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Energy Density and Dry Matter Content in Fish: New Observations and an Evaluation of Some Empirical Models

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Abstract

Energy density (ED) is an indicator of fish nutritional status, physiological status, and fitness. Estimates of ED of predators and prey are also needed for bioenergetics modeling, but direct measurements of ED are difficult to obtain. Hence, investigators often borrow published values from the same species or related species. Alternatively, models have been developed that predict ED from dry matter content (DM). The scarcity of published ED values makes data borrowing and the generality of predictive modeling difficult to evaluate. We report new ED measurements derived from bomb calorimetry for six freshwater fish species (Arctic Char *Salvelinus alpinus*, Brown Trout *Salmo trutta*, kokanee *Oncorhynchus nerka*, Lake Trout *Salvelinus namaycush*, Rainbow Trout *O. mykiss*, and White Sucker *Catostomus commersonii*) and compared them to previously published data. We used our data to validate existing ED:DM models and to fit new ones. We also quantified bias that could result from borrowing inappropriate ED values for bioenergetics modeling. We collected a range of fish sizes from two reservoirs of differing productivity and measured whole-body ED (wet-mass basis) and DM. Our data substantially increase the range of ED data for Arctic Char, kokanee, and White Suckers. Two multispecies ED:DM models predicted the ED of our samples accurately (mean root mean square error [RMSE] < 500 J/g), even at the extremes for the range of prediction where data used for model development were limited. Taxon-specific models performed less well (mean RMSE = 775 J/g), and some appeared highly biased (RMSE 956−1,900 J/g). Bioenergetics model simulations showed that Lake Trout prey consumption could be overestimated by as much as 22% when using borrowed EDs for Lake Trout and their prey, but prey consumption estimates fell within ±2% of observed when ED was predicted from DM. When direct measures of ED are unattainable, measurement of DM and prediction of ED from one of the published multispecies models offer a practical and accurate method for bioenergetics modeling and other studies requiring information on fish energy content.

Knowledge of the energy density (ED) of fishes is important from basic and applied perspectives. Energy storage is an important strategy for fishes because many experience stochastic food availability (Armstrong and Schindler 2013) and seasonal and ontogenetic changes in energy requirements related to survival, migration, and reproduction. Withstanding periods of starvation and surviving winters in temperate climates can depend on the level of energy reserves (Post and Evans 1989; Post and Parkinson 2001). The choice to migrate may depend on body condition (Jonsson and Jonsson 1993; Brodersen et al. 2008). Spawning may be contingent on females obtaining sufficient energy reserves (Thorpe 1994; Jorgenson et al. 2006). Climate change may increase metabolic costs and reduce energy reserves, with implications for growth, reproduction, and survival (Ficke et al. 2007). Thus, ED is an important indicator of the nutritional status, physiological status, and fitness of fishes.

Knowledge of ED is also required in predation studies because of its relationship to prey quality and because energy

is the common currency used to convert biomass of prey consumed to biomass of consumer growth in bioenergetics models (Jobling 1994; Hanson et al. 1997). Managing multi-faceted recreational fisheries (Pate et al. 2014), quantifying the effects of introduced predators on native fish (Ruzycki et al. 2003), planning the recovery of native fish (Sorel et al. 2016), and achieving an understanding of food web dynamics (Schoen et al. 2015) have all relied on accurate bioenergetics-derived estimates of predation. Because bioenergetics-derived estimates of prey consumption and contaminant bioaccumulation are sensitive to the EDs of predator and prey (Trudel and Rasmussen 2006; Breck 2008), accurate whole-body ED data are essential for applying bioenergetics models to a variety of fisheries management problems.

Energy density of fish is frequently estimated indirectly from proximate composition analysis (Brett 1995). Although proximate composition analysis can provide more detailed information on body condition than overall ED, this approach usually employs standard conversion factors for the EDs of lipid and protein, which may not be accurate (Brett 1995; Vollenweider et al. 2011). A few comparisons of ED calculated from proximate analysis with direct measurements obtained by bomb calorimetry showed that the former approach is subject to error, partly due to variation in the ED of lipids (Craig et al. 1978; Weatherley and Gill 1983; Schloesser and Fabrizio 2015). Thus, direct measurement of ED by bomb calorimetry is more reliable than ED estimation from proximate composition analysis unless the energy equivalents of body components are well known (Hartman and Brandt 1995).

Relatively few direct measurements of fish ED exist in the primary literature. This may have arisen in part because bomb calorimetry is time consuming, and lethal sampling and specialized equipment for sample preparation and analysis are required. In bomb calorimetry, a dried, pulverized, homogenized sample is combusted in a closed vessel that is pressurized with pure oxygen (Cummins and Wuycheck 1971). The heat of combustion is measured precisely to compute the energy content of the sample through well-known physical relationships (Parr Instrument Company 2013). The methodology is labor intensive and may be difficult for managers to justify, particularly when whole-body estimates of large fishes are required (Glover et al. 2010). Consequently, there is a dearth—and, for some species, a complete absence—of whole-body ED measurements derived from bomb calorimetry in the literature.

Alternatively, ED can be estimated from models that relate dry matter content (DM, %; sometimes called "percent dry weight") to ED (Hartman and Brandt 1995). This is possible because proximate analysis of fish body composition has demonstrated that in many fish, ED is inversely related to body water content (Love 1970; Breck 2008) and therefore is positively related to DM. Because determination of DM is much easier than measurement of ED, models that predict ED

from DM are an appealing alternative to calorimetry. However, limited empirical data on ED for many species of fish leave some uncertainty about the reliability of the modeling approach. Additional ED data could be used to evaluate the generality of ED:DM models.

In bioenergetics modeling (where ED values for the consumer and its prey are essential) and in some food web and fish nutrition studies, it is common practice for investigators to borrow published values for the same species or a closely related species as a surrogate for direct observations or estimates from an ED:DM model (Hansen et al. 1993; Hanson et al. 1997; Glover et al. 2010). For example, in an informal literature search with Google Scholar, we found that a single paper, Cummins and Wuycheck (1971), has been cited as a source for ED data in at least 95 articles published by the American Fisheries Society. More empirical ED data are needed to assess the variability across systems and among taxa before the propriety of borrowing ED values from the literature can be evaluated.

In this study, we measured whole-body DM and ED in six fish species found in coldwater systems across North America: the Arctic Char *Salvelinus alpinus*, Brown Trout *Salmo trutta*, kokanee (lacustrine Sockeye Salmon *Oncorhynchus nerka*), Lake Trout *Salvelinus namaycush*, Rainbow Trout *O. mykiss*, and White Sucker *Catostomus commersonii*. Relatively little published calorimetry data were available for wild individuals of any of these species outside of their native range, and no such data were available from populations in western North America, prompting our study. We used our measurements to (1) compare with existing ED data for each species, (2) evaluate whether ED varied with fish size and among water bodies, (3) validate predictions from models that estimate ED from DM (Hartman and Brandt 1995; Schreckenbach et al. 2001), and (4) evaluate the potential implications of borrowing ED estimates versus predicting ED from DM for the accuracy of bioenergetics model predictions of piscivore consumptive demand.

METHODS

Fish collection.—All fish capture, handling, and euthanasia procedures were approved by the Institutional Animal Care and Use Committee (Protocol Number 09-1408A) at Colorado State University and followed applicable state and federal regulations.

Fish for DM and ED determinations were collected as part of food web studies at two reservoirs west of the Continental Divide in the southern Rocky Mountains of Colorado. Blue Mesa Reservoir is one of the most productive coldwater fisheries in the state (Johnson and Martinez 2000; Pate et al. 2014), whereas Lake Dillon is less productive, in part because of tight nutrient controls in the watershed (Lewis et al. 1984; Olsen 2014). We anticipated that these systems would provide a wide range of fish ED values due to their contrasts in trophic

state, fish growth rates, thermal conditions, and prey density. Brown Trout, kokanee, Rainbow Trout, and White Suckers were collected from both reservoirs. Arctic Char were only present at Lake Dillon, and Lake Trout were only present in Blue Mesa Reservoir. None of the study species is native to western Colorado. Kokanee were introduced to Colorado from Flathead Lake, Montana, in 1952 and were first stocked into Blue Mesa Reservoir in 1966 and Lake Dillon in 1967 (Wiltzius 1974, 1985). Arctic Char were first stocked into Lake Dillon in 1990 and were obtained from Sun Valley Trout Farms, British Columbia, Canada, which collected the eggs from an anadromous stock in Nauyuk Lake, Northwest Territories, Canada (Olsen 2014). White Suckers were first detected in western Colorado during 1926 and are suspected to have been moved by bait anglers from east of the Continental Divide, where White Suckers are native (Wiltzius 1978). Lake Trout, Brown Trout, and Rainbow Trout were first brought to the state prior to 1900, and the source populations are unknown (Wiltzius 1985).

To collect the broadest possible size range, we sampled fish by using multimesh gill nets during spring, summer, and fall in 3 years (2011, 2012, and 2014) over a variety of depths (2–40 m). We measured each fish for TL (mm) and wet mass (WW; g) in the field and then stored whole fish individually in plastic bags at –20°C until they could be prepared for ED determination at the Fisheries Ecology Laboratory, Colorado State University.

Sample preparation.—We removed stomach contents before cutting partially frozen fish into 1.5-cm cubes, and all viscera and fluids were retained. This material was dried at 60°C for at least 72 h to a constant weight (Lantry and O'Gorman 2007). Drying of whole fish provides less-variable results than subsampling homogenized tissue prior to drying (Glover et al. 2010). Dried samples were then homogenized with a food processor. We computed DM as

$$DM(\%) = \frac{dry\ mass(g)}{WW(g)} \times 100. \quad (1)$$

Energy density.—Energy density (J/g dry mass) was measured with a Parr Instrument Company Model 1261 isoperibol bomb calorimeter maintained by the Animal Sciences Department at Colorado State University. A subsample of dried material (1.0 ± 0.1 g) from each fish was compressed into a pellet and placed in the combustion chamber, which was then charged to 30 atmospheres with pure oxygen and combusted. We combusted at least three subsamples from each fish, and we only used data from subsamples that underwent complete combustion (determined by the presence of pellet residue in the combustion chamber or a faulty fuse wire). Replicate measurements were averaged for each fish. A benzoic acid standard (Gundry et al. 1969) was used to verify accuracy and precision of the calorimeter. The mean difference between expected and measured EDs of the standard was 97.6 J/g (SD = 172.6 J/g) or 0.37%. Standards

were combusted at the beginning and end of each session as well as after every tenth fish sample. Energy density of each dry subsample was converted to ED on a WW basis by using the water content determined for the same fish.

Species-specific relationships between ED and WW were investigated using linear regression. We tested whether the ED of a particular species differed between the two reservoirs by using ANCOVA that accounted for lake-specific differences in fish mass. We used linear regression to fit ED versus DM relationships at the species level, as in Hartman and Brandt (1995). We evaluated the normality of residuals and fit a power function to the combined species data to compare with Hartman and Brandt (1995) and Schreckenbach et al. (2001). The level of statistical significance was set to an α of 0.05, and this value was adjusted with a Bonferroni correction for multiple comparisons when applicable.

We gathered ED values for the six species in our study from the literature to compare with our findings. The search was performed with Google Scholar, and the publication date was unconstrained. We included only studies that were published in the primary literature and that measured the whole-body EDs of wild fish directly by bomb calorimetry. We excluded laboratory studies because captive fish can have different body composition and EDs than wild fish (Simpkins et al. 2003; Copeland and Carline 2004; Morley et al. 2012). Because bioenergetics models require ED inputs for predator and prey to be on a whole-body, WW basis, and since piscivores consume prey in this form, we included only studies in which measurements were of whole fish (viscera included) and were reported on a WW basis or studies for which values could be computed from reported water content.

Dry matter relationships.—We validated predictions from published models that used DM to predict whole-body ED by comparing our measured ED values with those predicted by the models using our measured DM values. Hartman and Brandt (1995) presented 39 ED:DM models for individual fish species, families, and orders and a combined model for all species studied ($n > 34$). Their study combined some original data with published values and included freshwater and coastal marine taxa from North America. Schreckenbach et al. (2001) presented a multispecies model developed from 578 samples of 17 freshwater fish species sampled in Germany.

We assessed agreement between our observed ED values and predictions from the multispecies ED:DM model of Hartman and Brandt (1995) as

$$ED = 45.29 \times DM^{1.507}, \quad (2)$$

where ED is whole-body energy density (J/g WW) and DM is whole-body dry matter content (%). We also assessed agreement between our observed ED values and predictions from the multispecies ED:DM model of Schreckenbach et al. (2001),

$$ED = 0.0253 \times DM^{1.6783}, \tag{3}$$

where ED is whole-body energy density (MJ/kg WW) and DM is whole-body dry matter content (%).

We also compared our observed ED values to predictions from taxon-specific models (lowest taxonomic level available) reported by Hartman and Brandt (1995), which were all simple linear functions. Species-specific models were reported for Lake Trout, Rainbow Trout, and White Suckers:

$$\text{Lake Trout ED} = -3{,}809 + (397.9 \times DM), \tag{4}$$

$$\text{Rainbow Trout ED} = -2{,}457 + (347.8 \times DM), \tag{5}$$

$$\text{White Sucker ED} = 232 + (143.0 \times DM). \tag{6}$$

Species-specific models were not available for Arctic Char, kokanee, or Brown Trout. Therefore, we compared our observed ED values for these species to predictions from Hartman and Brandt's (1995) model for the family Salmonidae:

$$\text{Salmonid ED} = -3{,}632 + (386.7 \times DM). \tag{7}$$

We used two approaches to evaluate the existing ED:DM models. We used root mean square error (RMSE) for each fish species to quantify the overall agreement of model-predicted and observed values using the equation

$$\text{RMSE} = \sqrt{\frac{\sum \left[(ED_o - ED_p)^2 \right]}{n}}, \tag{8}$$

where ED_o is the observed ED value; ED_p is the value predicted by the model; and n is sample size. We also plotted the predicted versus observed values to look for evidence of systematic errors in model predictions, and we tested whether the relationship between predicted and observed values had a slope different from 1 and an intercept different from 0.

Bioenergetics modeling.—When applying bioenergetics models to fisheries management questions, investigators have two options for specifying ED values as model input in the absence of direct measures for key predators and prey: (1) measuring in situ DM and converting to ED by using species-specific or multispecies ED:DM models as outlined above; or (2) borrowing ED values from the same or similar species and size-groups of predator and prey from the literature. Option 1 should be less biased than option 2 or some combination thereof, but this presumption depends on the magnitude and direction of error in alternative ED predictions and the nature of the study questions. Regardless of how EDs are specified, bias may be inconsequential if small or if the conclusions from model simulations are robust to uncertainty in model inputs.

To identify when the method of alternative ED selection is important, we evaluated the potential implications of relying on ED:DM models versus borrowed ED values for the accuracy of bioenergetics model predictions of piscivore consumptive demand within the context of a real-world fisheries management problem. Using each method, we simulated and compared rates of kokanee consumption by Lake Trout in Blue Mesa Reservoir (Pate et al. 2014). Here, biologists manage for coexistence between naturally reproducing Lake Trout and hatchery-supported kokanee, the production of which can be limited when Lake Trout predation rates are too high. Thus, accurate estimates of Lake Trout consumptive demand are necessary to determine the level of population regulation that is needed to maintain stability in what can be a volatile predator–prey interaction (Martinez et al. 2009; Pate et al. 2014). Pate et al. (2014) used field data on diet, growth, distribution, spawning, abundance, and age structure to model Lake Trout predation by using direct estimates of ED (present study). Reconstructing these model simulations using EDs predicted from DM or borrowed from the literature provided an opportunity to assess the relative accuracy of these alternative approaches.

Construction of the bioenergetics model and model inputs are described in detail by Pate et al. (2014). In brief, annual per-capita consumption rates of kokanee and other non-focal prey, including Rainbow Trout, Yellow Perch *Perca flavescens*, crayfish, and other small invertebrates, were estimated for Lake Trout of ages 3–25. However, we restricted this analysis to age-15 and younger fish (i.e., 98% of the population) to avoid artificially inflating bias from uncertainty in the EDs and DM of older fish whose body sizes were at least two-fold greater than the maximum WW associated with an ED–DM observation in our data set. Age-specific simulations incorporated ontogenetic shifts in diet and ED (Appendix Tables A.1–A.3). Age-10 and older Lake Trout were mostly piscivorous, and kokanee represented over 90% of their diet by weight. The mean length of kokanee consumed by Lake Trout was equivalent to 33% of predator length. Because Lake Trout consumed larger kokanee as they grew, the ED of kokanee was adjusted for each age-class of Lake Trout. These adjustments were not needed for non-focal prey. Age-specific, per-capita biomasses of kokanee consumed were converted to numbers consumed based on the same prey length-to-predator length relationship. Numerical, per-capita consumption rates were scaled up to the population level based on estimates of Lake Trout mortality, age structure, and abundance.

First, we simulated the bioenergetics model of Pate et al. (2014), which incorporated direct measures of ED for Lake Trout and all prey, to generate a baseline for assessing accuracy. Baseline ED inputs for Lake Trout (Table A.2) were specified using the linear relationship between ED and WW mentioned previously. Paired ED:WW observations for small kokanee (i.e., <50 g) eaten by young Lake Trout in

Blue Mesa Reservoir were underrepresented in the corresponding relationship developed for kokanee. Thus, the fitted intercept may have been inflated, leading to overestimation of the EDs of small kokanee (see Results). To remain conservative and avoid artificially inflating the potential bias in estimates of per-capita and population-level consumption when specifying ED inputs using DM or by borrowing from the literature, we specified the baseline ED inputs for kokanee by using a linear relationship between ED and TL instead of WW because this relationship (1) generated ED estimates that were very close to those from the ED:WW relationship for large kokanee; and (2) generated ED estimates that resembled those from the mass-dependent equation of Beauchamp et al. (1989), the relationship used in the borrowed scenario (see below), for small kokanee (Table A.3).

Next, we reformulated baseline ED inputs by converting corresponding estimates of DM for Lake Trout and fish prey to EDs using the multispecies models of Hartman and Brandt (1995) and Schreckenbach et al. (2001), and we then re-implemented the simulations. Because we could not convert DM to ED for crayfish and other small invertebrates by using the multispecies models, we used the borrowed values for invertebrates in this scenario (see below). Lastly, we simulated the scenario in which all ED values were borrowed from the literature (Tables A.1–A.3). We examined previous studies of Lake Trout consumptive demand to guide our selection of borrowed ED values (Yule and Luecke 1993; Vidergar 2000; Ruzycki et al. 2003; Schoen et al. 2012). The sources of selected values were consistent across studies. We used the mass-dependent equations of Stewart et al. (1983) and Beauchamp et al. (1989) to estimate the ED dynamics of Lake Trout and kokanee, respectively (Tables A.2, A.3). The ED for Rainbow Trout was calculated from the mass-dependent equation of Rand et al. (1993) using the reconstructed mean lengths and weights of Rainbow Trout found in the stomach contents of Lake Trout (TL = 185 mm, WW = 59 g; n = 106; W. M. Pate, unpublished data). The ED for Yellow Perch was borrowed from Kitchell et al. (1977), the ED for crayfish was obtained from Stein and Murphy (1976), and the ED for other small invertebrates was the average across multiple studies (Baldwin et al. 2000, 2003; Beauchamp and Van Tassel 2001; Schoen et al. 2012; Hansen et al. 2013; Table A.1).

The bioenergetics simulations were designed to provide a minimum expectation for the potential degree of bias in estimated consumption demand on focal prey when direct measures of ED are lacking, thus forcing investigators to specify ED inputs by using alternative methods. However, predator diet composition, predator EDs, and focal and non-focal prey EDs can interact to influence the magnitude and direction of bias in complex ways. Therefore, we conducted a sensitivity analysis to identify the specific ED inputs that strongly influenced rates of kokanee consumption by Lake Trout in the

baseline model. We sequentially and individually increased (reflecting overestimation by the alternative selection approach) and decreased (reflecting underestimation) the predator and prey EDs by 20% and computed the percent change in resulting per-capita and population-level consumption demand. Lastly, we used results from the sensitivity analysis to help identify when the method of alternative ED selection is important for bioenergetics modeling studies of piscivore consumptive demand.

RESULTS

Energy Density Measurements

We measured the EDs of 299 fish, including juveniles and adults from each of the six species (Figure 1). The average within-fish coefficient of variation of ED measurements was 1.4%. Observed ED ranged from a low of 2,713 J/g (White Sucker) to a high of 14,837 J/g (kokanee). Kokanee showed the greatest range of EDs (3,773−14,837 J/g; Table 1). Arctic Char had the lowest range of EDs (3,486−7,475 J/g). Mean ED was greatest for kokanee (9,807 J/g) and Lake Trout (7,755 J/g) and was consistently lower for Rainbow Trout (5,648 J/g), White Suckers (5,585 J/g), Brown Trout (5,502 J/g), and Arctic Char (5,388 J/g). Energy density increased with fish mass in Brown Trout from Lake Dillon ($P < 0.001$) and in kokanee ($P < 0.001$), Lake Trout ($P < 0.001$), and White Suckers ($P < 0.001$) from Blue Mesa Reservoir (Figure 1). After accounting for differences in fish mass, the EDs of kokanee ($P = 0.0015$), Rainbow Trout ($P = 0.0008$), and White Sucker ($P = 0.0068$) were significantly greater in Blue Mesa Reservoir than in Lake Dillon, but no difference was observed between reservoirs for Brown Trout ($P = 0.4123$).

We found few direct measurements of wet-mass ED for wild-caught individuals of our six species in the literature. Several studies reported the EDs of Arctic Char in laboratories or hatcheries, but we found no published values for wild Arctic Char. We found no ED values for wild kokanee either, but Brett (1983) reported values of 4,971−7,766 J/g for wild Sockeye Salmon (Table 1). The literature-reported ED ranges for Brown Trout (3,920−7,720 J/g) and Rainbow Trout (3,806–6,870 J/g) were similar to the ranges we observed for these species (Table 1). The reported ED range for Lake Trout from the Laurentian Great Lakes was slightly less than we observed, but the range was greater if the siscowet morphotype of Lake Trout was included (Table 1). Cummins and Wuycheck (1971) reported a single ED value of 7,524 J/g for White Suckers, but they did not report the method of determination, so we excluded this value from our comparisons. One other study (Bryan et al. 1996) reported calorimetry-based values for White Suckers (3,586−3,694 J/g). Overall, the range of EDs we observed for each species examined was greater than that reported in the literature, including data from the studies used by Hartman and Brandt (1995) to develop species-specific ED:DM relationships. Literature values comprised only 29% of the range we observed for kokanee and 2%
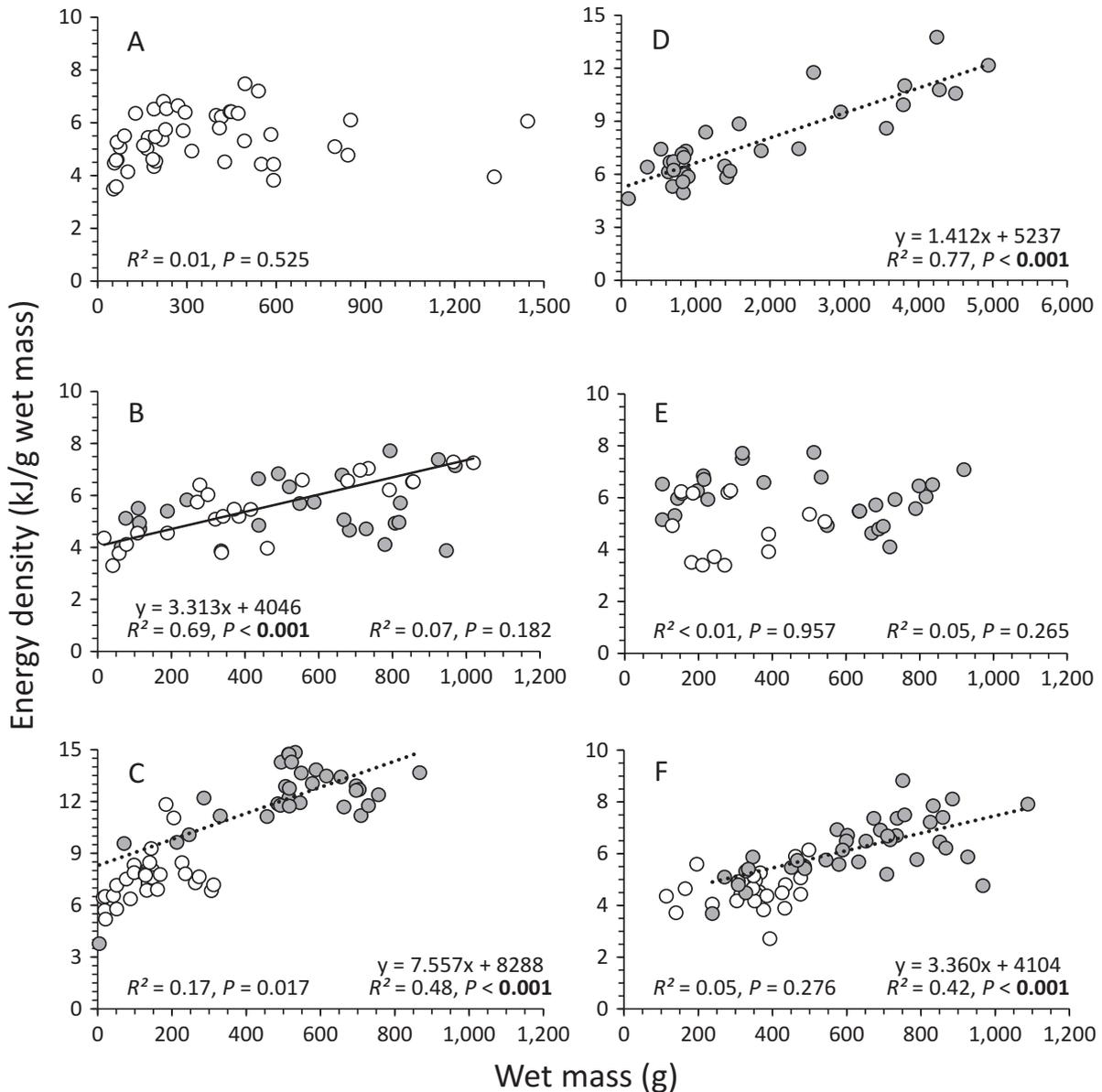
FIGURE 1. Measured energy densities of **(A)** Arctic Char, **(B)** Brown Trout, **(C)** kokanee, **(D)** Lake Trout, **(E)** Rainbow Trout, and **(F)** White Suckers from Blue Mesa Reservoir (shaded symbols, dotted line) and Lake Dillon (open symbols, solid line). Regression equations (left = Lake Dillon; right = Blue Mesa Reservoir) are in units of joules per gram (y) and grams (x). Significant P-values are shown in bold ($\alpha = 0.05$, adjusted for multiple comparisons). Note the difference in axis scales.

of the range we observed for White Suckers. Most of our measurements that were outside the reported range were higher than the previously reported maximum values.

Dry Matter : Energy Density Relationships

Dry matter content averaged 27.1% (SD = 5.9%) and ranged from a low of 15.5% (393-g White Sucker) to a high of 44.6% (588-g kokanee). Energy density was strongly related to DM in each species ($r^2 \geq 0.876$, $P < 0.0001$; Table 2). As was also found

by Hartman and Brandt (1995), the residuals of the linear model with all species combined ($n = 299$) indicated that $\log_{10}$ transformation was required. The transformed model for all species combined,

$$ED = 32.678 \times DM^{1.604}, \qquad (9)$$

had an r^2 of 0.955, and the residuals were normally distributed. This model was very similar to the multispecies models

TABLE 1. Whole-body energy density of 299 fish sampled from Blue Mesa Reservoir and Lake Dillon, Colorado, and literature values from studies of whole fish sampled from the wild and determined by bomb calorimetry.

| | | | Present study | | | | | | Literature | | | | |
| | | | | Energy density (J/g) | | | | | Wet mass (g), | | Energy density (J/g) | | |
Taxon	n	Wet mass (g)		Mean	SD	Range		n	TL (mm), or age	Mean	SD	Range	Source[a]
Arctic Char	45	53–1,445		5,388	987	3,486–7,475		–	–	–	–	–	–
Brown Trout	50	17–1,019		5,502	1,142	3,302–7,720		149	51–750 g	6,398	694	3,920–7,720	1, 2
Kokanee	68	4.2–867		9,736	2,934	3,773–14,837		–	–	–	–	–	–
Sockeye Salmon	–	–		–	–	–		32	1–2,270 g	6,684	787	4,971–7,766	3
Lake Trout	32	94–4,940		7,755	2,313	4,624–13,763		177	35–5,500 g	9,252	1,574	4,221–11,460	4, 5
Siscowet Lake Trout	–	–		–	–	–		68	156–7,500 g	10,789	2,802	5,025–17,216	5
Rainbow Trout	41	102–920		5,648	1,146	3,396–7,742		48	Age 0–3+	4,747	805	3,806–6,870	6, 7
White Sucker	63	114–1,088		5,585	1,265	2,713–8,826		9	79–119 mm	3,223	146	3,586–3,694	6

[a] Sources: (1) Lien (1978); (2) Pizzul et al. (2009); (3) Brett (1983); (4) Rottiers and Tucker (1982); (5) Johnson et al. (1999); (6) Bryan et al. (1996); and (7) Lowery and Beauchamp (2015).

TABLE 2. Models for estimating energy density (ED; J/g wet mass) from dry matter content (DM; %) in fish collected from two Colorado reservoirs ($P <$ 0.0001 for each model). All models are of the form ED = $a + (b \times$ DM), except the salmonid (family-level) and combined-species models, which are of the form ED = $a \times$ DM^b (a and b = empirically derived constants).

Taxon	r^2	n	a	b
Arctic Char	0.908	45	–2,831.2	347.4
Brown Trout	0.876	51	–2,514.6	330.0
Kokanee	0.921	67	–6,551.1	475.1
Lake Trout	0.979	32	–4,165.1	401.8
Rainbow Trout	0.928	41	–2,886.6	348.9
White Sucker	0.962	63	–3,945.4	378.0
Salmonidae	0.958	236	36.548	1.574
Combined species	0.955	299	32.678	1.604

reported by Hartman and Brandt (1995) and Schreckenbach et al. (2001; Figure 2).

The multispecies models of Hartman and Brandt (1995) and Schreckenbach et al. (2001) both performed reasonably well at predicting EDs across the range of our DM measurements for each species (Figure 3; Table 3). The mean RMSE across species was 435 J/g for the Schreckenbach et al. (2001) model and 448 J/g for the Hartman and Brandt (1995) model, and neither model had consistently higher RMSE across species (Table 3). The greatest difference in RMSE between the models was for White Suckers (RMSE of the Schreckenbach et al. [2001] model was 33% lower) and Arctic Char (RMSE of the Hartman and Brandt [1995] model was 26% lower). The

FIGURE 3. Observed energy density (ED) compared to the ED values predicted by the combined-species models of Hartman and Brandt (1995; open circles) and Schreckenbach et al. (2001; shaded squares). Species analyzed were (A) Arctic Char, (B) Brown Trout, (C) kokanee, (D) Lake Trout, (E) Rainbow Trout, and (F) White Sucker. Note the difference in axis scales. The diagonal represents a 1:1 line.

difference in RMSE between models was lowest for Brown Trout (RMSE of the Hartman and Brandt [1995] model was 4% lower). Predictions from both models were unbiased except those generated by the Hartman and Brandt (1995) model when applied to kokanee and White Suckers (Table 3).

None of the taxon-specific models of Hartman and Brandt (1995) fit our data as well as their multispecies model and, in most cases, the model of Schreckenbach et al. (2001; Table 3; Figure 4). The mean RMSE of the taxon-specific models was 774 J/g. There was large, systematic bias in predictions from the Hartman and Brandt (1995) species-specific model for White Suckers (Table 3; Figure 4), but the sample size in that study was only five fish. Bias was also evident in the salmonid model's predictions for kokanee, which tended to underestimate the EDs of small and large kokanee (Figure 4), indicating that a simple linear model may not be appropriate for this species.

Bioenergetics Modeling

Bioenergetics model predictions for the per-capita consumption rate of kokanee (number/year) by Lake Trout varied

FIGURE 2. Combined-species models of energy density (ED) and dry matter content (DM) from Hartman and Brandt (1995; equation 2: ED = 45.29 × DM$^{1.507}$), Schreckenbach et al. (2001; equation 3: ED = 0.0253 × DM$^{1.6783}$), and the present study (equation 9: ED = 32.678 × DM$^{1.604}$).

TABLE 3. Error (root mean square error [RMSE]) and bias (*P*-values of tests to determine whether the relationship between predicted and observed values had intercepts different from 0 [β_0] and slopes different from 1 [β_1]) of predictions from the combined-species models of Schreckenbach et al. (2001) and Hartman and Brandt (1995) and taxon-specific models of Hartman and Brandt (1995; family-level [Salmonidae] model for Arctic Char, Brown Trout, and kokanee; species-specific models for Lake Trout, Rainbow Trout, and White Suckers) applied to measured dry matter content and energy density data from two Colorado reservoirs. Asterisks denote significant differences; α was adjusted for multiple comparisons.

Species	Schreckenbach et al. (2001) combined model			Hartman and Brandt (1995) combined model			Hartman and Brandt (1995) taxon-specific models		
	RMSE	β_0	β_1	RMSE	β_0	β_1	RMSE	β_0	β_1
Arctic Char	374.6	0.749	0.207	296.1	0.013	0.008	340.8	0.834	0.786
Brown Trout	410.9	0.970	0.755	395.0	0.044	0.078	510.7	0.727	0.621
Kokanee	747.2	0.007	0.003	920.4	<0.0001*	<0.0001*	965.6	<0.0001*	<0.0001*
Lake Trout	450.9	0.003	0.009	377.3	0.573	0.174	404.0	0.029	0.242
Rainbow Trout	364.5	0.884	0.548	307.0	0.036	0.029	502.5	0.001	0.072
White Sucker	263.2	0.006	0.133	393.4	<0.0001*	<0.0001*	1,923.8	<0.0001*	<0.0001*
Mean	435.2			448.2			774.5		
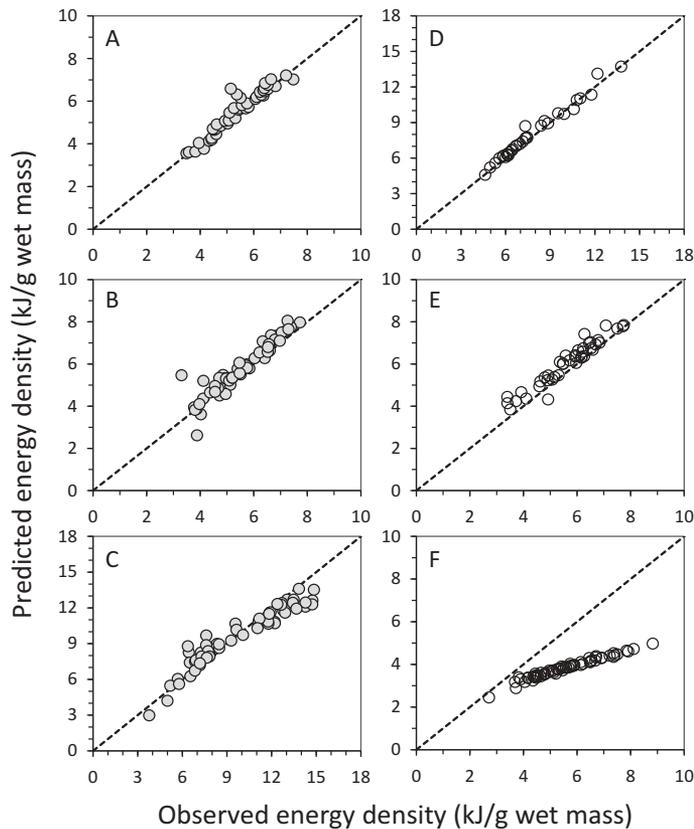
FIGURE 4. Observed energy density (ED) compared to the ED values predicted by the taxon-specific models of Hartman and Brandt (1995). Species analyzed were **(A)** Arctic Char (family-level [Salmonidae] model), **(B)** Brown Trout (family-level model), **(C)** kokanee (family-level model), **(D)** Lake Trout (species-level model), **(E)** Rainbow Trout (species-level model), and **(F)** White Sucker (species-level model). Note the difference in axis scales. The diagonal represents a 1:1 line.

by age-class and showed little deviation from the baseline model after predator and prey EDs were predicted from DM using the multispecies models of Hartman and Brandt (1995) and Schreckenbach et al. (2001). Conversely, per-capita consumption rates were overestimated when simulating ED values borrowed from the literature (Figure 5a, b). This outcome was driven by contradictory directional error in the literature-based ED predictions for Lake Trout and kokanee; contradictory error was nonexistent or less extensive within corresponding predictions from the Hartman and Brandt (1995) model and the Schreckenbach et al. (2001) model (Figure 5c). The mass-dependent equation from Stewart et al. (1983) overestimated EDs for most age-classes of Lake Trout in Blue Mesa Reservoir (by 48−2,879 J/g), while the equation from Beauchamp et al. (1989) underestimated the EDs of kokanee eaten by Lake Trout (by 927−4,271 J/g), thus amplifying the bias in consumption rates. Bias was greatest for age-classes of Lake Trout that consumed over 90% kokanee (Figure 5b). Deviations between baseline and borrowed EDs for non-focal fish prey were less extensive, and these fish also contributed less to the diets of Lake Trout (Table A.1). Similar patterns emerged after scaling up to population-level consumption demand, but error was less than that observed at the per-capita level. Estimates of population-level consumption decreased by 1.13% for the Hartman and Brandt (1995) model, increased by 0.81% for the Schreckenbach et al. (2001) model, and increased by 22.09% when predator and prey ED values were borrowed (Figure 5d).

The sensitivity analysis indicated that kokanee ED, followed by Lake Trout ED, had the greatest influence on the focal prey consumption rate in the baseline bioenergetics model (Table 4). Overestimation of Lake Trout ED by 20% corresponded to an approximately 7% increase in per-capita and population-level consumption, whereas underestimation
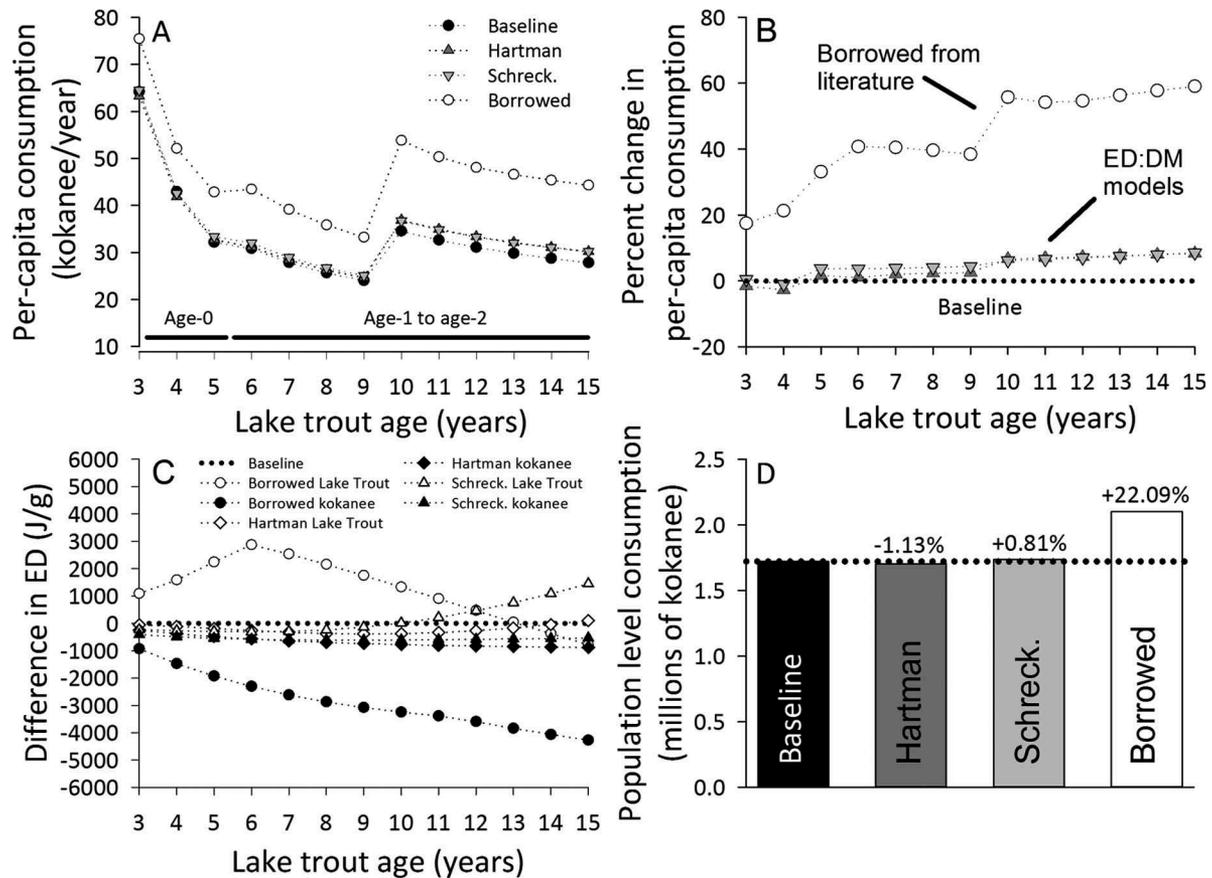
FIGURE 5. **(A)** Annual per-capita consumption rates of kokanee estimated from a bioenergetics model for different age-classes of Lake Trout in Blue Mesa Reservoir, Colorado, under the different energy density (ED) selection approaches, **(B)** percent changes in per-capita consumption from the baseline simulation for each ED selection approach, **(C)** differences between the selected and baseline EDs averaged across the start and end of the 1-year bioenergetics simulation for Lake Trout and kokanee prey, and **(D)** estimates of population-level consumption demand on kokanee under each ED selection approach. Solid black lines in panel A indicate the typical age-classes of kokanee consumed by different age-classes of Lake Trout. Values above each bar in panel D indicate the percent change from the baseline simulation. "Hartman" represents the approach of converting dry matter content to ED by using the multispecies model of Hartman and Brandt (1995); "Schreck." represents the same approach but with the multispecies model of Schreckenbach et al. (2001); and "borrowed" represents the case in which all EDs were taken from the literature.

of Lake Trout ED corresponded to a decrease in consumption of similar magnitude. The magnitude and direction of resulting bias from overestimating or underestimating ED were greater and reversed for kokanee. Thus, the overestimation of predator ED or prey ED while underestimating the other created contradictory directional error that amplified bias in consumption demand, whereas overestimating both or underestimating both created countervailing directional error that partially offset bias. For the latter case, the error in Lake Trout ED had to be two- to threefold greater than error in kokanee ED to fully offset bias in per-capita consumption rate. In general, 20% changes to the ED of non-focal prey had a negligible influence on resulting per-capita and population-level consumption of focal prey. However, because Yellow Perch constituted about 20–40% of the diet for Lake Trout younger than age 10 (the most abundant age-classes in the population), 20% changes to Yellow Perch ED for these age-classes influenced per-capita

and population-level consumption to a similar extent as Lake Trout ED (Table 4).

DISCUSSION

Although our work provides important new information on the EDs of the six fish species in our study, investigators should be cautious about borrowing ED data from our systems or other systems. We showed that the range of ED values for a species can be great (as high as 10,000 J/g in the case of kokanee and Lake Trout). We also found that the EDs of some species differed between our two systems and that ED varied with body size in some cases. Simulations demonstrated that borrowing inappropriate ED estimates for use in bioenergetics models can result in substantial errors in estimated consumption and inappropriate management conclusions. More empirical studies of ED would further our understanding of the

TABLE 4. Results from the sensitivity analysis evaluating the relative influence of overestimating or underestimating the energy density (ED) of Lake Trout and different prey by 20% on the per-capita and population-level rates of kokanee consumption by different age-classes of Lake Trout in the baseline bioenergetics model of Pate et al. (2014).

Altered ED input	Percent change in consumption of kokanee (number/year) by Lake Trout						
	Age 3	Age 4	Age 6	Age 9	Age 12	Age 15	Population level
Overestimation by 20%							
Lake Trout	6.20	5.92	6.74	7.19	7.54	7.88	6.15
Kokanee	–12.28	–11.10	–10.86	–11.43	–16.61	–16.62	–11.79
Rainbow Trout	–0.78	–1.19	–2.15	–1.97	–0.15	–0.14	–1.10
Yellow Perch	–4.55	–5.12	–5.58	–5.13	–0.30	–0.28	–4.82
Crayfish	–0.81	–1.24	–0.47	–0.43	–0.14	–0.14	–0.85
Small invertebrates	–0.52	–0.56	–0.08	–0.08	–0.00001	–0.00001	–0.45
Underestimation by 20%							
Lake Trout	–6.27	–5.97	–6.75	–7.17	–7.52	–7.86	–6.20
Kokanee	16.36	14.33	13.92	14.87	24.94	24.97	15.53
Rainbow Trout	0.79	1.22	2.25	2.05	0.15	0.14	1.13
Yellow Perch	5.02	5.72	6.29	5.72	0.30	0.28	5.35
Crayfish	0.82	1.27	0.48	0.44	0.14	0.14	0.87
Small invertebrates	0.53	0.57	0.08	0.08	–0.00001	–0.00001	0.46

factors that drive variation in ED and would provide more specific guidance on the factors that must be evaluated to minimize potential error when it is necessary to borrow ED values from other studies. In the meantime, we found that ED can be predicted relatively accurately from DM measurements, which are substantially easier to obtain than EDs from bomb calorimetry or proximate composition analysis.

We report the first calorimetry-based, whole-body ED estimates on a WW basis for wild Arctic Char—albeit for an unusual population well outside the species' native range. Given the diversity of life history types and the circumpolar distribution of Arctic Char (Johnson and Burns 1984), empirical data from other locations are needed to produce generalizations about expected EDs for the species. We also report the first ED measurements for kokanee on a WW basis. Historically, studies requiring EDs for kokanee have borrowed values for Sockeye Salmon (Brett 1983). We showed that the EDs of some kokanee can be almost twice as high as the maximum values reported for Sockeye Salmon. The range we observed suggests that (1) kokanee can attain extremely high EDs, which can make them particularly beneficial to their predators; and (2) borrowing ED data from Brett's (1983) Sockeye Salmon study may not be appropriate for some size-classes or age-classes of kokanee. We also observed a much greater range of EDs in White Suckers than has been reported previously, perhaps because our study included more individuals over a greater range of fish sizes. Our data suggest that the EDs of White Suckers can be similar to those of salmonids (excluding kokanee and Lake Trout) from the same system. White Suckers commonly co-occur with trout, so accurate ED data are needed to use bioenergetics models to estimate consumptive demand of piscivores that feed on catostomids and salmonids (e.g., Yule and Luecke 1993).

Ontogenetic changes in fish body composition (often an increase in the lipid fraction as the fish grow) are common (Johnson et al. 1999; Wuenschel et al. 2006; Harter et al. 2013). This suggests that for some species, ED varies with body size, and the use of a fixed ED from the literature will not accurately represent ED in a size- or age-structured population. In our study, EDs increased with body size in Brown Trout, kokanee, Lake Trout, and White Suckers. Thus, bioenergetics models for these species should consider incorporating mass-dependent EDs of the consumer and prey. Models for Sockeye Salmon (which are routinely used to model kokanee; Beauchamp et al. 1989) and Lake Trout (Stewart et al. 1983) do so, but we found that the slope of the mass dependency was higher for kokanee and lower for Lake Trout in our study (see bioenergetics implications below). Thus, site-specific data on the mass dependency of ED may be required in bioenergetics modeling of these species. In the future, investigators could conduct pilot studies employing ED:DM models before deciding whether site- and mass-specific EDs are required for a particular application. Additional studies investigating the relationship between ED and body size over a wide range of fish sizes could facilitate development of more general ED:WW functions.

We expected to find a strong relationship between ED and DM because previous work with a wide variety of species (Hartman and Brandt 1995; Schreckenbach et al. 2001) had reported high correlations ($r > 0.97$). However, we were surprised by the extent to which our multispecies model was similar to previously reported models, despite the fact that the

other models included many different freshwater, anadromous, and marine species from North America and Europe. The concordance of multispecies models developed for different sets of species suggests strong generality in the ED:DM relationship in fishes. Similarly, strong relationships between ED and DM have been shown for diverse invertebrate taxa (r^2 = 0.96; James et al. 2012), and Ciancio et al. (2007) developed a single predictive model (r^2 = 0.93) for marine and freshwater fishes, insects, crustaceans, mollusks, and annelids. Clearly, DM is useful for predicting ED in many aggregated taxa. Depending on the accuracy and precision needed for the question at hand, more taxon-specific models may be required.

Both the Hartman and Brandt (1995) and Schreckenbach et al. (2001) multispecies models applied to data from a single species had a mean RMSE less than 500 J/g (about 7% of the grand mean ED of 6,728 J/g). Error exceeded 1,500 J/g in some individuals. Bias was evident in predictions from Hartman and Brandt's (1995) combined-species model when applied to kokanee and White Suckers. This suggests that there may be differences in the ED:DM relationship for some species and that species-specific models may be more accurate for them. However, counter to expectation, the predictions from Hartman and Brandt's (1995) taxon-specific models always had greater error than predictions from their multispecies model, and predictions with the salmonid (family-level) and White Sucker models were biased. The bias in predictions from the Hartman and Brandt (1995) model for White Suckers strongly suggests an error in the reported model, which could have been due to the small sample size in the empirical study (n = 5). Overall, the poorer performance of taxon-specific models may be attributable to the smaller sample sizes and potentially fewer locations and seasons represented in studies at the species, family, or even order level (Hartman and Brandt 1995). Methodological differences (e.g., wet weights measured before versus after freezing; freezing the fish in water or not) could also have contributed to the lack of fit in some cases (Crane et al. 2016). Thus, current taxon-specific models may not accurately represent the range of EDs and DM exhibited by the taxon. For the six species in our study, the use of the multispecies ED:DM model from either Hartman and Brandt (1995) or Schreckenbach et al. (2001) is preferable to use of the previously published taxon-specific models. More ED measurements from diverse systems are needed to improve taxon-specific ED:DM models.

The bioenergetics simulations showed that predicting ED from DM by using the multispecies models of Hartman and Brandt (1995) and Schreckenbach et al. (2001) is a viable alternative for specifying ED inputs for bioenergetics models in the absence of direct measures of ED. Investigators run the risk of introducing considerable bias into estimates of per-capita consumption rate of focal prey that can propagate to the population level when borrowing ED inputs from the literature for large-bodied predators that selectively feed on large-bodied prey. Contradictory directional errors in the literature-based predictions for Lake Trout ED and kokanee ED combined with the high proportion of kokanee in the diets of Lake Trout were the primary drivers of bias observed in the borrowed ED scenario. However, overestimation observed at the population level was less than expected based on departures from the baseline model observed at the per-capita level. Inaccuracies observed at the per-capita level were tempered by mortality and age structure when scaling to the population level (i.e., overestimation was greatest for age-classes of Lake Trout with the lowest relative abundance in the population). Therefore, inference from studies interested in population-level effects is potentially less sensitive to bias arising from borrowed EDs than from studies where per-capita rates are of interest.

The sensitivity analysis indicated that the diet proportions of focal versus non-focal prey and the direction of error (overestimation versus underestimation) in alternative ED predictions for predator and prey can influence the consumption rates of focal prey for different age-classes of the predator in complex ways. For the Blue Mesa Reservoir example modeled here, bias was driven mostly by error in kokanee ED and less so by non-focal prey for all age-classes of Lake Trout but was amplified by contradictory directional error in Lake Trout ED. It is possible for errors in alternative ED inputs for predator and prey to offset each other by chance. According to results from the sensitivity analysis, however, error in Lake Trout ED would have had to be two- to threefold greater than error in kokanee ED to fully offset bias for different age-classes of predator. Thus, regardless of whether errors in alternative ED predictions happen to counteract or contradict, investigators should anticipate some level of bias when borrowing ED values for large-bodied prey that (1) fall outside the size range or geographic range of previously reported information for that species or a similar species and (2) constitute the majority of the predator's diet. For these situations, in situ measures of DM could be used to specify ED inputs or (at a minimum) to verify borrowed ED values for prey by sampling a few individuals across a range of body sizes if an accurate estimate of piscivore consumptive demand is necessary to achieve management objectives and if calorimetry is not possible. For small-bodied, non-focal prey that constitute less than 10% of the diet, accurate estimates of ED appear less critical, and borrowing values is probably sufficient for these prey groups. Overall, results from the bioenergetics simulations and sensitivity analysis indicate that the more site-specific ED data are used in model applications, the lower are the chances of developing inappropriate management conclusions.

In summary, our data showed that ED varies considerably across species, among locations, and in some cases, with body size. We also demonstrated that consumption estimates from bioenergetics models are sensitive to the EDs of both the consumer and the prey, and substantial errors can arise from borrowing inaccurate ED values. Before borrowing ED values

from other studies, investigators should (1) evaluate whether the environmental and demographic characteristics of their study system are comparable to those of the source of the borrowed values and (2) consider some verification by direct measurement. When direct measures of ED are unattainable, then the measurement of DM and prediction of ED from one of the published multispecies models constitute a practical and accurate method for bioenergetics modeling and other studies requiring information on fish energy content.

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REFERENCES

Armstrong, J. B., and D. E. Schindler. 2013. Excess digestive capacity in predators reflects a life of feast and famine. Nature 476:84−88.

Baldwin, C. M., D. A. Beauchamp, and J. J. Van Tassell. 2000. Bioenergetic assessment of temporal food supply and consumption demand by salmonids in the Strawberry Reservoir food web. Transactions of the American Fisheries Society 129:429−450.

Baldwin, C. M., J. G. McLellan, M. C. Polacek, and K. Underwood. 2003. Walleye predation on hatchery releases of kokanees and Rainbow Trout in Lake Roosevelt, Washington. North American Journal of Fisheries Management 22:660−676.

Beauchamp, D. A., D. J. Stewart, and G. L. Thomas. 1989. Corroboration of a bioenergetics model for Sockeye Salmon. Transactions of the American Fisheries Society 118:597−607.

Beauchamp, D. A., and J. J. Van Tassell. 2001. Modeling seasonal trophic interactions of adfluvial Bull Trout in Lake Billy Chinook, Oregon. Transactions of the American Fisheries Society 130:204−216.

Breck, J. E. 2008. Enhancing bioenergetics models to account for dynamic changes in fish body composition and energy density. Transactions of the American Fisheries Society 137:340−356.

Brett, J. R. 1983. Life energetics of Sockeye Salmon, Oncorhynchus nerka. Pages 29−63 in W. P. Aspey and S. I. Lustik, editors. Behavioral energetics: vertebrate costs of survival. Ohio State University Press, Columbus.

Brett, J. R. 1995. Energetics. Pages 3–68 in C. Groot, L. Margolis, and W. C. Clarke, editors. Physiological ecology of Pacific salmon. University of British Columbia Press, Vancouver.

Brodersen, J., P. A. Nilsson, L.-A. Hansson, C. Skov, and C. Brönmark. 2008. Condition-dependent individual decision-making determines cyprinid partial migration. Ecology 89:1195−1200.

Bryan, S. D., C. A. Soupir, W. G. Duffy, and C. E. Freiburger. 1996. Caloric densities of three predatory fishes and their prey in Lake Oahe, South Dakota. Journal of Freshwater Ecology 11:153−161.

Ciancio, J. E., M. A. Pascual, and D. A. Beauchamp. 2007. Energy density of Patagonian aquatic organisms and empirical predictions based on water content. Transactions of the American Fisheries Society 136:1415 −1422.

Copeland, T., and R. F. Carline. 2004. Relationship of lipid content to size and condition in Walleye fingerlings from natural and aquaculture environments. North American Journal of Aquaculture 66:237–342.

Craig, J. F., M. J. Kenley, and J. F. Talling. 1978. Comparative estimations of the energy content of fish tissue from bomb calorimetry, wet oxidation and proximate analysis. Freshwater Biology 8:585−590.

Crane, D. P., C. C. Killhourhy, and M. D. Clapsadl. 2016. Effects of three frozen storage methods on wet weight of fish. Fisheries Research 175:142–147.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitteilungen Internationale Vereinigung fur Theoretische und Angewandte Limnologie 18.

Ficke, A. D., C. A. Myrick, and L. J. Hansen. 2007. Potential impacts of global climate change on freshwater fisheries. Reviews in Fish Biology and Fisheries 17:51−613.

Glover, D., D. R. Devries, R. A. Wright, and D. A. Davis. 2010. Sample preparation techniques for determination of fish energy density via bomb calorimetry: an evaluation using Largemouth Bass. Transactions of the American Fisheries Society 139:671−675.

Gundry, H. A., D. Harrop, A. J. Head, and G. B. Lewis. 1969. Thermodynamic properties of organic oxygen compounds 21: enthalpies of combustion of benzoic acid, pentan-1-ol, octan-1-ol, and hexadecan-1-ol. Journal of Chemical Thermodynamics 1:321−332.

Hansen, A. G., D. A. Beauchamp, and C. M. Baldwin. 2013. Environmental constraints on piscivory: insights from linking ultrasonic telemetry to a visual foraging model for Cutthroat Trout. Transactions of the American Fisheries Society 142:300−316.

Hansen, M. J., D. Boisclair, S. B Brandt, S. W. Hewett, J. F. Kitchell, M. C. Lucas, and J. J. Ney. 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here? Transactions of the American Fisheries Society 122:1019–1030.

Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin Sea Grant Institute, Publication WISCU-T-97-001, Madison.

Harter, B. B., K. H. Elliott, G. J. Divoky, and G. K. Davorn. 2013. Arctic Cod (Boreogadus saida) as prey: fish length–energetics relationships in the Beaufort Sea and Hudson Bay. Arctic 66:191−196.

Hartman, K. J., and S. B. Brandt. 1995. Estimating energy density of fish. Transactions of the American Fisheries Society 124:347−355.

James, D. A., I. J. Csargo, A. V. Eschen, M. D. Thul, J. M. Baker, C. Hayer, J. Howell, J. Krause, A. Letvin, and S. R. Chipps. 2012. A generalized model for estimating the energy density of invertebrates. Freshwater Science 31:69−77.

Jobling, M. 1994. Fish bioenergetics. Chapman and Hall, London.

Johnson, B. M., and P. J. Martinez. 2000. Trophic economics of Lake Trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:115−131.

Johnson, L., and B. Burns, editors. 1984. Biology of the Arctic Charr. University of Manitoba Press, Winnipeg.

Johnson, T. B., D. M. Mason, S. T. Schram, and J. F. Kitchell. 1999. Ontogenetic and seasonal patterns in the energy content of piscivorous fishes in Lake Superior. Journal of Great Lakes Research 25:275−281.

Jonsson, B., and N. Jonsson. 1993. Partial migration: niche shifts versus sexual maturation in fishes. Reviews in Fish Biology and Fisheries 3:348−365.

Jorgenson, C., B. Ernande, O. Fiksen, and U. Dieckmann. 2006. The logic of skipped spawning in fish. Canadian Journal of Fisheries and Aquatic Sciences 63:200−211.

Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to Yellow Perch (Perca flavescens) and Walleye (Stizostedion vitreum vitreum). Journal of the Fisheries Research Board of Canada 34:1922−1935.

Lantry, B. F., and R. O'Gorman. 2007. Drying temperature effects on fish dry mass measurements. Journal of Great Lakes Research 33:606–616.

Lewis, W. M., J. F. Saunders, D. W. Crumpacker, and C. M. Brendecke. 1984. Eutrophication and land use: Lake Dillon, Colorado. Springer-Verlag, New York.

Lien, L. 1978. The energy budget of the Brown Trout population of Øvre Heimdalsvatn. Holarctic Ecology 1:279−300.

Love, R. M. 1970. The chemical biology of fishes. Academic Press, London.

Lowery, E. D., and D. A. Beauchamp. 2015. Trophic ontogeny of fluvial Bull Trout and seasonal predation on Pacific salmon in a riverine food web. Transactions of the American Fisheries Society 144:724−741.

Martinez, P. J., P. E. Bigelow, M. A. Deleray, W.A. Fredenberg, B. S. Hansen, N. J. Horner, S. K. Lehr, R. W. Schneidervin, S. A. Tolentino, and A. E. Viola. 2009. Western Lake Trout woes. Fisheries 34:424−442.

Morley, J. W., J. A. Buckel, and T. E. Lankford Jr. 2012. Comparing multiple predictors of energy content in juvenile Bluefish. Transactions of the American Fisheries Society 141:1109−1116.

Olsen, D. M. 2014. Arctic Char (Salvelinus alpinus) can enhance fisheries in reservoirs with trophic constraints. Master's thesis. Colorado State University, Fort Collins.

Parr Instrument Company. 2013. Introduction to bomb calorimetry. Available: http://www.parrinst.com/wp-content/uploads/downloads/2013/07/483M_Parr_Intro-to-Bomb-Calorimetry.pdf. (December 2016).

Pate, W. M., B. M. Johnson, J. Lepak, and D. Brauch. 2014. Managing for coexistence of kokanee and trophy Lake Trout in a montane reservoir. North American Journal of Fisheries Management 34:908−922.

Pizzul, E., M. Bertoli, A. Basset, F. Vignes, M. Calligaris, and E. Tibaldi. 2009. Energy densities of Brown Trout (Salmo trutta) and its main prey items in an alpine stream of the Slizza basin (northwest Italy). Journal of Freshwater Ecology 24:403−410.

Post, J. R., and D. O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year Yellow Perch (Perca flavescens): laboratory, in situ enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences 46:1958−1968.

Post, J. R., and E. A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. Ecology 82:1040−1051.

Rand, P. S., D. J. Stewart, P. W. Seelbach, M. L. Jones, and L. R. Wedge. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. Transactions of the American Fisheries Society 122:977−1001.

Rottiers, D. V., and R. M. Tucker. 1982. Proximate composition and caloric content of eight Lake Michigan Fishes. U.S. Fish and Wildlife Service Technical Paper 108.

Ruzycki, J. R., D. A. Beauchamp, and D. L. Yule. 2003. Effects of introduced Lake Trout on native Cutthroat Trout in Yellowstone Lake. Ecological Applications 13:23−37.

Schloesser, R. W., and M. C. Fabrizio. 2015. Relationships among proximate components and energy density of juvenile Atlantic estuarine fishes. Transactions of the American Fisheries Society 144:942–955.

Schoen, E. R., D. A. Beauchamp, A. R. Buettner, and N. C. Overman. 2015. Temperature and depth mediate resource competition and apparent competition between Mysis diluviana and kokanee. Ecological Applications 25:1962−1975.

Schoen, E. R., D. A. Beauchamp, and N. C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: pulsed predatory inertia of Lake Trout and decline of kokanee. Transactions of the American Fisheries Society 141:1191−1206.

Schreckenbach, K., R. Knosche, and K. Elbert. 2001. Nutrient and energy content of freshwater fishes. Journal of Applied Ichthyology 17:142−144.

Simpkins, D. G., W. A. Hubert, C. Martinez del Rio, and D. C. Rule. 2003. Physiological responses of juvenile Rainbow Trout to fasting and swimming activity: effects on body composition and condition indices. Transactions of the American Fisheries Society 132:576–589.

Sorel, M. H., A. G. Hansen, K. A. Connelly, A. C. Wilson, E. D. Lowery, and D. A. Beauchamp. 2016. Predation by Northern Pikeminnow and Tiger Muskellunge on juvenile salmonids in a high-head reservoir: implications for anadromous fish reintroductions. Transactions of the American Fisheries Society 145:521−536.

Stein, R. A., and M. L. Murphy. 1976. Changes in proximate composition of the crayfish Orconectes propinquus with size, sex, and life stage. Journal of the Fisheries Research Board of Canada 33:2450−2458.

Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for Lake Trout, Salvelinus namaycush: application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681−698.

Thorpe, J. E. 1994. Reproductive strategies in Atlantic Salmon, Salmo salar L. Aquaculture Research 25:77−87.

Trudel, M., and J. B. Rasmussen. 2006. Bioenergetics and mercury dynamics in fish: a modelling perspective. Canadian Journal of Fisheries and Aquatic Sciences 63:1890−1902.

Vidergar, D. T. 2000. Population estimates, food habits, and estimates of consumption of selected predatory fishes in Lake Pend Oreille, Idaho. Master's thesis. University of Idaho, Moscow.

Vollenweider, J. J., R. A. Heintz, L. Schauffler, and R. Bradshaw. 2011. Seasonal cycles in whole-body proximate composition and energy content of forage fish vary with water depth. Marine Biology 158:413–427.

Weatherley, A. H., and H. S. Gill. 1983. Protein, lipid, water and caloric contents of immature Rainbow Trout, Salmo gairdneri Richardson, growing at different rates. Journal of Fish Biology 23:653−673.

Wiltzius, W. J. 1974. Post impoundment fishery investigations, Curecanti Unit, Upper Colorado River Storage Project. Colorado Division of Wildlife, Final Report, Fort Collins.

Wiltzius, W. J. 1978. Some factors historically affecting the distribution and abundance of fishes in the Gunnison River. Colorado Division of Wildlife, Final Report, Fort Collins.

Wiltzius, W. J. 1985. Fish culture and stocking in Colorado, 1872–1978. Colorado Division of Wildlife, Report DOW-R-D-12-85, Fort Collins.

Wuenschel, M. J., A. R. Jugovich, and J. A. Hare. 2006. Estimating the energy density of fish: the importance of ontogeny. Transactions of the American Fisheries Society 135:379–385.

Yule, D. L., and C. Luecke. 1993. Lake Trout consumption and recent changes in the fish assemblage of Flaming Gorge Reservoir. Transactions of the American Fisheries Society 122:1058−1069.

Appendix: Age-Specific Lake Trout Bioenergetics Simulations

TABLE A.1. Diet composition of different size-groups and age-groups of Lake Trout used in bioenergetics simulations to estimate consumption demand on kokanee (KOK), Rainbow Trout (RBT), Yellow Perch (YPE), crayfish (CFI), and other small invertebrates (SMI) in Blue Mesa Reservoir, Colorado. The corresponding energy densities (EDs) of each prey group under the alternative ED selection approaches are also listed. Baseline ED values were estimated from prey captured in Blue Mesa Reservoir (present study). Energy density values were also generated from corresponding estimates of dry matter content (DM) by using the multispecies ED:DM models of Hartman and Brandt (1995; equation 2 in Methods) and Schreckenbach et al. (2001; equation 3). Borrowed ED values were obtained from Rand et al. (1993) for RBT, Kitchell et al. (1977) for YPE, and Stein and Murphy (1976) for CFI and were averaged across a number of studies for SMI (Baldwin et al. 2000, 2003; Beauchamp and Van Tassell 2001; Schoen et al. 2012; Hansen et al. 2013). Because the EDs of kokanee were adjusted for each age-class of Lake Trout, those values are listed in Table A.3.

Lake Trout TL (mm)	Lake Trout age (years)	Prey type				
		KOK	RBT	YPE	CFI	SMI
		Diet proportions				
332 to <409	3	0.576	0.034	0.266	0.058	0.066
409 to <478	4	0.478	0.053	0.307	0.091	0.072
409 to <740	5–9	0.458	0.110	0.381	0.039	0.012
≥740	≥10	0.937	0.012	0.031	0.019	
		Baseline energy density (J/g)[a]				
332 to <409	3	Table A.3	6,094	4,731	3,706	2,107
409 to <478	4		6,094	4,731	3,706	2,107
409 to <740	5–9		6,094	4,731	3,706	2,107
≥740	≥10		6,094	4,731	3,706	2,107
		Hartman and Brandt (1995) energy density (J/g)				
332 to <409	3	Table A.3	5,844	4,716	6,153	3,461
409 to <478	4		5,844	4,716	6,153	3,461
409 to <740	5–9		5,844	4,716	6,153	3,461
≥740	≥10		5,844	4,716	6,153	3,461
		Schreckenbach et al. (2001) energy density (J/g)				
332 to <409	3	Table A.3	5,672	4,467	6,153	3,461
409 to <478	4		5,672	4,467	6,153	3,461
409 to <740	5–9		5,672	4,467	6,153	3,461
≥740	≥10		5,672	4,467	6,153	3,461
		Borrowed energy density (J/g)				
332 to <409	3	Table A.3	5,822	4,186	6,153	3,461
409 to <478	4		5,822	4,186	6,153	3,461
409 to <740	5–9		5,822	4,186	6,153	3,461
≥740	≥10		5,822	4,186	6,153	3,461

[a]The EDs for RBT and YPE were modified slightly from those presented by Pate et al. (2014) to ensure consistency between the direct measures of ED selected for baseline simulations and the paired measures of DM used to estimate ED with the multispecies models of Hartman and Brandt (1995) and Schreckenbach et al. (2001). Paired measures of ED and DM from individual RBT and YPE falling within the range of reconstructed TLs observed in the diets of Lake Trout were averaged to develop the baseline, Hartman and Brandt (1995), and Schreckenbach et al. (2001) inputs.

TABLE A.2. Age-specific predator start and end weights and corresponding energy densities (EDs) under the alternative ED selection approaches and used as input into the bioenergetics model for estimating the annual per-capita consumption rate of kokanee and alternative prey by Lake Trout in Blue Mesa Reservoir, Colorado (Pate et al. 2014). Baseline ED values were estimated from Lake Trout captured in Blue Mesa Reservoir (present study). Energy density values were also generated from corresponding estimates of dry matter content (DM; %) by using the multispecies ED:DM models of Hartman and Brandt (1995; equation 2 in Methods) and Schreckenbach et al. (2001; equation 3). Borrowed ED values were generated from the mass-dependent relationship of Stewart et al. (1983).

Lake Trout age-class (years)	TL (mm)[a]	Wet mass (g)[b]		Baseline ED (J/g)[c]		Hartman and Brandt (1995) ED (J/g)[d]		Schreckenbach et al. (2001) ED (J/g)[e]		Borrowed ED (J/g)	
		Start	End	Start	End	Start	End	Start	End	Start	End
3	332	251	503	5,591	5,947	5,575	5,873	5,382	5,704	6,474	7,250
4	409	503	850	5,947	6,437	5,873	6,292	5,704	6,159	7,250	8,320
5	478	850	1,286	6,437	7,052	6,292	6,831	6,159	6,749	8,320	9,662
6	541	1,286	1,797	7,052	7,774	6,831	7,483	6,749	7,470	10,093	10,491
7	599	1,797	2,371	7,774	8,584	7,483	8,237	7,470	8,313	10,491	10,938
8	650	2,371	2,992	8,584	9,460	8,237	9,080	8,313	9,266	10,938	11,421
9	697	2,992	3,645	9,460	10,383	9,080	9,997	9,266	10,314	11,421	11,930
10	740	3,645	4,318	10,383	11,333	9,997	10,972	10,314	11,440	11,930	12,454
11	779	4,318	4,999	11,333	12,294	10,972	11,990	11,440	12,628	12,454	12,984
12	814	4,999	5,678	12,294	13,253	11,990	13,033	12,628	13,858	12,984	13,513
13	845	5,678	6,346	13,253	14,197	13,033	14,090	13,858	15,114	13,513	14,033
14	874	6,346	6,998	14,197	15,117	14,090	15,146	15,114	16,381	14,033	14,541
15	900	6,998	7,628	15,117	16,006	15,146	16,191	16,381	17,644	14,541	15,031

[a]Estimated using a von Bertalanffy growth function relating length to age, as presented by Pate et al. (2014).

[b]Estimated using a length–wet mass regression presented by Pate et al. (2014).

[c]Estimated using the linear regression relating ED (J/g) to wet mass (WW; g), presented in Results.

[d]Estimated by first using a linear regression relating DM to WW (DM = [0.0034 × WW] + 23.53; $n = 32$, $r^2 = 0.75$, $P < 0.001$) and then inserting DM into the multispecies model of Hartman and Brandt (1995).

[e]Estimated by first using the linear regression relating DM to WW and then inserting DM into the multispecies model of Schreckenbach et al. (2001).

TABLE A.3. Start and end weights of kokanee prey and corresponding energy densities (EDs) under the alternative ED selection approaches and used as input into the bioenergetics model for estimating the annual per-capita consumption rates by different age-classes of Lake Trout in Blue Mesa Reservoir, Colorado (Pate et al. 2014). Baseline ED values were estimated from kokanee captured in Blue Mesa Reservoir (present study). Energy density values were also generated from corresponding estimates of dry matter content (DM; %) by using the multispecies ED:DM models of Hartman and Brandt (1995; equation 2 in Methods) and Schreckenbach et al. (2001; equation 3). Borrowed ED values were generated from the mass-dependent relationship of Beauchamp et al. (1989).

Lake Trout age-class (years)	TL (mm)[a]	Wet mass (g)[b]		Baseline ED (J/g)[c]		Hartman and Brandt (1995) ED (J/g)[d]		Schreckenbach et al. (2001) ED (J/g)[e]		Borrowed ED (J/g)	
		Start	End	Start	End	Start	End	Start	End	Start	End
3	109	13	25	5,970	6,645	5,793	6,327	5,617	6,196	5,335	5,425
4	135	25	40	6,645	7,258	6,327	6,824	6,196	6,742	5,425	5,543
5	158	40	58	7,258	7,812	6,824	7,286	6,742	7,251	5,543	5,683
6	179	58	79	7,812	8,315	7,286	7,713	7,251	7,726	5,683	5,843
7	198	79	101	8,315	8,771	7,713	8,107	7,726	8,167	5,843	6,017
8	215	101	125	8,771	9,183	8,107	8,469	8,167	8,574	6,017	6,201
9	230	125	149	9,183	9,557	8,469	8,802	8,574	8,951	6,201	6,391
10	244	149	174	9,557	9,896	8,802	9,108	8,951	9,297	6,391	6,584
11	257	174	199	9,896	10,203	9,108	9,388	9,297	9,616	6,584	6,751
12	268	199	223	10,203	10,482	9,388	9,644	9,616	9,909	6,751	6,764
13	279	223	247	10,482	10,734	9,644	9,878	9,909	10,177	6,764	6,777
14	288	247	270	10,734	10,962	9,878	10,091	10,177	10,422	6,777	6,789
15	297	270	292	10,962	11,169	10,091	10,286	10,422	10,647	6,789	6,800

[a]Estimated as 33% of Lake Trout TL (mm; Pate et al. 2014).

[b]Estimated using the following TL–wet mass (WW; g) regression: $TL = 0.000008995 \times WW^{3.024}$.

[c]Estimated using the linear regression relating ED (J/g) to TL ($ED = [26.63 \times TL] + 3,054.4$; $n = 33$, $r^2 = 0.66$, $P < 0.001$).

[d]Estimated by first using a linear regression relating DM to TL ($DM = [0.0594 \times TL] + 18.50$; $n = 33$, $r^2 = 0.69$, $P < 0.001$) and then inserting DM into the multispecies model of Hartman and Brandt (1995).

[e]Estimated by first using the linear regression relating DM to TL and then inserting DM into the multispecies model of Schreckenbach et al. (2001).