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## Assessment of Seasonal Changes in Energy Density and Condition in Age-0 and Age-1 Muskellunge

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**Abstract.**—The objectives of this study were to evaluate seasonal changes in the energy density of age-0 and age-1 muskellunge *Esox masquinongy* and to compare energy density to various estimates of condition. Three treatment groups of muskellunge were evaluated to determine temporal changes in energy density (J/g wet weight [ww]), water content, condition factor ( $K_{TL}$ ;  $K = W/L^3$ , where  $W$  = weight and  $L$  = total length in centimeters), and relative weight ( $W_r$ ; ratio of actual to “standard” weight) through the first year following hatching. Treatment groups were (1) hatchery (muskellunge reared and maintained in hatchery ponds), (2) stocked (hatchery-reared muskellunge stocked in lakes), and (3) natural (muskellunge naturally produced in lakes). Energy levels and relative condition were compared for fish 4 and 11 months old. Differences in energy density were observed between all three treatment groups. An average overwinter reduction of  $494 \pm 192$  J/g ww in energy density was observed over all treatment groups combined. Natural fish lost less energy (8%) over winter than either hatchery (12%) or stocked fish (15%). A simple linear model effectively relates energy to indices of condition for muskellunge. A weak positive relation ( $P < 0.0001$ ,  $r^2 = 0.39$ ,  $0.40$ , and  $0.43$ ) was observed between dry weight energy density and three indicators of fish condition (percent water,  $K$ , and  $W_r$ ). Our results show that condition indices may not be the best indicators of seasonal fluctuations in total energy within and between fish populations. Seasonal fluctuations in energetic values for a population can be more accurately determined through assessment of percent water in individual fish.

Low survival after stocking is a problem for hatchery-reared muskellunge *Esox masquinongy* (Mather and Wahl 1989; Margenau 1992). Survival of stocked muskellunge may be related to the energy density or condition of fish stocked into lakes (Miranda and Hubbard 1994). The energy density of a fish may determine the ability of an individual to compete successfully for food resources and refugia, sustain growth, maintain and repair tissues, and cope with stresses induced by environmental changes (Brown and Murphy 1991). Flath and Diana (1985) found that seasonally low energy levels in alewives *Alosa pseudoharengus* corresponded with annual die-offs. Severe winter conditions reduce survival in a variety of fish species, especially among smaller individuals in a cohort (Reimers 1963; Hunt 1969; Toney and Coble 1979; Adams et al. 1982; Elrod et al. 1988; Post and Evans 1989; Thompson et al. 1991). Henderson et al. (1988) reported that late-spawned age-0 sand smelt *Atherina boyeri* had in-

sufficient fat reserves to survive a normal winter. Overwinter declines in condition of fish have been attributed to either reduced forage availability or decreased foraging efficiency of fish at low temperatures (Adams et al. 1982; Cunjack and Power 1987).

Overwinter survival is directly related to length in muskellunge and may also be related to greater energy stores in larger fish (Carline et al. 1986). Margenau (1992) found that most size-related effects on survival of stocked muskellunge fingerlings occurred before the onset of winter. Overwinter survival of these fish from October to May was still less than 50%. Size-dependent effects on growth and mortality of fall-stocked muskellunge have been amply demonstrated (Hanson et al. 1986; Margenau 1992; Johnson and Margenau 1993). Age-0 esocids grow rapidly in the fall, but growth declines substantially over winter (Wahl and Stein 1991; Margenau 1992). Both fish size and energy stores may determine whether fish will survive through the first winter.

Condition indices have been widely used as indicators of relative health for a variety of fish species (Brown and Murphy 1991; Childress 1991)

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and may be useful for investigating overwinter survival of muskellunge. However, the usefulness of condition indices to assess fish populations has been much debated, as has the best index to use in different situations (Cone 1989; Springer et al. 1990; Murphy et al. 1991). It is possible to define differences in the length-weight relation or form of a fish but much more risky to draw conclusions about relative health or condition of fish. Seasonal fluctuations in condition indices may correlate with important changes in fish energy density (LeCren 1951) or ontogenetic shifts in food use (Liao et al. 1995). Direct estimates of body composition were found to be most appropriate for determining condition in northern pike *Esox lucius*. Although water content and condition factor ( $K_{TL}$ ;  $K = W/L^3$ ; where  $W$  = weight and  $L$  = total length in centimeters) were also useful, greater error was associated with these estimates (Salam and Davies 1994). Relative weight ( $W_r$ ; ratio of actual weight to "standard" weight) was found to be useful in predicting the total body energy of striped bass *Morone saxatilis* and hybrid striped bass *M. chrysops*  $\times$  *M. saxatilis* (Brown and Murphy 1991). Seasonal fluctuations in condition indices should correlate with changes in energy density. Little is known about the seasonal variation in energy density of esocids, and even less is known about relations between muskellunge energy density and various condition indices.

The objectives of this study were to measure seasonal changes in the energy density of age-0 and age-1 muskellunge and determine the relation between energy density and various estimates of condition. Direct measurements of seasonal variation in energy density of muskellunge will enhance our understanding of the effects of the overwinter period on condition of young muskellunge. Comparisons between energy density, water content,  $K$ ,  $W_r$ , and length-weight regressions will help determine which measure most accurately reflects seasonal variation in muskellunge condition.

### Methods

Treatment groups were (1) hatchery (muskellunge maintained in hatchery ponds), (2) stocked (hatchery-reared muskellunge placed in lakes), and (3) natural (muskellunge produced by natural spawning in the study lakes). We monitored changes in energy density and various measures of condition for all three treatment groups from age 4 months (September 1990) to age 17 months (October 1991). Hatchery muskellunge were progeny of wild broodstock from Lac Courte Oreilles,

TABLE 1.—Number of hatchery-reared, stocked (ST), and natural (NA) muskellunge sampled for caloric analysis. In September 1990, hatchery fish were not yet stocked into lakes (NS).

Sampling date	Water body						
	Spooners Hatchery Pond	Lyman		Lake of the Pines		Lost Land	
		NA	ST	NA	ST	NA	ST
Sep 1990	10	7	NS	5	NS	2	NS
Oct 1990	5	4	5	5	5	3	5
May 1991	5	3	5	3	5	5	4
Oct 1991	3	3	3	2	4	1	3
Total	23	17	13	15	14	11	12

Wisconsin. Hatchery fish were reared on a minnow diet and retained in ponds until age 17 months. When the fish were age 4 months, a subsample was removed and stocked (typical stocking size for Wisconsin is 300 mm) in Lake of the Pines, Lost Land Lake, and Lyman Lake in northern Wisconsin. All three lakes were dark water, had good muskellunge populations, and had some level of natural recruitment. Annual stocking supplements natural reproduction in all three lakes. Stocked fish were given a fin clip for later identification. Hatchery, stocked, and natural fish were sampled at four intervals: early first fall (age 4 months, September), late first fall (age 5 months, late October), spring (age 11 months, May), and second fall (age 17 months, October). Fish were collected from hatchery ponds with a seine and from study lakes with an AC, boat-mounted electrofishing unit. The gear types used are widely accepted and were the most logical and efficient to collect fish for this study. At each sampling interval, we attempted to collect at least three fish from each treatment group (Table 1). All fish were wrapped in plastic wrap, then aluminum foil, and frozen immediately following sampling.

Total length (mm), wet weight (g), percent water, energy density (J/g),  $K$ , and  $W_r$  were determined for each fish collected. To determine water content, fish were ground in a 1-L blender and dried at 65–70°C in a drying oven. Ground fish were weighed daily beginning 3 d after drying. Samples were considered dry when there was no weight loss between consecutive daily weighings. To determine energy content, ground, dried fish samples were reground in a blender until a homogenous powder was obtained. Four 1-g pellets were formed with a press from each fish. Pellets were placed in a 65–70°C drying oven for at least 24 h. To eliminate error in energy measurements

resulting from water uptake, pellets were placed in desiccation chambers before being weighed to the nearest 0.01 g.

We performed bomb calorimetry with an adiabatic oxygen microbomb calorimeter using standard procedures (Anonymous 1968). Nitric acid and fuse wire corrections were performed for each 1-g sample. Sulfur levels were sufficiently low in fish samples that the sulfuric acid correction was not required (Gordon and Roberts 1977). Two samples were combusted for each fish collected, and an average value was obtained from the two samples. If the difference in values between the samples was greater than 420 J, a third sample was combusted and averaged.

A two-way analysis of variance (ANOVA; SAS Institute 1988) was used to compare the dependent variables (percent dry weight,  $W_r$ ,  $K$ , and wet weight energy density). Independent variables were date (October 1990, May 1991, and October 1991) and treatment (hatchery, stocked, and natural). September 1990 fish were not included in the analysis because fish had not been stocked on this date. Analysis of covariance (ANCOVA; SAS Institute 1988) was used to evaluate the effects of length on energy density. The covariate (length) was centered around its mean. A squared term was entered in the model to account for the curvilinear relation between the covariate length and energy density. Adjusted means incorporating the quadratic function were compared between independent variables ( $\alpha = 0.05$ ). The SAS "estimate" function was used to compare types of fish across dates in the covariance analysis. We specified the mean for each type of fish for which comparisons were made. October 1991 fish were not included in the ANCOVA because sample sizes were too small to test model assumptions. Analysis of covariance was not performed on  $K$  because length is included in the calculation of this index.

We observed seasonal changes in water content,  $K$ ,  $W_r$ , and length-weight regressions that occurred within and among groups of fish during the first year, and determined which of these measures most accurately reflected energy density. Length-weight regressions were calculated for each date for all treatment groups combined to examine general seasonal fluctuations. Analysis of covariance was used to determine whether the slopes were different for length-weight regressions on each date. Linear regression was used to determine the relation between dry weight energy density and  $K$ ,  $W_r$ , and percent dry weight for all fish. Error es-

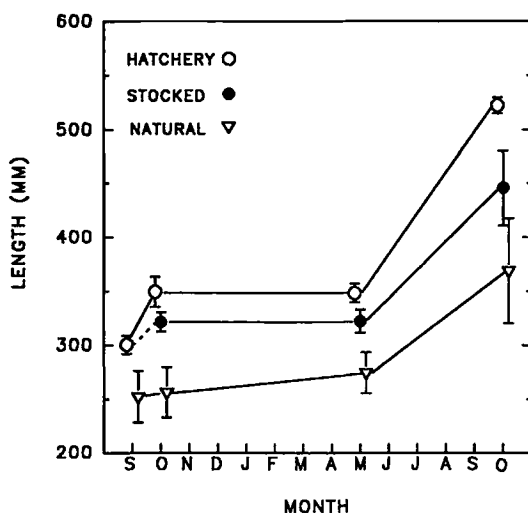


FIGURE 1.—Seasonal differences in mean total length (mm) of muskellunge in three treatment groups (hatchery, stocked, and natural). Error bars represent 95% confidence intervals. Hatchery muskellunge were first stocked into the lakes in September 1990.

timates provided are 95% confidence intervals for all mean values presented in the text.

## Results

Hatchery, stocked, and natural fish were markedly different from each other. Treatment groups of fish were distinct within each condition variable (ANOVA,  $P < 0.05$ ,  $df = 2$ , 72), except for stocked and natural fish, which could not be distinguished when  $W_r$  was used (ANOVA,  $P > 0.05$ ,  $df = 2$ , 72). Hatchery fish showed the highest  $W_r$  ( $94 \pm 4$ ), followed by stocked ( $82 \pm 2$ ) and then natural fish ( $80 \pm 3$ ). Hatchery fish showed the highest  $K$  ( $0.51 \pm 0.02$ ), followed by stocked ( $0.48 \pm 0.01$ ) and then natural fish ( $0.44 \pm 0.01$ ). Hatchery fish also had the highest percent dry weight ( $22.93 \pm 0.86$ ), followed by stocked ( $20.39 \pm 0.49$ ) and natural fish ( $18.99 \pm 0.58$ ). Wet weight energy density differed among treatment groups following the same pattern just described.

Length had a significant effect on wet weight energy density (ANCOVA,  $P < 0.0306$ ,  $df = 1$ , 52). Hatchery fish were longest ( $389 \pm 46$  mm), whereas natural fish were shortest ( $286 \pm 21$  mm; Figure 1). After the effects of length were removed, the overwinter reduction in energy density was still apparent for all treatment groups (ANCOVA,  $P = 0.0001$ ,  $df = 1$ , 52; Figure 2). Energy density declined over winter by an average of  $495 \pm 173$  J/g ww for all treatment groups combined.

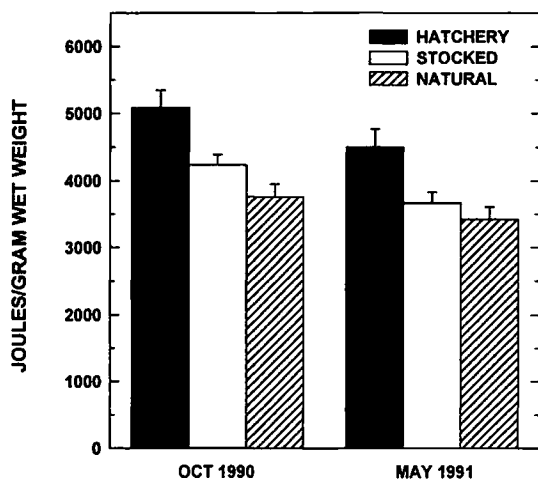


FIGURE 2.—Seasonal differences in wet weight energy density (J/g) of muskellunge in three treatment groups (hatchery, stocked, and natural). Results are from AN-COVA analysis with effects of length removed. Error bars represent the upper 95% confidence limit. Treatment groups should not be compared within a season. Means have been adjusted so that treatment groups can be compared across seasons.

Energy density declined sharply in stocked muskellunge from September (stocking) to October 1990, while increasing in natural fish. The overwinter reduction in energy content was greater for stocked ( $571 \pm 226$ ) and hatchery ( $577 \pm 380$ ) fish than for natural fish ( $338 \pm 278$ ).

The effects of overwintering on the other variables measured were not as clear. Overwinter differences were noted for all indices of condition (ANOVA,  $P < 0.05$ ,  $df = 2, 72$ ) except  $W_r$  (ANOVA,  $P > 0.05$ ,  $df = 2, 72$ ; Figure 3). In contrast to results observed for energy density, fish collected in spring had higher  $K$  ( $0.51 \pm 0.01$ ) than those collected the previous fall ( $0.48 \pm 0.01$ ). The slope of the length-weight regression line for fish in each season increased over winter, indicating healthier fish. Like energy density, percent dry weight decreased over winter from  $21.2 \pm 0.6$  to  $19.5 \pm 0.6$ . The magnitude of overwinter changes in water content differed across treatment groups of fish. For stocked fish, percent dry weight declined by 6% from September to October, and by 7% over the winter. In contrast, the percent dry weight of natural fish increased by 2% before winter but showed a similar decrease of 6% over the winter.

The energy density of muskellunge can be estimated from fish condition indices (Figure 4). Weak significant relations were observed between

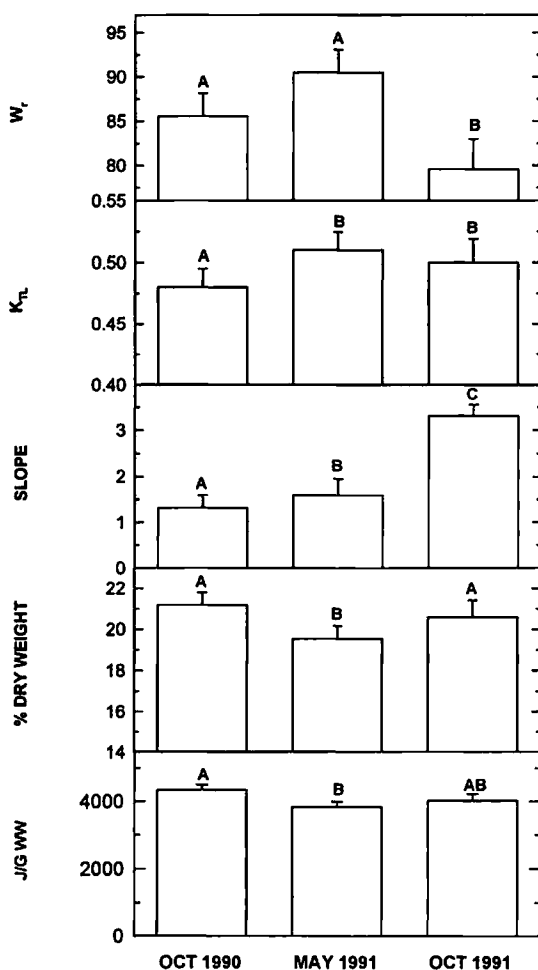


FIGURE 3.—Seasonal differences in  $W_r$ ,  $K$ , length-weight regression slopes, percent dry weight, and wet weight (ww) energy density (J/g) for all treatment groups (hatchery, stocked, and natural) combined. Error bars represent upper 95% confidence limit. Within a variable ( $W_r$ ,  $K$ , slope, percent dry weight, and J/g ww), values that do not share a common letter are significantly different ( $\alpha = 0.05$ ).

energy density and percent dry weight ( $P < 0.0001$ ,  $r^2 = 0.39$ ;  $Y = 408X + 11,340$ ),  $K$  ( $P < 0.0001$ ,  $r^2 = 0.41$ ;  $Y = 14,626X + 12,552$ ) and  $W_r$  ( $P < 0.0001$ ,  $r^2 = 0.43$ ;  $Y = 92.41X + 11,684$ ). Only the percent water was robust against seasonal deviations in energy density. The relation of percent dry weight,  $K$ , and  $W_r$  to wet weight energy density remained significant when determined within each season ( $P < 0.02$ ). Percent dry weight remained significant ( $P < 0.05$ ) when compared within each type of fish; however,  $K$  and  $W_r$  did not.

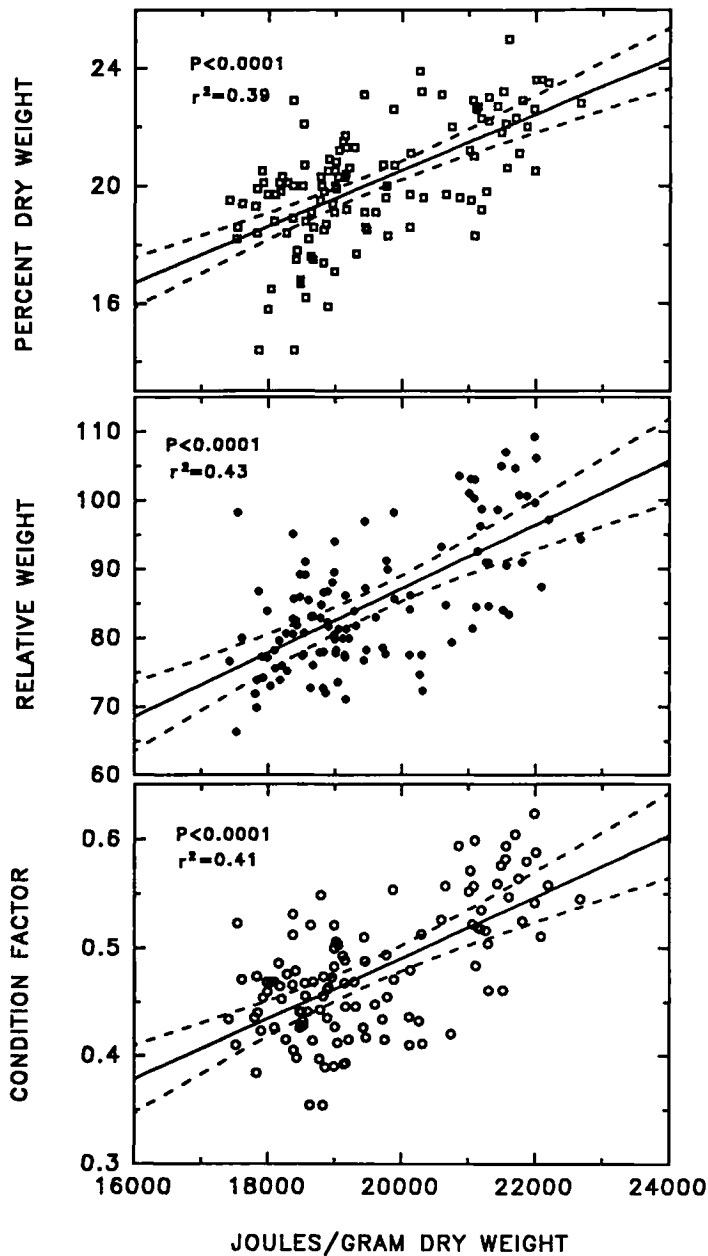


FIGURE 4.—Relation between  $K$ ,  $W_r$ , percent dry weight, and dry weight energy density (J/g) for all muskellunge collected. Broken lines are 95% confidence limits.

### Discussion

Mortality of stocked muskellunge is generally greatest sometime during the first several months after stocking (Hanson et al. 1986; Margenau 1992). Much of this mortality has been attributed to predation (Stein et al. 1981; Carline et al. 1986; Serns and Andrews 1986; Wahl and Stein 1989)

and stress (Mather and Wahl 1989). However, energy density and fish length may also play an important role (Carline et al. 1986). A baseline or maintenance energy density may be required by fish to survive over winter (Newsome and Leduc 1975; Hoar 1983; Thompson et al. 1991). Fish with energy densities below the levels we observed in

natural lakes may have experienced increased mortality. The natural fish we sampled may have been at or slightly above this threshold level, whereas fish reared under hatchery conditions were likely above this level. Our results show that the energy density of muskellunge declines after stocking and during the winter, and is more closely related to percent dry weight than to other measures of condition.

Distinct seasonal differences were observed in the energy density of muskellunge. Stocked muskellunge gained water and lost energy rapidly in fall following stocking. This rapid initial energy loss may have resulted from difficulties in obtaining food in the natural environment (Carline et al. 1986). Natural fish lost water and increased their energy density before winter. Fish from all treatments increased water content and decreased energy density over winter. Muskellunge held over winter in hatchery ponds lost energy at rates similar to those of stocked fish, yet the energy density and size of hatchery fish in early spring remained greater than those of stocked or natural fish.

Several factors other than limited food availability could account for the overwinter energy loss we observed. Muskellunge reared in hatchery ponds were supplied with abundant food and showed consistently greater energy densities than stocked or natural fish, yet the energy density of hatchery fish declined over winter. An early winter reduction in condition of brook trout *Salvelinus fontinalis* and brown trout *Salmo trutta* has been attributed to either an inability to assimilate ingested food or to insufficient energy intake to balance metabolic costs of fish acclimating to new climatic conditions (Cunjak and Power 1987).

A significant loss in energy over winter for all fish combined was observed when the effects of length were removed. Survival of fall-stocked muskellunge in Lake of the Pines is extremely low (2.3%), whereas larger spring-stocked fish with higher total body energy had higher survival (25.3%; Margenau 1992). In our study, fish grew faster in captivity, resulting in significant length differences among hatchery, stocked, and natural fish. Previous authors reported that size is an important factor influencing overwinter mortality (Post and Evans 1989; Miranda and Hubbard 1994). Johnson and Evans (1990) found that overwinter mortality of white perch *Morone americana* was related to body size, winter duration, temperature, and food availability. We did not evaluate the possible effects of length at stocking on sur-

vival, although other studies have shown potential effects (Oliver et al. 1979; Thompson et al. 1991).

In addition to seasonal variation in energy density, we observed seasonal differences in condition indices. Seasonal differences in condition indices have been reported for menhaden *Brevoortia* spp. (Dahlberg 1969) and Pacific herring *Clupea pallasii* (Hart et al. 1940) but have not been detected in other clupeids (Strange and Pelton 1987), striped bass *Morone saxatilis*, Atlantic herring *Clupea harengus*, or fry of thorn sturgeon *Acipenser nudiiventris* (Gershanovich et al. 1984). In our study, muskellunge collected in spring had significantly higher condition indices than those collected the previous fall, despite a decline in energy density during this period (Figure 1). Fish with a greater proportion of water weigh more (Gershanovich et al. 1984); this would explain our observation that higher condition indices were found in spring fish with depleted energy reserves and higher water content. Energy density was negatively correlated with the proportion of water in fish (Rottiers and Tucker 1982) and positively correlated with growth (Busacker et al. 1990). Results involving measures of  $W_r$  should be used with caution. In our study, some fish were below the length proposed (38 cm) for the  $W_r$  equation (Murphy et al. 1991; Neumann and Willis 1994).

We observed a positive relation between the percent dry matter and energy density of muskellunge, explaining 39% of the variance in muskellunge energy density. Relative weight explained 43% of the variance in energy density and  $K_{TL}$  explained 41%. It is more accurate to predict seasonal trends in condition of muskellunge populations with percent water estimates because it is more robust than  $K$  and  $W_r$  against seasonal variations in energy density of fish. Managers can conveniently estimate the energy content of muskellunge by determining percent dry weight rather than the more complex and laborious procedures required to measure energy density. Additional data collected with these simplified procedures will give us a better understanding of muskellunge ecology and its application to management.

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