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Article

Variation in relationships of $\delta^{13}C$ and $\delta^{15}N$ between lethal and nonlethal samples in fishes

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ABSTRACT

Objective: We summarized variation in muscle–fin isotope relationships in studies of freshwater fishes and evaluated whether season and body condition explained variation in muscle–fin relationships in a field study.

Methods: We reviewed published relationships of $\delta^{13}C$ and $\delta^{15}N$ values from muscle and fin tissue samples in fishes and compared them to relationships in a large sample of muscle and fin tissue samples that we collected from two small-bodied fishes, juvenile Brown Trout *Salmo trutta* and Mottled Sculpin *Cottus bairdii*. We evaluated the importance of season and body condition (dry matter content and C:N) in our muscle–fin relationships using multiple regression with model selection.

Results: Correlations between muscle and fin $\delta^{13}C$ and ^{15}N values within studies were high, but the variance in relationships across studies was large, even for the same species. Muscle and fin $\delta^{13}C$ and $\delta^{15}N$ values in our field study were also strongly positively correlated ($r \geq 0.89$), with minor muscle–fin differences for Brown Trout ($\Delta\delta^{13}C = -0.71 \pm 0.42‰$, $\Delta\delta^{15}N = 0.13 \pm 0.38‰$) and Mottled Sculpin ($\Delta\delta^{13}C = -0.73 \pm 0.29‰$, $\Delta\delta^{15}N = -0.21 \pm 0.31‰$). Slopes of our muscle–fin relationships for $\delta^{13}C$ ($\beta_1 = 0.796$-0.911) and $\delta^{15}N$ ($\beta_1 = 0.826$-0.872) were similar to average literature values ($\delta^{13}C$: $\bar{\beta}_1 = 0.824$; $\delta^{15}N$: $\bar{\beta}_1 = 0.875$), but again, the variance in published relationships was large. Incorporating season and body condition in models improved muscle–fin relationships.

Conclusions: High variance in muscle–fin isotopic relationships makes it difficult to rely on previously established models. We found that body condition improved the fit of muscle–fin relationships, suggesting that the large variance among the previous studies might be due to unmeasured predictors. Incorporating additional predictors, such as energy status, could reduce variation in muscle–fin relationships and increase their applicability across systems.

KEYWORDS: body condition, energy status, fin, meta-analysis, muscle

LAY SUMMARY

We showed that the relationship between fish muscle and fin isotope signatures is often strong but variable through time and space. Incorporating information on fish energy status can improve muscle–fin relationships and may increase the applicability of models that predict whole-body isotopic signatures from nonlethal samples such as fin clips.

INTRODUCTION

Stable isotope ratios of fish tissues can provide management insights useful for protecting native species and predicting impacts of invasive species (Dominguez Almela et al., 2021; Hickerson et al., 2019), determining stocking success (Rosinski et al., 2023; Wolff et al., 2013), identifying trophic pathways supporting fisheries (Frisch et al., 2014), and determining origins of invasive and illegally introduced fishes (Whitman et al., 2024; Wolff et al., 2012). A common application of isotope analysis is as a tool to understand trophic ecology because stable isotope ratios of a consumer's tissues can reflect those of its dietary sources (Peterson & Fry, 1987). Stable isotope analysis has been a tremendous boon for studying individual consumers' feeding habits partly because it can provide a more time-integrated view of diet than is possible by examining stomach contents (Peterson & Fry, 1987), which are transient and difficult to analyze (Baker et al., 2014). The isotope approach can also provide insights into trophic interactions, food web

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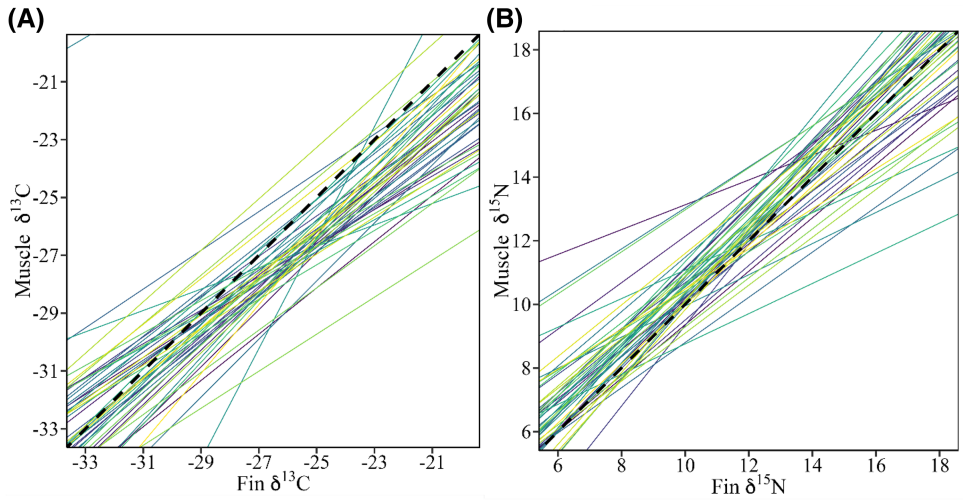

Figure 1. Plots of muscle–fin relationships with (A) $\delta^{13}C$ and (B) $\delta^{15}N$ from 17 studies of freshwater fish species listed in Table 2. The dashed line represents a 1:1 relationship.

structure, and ecosystem function (Peterson & Fry, 1987). For example, stable isotope ratios can be used to infer carbon sources ($\delta^{13}C$), trophic position ($\delta^{15}N$), trophic niche width, and dietary overlap with other species (Boecklen et al., 2011).

Whole-body or muscle samples are the most prevalent sample types used for stable isotope analysis in trophic ecology (Boecklen et al., 2011). In fishes, white epaxial (dorsal) muscle has been the preferred tissue for analysis because it is less variable than some other tissues, its fractionation behavior has been characterized, and it is easier to homogenize than whole bodies (Pinnegar & Polunin, 1999). However, obtaining muscle samples can be harmful or fatal to the fish, particularly for small species or juveniles, which may be undesirable from ethical, conservation, or practical standpoints. There is growing interest in alternative tissues that can be obtained more innocuously for addressing questions in fish trophic ecology with stable isotope analysis.

Fins can be readily sampled with minimal injury and are routinely used for marking, genetic studies, age determination, and disease monitoring in live fish. However, the utility of fins for trophic ecology questions depends on an understanding of how their isotope ratios compare to white muscle upon which most studies, mixing models, and theory are based. For example, tissues can differ in how they fractionate dietary inputs (the diet–tissue discrimination factor; Boecklen et al., 2011) and in their turnover rate of isotopes (Vander Zanden et al., 2015). These dynamics can change temporally (Finlay et al., 2002) and may be species-specific (Willis et al., 2013) and temperature dependent (Maitland et al., 2021). More work to identify patterns and mechanisms driving lethal–nonlethal tissue relationships would contribute to the transition away from harmful tissue sampling in fish trophic studies using stable isotope analysis.

Comparisons of lethal and nonlethal tissues have been performed on a broad phylogenetic range of freshwater and marine fishes, most commonly comparing fin tissue to muscle (Willis et al., 2013). Generally, studies have examined absolute differences between muscle and fin isotope values ($\Delta\delta^{13}C$ and $\Delta\delta^{15}N$) or they have fit simple linear regressions to describe the relationships between the isotopic values of muscle and fin tissue. In most cases, isotope ratios of muscle tissue have been found to be strongly correlated with fin values, but the relationship is rarely 1:1. In fact, the literature shows a surprising lack of coherence across studies in the relative isotopic composition of fins and muscle tissue (Figure 1). Uncertainty remains about factors that may drive variation in relationships of $\delta^{13}C$ and $\delta^{15}N$ from lethal and nonlethal samples in fish.

The goals of our study were to summarize findings from other studies on muscle–fin isotope relationships in freshwater fishes and to compare isotope ratios of muscle and fin tissue of juvenile Brown Trout *Salmo trutta* and Mottled Sculpin *Cottus bairdii* in a field study to determine if fin tissue could substitute for muscle for studying trophic interactions in our study system. We were interested in if and how muscle and fin $\delta^{13}C$ and $\delta^{15}N$ differed, if relationships varied by species, and how these relationships compared with findings from other studies. We were also interested in whether body condition covariates related to lipid content affected the relationships. Because fin and muscle tissue differ in how metabolically active they are (Graham et al., 2013) and have different biochemical composition, including the amount of lipid they possess (Galván et al., 2015; Larocque et al., 2021; Maktoof et al., 2020), a fish's body condition may affect $\delta^{13}C$ and $\delta^{15}N$ values in fin versus muscle tissue differentially. We hypothesized that two commonly used surrogates for lipid content, C:N ratio and dry matter content, could explain some of the variation in muscle–fin isotope relationships. Because lipid content often varies seasonally due to the reproductive cycle and changes in food availability and thermal conditions (Berg & Bremset, 1998; Nelson & McPherson, 1987; Spangenberg et al., 2023), we expected that muscle–fin relationships would change with season.

METHODS

Literature synthesis

Studies with freshwater fishes in which differences between muscle and fin isotope values ($\Delta\delta^{13}C$, $\Delta\delta^{15}N$), muscle–fin regressions, and/or tissue-specific C:N ratios were available were gathered from the literature using Google Scholar. Search terms included "Brown Trout," "C:N," "fin," "fish," "isotope,"

"lipid," "Mottled Sculpin," "muscle," "nonlethal," "tissue discrimination factor," and "turnover," and publication date was unrestricted. For each study we noted fins used and if lipid extraction or correction was performed. We excluded multispecies relationships and studies with sample sizes <5. Studies where adipose fins were used were not included in the summary because many species do not have adipose fins, and their anatomy and composition differ from rayed fins (Stewart et al., 2014). We tabulated reported $\Delta\delta^{13}C$ values, $\Delta\delta^{15}N$ values, linear regression models relating muscle $\delta^{13}C$ and $\delta^{15}N$ values to fin $\delta^{13}C$ and $\delta^{15}N$ values, and fin and muscle C:N for comparison with the findings from our field study. We also examined effect of lipid extraction/correction on $\Delta\delta^{13}C$ and the effect of lipid extraction on $\Delta\delta^{15}N$, as well as within-species differences in $\Delta\delta^{X}X$ for six species of salmonids in which there were multiple measurements for the same species.

Field study

The fieldwork for this study was conducted on the Blue River, a fifth-order tributary to the Colorado River near Kremmling, Colorado. We sampled five sites with a mean elevation of about 2,600 m above sea level that were approximately 10 km downstream from the dam at Green Mountain Reservoir (39°52′43.39″N, 106°19′58.65″W). River flow and temperature are regulated by the dam's hypolimnetic releases. The river is oligotrophic and cold, with about 1,400 annual growing degree-days (air, base = 5°C). Fish were collected with pulsed DC electrofishing during three time periods: May 24–28, August 2–6, and October 10–15, 2021. We sought to sample 15 individuals per species from each site and sampling date. The Mottled Sculpin ranged in size from 80 to 135 mm total length, and Brown Trout ranged in size from 80 to 194 mm total length. The fish were euthanized, measured in millimeters, and weighed in grams, and their stomach contents were collected via gastric lavage for another study. In the laboratory, we removed ~20% of the upper lobe of the caudal fin and a section of white epaxial muscle tissue without skin measuring approximately 5 × 5 mm for stable isotope analysis. Whole fish (for dry matter content analysis, below) and muscle and fin tissue samples (for isotope analysis) were dried at 60°C to constant weight.

Desiccated samples were ground to a homogeneous powder using a mortar and pestle, which were cleaned with ethanol between samples to avoid cross-contamination. Samples were then analyzed for percentage carbon (%C), percentage nitrogen (%N), and the relative abundance of stable carbon and nitrogen isotopes ($\delta^{13}C$ and $\delta^{15}N$ values) using a model NC2500 elemental analyzer (Carlo Erba, Milan, Italy) interfaced to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer (Thermo Fisher Scientific, Bremen, Germany) at the Cornell University Stable Isotope Laboratory (Ithaca, New York). Stable isotope compositions were expressed as parts per thousand (‰) using delta notation:

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 1{,}000, \quad (1)$$

where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ for the sample and standard. The standard for $\delta^{13}C$ values was Vienna Pee Dee Belemnite, and the standard for $\delta^{15}N$ values was atmospheric air.

Internal standards were analyzed after every 10 samples to maintain instrument accuracy and precision. The standard deviation of isotopic measurements of standards were 0.11‰ for $\delta^{15}N$, 0.268% for %N, 0.11‰ for $\delta^{13}C$, and 0.96% for %C values.

Lipid extraction or correction of carbon signatures for presumed lipid content based on C:N ratios were not performed for several reasons. Lipid corrections are normally performed on consumer and prey $\delta^{13}C$ values before making inferences about diets using mixing models, though a recent paper showed that lipid correction may be inappropriate even for this purpose (Arostegui et al., 2019). Our interest was in determining the relationship between fin and muscle isotope signatures, not diet. And chemical extraction of lipids can alter $\delta^{15}N$ values (Hicks et al., 2022; Larocque et al., 2021; Logan et al., 2008; Skinner et al., 2016; Smith et al., 2015). Alternatively, mathematical lipid correction models can perform poorly (Cloyed et al., 2020; Fagan et al., 2011; van der Merwe et al., 2022), implying that lipid correction of $\delta^{13}C$ values based on C:N ratios may require species-, population-, and tissue-specific functions (Logan et al., 2008), which were not available for juvenile Brown Trout and Mottled Sculpin.

Differences between muscle and fin isotope values ($\Delta\delta^{13}C$ and $\Delta\delta^{15}N$) were calculated as muscle value minus fin value. Simple linear regression was used to determine relationships between muscle and fin isotope values, with muscle as the dependent variable.

To investigate potential effects of fish energy status and lipid content on muscle–fin relationships, we computed dry matter content (DM; %), a body condition index that has been used as an indirect measure of both:

$$DM = DW/WW \times 100, \quad (2)$$

where DW is dry weight (g) and WW is wet weight (g). Wet and dry weights were of whole fish. The DM is strongly correlated with energy density in many fishes, including Brown Trout and sculpins *Cottus* spp. (Hartman & Brandt, 1995; Johnson et al., 2017; Rottiers & Tucker, 1982; Schreckenbach et al., 2001), and DM is a reliable surrogate for fish lipid content (Anthony et al., 2000; Breck, 2014; Peters et al., 2007; Post & Parkinson, 2001; Rottiers & Tucker, 1982; Trudel et al., 2005).

We used a multiple regression framework with model selection to examine potential factors affecting correspondence between fin and muscle isotope ratios. Our model selection protocol involved hypothesizing a set of predictors for each response variable, which included fin $\delta^{X}X$, fin C:N ratio, muscle C:N ratio, and DM. We also tested for seasonal effects (spring, summer, autumn). We examined collinearity among predictors and retained only one of the strongly correlated predictors ($|r| < 0.5$) in the global model. To evaluate multicollinearity among predictor variables, we ran variance inflation factor (VIF) tests and found that all continuous variables had variance inflation factor values below 3.3 (range = 1.08–3.29), demonstrating a lack of collinearity. We then fitted all possible main-effect models in R and used Akaike information criterion corrected for small sample size bias (AIC_c; Burnham & Anderson, 2002) to compare models. We computed ΔAIC_c,

the difference in AIC_c for a given model standardized to that of the model with the lowest AIC_c. Models with $\Delta AIC_c \leq 2$ were considered to have substantial evidence to support them (i.e., competing models; Burnham & Anderson, 2002). The likelihood of a particular model being the best in the candidate set was judged from AIC_c weight (Burnham & Anderson, 2002).

Predictor values were standardized with their mean and divided by standard deviation so model coefficients would be directly comparable. We removed extreme values (≥mean ± 2 SD) because we considered that they included values introduced by error. This process also improved normality of data, judged by the Shapiro–Wilk test. We developed separate models for each species because there was a significant species effect in initial modeling and a combined model would have little utility to other researchers. We developed models for each species and isotope separately. The global model was as follows:

$$\delta^{\chi}X_{muscle} = \delta^{\chi}X_{fin} + C{:}N_{fin} + C{:}N_{muscle} + DM + season, \quad (3)$$

where $\delta^{\chi}X$ is either $\delta^{13}C$ or $\delta^{15}N$, C:N ratio is carbon to nitrogen ratio of the tissue, DM is dry matter content (%), and season is categorical (spring [May], summer [August], or autumn [October]).

RESULTS

Literature synthesis

The difference between muscle and fin isotope values ($\Delta\delta^{\chi}X$) varied widely across studies encompassing 31 species (Table 1). For carbon, the mean difference (‰) was −0.88 (range = −2.97 to +0.40; $n = 40$), and for nitrogen, the mean difference (‰) was 0.21 (range = −1.30 to +1.26; $n = 40$). The mean $\Delta\delta^{13}C$ (‰) was similar for studies with (mean = −0.87; range = −1.77 to +0.4; $n = 23$) and without (mean = −0.90; range = −2.97 to +0.3; $n = 17$) lipid correction/extraction. The mean $\Delta\delta^{15}N$ (‰) with lipid extraction was −0.13 (range: −1.07 to +0.50; $n = 6$), and without lipid extraction, the mean was −0.02 (range: −1.3 to +1.21; $n = 17$). Among studies of the same species, the mean $\Delta\delta^{13}C$ (‰) was −0.73 (range = −1.14 to −0.25; $n = 6$), and for nitrogen, the mean difference was −0.06 (range = −5.25 to +0.55; $n = 6$).

Despite variation in species and the fins used, most studies found strong fits in linear regression models to convert fin $\delta^{13}C$ and $\delta^{15}N$ values to muscle values (Table 2). The average R^2 was 0.82 for $\delta^{13}C$ and 0.77 for $\delta^{15}N$. However, published equations varied widely in their parameters. For carbon, the mean β_0 was −5.42 (range = −17.44 to +21.61; $n = 50$) and the mean β_1 was 0.82 (range = 0.37–1.92; $n = 50$). For nitrogen, the mean β_0 was 1.79 (range = −3.32 to +9.23; $n = 50$) and the mean β_1 was 0.88 (range = 0.39–1.27; $n = 50$).

The C:N of fin and muscle tissue (without lipid extraction) was highly variable across 47 species (Table 3). The average C:N of fin tissue was 3.53 (range = 2.90–4.26) and muscle tissue was 3.66 (range = 3.20–8.02). Although the mean difference in C:N of fin and muscle tissue was only 0.14, the higher variation in muscle C:N drove a wide range in muscle – fin C:N values (range = −0.60 to +4.85) across studies. There were not enough studies of the same species to make meaningful comparisons within taxa.

Field study

In our field study, carbon isotope values of muscle ranged from −26.05‰ to −21.64‰ for Brown Trout ($n = 216$) and from −25.73‰ to −21.83‰ for Mottled Sculpin ($n = 163$). Nitrogen isotope values of muscle ranged from 10.66‰ to 14.52‰ for Brown Trout and from 11.54‰ to 14.76‰ for Mottled Sculpin. Differences between muscle and fin isotope values were relatively small and similar between the two species. Mean ± SD fin $\delta^{13}C$ values (Brown Trout: −23.28 ± 0.914‰, Mottled Sculpin: −23.20 ± 0.96‰) were enriched compared with muscle values (−23.98 ± 0.915‰ and −23.93 ± 0.954‰, respectively). The average difference was $\Delta\delta^{13}C = -0.706$‰ in Brown Trout and $\Delta\delta^{13}C = -0.726$‰ for Mottled Sculpin. Mean fin $\delta^{15}N$ values (Brown Trout: 12.54 ± 0.879‰, Mottled Sculpin: 13.56 ± 0.830‰) were depleted compared with muscle values for Brown Trout (12.67 ± 0.689‰) and enriched compared with muscle values for Mottled Sculpin (13.35 ± 0.690‰). Average differences in nitrogen values were smaller than for carbon: $\Delta\delta^{15}N = 0.128$‰ in Brown Trout and $\Delta\delta^{15}N = -0.207$‰ in Mottled Sculpin. Differences between muscle and fin $\delta^{15}N$ values were positive at low nitrogen fin values and negative at high fin nitrogen values for both species. There was a small effect of season on $\Delta\delta^{13}C$ ($P < 0.001$) and $\Delta\delta^{15}N$ ($P < 0.001$) for Brown Trout and on $\Delta\delta^{15}N$ ($P < 0.001$) for Mottled Sculpin (Figure 2).

Both $\delta^{13}C$ and $\delta^{15}N$ values of caudal fin tissue of Brown Trout and Mottled Sculpin in the Blue River were strongly positively correlated with those from muscle tissue. Linear regression models relating muscle isotope values to fin values were highly significant ($P < 0.001$) with high R^2 values for both isotopes and both species (Figure 3). The proportion of variance explained by the regression was slightly lower for Brown Trout ($\delta^{13}C$: $R^2 = 0.796$, $P < 0.001$; $\delta^{15}N$: $R^2 = 0.826$, $P < 0.001$) than for Mottled Sculpin ($\delta^{13}C$: $R^2 = 0.911$, $P < 0.001$; $\delta^{15}N$: $R^2 = 0.872$, $P < 0.001$). Slopes were all significantly different from 1.0 but were closer to 1.0 for $\delta^{13}C$ than for $\delta^{15}N$ (Brown Trout: $\beta = 0.893$ versus $\beta = 0.712$, Mottled Sculpin: $\beta = 0.949$ versus $\beta = 0.776$). Muscle–fin regression relationships did not differ by species.

Average muscle C:N ratio in samples from our field study was slightly higher (two-sample t-test: $t(377) = -13.594$; $P < 0.001$) for Mottled Sculpin (mean = 3.376 ± 0.067) than for Brown Trout (mean = 3.291 ± 0.056). Only 6% of Mottled Sculpin muscle samples exceeded the 3.5 C:N ratio threshold typically used for bias correction of $\delta^{13}C$ values due to high lipid content, and the maximum was C:N = 3.55. No Brown Trout muscle samples exceeded the C:N ratio correction threshold. Fin C:N ratios of Brown Trout were higher (mean = 3.470 ± 0.121) than muscle (paired t-test: $t(215) = -21.63$; $P < 0.001$) (Figure 4), and 39.8% of fin samples exceeded 3.5. Fin C:N ratios of Brown Trout were also higher (Welch two-sample t-test: $t(376.47) = 8.97$; $P < 0.001$) than those for Mottled Sculpin (mean = 3.374 ± 0.088). Fin C:N ratios showed a weak positive relationship with muscle C:N ratio for Brown Trout ($r = 0.158$, $P = 0.02$) and Mottled Sculpin ($r = 0.296$, $P < 0.001$), which could imply an effect of

Table 1. Differences (Δ = muscle – fin) in $\delta^{13}C$ and $\delta^{15}N$ of muscle and fin tissue of some freshwater fishes. Values are mean ± SD. Abbreviations are as follows: Y = yes, N = no, C = caudal fin, D = dorsal, P = pelvic, Pt = pectoral, and NR = not reported; "Lipid?" indicates if lipid extraction or correction was performed.

Species	Source	Lipid?	Fin	*n*	$\Delta\delta^{13}C$ (‰)	$\Delta\delta^{15}N$ (‰)
Lake Sturgeon (*Acipenser fulvescens*)	Smith et al., 2015	N	Pt	68	−2.97	−0.70
Lake Sturgeon	Smith et al., 2015	Y	Pt	68	−0.21	−0.46
Freshwater Drum (*Aplodinotus grunniens*)	Maitland & Rahel, 2021	Y	P	5	−1.77 ± 0.23	0.70 ± 0.17
Longnose Sucker (*Catostomus catostomus*)	Maitland & Rahel, 2021	Y	P	23	−1.03 ± 0.62	0.46 ± 0.43
White Sucker (*Catostomus commersonii*)	Maitland & Rahel, 2021	Y	P	42	−1.25 ± 0.59	0.31 ± 0.60
Lake Whitefish (*Coregonus clupeaformis*)	Hanisch et al., 2010	N	C	17	−1.11 ± 0.42	−0.22 ± 0.49)
Slimy Sculpin (*Cottus cognatus*)	Kelly et al., 2006	N	C	30	0.30 ± 0.50	−0.50 ± 0.50
Red Shiner (*Cyprinella lutrensis*)	Maitland & Rahel, 2021	Y	P	9	−0.57 ± 0.38	0.37 ± 0.17
Johnny Darter (*Etheostoma nigram*)	Maitland & Rahel, 2021	Y	P	16	−0.79 ± 0.29	0.86 ± 0.30
Brassy Minnow (*Hybognathus hankinsoni*)	Maitland & Rahel, 2021	Y	P	16	−1.11 ± 0.40	0.81 ± 0.27
Barramundi (*Lates calcarifer*)	Jardine et al., 2011	N	NR	18	−0.50 ± 0.60	0.00 ± 0.50
Spangled Perch (*Leiopotherapon unicolor*)	Jardine et al., 2011	N	NR	37	−0.50 ± 1.20	−1.10 ± 1.00
Asp (*Leuciscus aspius*)	Vašek et al., 2017	N	D	48	−1.40 ± 0.40	0.98 ± 0.28
Common Shiner (*Luxilus cornutus*)	Maitland & Rahel, 2021	Y	P	14	−1.20 ± 0.49	0.30 ± 0.30
Eastern Rainbowfish (*Melanotaenia splendida*)	Jardine et al., 2011	N	NR	45	−0.90 ± 0.90	0.70 ± 1.30
Smallmouth Bass (*Micropterus dolomieu*)	Maitland & Rahel, 2021	Y	P	6	−0.28 ± 0.07	0.30 ± 0.20
Shorthead Redhorse (*Moxostoma macrolepidotum*)	Maitland & Rahel, 2021	Y	P	9	−1.74 ± 0.65	0.96 ± 0.41
Hornyhead Chub (*Nocomis biguttatus*)	Maitland & Rahel, 2021	Y	P	17	−0.23 ± 0.40	0.43 ± 0.13
Bigmouth Shiner (*Notropis dorsalis*)	Maitland & Rahel, 2021	Y	P	8	−0.88 ± 0.69	0.54 ± 0.19
Sand Shiner (*Notropis stramineus*)	Maitland & Rahel, 2021	Y	P	12	−1.09 ± 0.31	0.88 ± 0.57
Coho Salmon (*Oncorhynchus kisutch*)	Larocque et al., 2021	Y	C	20	−0.79 ± 0.44	−1.07 ± 0.70
Rainbow Trout (*Oncorhynchus mykiss*)	Hanisch et al., 2010	N	C	55	−0.09 ± 1.00	−0.14 ± 0.63
Rainbow Trout	Sanderson et al., 2009	N	C	372	−0.52 ± 0.67	0.39 ± 0.58
Rainbow Trout	Larocque et al., 2021	Y	C	20	−0.90 ± 0.57	0.39 ± 0.57
Chinook Salmon (*Oncorhynchus tshawytscha*)	Sanderson et al., 2009	N	C	727	−0.77 ± 0.69	0.38 ± 0.58
Chinook Salmon	Larocque et al., 2021	Y	C	20	−0.22 ± 0.41	−0.37 ± 0.57
Fathead Minnow (*Pimephales promelas*)	Maitland & Rahel, 2021	Y	P	16	−1.55 ± 0.43	0.88 ± 0.35
Pygmy Whitefish (*Prosopium coulterii*)	Hanisch et al., 2010	N	C	26	−1.10 ± 0.67	1.21 ± 0.40
Longnose Dace (*Rhinichthys cataractae*)	Maitland & Rahel, 2021	Y	P	35	−1.09 ± 0.57	0.83 ± 0.47
Atlantic Salmon (*Salmo salar*)	Jardine et al., 2005	N	C	24	−0.21 ± 0.38	0.80± 0.35
Atlantic Salmon	Graham et al., 2013	Y	C	24	0.40 ± 0.10	0.80 ± 0.10
Atlantic Salmon	Larocque et al., 2021	Y	C	6	−0.94 ± 0.55	0.05 ± 0.96
Atlantic Salmon	Graham et al., 2013	N	C	24	−1.20 ± 0.10	−1.30 ± 0.70
Atlantic Salmon	Larocque et al., 2021	Y	C	20	−0.68 ± 0.44	0.50 ± 0.48
Brook Trout (*Salvelinus fontinalis*)	Hanisch et al., 2010	N	C	5	−1.63 ± 0.58	−0.74 ± 0.21
Brook Trout	Jardine et al., 2005	N	C	23	−0.65 ± 0.94	−0.31 ± 0.42
Lake Trout (*Salvelinus namaycush*)	Hanisch et al., 2010	N	C	15	−1.17 ± 0.61	−0.14 ± 0.54
Lake Trout	Larocque et al., 2021	Y	C	20	−0.93 ± 0.45	−0.28 ± 0.57
Creek Chub (*Semotilus atromaculatus*)	Maitland & Rahel, 2021	Y	P	59	−1.13 ± 0.72	0.47 ± 0.54
Freshwater Longtom (*Strongylura krefftii*)	Jardine et al., 2011	N	NR	11	−0.90 ± 1.00	0.30 ± 0.80
Mean					−0.88 ± 0.73	0.21 ± 0.54
Range					−2.97 to 0.40	−1.30 to 1.26
N					40	40

body lipid stores on fin C:N ratio. However, fin C:N ratio was not related to DM in Brown Trout ($P = 0.07$), which does not support that speculation.

The mean DM of Brown Trout (21.04 ± 1.13%; $n = 216$) and Mottled Sculpin (21.01 ± 1.12%; $n = 163$) in the Blue River did not significantly differ (two-sample *t*-test: $t(377) = 0.269$; $P = 0.79$). The lowest values of DM occurred in spring for Brown Trout (mean = 20.88%) and in autumn for Mottled Sculpin (mean = 20.77%) (Figure 5). Seasonal differences in DM were significant for Brown Trout (ANOVA: $F = 3.09$, $P = 0.048$) but not significant for Mottled Sculpin ($F = 2.57$, $P = 0.079$).

Including additional predictors in regression models explained more of the variance in muscle isotope ratios we measured in our field study (Table 4) compared to fin-only models, which were never included as competing models ($\Delta AIC_c > 2$). Fin $\delta^{13}C$ and $\delta^{15}N$ were always the strongest predictors of muscle isotope ratios in competing multivariate models. Slope coefficients for fin $\delta^{13}C$ with standardized data were approximately 0.91 for Brown Trout and approximately 0.92 for Mottled Sculpin. Slope coefficients for fin $\delta^{15}N$ with standardized data were lower than for fin $\delta^{13}C$ and averaged 0.63 for Brown Trout and approximately 0.65 for Mottled Sculpin. The DM was a significant predictor in all models for muscle $\delta^{15}N$ and in two out of three models for muscle $\delta^{13}C$. Muscle C:N ratio was a significant predictor in all $\delta^{15}N$ models but did not appear in $\delta^{13}C$ models. Fin C:N ratio was a significant predictor in five out of eight models and usually had the lowest slope coefficient of any predictor.

Table 2. Linear regression equations to convert fin $\delta^{13}C$ and $\delta^{15}N$ values to muscle values for some freshwater fishes. Abbreviations are as follows: Y = yes, N = no, C = caudal fin, D = dorsal, M = multiple, NR = not reported, P = pelvic, and Pt = pectoral; "Lipid?" indicates if lipid extraction or correction was performed.

					$\delta^{13}C$			$\delta^{15}N$		
Species	**Source**	**Lipid?**	**Fin**	***n***	β_0	β_1	R^2	β_0	β_1	R^2
Lake Sturgeon	Smith et al., 2015	Y	Pt	68	−8.13	0.80	0.32	0.96	0.84	0.46
Freshwater Drum	Maitland & Rahel, 2021	Y	P	4	−10.69	0.640	0.93	9.23	0.39	0.70
Alligator Gar (*Atractosteus spatula*)	Fredrickson et al., 2022	N	C	16	−2.23	0.99	0.94	−0.09	1.03	0.74
Stone Loach (*Barbatula barbatula*)	Tronquart et al., 2012	N	M	113	−6.89	0.77	0.86	1.42	0.97	0.94
Silver Bream (*Blicca bjoerkna*)	Tronquart et al., 2012	N	M	13	−3.02	0.94	0.60	4.84	0.73	0.22
Longnose Sucker	Maitland & Rahel, 2021	Y	P	18	−2.22	0.96	0.92	1.94	0.83	0.92
White Sucker	Maitland & Rahel, 2021	Y	P	34	−12.08	0.58	0.73	2.42	0.77	0.87
Lake Whitefish	Hanisch et al., 2010	N	C	17	−4.64	0.87	0.88	0.94	0.86	0.87
Slimy Sculpin	Kelly et al., 2006	N	C	84	−8.22	0.70	0.71	−3.32	1.27	0.81
European Bullhead (*Cottus gobio*)	Tronquart et al., 2012	N	M	61	−5.85	0.83	0.90	−0.01	1.00	0.99
Red Shiner	Maitland & Rahel, 2021	Y	P	7	−8.34	0.71	0.91	3.48	0.72	0.45
Johnny Darter	Maitland & Rahel, 2021	Y	P	13	−10.17	0.66	0.87	0.05	1.08	0.83
Gudgeon (*Gobio gobio*)	Tronquart et al., 2012	N	M	41	−7.73	0.76	0.81	1.35	0.98	0.96
Brassy Minnow	Maitland & Rahel, 2021	Y	P	13	−7.36	0.78	0.86	2.25	0.83	0.96
Barramundi	Jardine et al., 2011	N	NR	18	−7.40	0.67	0.69	1.71	0.83	0.40
Spangled Perch	Jardine et al., 2011	N	NR	37	−5.31	0.79	0.83	1.70	0.71	0.65
Spotted Gar	Fredrickson et al., 2022	N	C	104	−2.79	1.00	0.95	1.04	0.92	0.88
Pumpkinseed (*Lepomis gibbosus*)	Tronquart et al., 2012	N	M	5	−5.71	0.84	0.98	−1.72	1.17	0.99
Asp	Vašek et al., 2017	N	D	21	−7.43	0.74	0.64	6.59	0.64	0.42
Asp	Vašek et al., 2017	N	D	27	−5.82	0.78	0.57	2.93	0.86	0.90
Common Dace (*Leuciscus leuciscus*)	Tronquart et al., 2012	N	M	11	−8.38	0.72	0.81	1.27	0.95	0.95
Common Dace	Busst et al., 2015	N	P	5	0.00	0.59	0.99	−0.09	1.02	0.94
Common Shiner	Maitland & Rahel, 2021	Y	P	11	1.08	1.09	0.88	−0.56	1.09	0.85
Eastern Rainbowfish	Jardine et al., 2011	N	NR	45	−3.28	0.90	0.78	5.05	0.49	0.21
Smallmouth Bass	Maitland & Rahel, 2021	Y	P	5	−0.12	1.01	0.99	0.69	0.96	0.99
Shorthead Redhorse	Maitland & Rahel, 2021	Y	P	7	21.61	1.92	0.90	−1.20	1.22	0.99
Hornyhead Chub	Maitland & Rahel, 2021	Y	P	14	−3.83	0.85	0.92	1.56	0.90	0.98
Bigmouth Shiner	Maitland & Rahel, 2021	Y	P	6	−17.44	0.37	0.85	0.84	0.98	0.89
Sand Shiner	Maitland & Rahel, 2021	Y	P	10	−13.12	0.55	0.86	6.58	0.45	0.76
Rainbow Trout	Hanisch et al., 2010	N	C	55	−0.55	0.98	0.94	4.01	0.48	0.36
European Perch (*Perca fluviatilis*)	Tronquart et al., 2012	N	M	41	−1.86	0.96	0.89	0.44	1.02	0.95
Eurasian Minnow (*Phoxinus phoxinus*)	Tronquart et al., 2012	N	M	45	−4.38	0.87	0.79	0.74	1.06	0.93
Fathead Minnow	Maitland & Rahel, 2021	Y	P	13	0.33	1.07	0.92	0.28	1.06	0.94
Pygmy Whitefish	Hanisch et al., 2010	N	C	26	−12.46	0.60	0.60	3.23	0.77	0.74
Stone Moroko (*Pseudorasbora parva*)	Busst et al., 2015	N	P	21	−1.86	0.96	0.88	4.21	0.62	0.84
Longnose Dace	Maitland & Rahel, 2021	Y	P	28	−12.33	0.56	0.74	1.90	0.87	0.94
European Bitterling (*Rhodeus amarus*)	Tronquart et al., 2012	N	M	11	−12.45	0.57	0.44	6.37	0.66	0.66
Common Roach (*Rutilus rutilus*)	Tronquart et al., 2012	N	M	41	−3.72	0.91	0.91	1.60	0.94	0.89
Common Roach	Busst et al., 2015	N	P	8	−9.88	0.73	0.94	−1.93	1.20	0.66
Atlantic Salmon	Graham et al., 2013	Y	C	25	−13.73	0.64	0.64	1.59	0.77	0.36
Brown Trout (*Salmo trutta*)	Graham et al., 2013	N	C	25	−3.39	0.84	0.69	1.006	0.94	0.58
Brook Trout	Hanisch et al., 2010	N	C	5	−3.46	0.93	0.88	1.57	0.75	0.91
Pallid Sturgeon (*Scaphirhynchus albus*)	Andvik et al., 2010	N	Pt	15	−1.02	0.89	0.97	2.27	0.86	0.79
Creek Chub	Maitland & Rahel, 2021	Y	P	47	−5.18	0.84	0.58	2.68	0.78	0.80
Common Chub (*Squalius cephalus*)	Tronquart et al., 2012	N	M	34	−7.90	0.73	0.76	−1.27	1.11	0.85
Common Chub	Busst et al., 2015	N	P	5	−10.96	0.64	0.76	−1.18	1.13	0.93
Walleye (*Stizostedion vitreum*)	Fincel et al., 2011	N	P	44	−4.90	0.79	0.92	3.50	0.81	0.80
Freshwater Longtom	Jardine et al., 2011	N	NR	11	−3.99	0.88	0.96	4.18	0.63	0.56
Tench (*Tinca tinca*)	Busst et al., 2015	N	P	8	3.42	1.19	0.86	0.69	0.93	0.82
Mean					−5.42	0.82	0.82	1.79	0.88	0.77
Range					−17.44 to +21.61	0.37–1.92	0.32–0.99	−3.32 to +9.23	0.39–1.27	0.21–0.99
N					50	50	50	50	50	50

Table 3. Mean carbon : nitrogen (C:N) ratios of fin and muscle tissue (without lipid extraction) from some freshwater fishes. Abbreviations are as follows: C = caudal fin, D = dorsal, M = multiple, NR = not reported, P = pelvic, and Pt = pectoral.

				C:N		
Species	**Source**	**Fin**	***n***	**Fin**	**Muscle**	**Muscle – Fin**
Lake Sturgeon	Smith et al., 2015	Pt	68	3.43	7.81	4.38
Freshwater Drum	Maitland & Rahel, 2021	P	5	3.20	3.25	0.05
Stone Loach	Tronquart et al., 2012	M	126	3.80	3.60	−0.20
Silver Bream	Tronquart et al., 2012	M	14	3.40	3.60	0.20
Longnose Sucker	Maitland & Rahel, 2021	P	23	3.59	3.62	0.03
White Sucker	Maitland & Rahel, 2021	P	42	3.62	3.48	−0.14
Lake Whitefish (winter)	Roberts et al., 2022	C	8	3.20	3.20	0.00
Lake Whitefish (autumn)	Roberts et al., 2022	C	8	3.10	3.20	0.10
Lake Whitefish (spring)	Roberts et al., 2022	C	8	3.10	3.20	0.10
European Bullhead	Tronquart et al., 2012	M	68	3.20	3.70	0.50
Red Shiner	Maitland & Rahel, 2021	P	9	3.81	3.99	0.18
Fourfinger (Threadfin *Eleutheronema tetradactylum*)	Jardine et al., 2011	NR	3	3.50	3.20	−0.30
Northern Pike *Esox lucius* (autumn)	Roberts et al., 2022	C	20	3.20	3.20	0.00
Northern Pike (spring)	Roberts et al., 2022	C	20	3.30	3.20	−0.10
Northern Pike (winter)	Roberts et al., 2022	C	20	3.40	3.20	−0.20
Johnny Darter	Maitland & Rahel, 2021	P	16	3.73	3.61	−0.12
Gudgeon	Tronquart et al., 2012	M	46	3.50	3.40	−0.10
Brassy Minnow	Maitland & Rahel, 2021	P	16	3.56	3.76	0.20
Barramundi	Jardine et al., 2011	NR	18	3.50	3.40	−0.10
Spangled Perch	Jardine et al., 2011	NR	37	3.60	3.60	0.00
Pumpkinseed	Tronquart et al., 2012	M	6	3.40	3.20	−0.20
Asp	Vašek et al., 2017	D	21	3.66	3.39	−0.27
Asp	Vašek et al., 2017	D	27	3.74	3.22	−0.52
Common Dace	Tronquart et al., 2012	M	12	2.90	3.40	0.50
Common Shiner	Maitland & Rahel, 2021	P	14	3.92	3.46	−0.46
Eastern Rainbowfish	Jardine et al., 2011	NR	45	3.90	3.60	−0.30
Smallmouth Bass	Maitland & Rahel, 2021	P	6	3.81	3.29	−0.52
Shorthead Redhorse	Maitland & Rahel, 2021	P	9	3.61	3.43	−0.18
Hairback Herring (*Nematalosa come*)	Jardine et al., 2011	NR	8	3.40	3.50	0.10
Bony Bream (*Nematalosa erebi*)	Jardine et al., 2011	NR	11	3.50	3.60	0.10
Blue Salmon Catfish (*Neoarius graeffei*)	Jardine et al., 2011	NR	9	3.30	3.40	0.10
Hornyhead Chub	Maitland & Rahel, 2021	P	17	3.81	3.71	−0.10
Bigmouth Shiner	Maitland & Rahel, 2021	P	8	4.26	3.98	−0.28
Sand Shiner	Maitland & Rahel, 2021	P	12	4.26	3.84	−0.42
Coho Salmon	Larocque et al., 2021	C	20	3.15	3.32	0.17
Rainbow Trout	Larocque et al., 2021	C	20	3.09	3.49	0.40
Chinook Salmon	Larocque et al., 2021	C	20	3.32	4.50	1.18
Sleepy Cod (*Oxyeleotris lineolatus*)	Jardine et al., 2011	NR	8	3.50	3.30	−0.20
Blackbanded Gudgeon (*Oxyeleotris selheimi*)	Jardine et al., 2011	NR	4	3.30	3.40	0.10
Yellow Perch (*Perca flavescens*) (autumn)	Roberts et al., 2022	C	11	3.50	3.20	−0.30
Yellow Perch (spring)	Roberts et al., 2022	C	11	3.70	3.30	−0.40
Yellow Perch (winter)	Roberts et al., 2022	C	11	3.70	3.30	−0.40
European Perch	Tronquart et al., 2012	M	46	3.10	3.40	0.30
European Perch	Tronquart et al., 2012	M	50	4.00	3.40	−0.60
Fathead Minnow	Maitland & Rahel, 2021	P	16	3.77	3.54	−0.23
Longnose Dace	Maitland & Rahel, 2021	P	35	4.12	3.61	−0.51
European Bitterling	Tronquart et al., 2012	M	12	3.80	3.40	−0.40
Common Roach	Tronquart et al., 2012	M	46	3.60	3.40	−0.20
Atlantic Salmon	Graham et al., 2013	C	25	3.69	3.46	−0.23
Atlantic Salmon	Larocque et al., 2021	C	6	3.25	3.55	0.30
Brown Trout	Larocque et al., 2021	C	20	3.27	5.41	2.14
Lake Trout	Larocque et al., 2021	C	20	3.17	8.02	4.85
Creek Chub	Maitland & Rahel, 2021	P	59	3.78	3.48	−0.30
European Chub	Tronquart et al., 2012	M	38	3.50	3.40	−0.10
Freshwater Longtom	Jardine et al., 2011	NR	11	3.50	3.40	−0.10
Mean				3.53	3.66	0.14
Range				2.90–4.26	3.20–8.02	−0.60 to +4.85
N				55	55	55

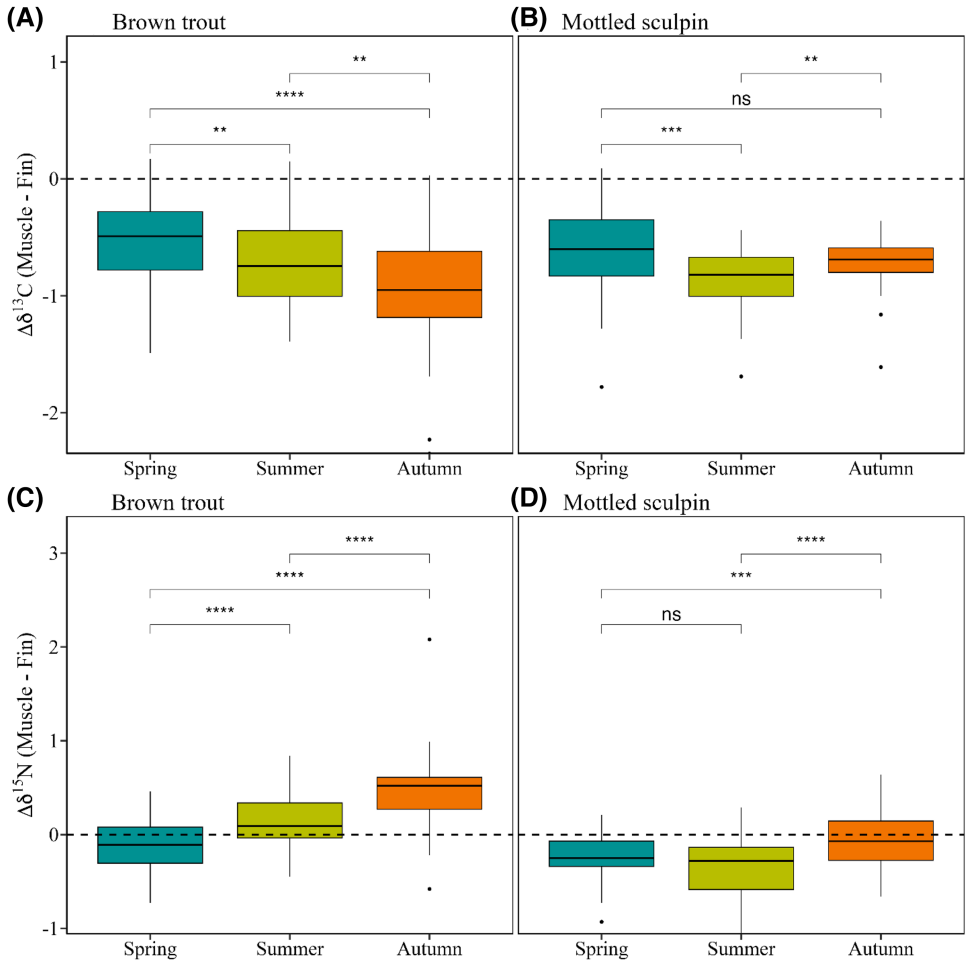

Figure 2. Box plots of the difference between muscle and fin isotope ratios (Δδ; ‰) of (A, C) Brown Trout and (B, D) Mottled Sculpin sampled from the Blue River, Colorado. Horizontal lines in the boxes represent the median, boxes show the interquartile range (IQR), vertical lines show minimum value (Q1 [first quartile] − 1.5 × IQR) and maximum value (Q3 [third quartile] + 1.5 × IQR), and points are outliers. Significant differences are denoted with asterisks (ns = not significant, one asterisk = $P \leq 0.05$, two asterisks = $P \leq 0.01$, three asterisks = $P \leq 0.001$, four asterisks = $P \leq 0.0001$).

DISCUSSION

Many studies have investigated the relationship between muscle and fin stable isotope values in freshwater fishes to evaluate if fin samples can substitute for more harmful muscle samples in trophic ecology studies. Because the existing literature on the use of stable isotopes of consumers to make inferences about diet and trophic position is primarily based on the isotopic composition of muscle, differences between muscle and fin isotope values necessitate the adjustment of fin values before they can substitute for muscle values. We found that published muscle–fin relationships are usually precise, but these relationships vary greatly across studies, even within the same species and in some cases within the same population.

The small average differences in $\delta^{13}C$ values of caudal fin and dorsal muscle tissue of juvenile Brown Trout and Mottled Sculpin in our field study were consistent with findings in studies of other species. On average, for both species, the carbon ratios of muscle tissue were depleted compared with fin tissue, which is consistent with other studies of freshwater fishes. The mean difference between muscle and caudal fin $\delta^{13}C$ values in our Brown Trout and Mottled Sculpin samples was similar to what has been previously demonstrated in other muscle–caudal fin comparisons in salmonids without lipid extraction/correction (Hanisch et al., 2010; Jardine et al., 2005; Sanderson et al., 2009) and in Slimy Sculpin *Cottus cognatus* (Kelly et al., 2006), a close relative of Mottled Sculpin. Slightly higher negative offsets have been observed in studies with other species and fins sampled (Hanisch et al., 2010; Jardine et al., 2011; Maitland & Rahel, 2021; Vašek et al., 2017).

The average differences in nitrogen isotope ratios of muscle and fin of Brown Trout and Mottled Sculpin in the Blue River were smaller than we observed for carbon. The average difference for our Brown Trout samples was similar to $\Delta\delta^{15}N$ observed with other salmonids and slightly lower than the average across other freshwater species we reviewed. The $\Delta\delta^{15}N$ we found for Mottled Sculpin was about double that observed in Slimy Sculpin (Kelly et al., 2006). In our study and others, fin samples with relatively low $\delta^{15}N$ values were usually depleted compared with muscle, and fin samples with higher fin $\delta^{15}N$ values tended to be enriched compared with muscle. Thus, the use of average $\Delta\delta^{15}N$ to predict muscle isotope ratios from fins

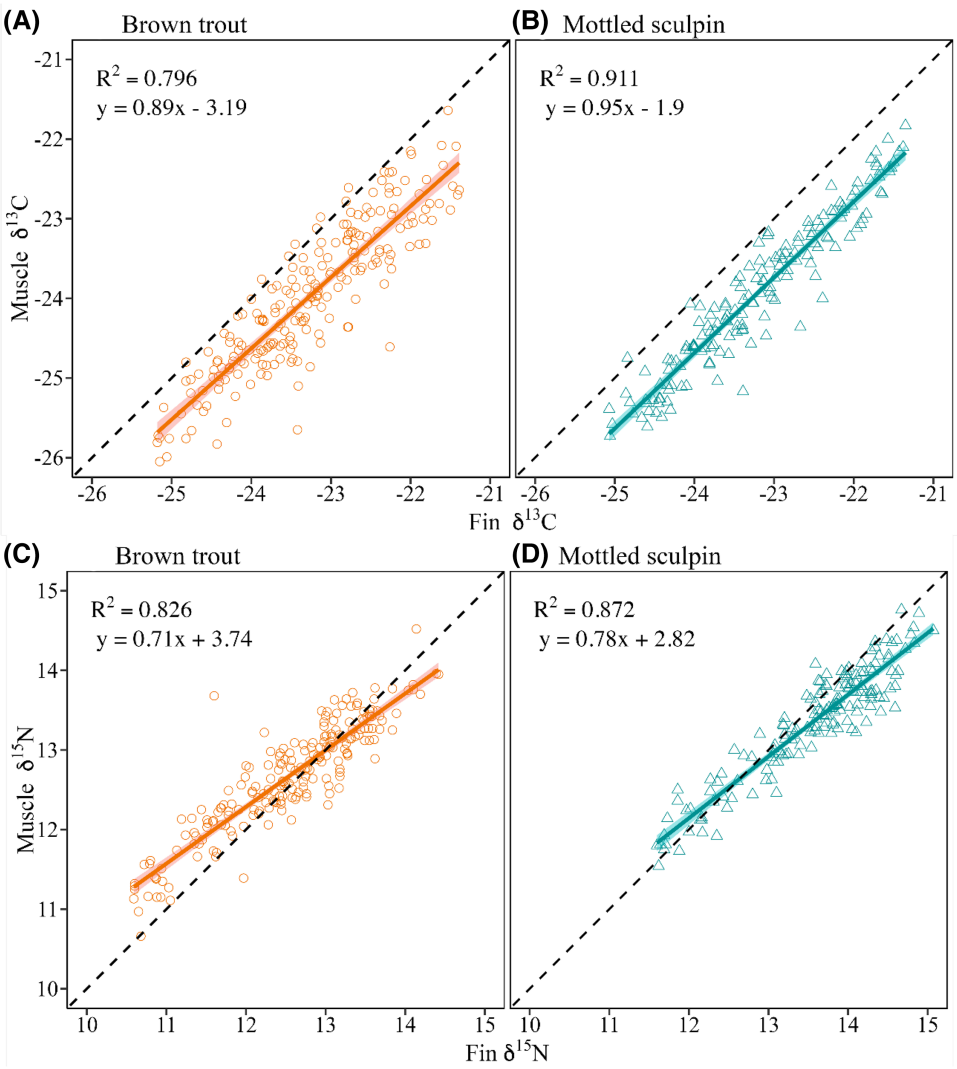

Figure 3. Relationships between fin and muscle $\delta^{13}C$ and $\delta^{15}N$ signatures for (A, C) Brown Trout and (B, D) Mottled Sculpin. Dashed lines indicate 1:1 relationships, solid lines represent estimated linear regressions, and shading represents 95% confidence intervals. Regression equations and R^2 values are included in each plot.

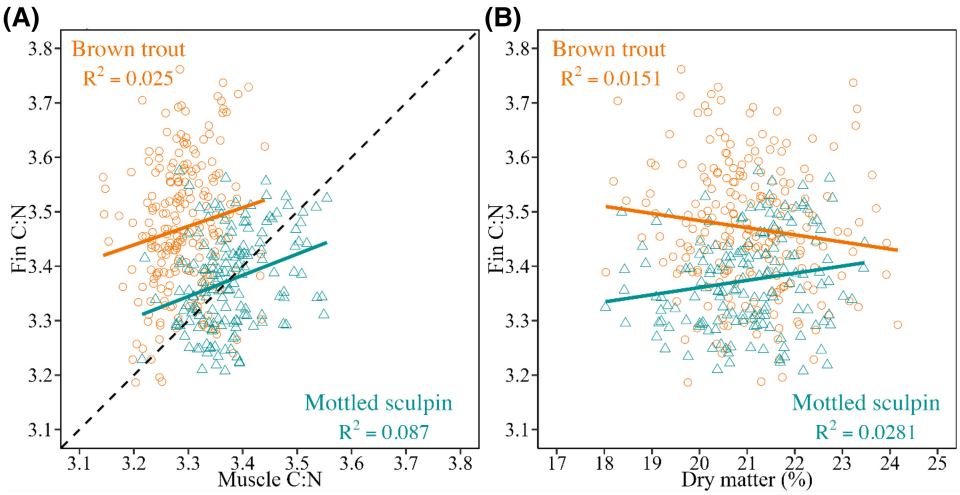

Figure 4. (A) Carbon : nitrogen ratio of muscle and fin tissue from Brown Trout (orange symbols; $n = 216$) and Mottled Sculpin (blue symbols; $n = 163$). The dashed line represents a 1:1 relationship. (B) Dry matter content (%) compared to fin C:N ratio for Brown Trout (orange symbols; $n = 216$) and Mottled Sculpin (blue symbols; $n = 163$).

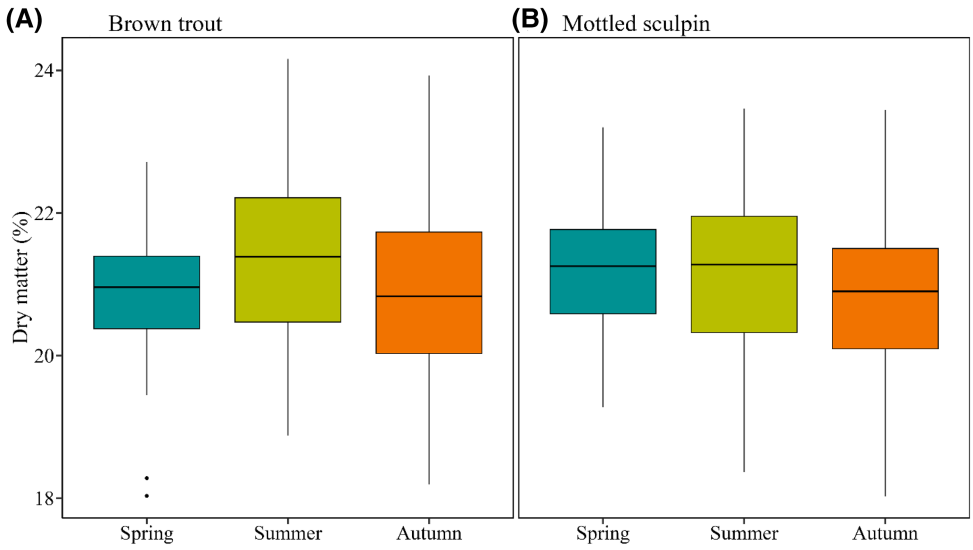

Figure 5. Box plots of whole-body dry matter content of (A) Brown Trout and (B) Mottled Sculpin sampled for stable isotope analysis over three seasons in the Blue River, Colorado. Horizontal lines in the boxes represent the median, boxes show the interquartile range (IQR), vertical lines show minimum value (Q1 [first quartile] – 1.5 × IQR) and maximum value (Q3 [third quartile] + 1.5 × IQR), and points are outliers.

instead of using slope and intercept of the relationship could lead to inaccurate estimates of muscle values and incorrect diet inferences.

Overall, the range in muscle–fin carbon differences across studies (3.37‰) is an order of magnitude larger than the expected trophic fractionation of $\delta^{13}C$ in muscle (0.39 ± 1.3‰; DeNiro & Epstein, 1977; Post, 2002). For nitrogen, the range in muscle–fin differences across studies (2.56‰) is similar to the expected change in trophic position of a predator and its prey (Post, 2002). Thus, inferences about diet could be highly biased if fin isotope signatures are converted to muscle signatures without verification. For example, subtle differences in trophic niche overlap of Mottled Sculpin and Brown Trout in our study system (Platis et al., 2024) would be completely obscured by error if fin $\delta^{13}C$ and $\delta^{15}N$ values were converted to muscle values using published muscle–fin relationships. Thus, investigators should be cautious about borrowing stable isotope offsets from other studies to estimate muscle values from fin samples.

Most of the variance in muscle $\delta^{13}C$ and $\delta^{15}N$ values of Brown Trout and Mottled Sculpin in our field study was explained by fin isotope ratios in simple linear regressions, and other investigators have generally found high (>0.77) R^2 values for these relationships as well. The strong relationships between muscle and fin isotope ratios that we and others have observed lend support to the practice of using fin tissue as a nonlethal proxy for dorsal muscle for trophic ecology questions. While several investigators have suggested that fin isotope ratios could, in at least some cases, substitute for muscle ratios without adjustment (Alvarez & Ward, 2019; Cucherousset et al., 2007, 2020; Curry et al., 2014; Evangelista et al., 2014; Fredrickson et al., 2022; Frossard et al., 2021; Hanisch et al., 2010; Hicks et al., 2022; Jackson et al., 2016; Kupilas et al., 2021; Musseau et al., 2018; Roon et al., 2022; Smith et al., 2015; Závorka et al., 2017), the wide range in muscle–fin offsets and regression models we reviewed suggest that this practice could produce erroneous estimates of muscle isotope ratios and trophic inferences.

Models that predict muscle from fin values would be most useful if the relationships were similar within a species, if not across species, and stable in space and time so that lethal sampling to verify muscle–fin relationships need not be repeated in every study. The literature suggests that although muscle–fin relationships are frequently quite precise, it is unclear how transferable they are across studies. Muscle–fin relationships of Brown Trout and Mottled Sculpin in the Blue River did not differ, but the broad range in muscle–fin $\Delta\delta^{13}C$, $\Delta\delta^{15}N$, and regression coefficients for both carbon and nitrogen across species we reviewed do not support an expectation of developing general, multispecies models for predicting muscle isotope values from fin tissue alone, nor do they support the practice of using simple correction factors or offsets to convert measured fin clip isotopic ratios to expected muscle isotopic ratios, particularly for $\delta^{15}N$. While the average slopes in muscle–fin relationships for $\delta^{13}C$ and $\delta^{15}N$ across studies were close to 1.0, they varied widely from 0.370 to 1.920 for $\delta^{13}C$ and 0.390 to 1.266 for $\delta^{15}N$, and intercepts varied from −17.44 to +21.61 for $\delta^{13}C$ and −3.323 to +9.230 for $\delta^{15}N$. Some of this variation across studies can be attributed to whether samples were adjusted for lipid content, either by extraction or mathematical normalization. However, several studies comparing muscle–fin models across species using the same lipid protocol also found high interspecies variance and concluded that species-specific models were preferable over multispecies models (Busst et al., 2015; Galván et al., 2015; Maitland & Rahel, 2021; Roberts et al., 2022) or that the use of multispecies models is not justified (Larocque et al., 2021; Tronquart et al., 2012; Willis et al., 2013).

Within-species variation in muscle–fin $\Delta\delta^{13}C$, $\Delta\delta^{15}N$, and regression coefficients among populations is also substantial

Table 4. Competing multiple linear regression models ($\Delta AIC_c \leq 2$) for the relationship between muscle and fin tissue $\delta^{13}C$ and $\delta^{15}N$ for juvenile Brown Trout and Mottled Sculpin from the Blue River, Colorado. Covariates included fin $\delta^{13}C$ or $\delta^{15}N$ ($FIN_{13C\ or\ 15N}$), fin C:N ratio ($FIN_{C:N}$), muscle C:N ratio ($MUS_{C:N}$), dry matter content (DM), and season (spring, summer, autumn). Season was modeled categorically, with spring as the reference level and summer and autumn as binary dummy variables; thus, intercepts refer to the mean muscle $\delta^{13}C$ and $\delta^{15}N$ values in spring, and coefficients for summer and autumn are the differences in the mean $\delta^{13}C$ and $\delta^{15}N$ values relative to spring. For comparison, models with only fin $\delta^{13}C$ or $\delta^{15}N$ ($FIN_{13C\ or\ 15N}$) were presented, although they were not competing models. Abbreviations are as follows: Loglik = model log-likelihood, AIC_c = Akaike's information criterion adjusted for small sample sizes, ΔAIC_c = difference in AIC_c between the given model and the most parsimonious model, and ω_i = Akaike weights.

Species	Stable isotope	Model structure	R^2	Loglik	AIC_c	ΔAIC_c	ω_i
Brown Trout	$\delta^{13}C$	$MUS_{13C} = -23.8 - 0.25 \times SUMMER - 0.32 \times AUTUMN + 0.91 \times FIN_{13C} - 0.04 \times DM + 0.24 \times FIN_{C:N}$	0.884	−51.5	117.5	0.00	0.532
		$MUS_{13C} = -24 + 0.82 \times FIN_{13C}$	0.795	115	236.2	118.7	0
	$\delta^{15}N$	$MUS_{15N} = 12.7 + 0.61 \times FIN_{15N} + 0.073 \times DM + 0.050 \times MUS_{C:N}$	0.842	−24.9	60.1	0.00	0.376
		$MUS_{15N} = 12.6 + 0.06 \times SUMMER - 0.16 \times AUTUMN + 0.66 \times FIN_{15N} + 0.066 \times DM + 0.056 \times MUS_{C:N}$	0.843	−23.1	60.8	0.67	0.269
		$MUS_{15N} = 12.7 + 0.61 \times FIN_{15N} - 0.071 \times DM + 0.052 \times MUS_{C:N} - 0.014 \times FIN_{C:N}$	0.841	−24.7	61.7	1.60	0.169
		$MUS_{15N} = 12.67 + 0.63 \times FIN_{15N}$	0.825	−36.77	79.6	19.5	0
Mottled Sculpin	$\delta^{13}C$	$MUS_{13C} = -23.8 - 0.27 \times SUMMER - 0.14 \times AUTUMN + 0.92 \times FIN_{13C} + 0.11 \times FIN_{C:N}$	0.931	−2.86	18.3	0.00	0.466
		$MUS_{13C} = -23.8 - 0.27 \times SUMMER - 0.15 \times AUTUMN + 0.92 \times FIN_{13C} - 0.021 \times DM + 0.15 \times FIN_{C:N}$	0.931	−2.31	19.3	1.09	0.270
		$MUS_{13C} = -23.93 + 0.91 \times FIN_{13C}$	0.911	−25.7	57.5	39.29	0
	$\delta^{15}N$	$MUS_{15N} = 13.4 - 0.13 \times SUMMER + 0.01 \times AUTUMN + 0.66 \times FIN_{15N} + 0.052 \times DM - 0.049 \times MUS_{C:N} + 0.038 \times FIN_{C:N}$	0.888	11.5	−6.0	0.00	0.494
		$MUS_{15N} = 13.4 - 0.11 \times SUMMER + 0.03 \times AUTUMN + 0.65 \times FIN_{15N} + 0.058 \times DM - 0.040 \times MUS_{C:N}$	0.887	9.75	−4.8	1.25	0.265
		$MUS_{15N} = 13.35 + 0.64 \times FIN_{15N}$	0.871	−2.89	11.9	17.95	0

across studies. This implies that local environmental conditions and population characteristics may be important drivers of factors that affect isotopic signatures such as diet, fractionation and turnover, lipid content, and C:N ratios (Boecklen et al., 2011; Shipley & Matich, 2020) and, therefore, muscle–fin relationships. For example, differences in the quantity and quality of food and suitability of thermal conditions affect the balance of anabolic and catabolic processes in the fish and the amount of surplus energy available to allocate to lipid storage (Jobling, 1994).

Populations can also experience changes in environmental conditions that affect the energy status of members, and this could lead to temporal variation in muscle–fin relationships. Relatively few studies have examined temporal variation in muscle–fin relationships, and the results are mixed. Sanderson et al. (2009) found that species-specific relationships for two salmonid species in 21 locations were not different over 3 years, but Finlay et al. (2002) concluded that annual reevaluation of relationships was necessary. We detected an effect of season on muscle–fin relationships, and Hanisch et al. (2010) and Roberts et al. (2022) also reported seasonal changes in relationships. Thus, even population-specific models may perform poorly when applied under different conditions than those under which the models were developed. Differences in energy storage could explain some of the intraspecific and temporal variation in muscle–fin relationships and prompted our interest in determining if fish energy status, as indicated by DM and fin and muscle ratio, could explain some of the variation in muscle–fin relationships.

Incorporating information about the energy status of the Brown Trout and Mottled Sculpin we studied improved the fit of muscle–fin relationships, confirming our hypothesis that fish body condition affects these relationships. The DM was a significant predictor in all four competing models for Brown Trout $\delta^{13}C$ and $\delta^{15}N$ and in three of the four models for Mottled Sculpin $\delta^{13}C$ and $\delta^{15}N$. Muscle C:N ratio, which is assumed to be proportional to lipid content (Logan & Lutcavage, 2008; Post et al., 2007), was also a significant predictor in most of the models. Given that fish energy status, and more specifically lipid content, can explain some of the residual variation in simple linear regressions for muscle–fin relationships and given the disagreement among investigators about how and when to correct tissue samples for lipid content (Tables 2, 3; Arostegui et al., 2019; Logan & Lutcavage, 2008), future studies should consider incorporating information about fish energy status rather than removing it by normalizing tissue isotope values through chemical extraction or mathematical adjustments. Of course, adopting measurements such as whole-body DM or lipid content as predictors defeats the purpose of seeking muscle–fin relationships to alleviate the need for lethal sampling. If the importance of energy status for improving muscle–fin relationships is verified in future studies, then the use of biopsy punches for obtaining nonlethal muscle samples or other nonlethal measures, such as various forms of allometric condition indices, including scaled mass index (Peig & Green, 2009), microwave energy meters (Crossin & Hinch, 2005), and bioelectrical impedance meters (Hartman et al., 2015), could be explored.

Persistent uncertainties and unknowns about muscle–fin relationships suggest that more research is still required before fin isotope ratios can be reliably substituted for muscle without verification. An alternative approach would be to move

away from using fins as proxies for muscle and focus instead on research to allow for the use of fin samples directly in trophic ecology studies. Such efforts could include standardizing fin sampling protocols (see Hayden et al., 2015), seeking better quantification of isotopic turnover time in fins, improving understanding of diet–tissue discrimination factors, and developing accompanying theory for interpretation of fin isotope values for making inferences about trophic ecology. Besides the obvious advantage of using fin sampling to reduce harm, the ability to resample individuals provides a means to address questions about how temporal changes in fish diet, condition, and environment affect values of trophic isotopes in tissues of individuals.

There are a few caveats about our findings. Although the sample sizes in our field study were larger than those of nearly all previous studies we summarized, our investigation was restricted to a single river, in a single year. We would not recommend use of our muscle–fin relationships for other populations of Brown Trout and Mottled Sculpin without verification that the relationships are applicable. We only looked at juvenile Brown Trout, and DM, lipid content, diet, and presumably isotope ratios could be different in adult fish. The mean DM of Brown Trout and Mottled Sculpin in our study was slightly lower than that observed in juvenile Brown Trout in three Scandinavian studies (22.59%; Mortensen, 1985; Jonsson & Jonsson, 1998, 2005) and in Slimy Sculpin (23.8%; Rottiers & Tucker, 1982), suggesting that fish in our study were in slightly poorer condition and therefore lower in lipid than these other populations. Future studies investigating the role of energy status in muscle–fin isotope relationships should include fish over a wider range of DM and condition. Although determining lipid content is more difficult, substituting it as a predictor would be a more direct evaluation of the hypothesis that fish energy status affects the muscle–fin relationship.

In conclusion, muscle–fin isotope relationships are characterized by strong positive correlations. High coefficients of determination in models for converting fin isotopic ratios to muscle limit the prediction error under conditions for which the model was developed. However, when conditions change, model performance can weaken and inferences about diet will be less accurate. Large differences in the slope and intercept for muscle–fin relationships across species and populations of the same species suggest that investigators should be cautious about borrowing muscle–fin models from other studies without some local verification of the applicability of the model. Incorporating additional predictors in muscle–fin relationships, such as measures of energy status, could improve the generality of the models and expand their applicability across studies.

DATA AVAILABILITY

The data sets used and/or analyzed during the current study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

All fish capture, handling, and euthanasia procedures were approved by the Institutional Animal Care and Use Committee at Colorado State University (IACUC protocol number 1677) and followed applicable state regulations (Colorado Parks and Wildlife Aquatic Scientific Collection License Number 1982079811).

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CONFLICTS OF INTEREST

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