.

Predator and prey fishes were collected with experimental gill nets. Fishes were measured and weighed, and scales and/or otoliths were removed for aging. Relative weight (W_r), of lake trout was computed from the standard weight (W_s equation of Piccolo et al. (1993):

$$W_r = 100 \cdot \frac{W_s}{W_{\text{observed}}},$$

where $\log_{10} W_s = -5.681 + 3.2462 \log_{10} \text{TL}$, W_s and W_{observed} are wet weights in grams, and TL is total length in millimeters. We assumed that W_r would increase with the amount of lipid in a lake trout, and hence, we used it as a surrogate for lipid content. A small (about 1 cm^3) muscle plug without skin was removed from each fish below dorsal fin and above the lateral line for stable isotope analysis. A portion of the liver was also removed from lake trout. Muscle and liver tissue samples were frozen in the field and stored frozen until they could be processed. Kokanee fry (50–80 mm TL) obtained from the Roaring Judy State Fish Hatchery were frozen whole before subsequent isotope analysis. A sample of their pelleted food was also analyzed for stable isotopes.

Stomach contents of rainbow trout and lake trout were removed and preserved in 10% formalin for subsequent identification in the laboratory. Extensive stomach sampling of kokanee from Blue Mesa Reservoir was performed in 1995 for diet analysis (Johnson et al., Colorado State University, unpublished) and in 1997 for gastric evacuation rates (Stockwell and Johnson 2000). However, only in 1995 was diet composition analyzed quantitatively because there was no indication in 1997 that kokanee food habits had changed from 100% zooplanktivory.

Tissue isotope samples were dried at 60°C for 24 h and then ground to a flour-like consistency with a mortar and pestle. A 1–2 mg sample of each tissue was placed in tin cup and processed for $\delta^{13}C$ and $\delta^{15}N$ signatures in a VG Isochrom mass spectrometer with Carlo-Erba NA1500 elemental analyzer. The quantity measured in stable isotope analysis, δ, is the relative difference between isotope ratios of the sample and a standard:

$$\delta = \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \cdot 10^3,$$

where δ (‰) is the per mil difference, R_{sample} is the isotopic ratio of the sample, and R_{standard} is the isotopic ratio of the standard.

Standards employed were Vienna Pee Dee Belemnite for $^{13}C/^{12}C$ and atmospheric N_2 for $^{15}N/^{14}N$ (Lajtha and Michener 1994). Samples were denoted as ''enriched'' or ''heavier'' if they contained more of the heavy isotope than other samples, and samples were denoted as ''depleted'' or **''**lighter**''** if they contained less of the heavy isotope. The mass spectrometer was calibrated using a glycine standard at the start of each session and after approximately every 10 samples. Accuracy of the mass spectrometer was maximized by processing separate subsamples for each isotope. Analytical precision was high; mean coefficient of variation (CV) among replicate tissue samples analyzed on different days and by different operators was 0.47% for $\delta^{13}C$ ($N = 97$ samples with replicate runs) and 1.8% for $\delta^{15}N$ ($N = 5$ samples with replicate runs).

Lake trout diet analysis methods and results are provided in Johnson and Martinez (2000). Rainbow trout and kokanee stomach samples were processed individually by sorting gut contents into four categories: crustacean zooplankton, aquatic macroinvertebrates (mainly amphipods and chironomid larvae and pupae), terrestrial insects, and fish. We then estimated the percent composition of each prey category by volume and summarized across fish sizes and seasons.

We categorized isotope samples by the season in which they were taken: April–May (spring samples), June–August (summer samples), and September–October (fall samples). Lake trout samples were partitioned into small (<425 mm TL), medium (425–600 mm TL), and large (>600 mm TL) length-classes for some analyses, in accordance with diet analyses in Johnson and Martinez (2000). We used a general linear models approach to assess whether isotopic signatures varied across species, by size or body condition, seasonally, and between lakes (Proc GLM, SAS 1990). Models were de-

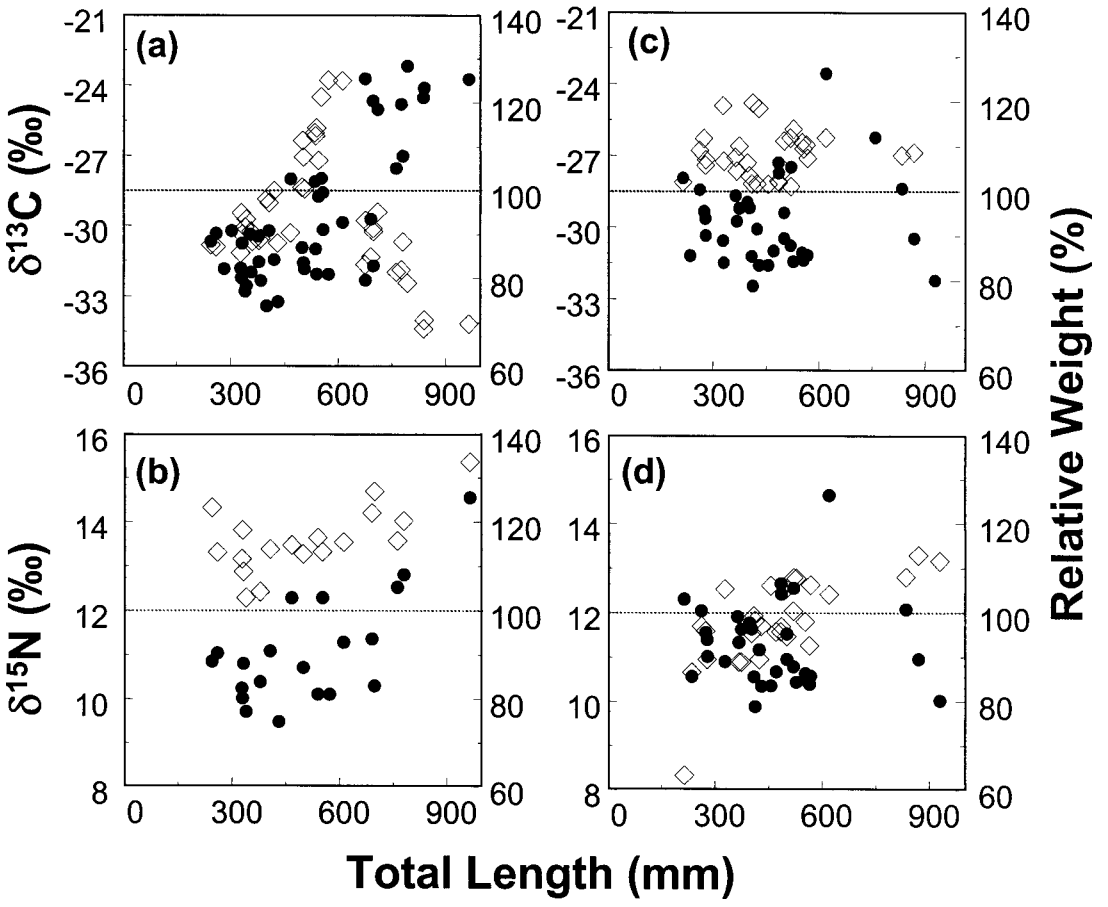

FIGURE 1.—**(a)** Carbon ($\delta^{13}C$) and **(b)** nitrogen ($\delta^{15}N$) isotope signatures (diamonds) of lake trout muscle tissue samples and relative weight (closed circles) as a function of fish length for lake trout sampled in Blue Mesa Reservoir, Colorado, in 1997; **(c)** and **(d)** show similar results for Lake Granby.

veloped iteratively starting with the full model, including all possible interactions. Significant factors ($\alpha = 0.05$) were retained and models were rerun; means were adjusted for the effects of other factors using least squares means (LSMEANS) command in the general linear models procedure.

Results

Carbon signatures of lake trout muscle and liver tissue were related to fish length, lake, length^2 and the length^2 × lake and length × lake interactions (muscle, $P \leq 0.0001$; liver, $P \leq 0.007$). Carbon muscle signatures were significantly lower for lake trout at Blue Mesa Reservoir than at Lake Granby ($P < 0.05$; Figure 1a, c). There was no significant seasonal variation in carbon signatures of either tissue. The liver: muscle carbon signature was significantly related only to fish length ($F = 6.53$, $P = 0.0129$). Carbon muscle signature of lake trout in Blue Mesa Reservoir increased with fish length from about 200–600 mm and then decreased thereafter (Figure 1a). A change in W_r appeared to be associated with the change in carbon signature for medium to large lake trout in Blue Mesa Reservoir (Figure 1a), high W_r and low carbon signatures occurring in large lake trout. Carbon signatures of Lake Granby lake trout, where W_r was relatively low across all sizes of fish, showed no trend with fish size (Figure 1c).

Nitrogen signatures of lake trout muscle tissue were related to fish length ($F = 34.0$, $P \leq 0.0001$) and lake ($F = 67.6$, $P \leq 0.0001$). Nitrogen muscle signatures increased with fish length ($\beta_1 = 0.0032$, $P \leq 0.0001$) and averaged about 1.70‰ higher at Blue Mesa Reservoir ($P \leq 0.0001$; Figure 1b, d). Nitrogen signatures of lake trout liver tissue were also related to fish length ($F = 70.4$, $P \leq 0.0001$) and lake ($F = 112.5$, $P \leq 0.0001$). Nitrogen liver

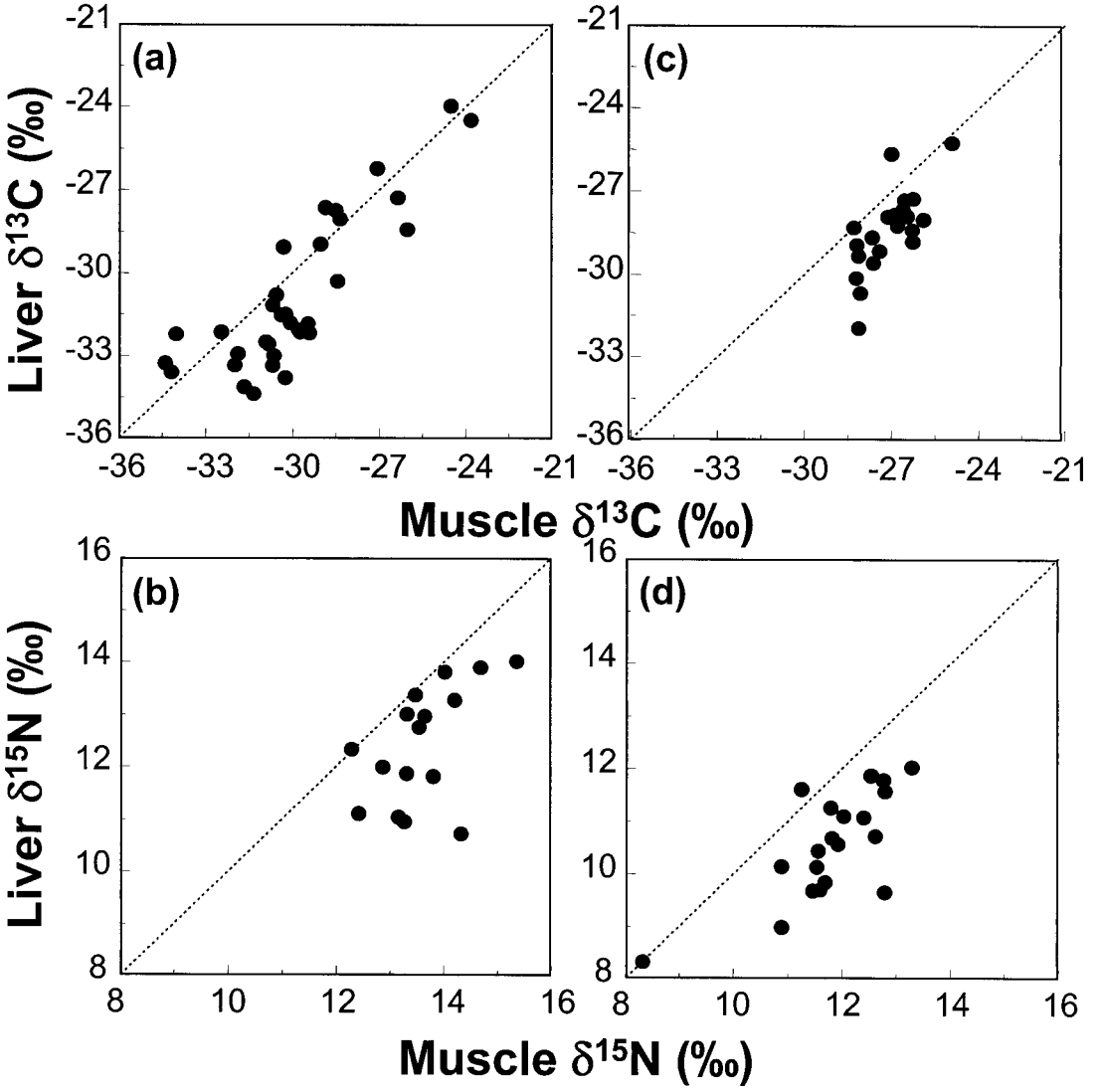

FIGURE 2.—Lake trout liver and muscle isotope ratios—**(a)** $\delta^{13}C$ and **(b)** $\delta^{15}N$ —for tissue samples taken from Blue Mesa Reservoir, Colorado, in 1997; **(c)** and **(d)** show similar ratios for Lake Granby. Dotted lines represent 1:1 correspondence.

signatures increased with fish length ($\beta_1 = 0.0042$, $P \leq 0.0001$) and averaged 1.92‰ higher at Blue Mesa Reservoir ($P < 0.0001$). Seasonal variation was not significant in signatures of either tissue. Liver carbon and nitrogen signatures were consistently lower than muscle signatures from the same fish over lakes (Figure 2). The liver: muscle nitrogen signature was weakly and positively related to fish length ($F = 3.81$, $\beta_1 = 0.00009$, $P = 0.0576$) but did not differ seasonally or between lakes ($P > 0.10$).

Overall, nitrogen signatures of muscle tissue varied by species ($F = 49.4$, $P \leq 0.0001$), lake ($F = 48.2$, $P \leq 0.0001$) and less so by season ($F = 4.53$, $P = 0.0135$). In Blue Mesa Reservoir, nitrogen signature was most variable for kokanee, but only one sample in spring and two samples in fall were analyzed (Table 1). In Lake Granby seasonal variation was highest for catostomids (Table 2). A significant species × season interaction was primarily due to an unusual seasonal pattern in the signatures of longnose suckers *Catostomus catostomus*. When we removed longnose suckers from the data set, we were able to estimate mean iso-

TABLE 1.—Mean carbon ($\delta^{13}C$, ‰) and nitrogen ($\delta^{15}N$, ‰) signatures of seven organisms from Blue Mesa Reservoir, Colorado, by season, and number of individuals composing each mean (*N*).

Organism	Isotope signature	Spring		Summer		Fall	
		Mean	*N*	Mean	*N*	Mean	*N*
Decapods	$\delta^{13}C$		0	−28.2	5	−27.1	6
	$\delta^{15}N$	9.62	1		0	9.60	4
Kokanee	$\delta^{13}C$	−32.0	8	−32.2	11	−32.8	11
	$\delta^{15}N$	13.1	1	11.8	11	10.6	2
Lake trout	$\delta^{13}C$	−29.5	16	−29.5	15	−29.7	9
	$\delta^{15}N$	13.16	2	13.7	15	−13.2	1
Longnose sucker	$\delta^{13}C$	−28.8	8	−28.5	10	−28.8	6
	$\delta^{15}N$		0	10.6	10	9.31	5
Rainbow trout	$\delta^{13}C$	−29.2	6	−26.0	10	−25.6	9
	$\delta^{15}N$	11.2	3	10.9	10	10.4	4
White sucker	$\delta^{13}C$	−28.3	2		0	−27.9	7
	$\delta^{15}N$		0		0	9.76	4
Zooplankton	$\delta^{13}C$	−33.4	2	−32.3	2		0
	$\delta^{15}N$		0	7.39	2		0

topic signatures for the other fish species, adjusted for season and lakes (Figure 3). Least squares means could not be estimated for the invertebrate species because each was sampled in one of the two lakes and in only one or two seasons. Simple mean isotopic signatures for longnose suckers and the invertebrates are presented in Figure 3.

Seasonal variation in carbon signatures was not significant ($F = 0.96$, $P = 0.38$), but carbon signatures did differ among species ($F = 10.3$, $P \leq 0.0001$) and lakes ($F = 81.5$, $P \leq 0.0001$). Variation between spring and fall was higher at Lake Granby, particularly among catostomids (Table 2). The high carbon signature for white suckers *Catostomus commersoni* in Lake Granby in fall was partially due to high values from two fish (<200 mm TL); white suckers of that size were not present in samples from other seasons or at all in samples from Blue Mesa Reservoir. Significant species × season and species × lake interactions dropped out when rainbow trout were omitted from the data set, so we could estimate adjusted mean signatures for the remaining fish species. As with nitrogen, we could not estimate adjusted mean carbon signatures for rainbow trout or invertebrates, and their simple means are presented in Figure 3.

Carbon and nitrogen signatures of muscle tissue from prey fish (kokanee, rainbow trout, and catsotomids) were not related with fish length ($P > 0.26$). Mean carbon muscle signatures of all prey species except rainbow trout ($P = 0.229$) were distinctly higher in Lake Granby than in Blue Mesa Reservoir ($P \leq 0.0001$). Nitrogen muscle signatures of kokanee, rainbow trout, and white suckers were all higher at Blue Mesa Reservoir than Lake Granby ($P \leq 0.0007$). Carbon signatures of rainbow trout appeared to be segregated into two groups in Blue Mesa Reservoir (Figure 4) not related to fish size ($P = 0.089$). Mean carbon signature of rainbow trout was significantly lower in

TABLE 2.—Mean carbon ($\delta^{13}C$, ‰) and nitrogen ($\delta^{15}N$, ‰) signatures of six organisms from Lake Granby, Colorado by season, and number of individuals composing each mean (*N*).

Organism	Isotope signature	Spring		Summer		Fall	
		Mean	*N*	Mean	*N*	Mean	*N*
Lake trout	$\delta^{13}C$	−26.9	20		0	−27.0	14
	$\delta^{15}N$	12.0	15		0	11.5	14
Longnose sucker	$\delta^{13}C$	−24.8	6		0	−26.1	6
	$\delta^{15}N$	8.36	5		0	9.14	6
Kokanee	$\delta^{13}C$	−25.8	2		0	−26.4	3
	$\delta^{15}N$	9.72	1		0	9.52	3
Mysis relicta	$\delta^{13}C$	−30.4	2	−30.4	1		0
	$\delta^{15}N$	8.75	2	6.52	1		0
Rainbow trout	$\delta^{13}C$		0		0	−25.5	4
	$\delta^{15}N$		0		0	8.94	4
White sucker	$\delta^{13}C$	−24.7	6		0	−21.3	5
	$\delta^{15}N$	8.46	4		0	7.67	5

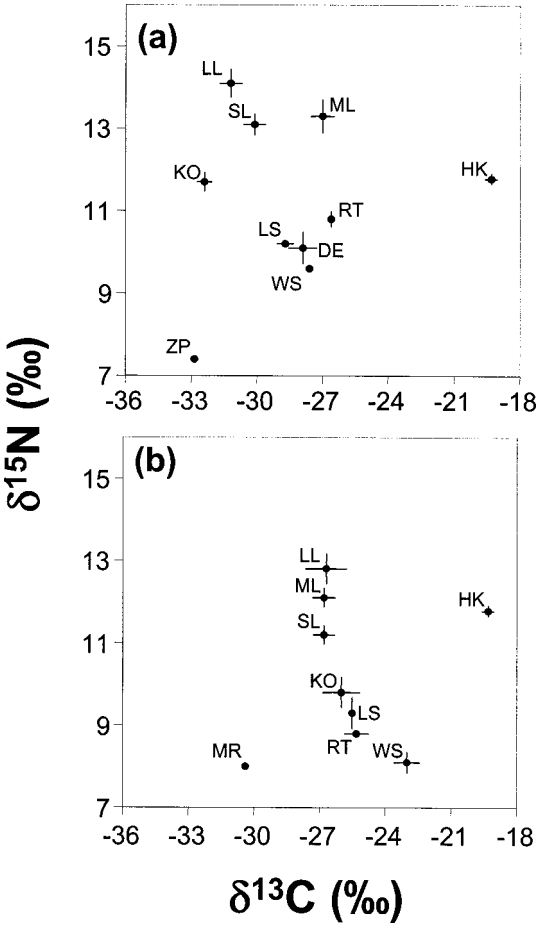

FIGURE 3.—Least squares means (with error bars; ±1 SE) or simple means (without error bars) for carbon and nitrogen isotope ratios of biota from **(a)** Blue Mesa Reservoir and **(b)** Lake Granby, Colorado, sampled in 1997. Abbreviations are as follows: ZP = zooplankton, KO = kokanee, MR = *Mysis relicta*, DE = decapods, LS = longnose sucker, WS = white sucker, RT = rainbow trout, SL = small lake trout (<426 mm), ML = medium lake trout (426–600 mm), and LL = large lake trout (>600 mm).

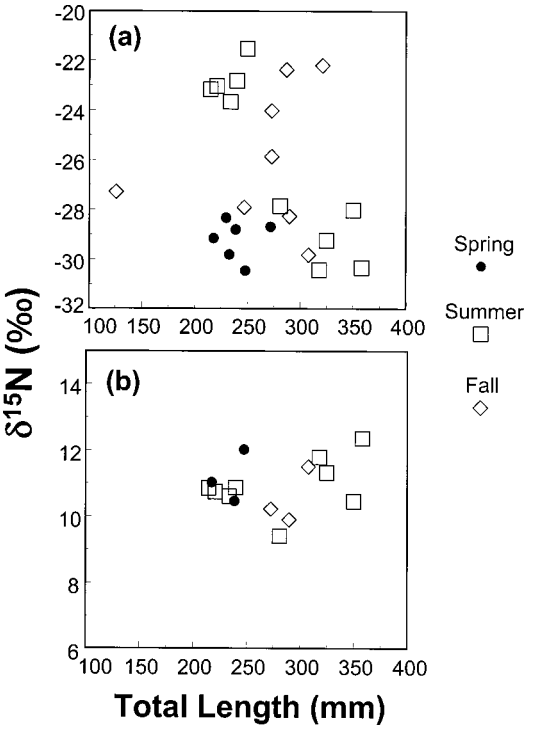

FIGURE 4.—**(a)** Carbon and **(b)** nitrogen signatures of rainbow trout muscle tissue as a function of fish total length. Tissue samples were taken in three seasons from Blue Mesa Reservoir, Colorado.

spring than summer (P = 0.041) or fall (P = 0.025). Rainbow trout carbon values were intermediate between these groups at Lake Granby.

Kokanee had lower carbon signatures than rainbow trout in Blue Mesa Reservoir; longnose and white suckers had similar carbon values within a lake, but both were lower in Blue Mesa Reservoir (Figure 3). Hatchery kokanee (mean length = 77 mm) had very distinct carbon signatures (mean $\delta^{13}C = -19.3$) that were 4–13‰ higher than other fishes or invertebrates (Figure 3). Nitrogen signatures of hatchery (mean $\delta^{15}N = 11.8$) and wild (mean length = 292 mm) kokanee were similar in Blue Mesa Reservoir, but hatchery kokanee had almost a 3-unit higher nitrogen signature than wild kokanee at Lake Granby (mean length = 225 mm; Figure 3). The isotopic signature of the hatchery food was $\delta^{15}N = 8.1$, $\delta^{13}C = -19.7$. Nitrogen and carbon signatures of hatchery kokanee were enriched relative to their food by about 3.7‰ and 0.4‰, respectively.

Low sample size and absence of species from one lake or the other limited our analysis of factors affecting invertebrate signatures. Zooplankton had the lowest carbon and nitrogen signatures of all consumers at Blue Mesa Reservoir (Figure 3). Large zooplankters were extremely scarce in Lake Granby; despite sampling on several occasions, we were unable to obtain a sample quantity sufficient to analyze for isotopic signatures. *Mysis relicta* had the lowest carbon signature of all consumers in Lake Granby and a similar nitrogen signature to kokanee, rainbow trout, and catostomids. Decapods were only sampled at Blue Mesa Reservoir, and they had carbon and nitrogen signatures similar to those of the two catostomids (Figure 3).

TABLE 3.—Diet composition (percent by volume) of kokanee (May–September 1995), rainbow trout (May–September 1997), and three size classes of lake trout (April–October 1994–1997) from Blue Mesa Reservoir, Colorado; N = the number of stomachs containing food.

			Lake trout		
Prey taxa	Kokanee N[a] = 130	Rainbow trout N = 28	<426 mm N = 20	426–600 mm N = 22	>600 mm N = 9
Zooplankton[a]	99.7	40	0	0	0
Aquatic invertebrates[b]	0.3	19	43	17	21
Terrestrial insects	0	38	5	1	0
Decapods	0	0	30	10	1
Fish	0	3	22	72	78

[a] Mainly *Daphnia* spp.
[b] Mainly amphipods and chironomid larvae and pupae.

Stomach content analysis showed that rainbow trout diet in Blue Mesa Reservoir consisted of approximately 40% crustacean zooplankton, 19% aquatic macroinvertebrates, 38% terrestrial insects, and 3% fish (Table 3). Blue Mesa Reservoir kokanee of all sizes and in all seasons were virtually entirely zooplanktivorous, the diet being composed of *Daphnia pulicaria* and *D. galeata mendotae*. Lake trout diet in Blue Mesa Reservoir changed with lake trout size. Small (<425 mm TL) lake trout consumed mostly aquatic invertebrates (amphipods, chironomids, and decapods), with some (22%) fish. Medium-sized lake trout (425–600 mm) ate fewer aquatic invertebrates and about 72% fish. Large lake trout (>600 mm) ate 78% fish and 22% aquatic invertebrates.

Discussion

Stable isotope analysis offers the opportunity for a more comprehensive picture of food web structure than is usually possible with diet studies. Because isotope signatures are more temporally integrative than diet analysis, it is important to understand how isotope signatures of consumers respond to changes in their diet. Seasonal changes in carbon isotope signatures could indicate that consumers were changing their diet in response to typical windfalls in resource availability, such as springtime zooplankton blooms, pulses in fish recruitment (natural or from stocking), or summer influxes of terrestrial insects. Because of enormous changes in body size and therefore gape, most predatory fishes undergo a trophic ontogeny, and the progression from small to large prey could be reflected in the isotopic signature of the consumer throughout its life (vander Zanden et al. 1998).

We found no evidence for significant seasonal variation in carbon signatures in the study reservoirs in 1997, except for rainbow trout in Blue Mesa Reservoir (a similar pattern may have existed in Lake Granby but only fall samples of rainbow trout were available). Significantly lower carbon signatures of rainbow trout sampled in spring compared with summer and fall may have been a result of the stocking regime in these reservoirs. We know that kokanee fry and their hatchery food had distinctly higher carbon signatures than any fish or invertebrates sampled from the lakes. Recently stocked rainbow trout probably also have this anthropogenic hatchery signature; those we sampled in spring had low carbon signatures, but they may have been stocked as subcatchables in the previous year and subsequently lost their hatchery signature during growth in the reservoir. In 1997, about 226,000 catchable rainbow trout were stocked in Blue Mesa Reservoir during June–August. The unusually high carbon signatures of some fish in summer and fall samples may have been from recently stocked catchables. The largest sizes of rainbow trout sampled in summer had a low signature similar to that of the spring fish, suggesting that they came from fish stocked as subcatchables. No such pattern existed in carbon signatures of stocked kokanee, presumably because kokanee are always stocked at a small size (about 50 mm) and we did not sample any kokanee less than 172 mm TL. Thus, the kokanee we sampled had grown sufficiently to have completely replaced their initial hatchery signature with a signature derived entirely from within-reservoir production.

The rate of change of isotopic signatures in response to a change in diet is proportional to the change in prey signatures but also to the amount of tissue generated from the new food resource. Because larger fish have lower specific growth rates, their body composition should be less responsive to changes in diet than smaller fish over the short duration of a growing season. However, metabolic turnover rates differ across tissues in

most animals (Lajtha and Michener 1994). In birds (Hobson and Clark 1992) and mammals (Tieszen et al. 1983), liver isotope signatures change in response to changes in food more quickly than do muscle values. Because most of the fish in our samples were relatively large, especially the lake trout, we wondered if liver samples might be more responsive to changes in diet and provide finer temporal resolution in diet inferences.

Although lake trout liver signatures were usually lower than muscle signatures, liver $\delta^{13}C$ is usually expected to be 0.5–4.1‰ lower than muscle tissue, in part due to higher lipid content (Pinnegar and Polunin 1999). We did not see any evidence of systematic seasonal variation in liver carbon signature, nor did the ratio of liver: muscle isotope signature change seasonally in either reservoir over a 6-month period. Thus, lake trout diets either did not change enough on a seasonal basis to be reflected in isotope signatures of either tissue or metabolic turnover in the liver provides no additional temporal resolution over muscle samples. In controlled feeding experiments on broad whitefish *Coregonus nasus*, body carbon signatures did not reach equilibrium with a new food source within 1 year after a change in diet of −5‰ (Hesslein et al. 1993); in addition, most of the change in isotope signatures was due to growth, not metabolic tissue replacement, which explains why liver signatures did not change more rapidly than muscle during the experiment. The results of our analyses on paired muscle–liver samples from lake trout are consistent with their findings and tend to support the conclusion of Hesslein et al. (1993) that liver samples appear to offer no advantage over muscle samples for detecting short-term changes in diet of relatively fast-growing fishes.

Because dietary changes over a lifetime probably would be more detectable than prey switching over a growing season, we examined the relationship between fish length and isotopic signatures. Generally, carbon signatures were not related to fish size, but again, the lack of any young-of-year fishes in our samples hampered our ability to detect time- or size-related changes in carbon signatures. We found an unusual relationship between $\delta^{13}C$ and fish length in lake trout from Blue Mesa Reservoir. The large drop in $\delta^{13}C$ between intermediate and large lake trout could be indicative of trophic differences, or it may simply be a function of changing lipid content. If relative weight was a reasonable surrogate for lipids, then in Blue Mesa Reservoir it appears that large lake trout were more lipid-rich than smaller lake trout. Because lipid $\delta^{13}C$ tends to be 2–3.5‰ lower than muscle (Gearing 1991) and if large lake trout have considerably more lipid per unit mass, then we would expect $\delta^{13}C$ to decrease with fish size, as appears to have occurred in the Blue Mesa Reservoir data. This conjecture could be tested in future studies by comparing signatures of unmodified tissue samples with those from the same samples after lipids have been chemically extracted. Alternatively, it may be that the intermediate-sized lake trout possess an unusually high $\delta^{13}C$ compared with smaller and larger fish. This could be explained if the intermediate fish exploited a higher fraction of recently stocked fishes (which had high $\delta^{13}C$ signatures) and small and large lake trout relied more heavily on prey biomass produced within the reservoir. Better understanding of how lipid content affects carbon signature is needed because both lipid content and prey selection tend to covary with predator size, and lipid content could confound diet assessments based on isotopes.

We hypothesized that $\delta^{13}C$ signatures would differ across organisms with a similar trophic position in reservoir food webs because of differences in the source of primary production in food chains within the webs. Carbon isotope signatures of phytoplankton, periphyton, and various terrestrial plants differ because of characteristic differences in carbon fractionation during photosynthesis (Ehleringer 1991; Hecky and Hesslein 1995). Cladocerans, the preferred prey of most planktivorous fishes, typically feed on phytoplankton-produced carbon (Balcer et al. 1984), whereas *M. relicta* may consume benthic carbon derived from periphyton, phytoplankton, and detritus (Lasenby 1991). Terrestrial insects, an important neustonic food source for some fishes in lakes and reservoirs, import a signature derived from terrestrial-based primary production.

Kokanee are usually highly zooplanktivorous (Rieman and Bowler 1980; Martinez and Bergersen 1991) and should incorporate a phytoplankton-derived carbon signature into their flesh, whereas rainbow trout in reservoirs typically feed on some combination of terrestrial insects and zooplankton (Trojnar and Behnke 1974; Lynott et al. 1995), imparting a composite of terrestrial and pelagic carbon signatures. Catostomids are more benthic in their habits and probably derive energy from benthic pathways (Hecky and Hesslein 1995), although longnose suckers are known to consume zooplankton in Colorado reservoirs (Trojnar and Behnke 1974; B. M. Johnson, personal observa-

tion). Assuming $\delta^{13}C$ signatures differ among the various primary producers in our food webs, then we would expect differences in carbon signatures of primary and secondary consumers.

Patterns in carbon isotope signatures were readily interpretable on the basis of feeding ecology of the resident species and production pathways in these reservoirs. Carbon isotope signatures of prey fishes were not variable within a taxon by size or season, but large differences in $\delta^{13}C$ existed among zooplankton, kokanee, catostomids and rainbow trout from Blue Mesa Reservoir. Kokanee, rainbow trout, and catostomids had $\delta^{13}C$ signatures in Lake Granby were similar, but they were distinct from *M. relicta*. These findings suggested greater segregation of prey resources in Blue Mesa Reservoir than at Lake Granby. Kokanee carbon signature in Blue Mesa Reservoir was consistent with a pelagic-based production pathway, whereas carbon signatures of rainbow trout and catostomids suggested a diet composed of prey of benthic or terrestrial origin. Carbon signatures in Lake Granby suggested that kokanee, rainbow trout, and catostomids consumed few zooplankton and probably all shared prey derived from benthic or terrestrial sources. Lake trout carbon values indicated that kokanee were important prey for small and large lake trout in Blue Mesa Reservoir; carbon values from Lake Granby suggested that all sizes of lake trout consumed a diet consisting of *M. relicta* and a combination of salmonid and catostomid fish prey.

Though considered a reliable indicator of trophic position (Lajtha and Michener 1994; vander Zanden and Rasmussen 1996) nitrogen signatures of a particular species or trophic guild are known to vary from place to place due to differences in ''baseline'' or source signatures at the base of the food web (Kendall 1998). Nitrogen signatures of a predator consuming the same prey species in two different lakes can differ if the isotopic signatures of the primary producers differ. For example, cultural eutrophication from fertilizers or animal waste (Kendall 1998) or atmospheric nitrogen deposition (Jassby et al. 1994) can impart a higher than natural nitrogen signature to the plants, which is then transported up the food chain. Thus, it may not be informative to compare nitrogen signatures across lakes. Rather, the trophic position (i.e., the enrichment of nitrogen relative to the baseline producer signatures) can be compared across systems.

Nitrogen isotope signatures of all consumers were lower in Lake Granby than in Blue Mesa Reservoir. However, the characteristic 3–4‰ increase across presumed trophic levels occurred in both reservoirs. Kokanee in Blue Mesa Reservoir had a nitrogen signature about 4‰ above zooplankton, and lake trout were about 2‰ above kokanee and 4‰ above rainbow trout, catostomids, and decapods. In Lake Granby, *M. relicta*, kokanee, rainbow trout, and catostomids all had similar nitrogen signatures, indicating that they occupied nearly the same trophic position in the food web. As for Blue Mesa Reservoir, Lake Granby lake trout had nitrogen signatures 2–4‰ above the signature of the prey assemblage. In both reservoirs, mean lake trout nitrogen signature, and presumably trophic position, increased with lake trout size. These patterns indicate that even the smallest lake trout in our samples were at least partially piscivorous but that lake trout became progressively more piscivorous as they grew.

Diet data for sport fishes from Blue Mesa Reservoir supported our conclusions about trophic linkages derived from isotope analysis. In Blue Mesa Reservoir, kokanee consumed cladocerans almost exclusively, and rainbow trout diet was about half zooplankton and half insects. Although diet data were not available, macrozooplankton have been extremely scarce in Lake Granby in recent years due to high *M. relicta* density. Annual zooplankton surveys at Lake Granby (Martinez, unpublished) documented densities of 1.3, 0.12, and 0.15 daphnia/L during 1995, 1996, and 1997, respectively. Consequently, both kokanee and rainbow trout at Lake Granby are probably relegated to feeding on insects (Martinez and Bergersen 1991). Research at Lake Granby (Martinez and Bergersen 1991) and elsewhere (Beattie and Clancey 1991; Bowles et al. 1991) has shown that these fishes rarely exploit *M. relicta*. Diet analysis showed that juvenile lake trout fed heavily on *M. relicta* in Lake Granby (Johnson and Martinez 2000) and mainly on insects, decapods, and some fish in Blue Mesa Reservoir (Table 3); lake trout diet switched to an increasing fraction of fish as they grew.

Isotope signatures from the Lake Granby food web suggested large differences in energy and materials pathways relative to those at Blue Mesa Reservoir. These differences in trophic structure have important implications for the sport fisheries. In Blue Mesa Reservoir, where *M. relicta* were not present, prey fishes were able to partition food resources; kokanee specialized on zooplankton and rainbow trout and catostomids also exploited alternate prey. Growth rates, density, and harvest of kokanee at Blue Mesa Reservoir are among the

highest in the region (Johnson and Martinez 2000) indicating that pelagic production in these coldwater reservoirs can be an extremely important source of energy to the food web and fishery. At Lake Granby, where *M. relicta* nearly eliminated pelagic macrozooplankton, there appeared to be fewer trophic links and greater overlap in diet of consumers at each trophic level. Nitrogen signatures indicate that *M. relicta* contributed very little to kokanee or rainbow trout diets, as other food habits studies have shown (Rieman and Falter 1981; Lasenby et al. 1986; Spencer et al. 1991). In fact, it appears that *M. relicta*, kokanee, rainbow trout and catostomids all occupied a similar trophic position in the food web and probably competed to varying degrees for benthic prey—to the detriment of the kokanee, in particular. Martinez and Wiltzius (1995) showed that when Lake Granby's thermal conditions enable *M. relicta* to access the epilimnion, they strip the lake of large zooplankton, resulting in poor growth and survival of kokanee. Because of their diel vertical migrations, in which feeding occurs in epilimnetic waters and digestion and excretion occur near the lake bottom, *M. relicta* appear to sequester pelagic production into the hypolimnion and tend to shift the food web towards a greater reliance on benthic energy pathways (Chess and Stanford 1998; Jassby 1998). Rather than diversifying trophic structure by providing an alternative food source for planktivorous sport fish, as originally intended by the introduction, stable isotope analysis suggested that the presence of *M. relicta* in Lake Granby short-circuited a major energy conduit—zooplankton—from channeling pelagic primary production into sport fish biomass.

Although laboratory studies are needed to continue to uncover the intricacies of isotopic fractionation and turnover by consumers (Gannes et al. 1997), isotope analysis enabled food webs in coldwater reservoirs to be compared without major field and laboratory effort. Changes in trophic structure of the reservoirs, resulting from changes in water management or fish stocking rates, for example, could be readily monitored with additional isotope analyses. Stable isotope approaches to understanding trophic dynamics are complementary to, not substitutes for, traditional diet studies. Isotope analysis usually cannot provide the fine-grained taxonomic resolution available from diet analysis. However, in very simple food webs, such as mountain reservoirs, stable isotope analysis offers a relatively easily obtained and temporally integrative assessment of food web structure.

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