Journal of Fish Biology (2005) **66,** 1060–1072
doi:10.1111/j.1095-8649.2005.00660.x, available online at http://www.blackwell-synergy.com

Temporal changes in the relationship between condition indices and proximate composition of juvenile *Coregonus artedi*

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(Received 5 February 2004, Accepted 1 December 2004)

The Fulton-condition factor (*K*) and per cent whole-body water content were examined to determine whether these indices can estimate the proximate composition of juvenile lake herring *Coregonus artedi* exposed to a simulated Lake Superior winter over a 225 day laboratory experiment. The *K* was positively correlated to whole-body crude lipid, crude protein, and gross energy content and negatively correlated to whole-body water content for each sampling period of the experiment (days 75, 150 and 225). In contrast, there was only a weak positive correlation between *K* and whole-body ash content. While per cent water content was negatively correlated with crude lipid, crude protein and gross energy content for each of the three sampling periods, the correlation between this predictor and ash content was only weakly negative. The indices can be used to accurately estimate temporal changes in proximate composition of juvenile lake herring during winter periods.

Key words: *Coregonus artedi*; Fulton condition factor; lake herring; proximate composition; water content.

INTRODUCTION

Survival of fishes at temperate latitudes during their first winter of life is strongly linked to body-tissue composition, particularly lipid, protein and gross-energy stores. The availability of these reserves subsequently affects the ability of individual fish to survive this critical period, maintain and repair body tissues, suppress disease and cope with stressors induced by environmental variability (Cunjak & Power, 1986; Seelbach, 1987; Henderson *et al.*, 1988; Brown & Murphy, 1991). As a result, fishes that deplete their energy stores below a critical threshold typically exhibit low survival (Oliver *et al.*, 1979; Cunjak, 1988; Post & Evans, 1989; Johnson & Evans, 1991; Cargnelli & Gross, 1997; Hurst *et al.*, 2000; Sutton & Ney, 2001; Pangle *et al.*, 2004). Because proximate composition of body tissues often determines recruitment

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success of age-0 year fishes, measurements of proximate composition can often be used to forecast year-class strength and recruitment to age 1 year (Wicker & Johnson, 1987; Thompson *et al*., 1991; Miranda & Hubbard, 1994; Jonas *et al*., 1996; Sutton *et al*., 2000).

The composition of fish tissues can be determined directly through proximate analyses or estimated indirectly using indices of physiological body condition (Brown & Murphy, 1991; Childress, 1991; Foster *et al*., 1993; Jonas *et al*., 1996; Lambert & Dutil, 1997; Fitzgerald *et al*., 2002). These condition indices are commonly used because they provide a time-efficient, cost-effective and non-lethal means of predicting relative fish health (Bolger & Connolly, 1989; Brown & Murphy, 1991; Ney, 1993). For example, previous studies have shown that condition indices accurately predicted the chemical composition of body tissues for plaice *Pleuronectes platessa* L. (Costopoulos & Fonds, 1989), striped bass *Morone saxatilis* (Walbaum) (Brown & Murphy, 1991), hybrid striped bass *M. saxatilis* × *Morone chrysops* (Rafinesque) (Brown & Murphy, 1991), largemouth bass *Micropterus salmoides* (Lacépède) (Brown & Murphy, 1994), Atlantic cod *Gadus morhua* L. (Lambert & Dutil, 1997), pike *Esox lucius* L. (Salam & Davies, 1994) and Atlantic salmon *Salmo salar* L. (Sutton *et al*., 2000). Further, per cent water content of Atlantic salmon, striped bass, hybrid striped bass and Atlantic cod has also been used to accurately predict lipid, protein and gross-energy content (Brown & Murphy, 1991; Herbinger & Friars, 1991; Lambert & Dutil, 1997; Sutton & Ney, 2001). Based on the results of these studies, condition indices and per cent water content can be used to assess the physiological status of individual fish within a population.

Condition indices are particularly useful for monitoring temporal changes in proximate-composition variables such as lipid and energy density (Hart *et al*., 1940; Wicker & Johnson, 1987; Pulliainen & Korhonen, 1990; Jonas *et al*., 1996). The accuracy of these predictions, however, often assumes that a constant, linear relationship exists between the predictor and response variables (Cone, 1989; Murphy *et al*., 1991; Springer *et al*., 1991). Although temporal changes in the body composition of fishes during early life stages may subsequently change the nature of the relationship between body condition and proximate composition, few studies have examined whether seasonal variations in condition indices are correlated with changes in lipid, protein and gross-energy content. For example, Jonas *et al*. (1996) found that changes in Fulton-condition factor (K) and relative mass of age 0 and 1 year muskellunge *Esox masquinongy* Mitchill were associated with fluctuations in energy density. Although this study demonstrated the existence of a temporal relationship between body condition and one proximate-composition variable (*i.e*. energy density), additional analyses are required to further characterize these relationships for fishes.

For this study, the empirical relationship between indices of condition and proximate composition of juvenile lake herring *Coregonus artedi* Lesueur was examined over a range of body sizes, feeding levels and changes in winter thermal regime that would be observed in natural populations. This laboratory experiment was designed to encompass the high degree of physiological variation exhibited by lake herring encountering their first winter of life (Anderson & Smith, 1971; Selgeby *et al*., 1978; Kinnunen, 1997). Recent findings have indicated that this variability, particularly in terms of lipid content, can strongly influence winter survival of juvenile lake herring (Pangle *et al.*, 2004). Subsequently, winter survival may be a key underlying factor that regulates year-class strength of this species (Pritchard, 1931; Scott, 1951; Selgeby, 1982; Hoff, 2004). By investigating the relationship between condition and proximate-composition indices, the aim of the study was to provide a means of evaluating recruitment dynamics in the field. Specific objectives of this research included the examination of temporal changes in the correlation between: (1) K and proximate composition (*i.e.* crude lipid, crude protein, gross energy, ash and water content) and (2) per cent whole-body water content and proximate composition (i.e. crude lipid, crude protein, gross energy and ash content) of juvenile lake herring over a 225 day laboratory experiment. With this information, the reliability of predicting proximate-composition constituents of juvenile lake herring was assessed using these indices of condition within the context of winter survival and recruitment to age 1 year.

MATERIALS AND METHODS

EXPERIMENTAL DESIGN

Lake herring were cultured from gametes obtained from spawning adults collected in commercial gillnets from Keeweenaw Bay (46°55′ N; 88°19′ W), Lake Superior, in December 2001. Fertilized eggs were incubated at the Red Cliff Tribal Hatchery (Bayfield, WI, U.S.A.) in 6 l hatching jars at 8° C until they reached the eyed stage. Eggs were then transported to the Purdue University Aquaculture Research Laboratory (West Lafayette, IN, U.S.A.) and incubated in similar conditions. Following hatching, larvae were reared in four 650 l flow-through aquaria and fed an *ad libitum* diet of live *Artemia* sp. nauplii (Summit Artemia, Instar, Technologies, Hyrum, UT, U.S.A.) and a moist formulated feed (Bio-Grower feed, Bio-Oregon, Inc., Warrenton, OR, U.S.A.). Water temperature and dissolved oxygen content in the rearing aquaria was maintained at 13° C, range ±1° C and >8·5 mg l^{-1}, respectively. A photoperiod of 16L : 8D was maintained for the duration of the rearing period, and water flow to each aquarium was maintained at 6 l min^{-1}. Lake herring were reared at these conditions for 180 days until they reached 50 to 129 mm total length (L_T) in late August 2002.

The laboratory experiment was conducted in a recirculating culture system containing 16 110 l aquaria. Outflow from each aquarium was controlled using a 26 mm diameter standpipe enclosed by a 78 mm diameter Venturi tube which drained into three 800 l settling chambers, each which contained biomedia and supplemental aeration from air stones. Before returning to each tank, water was passed through mechanical particle filters and an ultraviolet sterilizing chamber using a 1·5 hp electric pump. Water flow to each aquarium was maintained at 3·8 l min^{-1}, and temperature was controlled using three submersible chiller units (Frigid Units, Inc., Toledo, OH, U.S.A.). Photoperiod was controlled using the computer programme ModScan32 (WinTECH Software Design, Lewisburg, WV, U.S.A.) to correspond with the light regime at 46·5° N latitude from October to April.

Prior to the start of the experiment, juvenile lake herring were separated into a small (range, 50 to 85 mm L_T) and large (range, 86 to 129 mm L_T) size class. These size classes encompassed the range of L_T that would be expected for age 0 year lake herring in Lake Superior immediately prior to the onset of winter (Kinnunen, 1997). Thirty small or 15 large fish were randomly allocated to each aquarium (eight aquaria per size class) so that the biomass in each tank was the same between the two size treatments (mean ± S.E. 0·92 ± 0·02 g l^{-1}; ANOVA, $F_{1,14}$, $P = 0·08$). In addition, the following two feeding regimes were examined during the laboratory experiment: an *ad libitum* ration of *Artemia* sp.

nauplii fed to fish twice each day (0800 and 1600 hours) and starvation (*i.e.* no food). This broad range in daily ration was chosen because it is not known whether juvenile lake herring feed during winter months. Each feeding regime was randomly assigned to four aquaria within each size class. Thus, a 2×2 (body size $\times$ feeding ration) block design was conducted, with each treatment having four replicates.

Following a 14 day acclimation period, lake herring were subjected to the thermal regime that they would encounter in Lake Superior from October to April. Over a 52 day period, water temperature was decreased from 10 to 2° C at a rate of 0·15° C day^{-1} to represent cooling during autumn months. Water temperature was allowed to remain constant at 2° C for 130 days for the entire duration of the winter. For the spring warming period, water temperature was increased over a 43 day period to 10° C at a rate of 0·19° C day^{-1}. During the experiment, uneaten food and faecal material was removed by siphon from the aquaria on a daily basis, and dead fish were removed from each aquarium twice each day. On days 75 and 150 of the experiment, 25% of the fish in each aquarium were sacrificed, measured for L_T (to the nearest 1 mm) and wet mass (M, to the nearest 0·01 g), and frozen at −80° C for subsequent proximate-composition analyses. All fish remaining at the end of the experiment (day 225) were sacrificed, measured for L_T and M as described previously, and frozen prior to analyses of proximate composition.

ANALYSES OF CONDITION AND PROXIMATE COMPOSITION

The L_T and M data from individual lake herring sampled on days 75, 150 and 225 of the experiment were used to calculate K of individual fish as: $K = 10^5 M L_T^{-3}$,The constant 10^5 was a multiplier used to convert small decimals to mixed numbers for easier comprehension (Anderson & Neumann, 1996). Although a standard mass equation has been previously developed to assess lake herring body condition, relative mass could not be estimated from fish in this study due to biases associated with the standard mass relationship for fish <100 mm L_T (Fisher & Fielder, 1998).

Proximate composition of lake herring was estimated following standard AOAC (1990) procedures. To determine whole-body water content, each fish was oven dried to a constant mass at 100° C over a 24 h period and reweighed to the nearest 0·0001 g. Whole fish were individually homogenized using a commercial Waring blender and pooled with other individuals from the same treatment replicate. The ash fraction of each replicate was determined by combusting a 1 g homogenate sample to a constant mass (*c.* 3 h) at 550° C in a muffle furnace. A separate 1 g homogenate sample of each treatment replicate was placed in a Soxhlet lipid extraction apparatus, and lipid was extracted over a 24 h period using a 2 : 1 solution of chloroform and methanol as the solvent (Folch *et al.*, 1957). Following extraction, the crude lipid fraction (y) of each sample was calculated as: $y = 100(M_i - M_e)M_i$, where M_i and M_e were the initial and extracted masses (mg), respectively. A Perkin-Elmer 2410 Series II nitrogen analyser (Norwalk, CT, U.S.A.) was used to combust 0·2 g homogenate samples of each treatment replicate to estimate total nitrogen content, and these data were converted to total protein equivalents using the following relationship: percentage crude protein = percentage nitrogen $\times$ 6·25 (AOAC, 1990). Gross-energy content (J g^{-1} wet body mass) of a 1 g homogenate sample of each replicate was determined using a Parr Oxygen Combustion Bomb Calorimeter (Parr Instruments, Moline, IL, U.S.A.) following procedures described by Pierce *et al.* (1980). All proximate-composition variables, with the exception of gross energy (J g^{-1}), were reported as a percentage of lake herring wet body mass.

STATISTICAL ANALYSES

A linear regression was used to determine the relationship between mean whole-body crude lipid, crude protein, gross energy, ash and water content of individual lake herring treatment replicates during each of the three sampling periods (days 75, 150 and 225) and mean K and per cent whole-body water content. For all regression analyses, generalized linear model (GLM) procedures were used to identify the significance ($P \leq 0.05$) of correlation coefficients for the estimated regression relationships during each sampling period. Analysis of covariance (ANCOVA) was used to determine whether the slopes of the regression relationships between the response (proximate composition) and predictor (K and per cent whole-body water content) variables were different among the three sampling periods. For ANCOVA analyses, proximate composition was compared over sampling periods (*i.e.* days 75, 150 and 225), with indices of condition as the covariate. All data analyses were conducted using the SAS statistical analysis programme (SAS, 1990), and methods of statistical testing followed those as outlined in Zar (1999).

RESULTS

RELATIONSHIP OF K TO PROXIMATE COMPOSITION COMPONENTS

Crude-lipid content of juvenile lake herring was positively correlated with K on days 75, 150 and 225 of the laboratory experiment (ANOVA, $F_{1,44}$, all $P < 0.001$; Table I). Over the experimental period, the slope of the regression relationship increased from 9·845 (day 75) to 15·634 (day 225) and the intercept values decreased from 0·599 (day 75) to −1·994 (day 225). The slopes of the regression relationships between crude lipid content and K were significantly different (ANCOVA, d.f. = 2, $P < 0.001$) among sampling periods.

Although crude protein content of juvenile lake herring was not significantly correlated with K on day 75 of the laboratory experiment (ANOVA, $F_{1,44}$, $P < 0.076$), there was a positive correlation between these two variables on

TABLE I. Linear-regression variables of the relationships for crude lipid, crude protein, gross energy, ash and water content and the Fulton-condition factor (K) for juvenile lake herring on days 75, 150 and 225 of the laboratory experiment. Crude lipid, crude protein, ash and water content were expressed as percentages of wet body mass, while gross energy was expressed as J g^{-1} wet body mass

Day of experiment	Linear-regression equation	MS error	S.E. of K coefficient	r^2	P
75	Crude lipid = 0·599 + 9·845K	1·482	1·218	0·612	<0·001
	Crude protein = 12·059 + 2·208K	1·644	0·669	0·208	0·076
	Gross energy = 332·8 + 1153·5K	38 766·324	196·892	0·453	0·004
	Ash = 4·232 + 1·666K	1·152	2·258	0·112	0·642
	Water = 86·417 − 8·888K	26·169	1·528	0·435	0·005
150	Crude lipid = 0·305 + 11·222K	1·458	1·208	0·615	<0·001
	Crude protein = 10·789 + 7·353K	13·995	0·716	0·661	<0·001
	Gross energy = −339·8 + 2687·9K	47 745·583	218·508	0·737	<0·001
	Ash = 4·377 + 0·868K	0·154	0·559	0·039	0·496
	Water = 90·704 − 20·687K	117·246	1·722	0·748	<0·001
225	Crude lipid = −1·994 + 15·634K	1·781	1·335	0·640	<0·001
	Crude protein = 8·173 + 13·631K	13·995	0·716	0·674	<0·001
	Gross energy = −683·2 + 3577·1K	72 530·75	269·315	0·695	<0·001
	Ash = 2·962 + 4·464K	3·472	0·894	0·250	0·058
	Water = 93·222 − 27·189K	132·963	2·048	0·697	<0·001

days 150 and 225 (both $P < 0.001$; Table I). Regression slopes increased from 7·353 (day 150) to 13·631 (day 225) over the experiment, while intercept values decreased from 10·789 (day 150) to 8·173 (day 225). The slopes of the regression relationships between crude protein content and K were significantly different (ANCOVA, d.f. = 2, $P < 0.001$) among sampling periods.

Gross energy content of juvenile lake herring was positively correlated with K for each of the three sampling periods (ANOVA, $F_{1,44}$, all $P < 0.004$; Table I). Over the experimental period, the regression slopes increased from 4829·5 (day 75) to 14 976·6 (day 225) and values for the intercept variables decreased from 1393·3 (day 75) to −2860·3 (day 225). Regression relationship slopes between gross-energy content and K were significantly different (ANCOVA, d.f. = 2, $P < 0.001$) among days 75, 150 and 225. There was no significant relationship between ash content and K for juvenile lake herring on days 75, 150 and 225 of the laboratory experiment (ANOVA, $F_{1,44}$, all $P > 0.058$; Table I).

Water content was negatively correlated with K for juvenile lake herring on days 75, 150 and 225 of the laboratory experiment (ANOVA, $F_{1,44}$, all $P < 0.005$; Table I). Over the experimental period, the slope of the regression relationship decreased from −8·888 (day 75) to −27·189 (day 225) and the intercept values increased from 86·417 (day 75) to 93·222 (day 225). The slopes of the regression relationships between water content and K were significantly different (ANCOVA, d.f. = 2, $P < 0.001$) among days 75, 150 and 225.

RELATIONSHIP OF WATER TO PROXIMATE COMPOSITION COMPONENTS

Crude lipid content of juvenile lake herring was negatively correlated with water content for each of the three sampling periods (ANOVA, $F_{1,44}$, all $P < 0.039$; Table II). Regression slopes decreased from −0·478 (day 75) to −0·542 (day 225) over the experiment, while intercept values increased from 46·661 (day 75) to 49·698 and 49·032 (days 150 and 225, respectively). The slopes of the regression relationships between crude-lipid and water content were not significantly different (ANCOVA, d.f. = 2, $P < 0.001$) among days 75, 150 and 225.

Crude protein content of juvenile lake herring was negatively correlated with water content on days 75, 150 and 225 (ANOVA, $F_{1,44}$, all $P < 0.012$; Table II). Over the experimental period, the slope of the regression relationship decreased from −0·228 (day 75) to −0·486 (day 225) and the intercept values increased from 31·924 (day 75) to 53·699 (day 225). The slopes of the regression relationships between crude-protein and water content were significantly different (ANCOVA, d.f. = 2, $P < 0.001$) among sampling periods.

Gross energy content was negatively correlated with per cent water content for juvenile lake herring on days 75, 150 and 225 (ANOVA, $F_{1,44}$, all $P < 0.001$; Table II). The slope of the regression relationship decreased from −434·3 (day 75) to −540·4 (day 225) and the intercept values increased from 39 747·3 (day 75) to 47 674·8 (day 225) over the experimental period. The slopes of the regression relationships between gross-energy and water content were significantly different (ANCOVA, d.f. = 2, $P = 0.036$) among sampling periods.

TABLE II. Linear-regression variables of the relationships for crude lipid, crude protein, gross energy and ash content, and whole-body water content (W, %) for juvenile lake herring on days 75, 150 and 225 of the laboratory experiment. Crude lipid, crude protein, ash and water content were expressed as percentages of wet body mass, while gross energy was expressed as J g^{-1} wet body mass

Day of experiment	Linear-regression equation	MS error	S.E. of W	r^2	P
75	Crude lipid = 46·661 − 0·478W	14·34	1·671	0·262	0·039
	Crude protein = 31·924 − 0·228W	2·961	0·594	0·403	0·012
	Gross energy = 9493·5 − 103·74W	23876·5	154·526	0·665	<0·001
	Ash = 23·176 − 0·223W	6·446	2·289	0·579	0·285
150	Crude lipid = 49·698 − 0·532W	41·492	0·907	0·791	<0·001
	Crude protein = 41·164 − 0·331W	16·949	0·550	0·766	<0·001
	Gross energy = 11358·4 − 128·79W	10241·612	101·201	0·968	<0·001
	Ash = 11·672 − 0·087W	1·125	0·463	0·274	0·038
225	Crude lipid = 49·032 − 0·542W	56·34	0·960	0·815	<0·001
	Crude protein = 53·699 − 0·486W	45·421	0·571	0·907	<0·001
	Gross energy = 11386·9 − 129·06W	9695·38	98·465	0·960	<0·001
	Ash = 15·914 − 0·134W	3·465	0·895	0·246	0·048

Although ash content of juvenile lake herring was not significantly correlated with water content on day 75 (ANOVA, $F_{1,44}$, $P = 0{\cdot}285$), there was a positive correlation between these two variables on days 150 and 225 (ANOVA, $F_{1,44}$, both $P < 0{\cdot}048$; Table II). Regression slopes increased and intercept values decreased from days 150 (−0·087 and 11·672, respectively) to 225 (−0·134 and 15·914, respectively). The slopes of the regression relationships between ash and water content were not significantly different (ANCOVA, d.f. = 2, $P = 0{\cdot}165$) among sampling periods.

DISCUSSION

This study demonstrates that indices of condition, such as the K and per cent whole-body water content, can be used to accurately assess some proximate constituents of juvenile lake herring. These results agree with previous studies in which indices of condition have been used to estimate the proximate composition of juvenile fishes (Costopoulos & Fonds, 1989; Brown & Murphy, 1991; Foster *et al.*, 1993; Jonas *et al.*, 1996; Grant & Brown, 1999; Sutton *et al.*, 2000; Fitzgerald *et al.*, 2002). In addition, these indices can also be used to monitor temporal changes in the proximate composition of juvenile lake herring during periods of rapid energy change, such as the first winter of life. As a result, estimates of K and per cent whole-body water content can also be used as an indicator of the potential for winter survival and consequent recruitment to age 1 year (Wicker & Johnson, 1987; Thompson *et al.*, 1991; Miranda & Hubbard, 1994; Jonas *et al.*, 1996; Sutton *et al.*, 2000).

Results from previous studies have reported that lipid, protein and energy content are positively related to fish body condition (Costopoulos & Fonds, 1989; Brown & Murphy, 1991; Salam & Davies, 1994; Jonas *et al.*, 1996;

Lambert & Dutil, 1997; Grant & Brown, 1999; Sutton *et al*., 2000). Similar results were observed during the present study, as whole-body crude lipid and gross energy of juvenile lake herring were positively and significantly related to K on all sampling periods of the laboratory experiment. Although whole-body crude protein was also positively related to K, this relationship was not significant until day 150. Because lipids have a higher energy content than proteins (33 500 *v*. 29 600 J g^{-1}, respectively), they serve as the primary energy source utilized by fishes during periods of limited food availability and the first storage reserve utilized to meet metabolic demands (Pierce *et al*., 1980; Adams *et al*., 1982; Post & Evans, 1990). As a result, the continued utilization of this energy source by juvenile lake herring over the experiment is reflected by an increase in the slope of the lipid-condition relationship. Further, the utilization of proteins, as noted by the protein and condition regression relationship which was significant from day 150, also indicates a decline in the lipid reserves (Savitz, 1971; Costopoulos & Fonds, 1989; Kirjasniemi & Valtonen, 1997). Since proteins cannot sustain the energetic demands of fishes for prolonged periods of time, fishes must maintain a baseline level of lipid stores during periods of low energy consumption (Chang & Idler, 1960; Jobling, 1980; Hoar, 1983). Therefore, the protein content of fishes typically does not change until lipid reserves are depleted, at which point this component is catabolized to maintain basal metabolic processes (Jobling, 1980; Brown & Murphy, 1991; Sutton *et al*., 2000). Because lipid, and to some extent protein, comprise the primary energy sources in fishes, changes in the relationships of these two proximate-composition constituents are paralleled by similar changes in whole-body gross energy. As a result, it would appear that K can be used to estimate temporal changes in whole-body crude lipid, crude protein and gross energy for juvenile lake herring during winter periods.

Brown & Murphy (1991) reported that water content was inversely related to relative mass for juvenile striped bass and hybrid striped bass. The present results are in agreement with this study as whole-body water content of juvenile lake herring was inversely related to K. Further, per cent whole-body water content was a good predictor of whole-body crude lipid, crude protein and gross energy content of juvenile lake herring at all sampling periods. These results appear to be related to changes in proximate composition of juvenile lake herring. As fish energy stores are depleted through catabolism, they are gradually replaced by water due to large-scale cellular shrinkage that occurs with a concurrent increase in extracellular fluid (Idler & Bitners, 1959; Love, 1970; Niimi, 1972). Subsequently, the water content of juvenile lake herring in the present study increased as lipid, protein and gross-energy reserves were depleted over the winter period. Similarly, other studies have also shown an inverse relationship between lipid, protein and energy content with per cent body water in fishes (Love, 1970; Niimi, 1972; Craig *et al*., 1978; Flath & Diana, 1985; Brown & Murphy, 1991; Salam & Davies, 1994; Jonas *et al*., 1996; Sutton & Ney, 2001). These results suggest that the whole-body water can serve as a reliable estimator for temporal changes in whole-body crude lipid, crude protein and gross energy for juvenile lake herring during periods of limited energy uptake such as winter.

Depletion of lipid stores and energy density by juvenile fishes over the course of winter has been identified as a significant cause of mortality during this time period (Oliver *et al.*, 1979; Henderson *et al.*, 1988; Thompson *et al.*, 1991; Miranda & Hubbard, 1994; Johnson & Evans, 1996; Ludsin & DeVries, 1997; Fullerton *et al.*, 2000; Hurst *et al.*, 2000; Sutton & Ney, 2001). As a result, assessing declines in these energy stores over the winter can provide a mechanism for predicting year-class strength and recruitment to age 1 year. For the present study, the relationship between crude lipid, crude protein and gross energy content was strongly correlated to the two condition indices. Further, these relationships changed over the experiment as juvenile lake herring gradually depleted their energy stores (Pangle *et al.*, 2004). These differences are reflected by the progressive steepening of the regression coefficients between proximate composition and indices of condition. Similar changes between fish energy stores and body condition over the winter have been documented and directly linked to different utilization patterns of these storage reserves and subsequent rates of winter mortality between small and large individuals within an age-0 year cohort (Oliver *et al.*, 1979; Henderson *et al.*, 1988; Thompson *et al.*, 1991; Miranda & Hubbard, 1994; Cargnelli & Gross, 1997; Sutton & Ney, 2001).

Although the crude lipid, crude protein, and gross energy of juvenile lake herring were significantly correlated with *K* and per cent whole-body water content, the accuracy of both indices changed over the experimental period. With the exception of crude lipid on day 75 of the experiment, the correlation coefficients were greater for the proximate composition-water regression relative to those observed for *K*. Brown & Murphy (1991) found that water content more accurately estimated crude lipid and crude protein content of age-0 year striped bass and hybrid striped bass than relative mass. In addition, gross-energy content was more highly correlated to moisture content than the *K* for Atlantic cod (Lambert & Dutil, 1997). Jonas *et al.* (1996) found that seasonal trends in energy density of muskellunge were more accurately predicted with estimates of per cent water than *K* or relative mass. Therefore, the intrinsic attributes associated with water content indicate that this condition index is more robust against seasonal dynamics in proximate composition than *K*.

Indices of condition, such as the *K* and per cent whole-body water content, are reliable estimators of fish proximate composition. Because violations of the assumptions of these indices can bias subsequent results, however, caution must be used when evaluating temporal changes in these relationships. For example, *K* is based on the assumption that fishes exhibit isometric growth (*i.e.* the slope of the mass and length relationship = 3) and that deviations of the regression coefficients from this value do not result in length-dependent trends in condition (Bolger & Connolly, 1989; Anderson & Neumann, 1996). This assumption may be violated because fishes undergo different dimension changes over time resulting from allometric growth (Bagenal & Tesch, 1978). In the present study, *K* was independent of juvenile lake herring L_T throughout the duration of the laboratory experiment. Further, the regression coefficients between juvenile lake herring wet mass and L_T did not seriously deviate from a value of 3 (range, 2·99 to 3·20). Based on these results, the *K* serves as an unbiased index of condition for juvenile lake herring.

A caveat to the experimental design was combining lake herring in each aquarium for proximate-composition analyses. Although maintaining individual fish in separate tanks would have been the ideal situation, keeping multiple fish in each tank was necessary to allow lake herring to exhibit schooling behaviour as they would in Lake Superior at this life-history stage. Keeping individual lake herring in a tank would most probably have resulted in different responses as individual fish would have been stressed which might have caused greater reductions in proximate-composition variables. In order to avoid pseudo-replication, it was necessary to treat each tank as an experimental unit instead of each fish.

The results of this study demonstrate that *K* provides a viable alternative for the estimation of proximate composition of juvenile lake herring body tissues. In addition, measurements of per cent whole-body water content also provide an accurate means of estimating proximate-composition constituents for this species. Because estimates of body condition and water content can be used to reliably assess temporal changes in proximate composition, these indices could be used to monitor the status of age-0 year lake herring energy reserves. Further, mortality of lake herring during their first winter of life in Lake Superior is strongly dependent on physiological condition and adequacy of crude lipid, crude protein and gross energy stores (Pangle *et al.*, 2004).

We thank R. Kinnunen, W. Mattes and G. Fischer for assistance in the collection and incubation of the lake herring eggs used in this study. We would also like to acknowledge the efforts of L. Jefferson, J. Bobb, W. Shull, A. Benson, N. Gould and K. Wilson for their assistance in fish rearing and maintenance. Constructive comments on an earlier draft by R. Kinnunen, M. Bremigan, B. Young, D. Daugherty and E. Volkman improved this manuscript. Funding for this study was provided by the Michigan Sea Grant College Program and the Purdue University Department of Forestry and Natural Resources. This research was approved for publication as manuscript 17406 by the Purdue University Agricultural Research Program.

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