Energy Density of Three *Prosopium* Fish Species Endemic to Bear Lake, Utah–Idaho

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Abstract

We used bomb calorimetry to quantify the energy density of three *Prosopium* fish species endemic to Bear Lake, Utah–Idaho, that we collected in 2020–2021: Bear Lake Whitefish *Prosopium abyssicola*, Bonneville Whitefish *Prosopium spilonotus*, and Bonneville Cisco *Prosopium gemmifer*. We found that mean ± standard deviation wet weight energy densities were 6,312 ± 760 J/g for Bear Lake Whitefish; 5,301 ± 778 J/g for Bonneville Whitefish; and 4,743 ± 443 J/g for Bonneville Cisco. We built linear mixed models and found relationships between energy density and dry matter ratio (i.e., ratio of dried weight to wet weight of a fish) for all three species, suggesting that the energy density of future samples collected in Bear Lake could potentially be determined from comparisons between the dried and wet weight of fishes belonging to these species. Our results are useful for future bioenergetics modeling with these three Bear Lake endemic species and potentially with others species in related genera that share similar feeding, behavior, and life-history traits.

Keywords: energy density; U.S. Intermountain West; Bear Lake; *Prosopium*; bioenergetics

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Introduction

Energy density (ED) values provide information on the energetic properties of an organism. These values are useful for evaluating the condition of an individual or population compared with reference values (Pothoven et al. 2006; Johnson et al. 2017) and provide the energetic data needed to complete predation and consumption studies such as bioenergetics modeling efforts (Deslauries et al. 2017). For fishes, determining ED generally involves the collection of whole fish that are dried and ground into a homogenous mixture (for an example of methods, see Glover et al. [2010]), followed by combustion of small subsamples of each fish to determine the energy content. Extrapolation of results can represent "whole fish" ED as a function of wet or dry weight. The equipment required for ED analyses is expensive; thus, as an alternative, it is sometimes possible to use published values from previous studies. A variety of fishes and other organisms have undergone ED analyses (see Cummins and Wuycheck [1971] for an extensive overview); however, researchers and managers must use surrogate values from related species when species-specific values are not available. Although useful and justified in some instances, substitution of ED values can lead to erroneous study results. For example, Johnson et al. (2017) tested generalized ED models for several fishes and showed the cause-and-effect relationship between poor model applicability and skewed bioenergetics consumption estimates for some species.

Lakes and reservoirs in the U.S. Intermountain West region often exhibit low productivity and limited species richness, making management of food web dynamics a high priority for sportfish managers. Bear Lake, Utah–Idaho, is a large (∼28,230-ha) natural lake that provides a popular recreational salmonid fishery (Figure 1). In this system, there are three endemic species in the genus *Prosopium*: Bear Lake Whitefish *Prosopium abyssicola*, Bonneville Whitefish *Prosopium spilonotus*, and Bonneville Cisco *Prosopium gemmifer* (Sigler and Miller 1963; Sigler and Sigler 1987). Within the Utah Wildlife Action Plan (2015), each of these species is at the S1 state level or "critically imperiled" due to their small native distributions (Bear Lake). Consequently, preservation of *Prosopium* populations in Bear Lake is a high conservation priority. In addition, these species are prey for native Bonneville Cutthroat Trout *Oncorhynchus clarkii utah* and introduced Lake Trout *Salvelinus namaycush* (Ruzycki et al. 2001), both of which are popular sport fishes. Because of the recreational importance of Bear Lake to anglers and the conservation importance of Bear Lake Whitefish, Bonneville Whitefish, and Bonneville Cisco, maintaining a balanced food web in this ecosystem has been the focus of several studies. Bioenergetics work conducted in Bear Lake during 1993 and 1994 assessed predation rates on Bear Lake Whitefish, Bonneville Whitefish, Bonneville Cisco, and Bear Lake Sculpin *Cottus extensus* (Ruzycki et al. 2001). Unfortunately, ED values for Bear Lake *Prosopium* species were not available at that time and the authors used surrogate values from species that were within the same subfamily (Coregoninae; Hewett and Johnson 1992). With increasing recreational pressure on the fishery, changing climate, and anthropogenic effects in the Bear Lake drainage, continued monitoring of these species (both as forage and as a conservation priority) is necessary to ensure sustainability of the resource. Relevant, novel ED values for Bear Lake endemic *Prosopium* species are needed for future bioenergetics modeling efforts of the food web in this lake.

The objective of our study was to determine the ED of Bear Lake Whitefish, Bonneville Whitefish, and Bonneville Cisco in Bear Lake. We examined ED in relation to species and three predictor variables: total length (TL, in millimeters), fish wet weight (in grams), and the dried weight of fishes divided by their wet weight (hereafter dry–wet ratio, expressed as a decimal) of each fish. We provide current and species-specific ED values for the forage base of Bear Lake that can be used for future bioenergetics evaluations in this system. More broadly, our results could indicate relationships between ED and predictor variables that may allow for future ED calculation without the need for additional bomb calorimetry analysis.

Methods

We used gill nets and dip nets to collect fishes for bomb calorimetry during 2020 and 2021. We collected Bear Lake Whitefish and Bonneville Whitefish in Bear Lake during a 1-wk period in October 2020 by using American Fisheries Society standard sinking gill nets (appendix A in Bonar et al. [2009]). We placed nets at 5-m-depth increments (15–50 m) throughout Bear Lake. We assigned two sites for each depth, and we fished nets for two nights at each site. We collected Bonneville Cisco in January from shore by using dip nets when individuals moved into shallow, rocky areas to spawn. For each species, we attempted to collect 20 individuals across a range of sizes common to diets of Cutthroat Trout and Lake Trout (<250 mm TL; McConnell et al. 1957; Nielson and Archer 1976). We measured fish for TL and weighed them to the nearest gram in the field to avoid effects of freezing on length, weight, and subsequent dry–wet ratio metrics (Baltasar et al. 2021). We assumed that all fish of each species included in this study were sexually mature (based on TL exceeding what is common for immature fish; Utah Division of Wildlife Resources, unpublished data). Collected fish were in "prespawn" condition (Whitefishes) or "spawn" condition (Bonneville Cisco). We blotted fish dry, individually wrapped them, and froze them for later processing and analysis.

To prepare samples for bomb calorimetry, we thawed fish and cut them into 2.5-cm cubes (Glover et al. 2010). We did not examine gonads for sex determination; thus, we generalized the reported ED values between male and female. We placed cubed samples in foil pans and dried them in an oven set to 60°C (Johnson et al. 2017). Once drying had begun, we followed the methods of Glover et al. (2010) to prepare all samples. In brief, we weighed samples daily while drying until the weight remained constant over two consecutive days (±0.01 g). We ground dried samples to a homogenous mixture by using a commercially available coffee grinder set to the finest grind. We estimated ED by using a semimicro oxygen bomb calorimeter (Parr Instruments, Moline, IL) to combust approximately 0.1–0.2 g of each sample. We analyzed a minimum of two subsamples from each fish; however, we included a third subsample if the first two energy measurements were different by 2.0% or more (Glover et al. 2010). We recorded results as calories per gram (dry weight). We converted all data points to wet weight by multiplying each estimate by the dry–wet ratio of that individual fish (see below). In addition, we converted estimates of calories per gram to joules per gram to match units required for common bioenergetics analyses (Deslauriers et al. 2017).

We used linear regression to evaluate potential relationships between ED and three predictor variables known to relate to energy content of fishes. The predictor variables that we chose were as follows: 1) fish TL (Anthony et al. 2000), 2) fish wet weight (Pothoven et al. 2006), and 3) dry–wet ratio (i.e., dried sample weight/initial wet weight; Pothoven et al. 2006; Glover et al. 2010; Johnson et al. 2017). Given our limited data set (∼20 fish per species) and correlation between predictor variables, we evaluated each predictor variable separately using candidate models. We included quadratic effects for each variable to investigate potential nonlinear relationships with ED (e.g., weight; Pothoven et al. 2006). Within our data set, Bear Lake Whitefish and

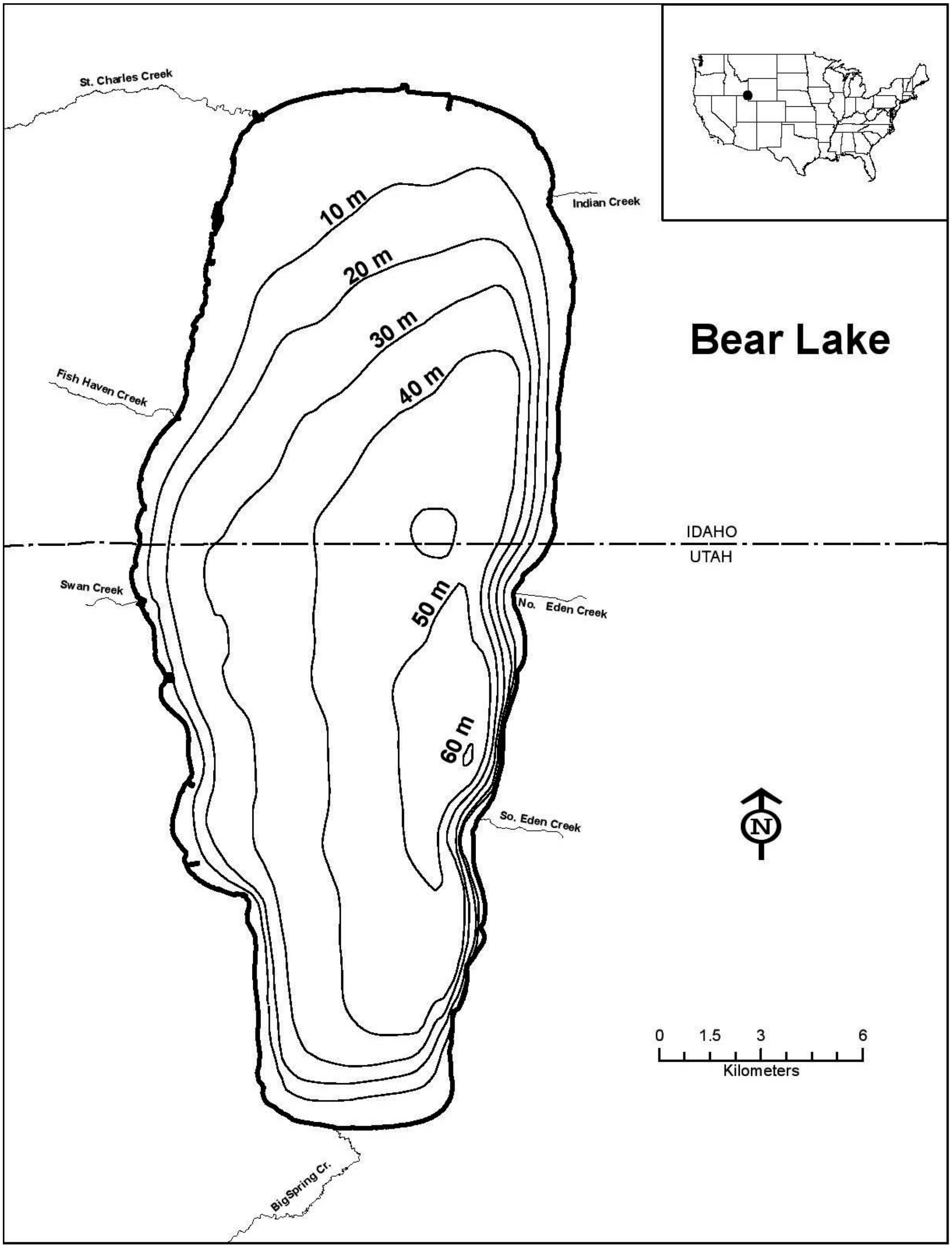

Figure 1. Map of Bear Lake Utah–Idaho, located in the Intermountain West region of the United States, where samples of three *Prosopium* species were collected and analyzed to determine energy density values for each species during 2020–2021.

Bonneville Whitefish shared similar TL, wet weight, and dry–wet ratio distributions. Consequently, we investigated ED relationships of these two closely related species by using the same model (hereafter Whitefish model) and included a species-specific intercept in some candidate models to investigate whether species-specific differences were present or whether ED relationships with predictors could be generalized between the two species. Because Bonneville Cisco has a smaller length and weight range than the other two species, we chose

Table 1. Mean (SD) of raw data determined from three Bear Lake *Prosopium* species collected during October 2020–January 2021 in Bear Lake Utah–Idaho. The Sa. no. column refers to the number of fish per species processed. The Obs. no. column refers to the total number of bomb calorimetry measurements for that species. The J/g column refers to the average wet weight energy density. The dry–wet ratio column refers to the average ratio of dry-to-wet weight of each fish, expressed as a decimal for simplicity. The TL column refers to the average total length of fish samples. The Wt column is the average wet weight of fish samples. Combined Whitefish represents the data set used to develop the Whitefish model for this study (i.e., both species combined).

Species	Sa. no.	Obs. no.	J/g	Dry–wet ratio	TL (mm)	Wt (g)
Bear Lake Whitefish	15	37	6,312 (759.6)	0.2670 (0.02837)	202.7 (23.37)	65.73 (29.40)
Bonneville Whitefish	19	47	5,301 (777.9)	0.2466 (0.03447)	225.8 (28.32)	95.45 (39.94)
Combined Whitefish	34	84	5,746 (916.8)	0.2556 (0.03334)	215.6 (28.55)	82.36 (38.46)
Bonneville Cisco	20	49	4,743 (443.1)	0.2200 (0.01283)	180.4 (12.84)	38.94 (8.467)

to model this species separately (hereafter Cisco model) to avoid making model predictions outside the range of realistic values. We incorporated uncertainty with our bomb calorimetry measurements by including all measurements for each fish (i.e., two to three per fish, as opposed to using a mean value). To control for nonindependence between these individual measurements, we included a random grouping factor (random intercept) for each fish that accounted for the nested nature of these data points.

To select a top model for each of our data sets, we fit candidate models, ranked each, and evaluated the model fit to ensure that linear regression assumptions were met. We fit linear mixed models by using package lme4 (Bates et al. 2015) in program R (version 3.6.3; R Development Core Team 2020). To facilitate model convergence, easier coefficient interpretation, and inclusion of interactive and polynomial terms in some models (Schielzeth 2010), we standardized and centered each continuous variable (TL, wet weight, and dry–wet ratio) to a mean of 0 and standard deviation (SD) of 1. Our candidate model set consisted of 20 models for Whitefish and 7 models for Cisco. We ranked models in each candidate model set by using Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson 2002). We considered a top model to be well supported if ΔAICc differed by more than 2 between the top model and the next-ranked model (Burnham and Anderson 2002). We evaluated the fit of our top models by using marginal and conditional R^2, and we plotted residual points to ensure random distribution of error. Marginal R^2 accounts for variation explained by fixed predictors (e.g., species, TL, wet weight, and dry–wet ratio), whereas conditional R^2 considers both the effect of fixed and random (e.g., fish ID grouping factor) predictors on model fit.

Results

We analyzed data from 15 Bear Lake Whitefish, 19 Bonneville Whitefish, and 20 Bonneville Cisco collected in Bear Lake (Table 1; Data S1, *Supplemental Material*). Average TL, wet weight, and dry–wet ratio were similar for Bear Lake Whitefish and Bonneville Whitefish, but were generally lower for Bonneville Cisco across all variables (Table 1). We ignited multiple subsamples from each fish, for a total sample size of 37, 47, and 49 for Bear Lake Whitefish, Bonneville Whitefish, and Bonneville Cisco, respectively. We found that Bear Lake Whitefish had the highest average ED, followed by Bonneville Whitefish and Bonneville Cisco (Table 1).

Percent dry weight was the best predictor of ED content for each of the three species examined (Tables 2 and 3). Our top-ranked Whitefish model retained terms for dry–wet ratio and a quadratic term for dry–wet ratio, along with a species-specific intercept that interacted with each of the dry–wet ratio variables (Table 4). The resulting equation for our top Whitefish model can be expressed as follows:

$$\begin{aligned} y = \alpha_0 &+ \left(\alpha 1_{\text{spp}} \times (\text{spp})\right) + \left(\beta 1_{\text{dry}} \times (\text{dry})\right) \\ &+ \left(\beta 2_{\text{quad}-\text{dry}} \times (\text{dry}^2)\right) + \left(\text{spp} \times \beta 3_{\text{spp:dry}} \times (\text{dry})\right) \\ &+ \left(\text{spp} \times \beta 4_{\text{spp:quad}-\text{dry}} + (\text{dry}^2)\right) \end{aligned} \tag{1}$$

where *y* is predicted ED, α is the model intercept, spp is a factor where 1 is input to solve for Bonneville Whitefish and 0 is input to solve for Bear Lake Whitefish, β are slopes associated with main effects and species-specific interactions (Table 4), and dry is a standardized variable of dry–wet ratio. Standardization of new values is achieved using the mean and SD calculated in this study. Consequently, a researcher or manager interested in applying our equation to a new data set would calculate dry as follows:

$$\text{dry} = (x - \mu)/\sigma \tag{2}$$

where *x* is the measured value of dry–wet ratio to be standardized, μ is 0.2556, and σ is 0.03334. For Bear Lake Whitefish, the equation is simplified and solved by

$$y = 5,973 + 823.9(\text{dry}) + 70.30(\text{dry}^2) \tag{3}$$

where dry = (*x* – 0.2556)/0.03334.

For Bonneville Whitefish, the species intercept and interactions are included; thus, the equation is simplified and solved by

$$\begin{aligned} y = 5,973 + -463.7 + 823.9(\text{dry}) + 70.30(\text{dry}^2) \\ + -80.40(\text{dry}) + -83.31(\text{dry}^2) \end{aligned} \tag{4}$$

where dry = (*x* – 0.2556)/0.03334.

For our top-ranked Cisco model, we also retained dry–wet ratio and quadratic dry–wet ratio (Table 5). The resulting equation for the Cisco model was as follows:

Table 2. Candidate model set ($n = 20$) used to evaluate energy density relationships for Bear Lake Whitefish *Prosopium abyssicola* and Bonneville Whitefish *Prosopium spilonotus* collected during October 2020 in Bear Lake Utah–Idaho. In each model equation, α_0 is the model intercept, α_{spp} is a species-specific intercept for Bonneville Whitefish, and β_X are slopes for the predictor variables included in each model: TL (mm), wet weight (WT, g), and dry–wet ratio (dry). Slopes associated with quadratic effects of each variable are indicated by quad-x in some equations. In models where α_{spp} is included, it is either an additive effect (α_{spp} +, addition of one parameter) or an interactive effect that varies with included predictors (α_{spp} ×, addition of two or three parameters). Because we collected multiple data points on each fish (two or three bomb calorimetry estimates per sample), we include a grouping factor for each fish sample (μ_{fish}) as a random effect in all model equations. We denote residual error as ε. We present the total number of fixed predictors included in each model (i.e., excludes μ_{fish} or ε) in column *K*. We ranked models using Akaike's Information Criterion corrected for small sample size (AICc), with differences in ΔAICc greater than 2 indicating substantial support for the top-ranked model (Burnham and Anderson 2002). Weight indicates the relative likelihood of each model, relative to the entire model set.

Model equation	Model	K	AICc	ΔAICc	Weight
$y \sim \alpha_0 + \alpha_{spp} \times \beta_{dry} + \beta_{quad\text{-}dry} + \mu_{fish} + \varepsilon$	3	6	1,083.45	0.00	1.00
$y \sim \alpha_0 + \alpha_{spp} \times \beta_{dry} + \mu_{fish} + \varepsilon$	6	4	1,099.09	15.64	0.00
$y \sim \alpha_0 + \alpha_{spp} + \beta_{dry} + \beta_{quad\text{-}dry} + \mu_{fish} + \varepsilon$	9	4	1,104.60	21.16	0.00
$y \sim \alpha_0 + \alpha_{spp} + \beta_{dry} + \mu_{fish} + \varepsilon$	12	3	1,110.32	26.87	0.00
$y \sim \alpha_0 + \beta_{dry} + \beta_{quad\text{-}dry} + \mu_{fish} + \varepsilon$	15	3	1,148.69	65.25	0.00
$y \sim \alpha_0 + \beta_{dry} + \mu_{fish} + \varepsilon$	18	2	1,156.73	73.28	0.00
$y \sim \alpha_0 + \alpha_{spp} \times \beta_{WT} + \beta_{quad\text{-}WT} + \mu_{fish} + \varepsilon$	2	6	1,163.64	80.20	0.00
$y \sim \alpha_0 + \alpha_{spp} \times \beta_{TL} + \beta_{quad\text{-}TL} + \mu_{fish} + \varepsilon$	1	6	1,168.16	84.71	0.00
$y \sim \alpha_0 + \alpha_{spp} + \beta_{WT} + \beta_{quad\text{-}WT} + \mu_{fish} + \varepsilon$	8	4	1,187.06	103.61	0.00
$y \sim \alpha_0 + \alpha_{spp} \times \beta_{WT} + \mu_{fish} + \varepsilon$	5	4	1,188.66	105.22	0.00
$y \sim \alpha_0 + \alpha_{spp} \times \beta_{TL} + \mu_{fish} + \varepsilon$	4	4	1,191.10	107.66	0.00
$y \sim \alpha_0 + \alpha_{spp} + \beta_{TL} + \beta_{quad\text{-}TL} + \mu_{fish} + \varepsilon$	7	4	1,191.24	107.80	0.00
$y \sim \alpha_0 + \alpha_{spp} + \beta_{WT} + \mu_{fish} + \varepsilon$	11	3	1,199.74	116.29	0.00
$y \sim \alpha_0 + \alpha_{spp} + \beta_{TL} + \mu_{fish} + \varepsilon$	10	3	1,202.20	118.76	0.00
$y \sim \alpha_0 + \beta_{WT} + \beta_{quad\text{-}WT} + \mu_{fish} + \varepsilon$	14	3	1,205.52	122.07	0.00
$y \sim \alpha_0 + \beta_{TL} + \beta_{quad\text{-}TL} + \mu_{fish} + \varepsilon$	13	3	1,209.08	125.64	0.00
$y \sim \alpha_0 + \alpha_{spp} + \mu_{fish} + \varepsilon$	19	2	1,214.32	130.87	0.00
$y \sim \alpha_0 + \beta_{WT} + \mu_{fish} + \varepsilon$	17	2	1,217.10	133.65	0.00
$y \sim \alpha_0 + \beta_{TL} + \mu_{fish} + \varepsilon$	16	2	1,219.75	136.31	0.00
$y \sim \alpha_0 + \mu_{fish} + \varepsilon$	Null	1	1,235.41	151.97	0.00

$$y = \alpha_0 + \left(\beta 1_{dry} \times (dry)\right) + \left(\beta 2_{quad-dry} \times (dry^2)\right) \quad (5)$$

where y is predicted ED, α is the model intercept, β are slopes associated with main effects, and dry is a standardized variable of dry–wet ratio, where standardization is achieved using the same equation above with μ as 0.2200 and σ as 0.01283. The equation is simplified and solved by

$$y = 4,742 + 386.9(dry) + 1.770(dry^2) \quad (6)$$

where dry = (x – 0.2200)/0.01283.

For all species, ED increased with dry–wet ratio (Figure 2). We assessed model fit and found marginal and conditional R^2 to be 0.95 and 0.97, respectively, for the Whitefish model. Marginal and conditional R^2 values were 0.79 and 0.92, respectively, for the Cisco model, suggesting a greater amount of unexplained variation

Table 3. Candidate model set ($n = 7$) used to evaluate energy density relationships for Bonneville Cisco *Prosopium gemmifer* collected during January 2021 in Bear Lake Utah–Idaho. In each model equation, α_0 is the model intercept and β_X are slopes for the predictor variables included in each model: total length (TL, mm), wet weight (WT, g), and dry–wet ratio (dry). Slopes associated with quadratic effects of each variable are indicated by quad-x in some equations. Because we collected multiple data points on each fish (two or three bomb calorimetry estimates per sample), we included a grouping factor for each fish sample (μ_{fish}) as a random effect in all model equations. Residual error is denoted ε. We present the total number of fixed predictors included in each model (i.e., excludes μ_{fish} or ε) in column *K*. We ranked models by using Akaike's Information Criterion corrected for small sample size (AICc), with differences in ΔAICc greater than 2 indicating substantial support for the top-ranked model (Burnham and Anderson 2002). Weight indicates the relative likelihood of each model, relative to the entire model set.

Model equation	Model	K	AICc	ΔAICc	Weight
$y \sim \alpha_0 + \beta_{dry} + \beta_{quad\text{-}dry} + \mu_{fish} + \varepsilon$	3	3	623.36	0.00	0.96
$y \sim \alpha_0 + \beta_{dry} + \mu_{fish} + \varepsilon$	6	2	629.49	6.13	0.04
$y \sim \alpha_0 + \beta_{WT} + \beta_{quad\text{-}WT} + \mu_{fish} + \varepsilon$	2	3	655.71	32.35	0.00
$y \sim \alpha_0 + \beta_{TL} + \beta_{quad\text{-}TL} + \mu_{fish} + \varepsilon$	1	3	656.28	32.92	0.00
$y \sim \alpha_0 + \beta_{WT} + \mu_{fish} + \varepsilon$	5	2	664.04	40.67	0.00
$y \sim \alpha_0 + \beta_{TL} + \mu_{fish} + \varepsilon$	4	2	664.42	41.06	0.00
$y \sim \alpha_0 + \mu_{fish} + \varepsilon$	Null	1	673.08	49.72	0.00

Table 4. Coefficient estimates and associated SE for our top model evaluating energy density of Bear Lake Whitefish *Prosopium abyssicola* (model intercept, α_0) and Bonneville Whitefish *Prosopium spilonotus* (species-specific intercept, $\alpha1_{\mathrm{spp}}$) that we collected from Bear Lake, Utah–Idaho, during October 2020. We standardized the continuous main effects for dry ratio ($\beta1_{\mathrm{dry}}$) and quadratic dry ratio ($\beta2_{\mathrm{dry}}$) and interactions ($\beta3_{\mathrm{spp:dry}}$ and $\beta4_{\mathrm{spp:quad\text{-}dry}}$) to a mean of 0 and SD of 1.

Coefficient	Estimate	SE
α_0	5,973	58.15
$\alpha1_{\mathrm{spp}}$	−463.6	78.69
$\beta1_{\mathrm{dry}}$	823.9	54.33
$\beta2_{\mathrm{quad\text{-}dry}}$	70.30	43.78
$\beta3_{\mathrm{spp:dry}}$	−80.40	69.19
$\beta4_{\mathrm{spp:quad\text{-}dry}}$	−83.31	50.06

attributed to our random effect for individual fish ID in Bonneville Cisco. Residual plots indicated random distribution of residual error and suggested that our model structure adequately fit our data.

Discussion

We found the ED of three Bear Lake endemic species to be related to the ratio of dry matter retained in samples. Our study provides data that are useful for future management of Bear Lake, particularly in the context of future diet and bioenergetics work for predatory species (Cutthroat Trout and Lake Trout) that rely on *Prosopium* spp. as their main forage. Although species-specific values are often best, our study may also be useful for inference on ED values of additional *Prosopium* spp. in other large oligotrophic lakes where fish may have similar diets and experience similar environmental (e.g., thermal) conditions to those encountered in Bear Lake. For example, ED values for *Prosopium* spp. in the Intermountain West are lacking (but see Lance and Baxter [2001] for Mountain Whitefish *Prosopium williamsoni*, reported as 5.3 kcal/g dry weight or approximately 6,187 J/g wet weight). Our study may provide more realistic surrogates for these species, relative to those derived from *Coregonus* spp. that are more common to the literature and report a range of values depending on species, location, and size. For example, ED values for Bloaters *Coregonus hoyi* ranged from approximately 5,000 to 7,000 J/g (Pothoven et al. 2012) and Lake Whitefish *Coregonus clupeaformis* averaged 5,000–8,000 J/g (but were variable depending on location; Pothoven et al. 2006) and in some cases, up to approximately 12,000 J/g (Rottiers and Tucker 1982). In additional evaluations, Fraley et al. (2021) found that diadromous *Coregonus* spp. had ED values ranging from approximately 8,000 to 12,000 J/g (e.g., Bering Cisco *Coregonus laurettae* and Least Cisco *Coregonus sardinella*). We found that ED values were generally lower in our study, particularly for Bonneville Cisco, an important prey item in Bear Lake. Assuming a standard bioenergetics approach, use of inflated ED values to represent Bear Lake endemics would likely result in an underestimate of consumption of the three species examined during our study.

Table 5. Coefficient estimates and associated SE for our top model evaluating energy density of Bonneville Cisco *Prosopium gemmifer* that we collected from Bear Lake, Utah–Idaho, during January 2021. We standardized the continuous main effects for dry ratio ($\beta1_{\mathrm{dry}}$) and quadratic dry ratio ($\beta2_{\mathrm{quad\text{-}dry}}$) to a mean of 0 and SD of 1.

Coefficient	Estimate	SE
α_0	4,742	49.43
$\beta1_{\mathrm{dry}}$	386.9	38.94
$\beta2_{\mathrm{quad\text{-}dry}}$	1.770	29.94

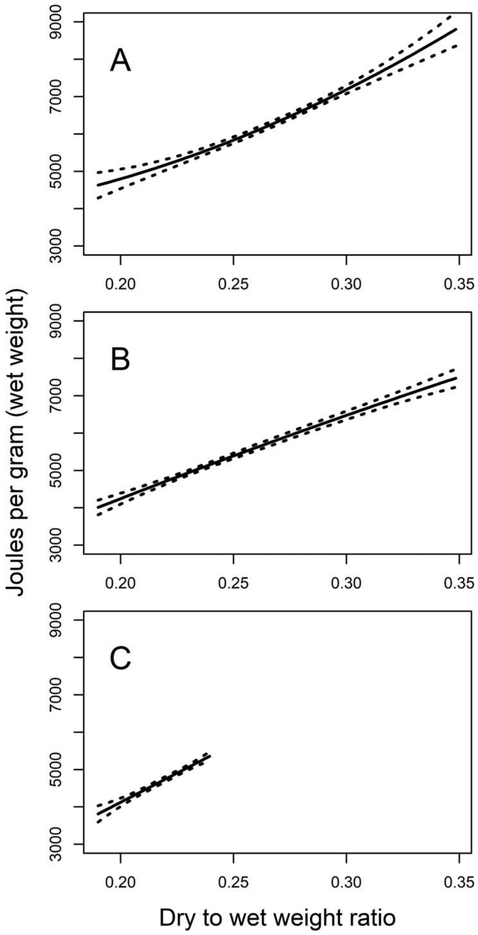

Figure 2. Predicted relationship between dry weight as a ratio of wet weight (expressed as a decimal for simplicity) and energy density (joules per gram) for three *Prosopium* species in Bear Lake, Utah–Idaho: (**A**) Bear Lake Whitefish *Prosopium abyssicola*, (**B**) Bonneville Whitefish *Prosopium spilonotus*, and (**C**) Bonneville Cisco *Prosopium gemmifer*. We collected Bear Lake Whitefish and Bonneville Whitefish during October 2020. We collected Bonneville Cisco during January 2021. Dashed lines indicate 95% confidence intervals around the predictions. Model predictions for each species are limited to dry–wet ratios encountered during this study.

The relationship between dry–wet ratio and energy content is well supported and has useful implications for future ED work in Bear Lake. Measures of dry–wet ratio serve as a surrogate for fat storage (Hartman and Brandt

1995), with higher dry–wet ratio values generally relating to lower water content and thus higher lipid content in fish tissue (Flath and Diana 1985). Studies document several generalized models between ED and dry–wet ratio (e.g., Hartman and Brandt 1995; Schreckenbach et al. 2001) that perform well in subsequent evaluations (e.g., Johnson et al. 2017). Bomb calorimetry is time intensive and costly (Hartman and Brandt 1995), but it is relatively easy and inexpensive for fishery researchers and managers to collect, weigh, and dry samples to achieve estimates of dry–wet ratio. Consequently, predictive models that relate dry–wet ratio to ED are useful alternatives for determining ED values for new species or across a range of seasons for previously analyzed species. However, careful consideration and evaluation should be given to the limitations of this approach (e.g., Johnson et al. 2017), and bomb calorimetry is likely needed when the species of interest differs in terms of diet, environmental conditions, or life history relative to available reference species.

Interestingly, our Whitefish model suggested species-specific differences in ED between Bear Lake Whitefish and Bonneville Whitefish, two closely related species. Differences in diet between the two species (Tolentino and Thompson 2004) may be responsible for differences in energy content. For example, Bear Lake Whitefish diets consist predominantly of ostracods, whereas Bonneville Whitefish in the size range that we examined have mixed diets consisting of high proportions of clams, along with terrestrial insects, chironomids, and ostracods (Tolentino and Thompson 2004). Pothoven et al. (2006) speculated that high consumption of mollusks resulted in lower ED of Lake Whitefish *Coregonus clupeaformis* in Lake Huron than Lake Michigan due to increased energy expenditure needed to feed on prey with indigestible shells. Similar diet mechanisms between Bonneville Whitefish and clams may contribute to lower average EDs.

Differences in depth use between Bear Lake Whitefish and Bonneville Whitefish may also contribute to observed ED and size differences. Bear Lake Whitefish occupy deeper portions of the lake below the thermocline (Tolentino and Thompson 2004) and therefore experience more consistent temperature regimes year-round. Correlation between water temperature and fish metabolism is well established (Volkoff and Ronnestad 2020), and more consistent thermal conditions as well as a documented selection of benthic habitat below the thermocline could allow the Bear Lake Whitefish to feed at optimal levels, albeit in a habitat with less food availability (Thompson 2003). However, Bear Lake Whitefish can store fat year-round while residing in these deeper habitats, while being exposed to a lower predation risk by Cutthroat Trout and Lake Trout (Kennedy 2005; Kennedy et al. 2006). By contrast, Bonneville Whitefish typically occupy warmer, more productive waters with a higher food availability at or near the thermocline when the lake is thermally stratified (Sigler and Miller 1963). This may contribute to a higher metabolism and faster growth, but they are exposed to a higher predation risk (Kennedy 2005). For example, Bonneville Whitefish are able to reach lengths greater than 600 mm TL, relative to Bear Lake Whitefish, which rarely exceed 250 mm TL (Tolentino and Thompson 2004). Consequently, energy acquired by Bonneville Whitefish may primarily be for growth under increased predation pressure and satisfy the higher metabolic requirements associated with warmer temperatures.

We found Bonneville Cisco to have the lowest average ED among the three species studied, likely relating to its diet and lower trophic position in the Bear Lake food web. Bonneville Cisco feed primarily on zooplankton and play an important role in converting this prey to fish biomass, in turn, providing forage for Cutthroat Trout and Lake Trout (Lentz 1986). The Utah Division of Wildlife Resources annually collects diet data for both Cutthroat Trout and Lake Trout (Nielson and Archer 1976; Tolentino 2008). These data show that both species' diets were mainly composed of fish, with a strong preference for Bonneville Cisco and Bear Lake Sculpin (the latter species was not part of this study). In addition, Whitefish (Bear Lake and Bonneville species) comprise an important, although less frequent, part of both Cutthroat Trout and Lake Trout diets. Zooplankton, although numerous, have lower ED values ($\sim$3,000 J/g) than larger and more diverse prey items found in the diets of Bonneville Whitefish and Bear Lake Whitefish (Cummins and Wuycheck 1971; Tolentino and Thompson 2004). We speculate that lower energy intake associated with zooplankton consumption relates to the lower Bonneville Cisco ED measurements found during this study.

Our study is limited to a single season and year of sample collection, and it is unknown whether temporal differences in ED occur among the three species that we studied in Bear Lake. Future research could address seasonal differences in ED and evaluate the usefulness of the predictive dry–wet ratio models developed during this study across a range of seasons. There may be a relationship between seasonal differences in ED and shifts in diet (Pothoven et al. 2006; Herbst et al. 2013) or reproductive status in mature individuals (Vondracek et al. 1996; Pedersen and Hislop 2001). Differences among years may occur because of potentially changing environmental conditions in Bear Lake (e.g., warmer water temperatures, less winter ice cover or duration of ice cover) that could affect the metabolic requirements of fishes (Ficke et al. 2007). We believe that any potential seasonal ED differences would be minimal for Bear Lake Whitefish and Bonneville Cisco given the relatively consistent diets year-round (Tolentino and Thompson 2004; Kennedy 2005; Kennedy et al. 2006); however, ED could still vary as a function of temperature and metabolism under a consistent diet. The diet of Bonneville Whitefish has greater seasonal variation (mentioned above) and may be best suited for an initial evaluation of potential seasonal differences in ED within Bear Lake. For all three species, we did not examine the effect of maturity, sex, and time to spawning and they may be useful as part of another evaluation in future studies of Bear Lake endemic fishes. Bear Lake Whitefish, Bonneville Whitefish, and Bonneville Cisco represent three species of conservation concern in Utah; thus, periodic monitoring of ED values may provide additional information about the condition of Bear Lake's endemic Whitefish populations (Johnson et al. 2017) that can be used to monitor and maintain native biodiversity in this unique lake ecosystem.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content of functionality of any supplemental material. Queries should be directed to the corresponding author.

Data S1. Energy density samples indexed to fish ID and associated predictor variables for three species of *Prosopium* collected in Bear Lake, Utah–Idaho, as part of an energy density study conducted in 2020–2021. We collected fishes from October 2020 to January 2021 (Bear Lake Whitefish *Prosopium abyssicola*, Bonneville Whitefish *Prosopium spilonotus*, and Bonneville Cisco *Prosopium gemmifer*). We then dried them and analyzed subsamples from each fish to determine energy density content (joules per gram, wet weight) by using bomb calorimetry. We recorded multiple bomb calorimetry samples for each fish to obtain a more accurate approximation of average energy density. We used covariates collected in the field (total length [T] and weight [Wt]) and determined in the lab (dry–wet ratio, dried weight of fish divided by the wet weight of the fish recorded in the field) to build linear models that investigated relationships between each predictor variable and energy density measurements. Column headers within the spreadsheet are column A, Sample ID = unique identification for each energy density measurement; column B, Fish = identification code for each fish collected from Bear Lake, which consists of a species code and unique ID; column C, Spp = species code; column D, Collection_month = sample collection month; column E, Year = year of collection of the sample; column F, Lake = source of the samples, with all samples collected in Bear Lake, Utah–Idaho; column G, Joules_wet = energy content of sample determined by bomb calorimetry, where all measurements refer to joules per gram wet weight; column H, TL_field = total length of the sample measured during collection, with units in millimeters; column I, Wt_field = total weight of the fish measured during collection, with units in grams; and column J, per_DryWeight_field = weight of the dried sample, divided by its initial wet weight measured in the field.

Available: https://doi.org/10.3996/JFWM-22-020.S1 (15 KB XLSX)

Reference S1. McConnell WJ, Clark WJ, Sigler WF. 1957. Bear Lake, its fish and fishing. Utah State Department of Fish and Game, Idaho Department of Fish and Game, Utah State Agricultural College.

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Reference S2. Nielson BR, Archer DA. 1976. Bear Lake cutthroat trout fisheries enhancement program: performance report 1968–1975. Salt Lake City: Utah State Department of Natural Resources, Division of Wildlife Resources. Publication 76-5.

Available: https://doi.org/10.3996/JFWM-22-020.S3 (5.421 MB PDF)

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