

Relationships Between Body Condition Indices and Proximate Composition in Adult Walleyes

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Abstract.—Relationships between indices of condition and measures of proximate body composition were examined among and within nine populations of mature walleyes *Sander vitreus* that varied widely in growth rate and lipid status. Body condition, measured as the residuals from mass versus length regressions, was negatively related to mean water content and positively related to mean lipid content among populations. When the roles of water and lipid content were examined simultaneously within populations, most of the variance in condition was accounted for by lipid content. The strength of the relationships between various condition indices and body proximate composition varied considerably among populations but less between sexes within populations. Furthermore, the strength and nature of these relationships was not strongly influenced by the choice of mass-at-length index (residuals, relative condition, relative weight, or Fulton's *K*). The visceral-somatic index and muscle lipid content both exhibited slightly stronger relationships with body proximate composition than did mass-at-length condition indices for both sexes. The hepatosomatic index was more consistently related to somatic lipid content for females than for males in most populations. Relatively simple condition indices can provide reliable surrogates of body proximate composition in many adult walleye populations, but caution should be exercised in extrapolating from condition-composition relationships among populations.

The term “condition” is widely used in ecological studies to refer to the state of an animal's general health or, more commonly, its energy or nutrient reserves (Schulte-Hostedde et al. 2005). High body condition (i.e., high energy or nutrient reserves) is thought to be a direct consequence of an animal's ability to acquire resources (Baker 1989), which can then be used to meet the energetic demands of increased fitness (Jakob et al. 1996). Animals of higher condition are expected to have greater probabilities of survival and future reproductive success. Thus, condition is of interest to a variety of research questions. Though simple in concept, condition is not necessarily simple to

determine directly. Some measures of an animal's condition, such as whole-body lipid content or energy density, require lethal sampling followed by considerable tissue processing and analysis. This has led some to use nonlethal and simpler alternate measures of condition.

A condition index is a measure of an individual's relative plumpness and is usually estimated as the observed mass of an individual relative to a standard or predicted mass. Condition indices differ from each other in how the mass of the standard individual is calculated and in how the two masses are compared (i.e., difference or ratio). The standard mass is usually predicted from a theoretical or empirical relationship between body mass and some linear measure of body size. In animal ecology there has been considerable debate around the appropriate linear measure of body

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size to use in estimating mass at size (Green 2001; Schulte-Hostedde et al. 2005). Conversely, in fisheries research, predicted mass is almost always estimated from some measure of body length (total, fork, or standard). For example, one of the most common condition indices used in fisheries research, Fulton's condition factor (K), is calculated as the ratio of the mass of an individual to the cube of its length (Ricker 1975). Two similar indices, relative condition (Le Cren 1951) and relative weight (Murphy et al. 1990), are ratios of the mass of an individual to the predicted mass for its length based on a sample-specific (relative condition) or species-specific (relative weight) mass-length regression. The merits and shortcomings of each of these indices have been critiqued previously (Bolger and Connolly 1989; Cone 1989; Springer et al. 1990). However, the value of condition indices to ecological research ultimately depends on how well they reflect the particular body traits of interest.

Lipids are the primary energy storage material in fish (Love 1970; Adams 1999; Tocher 2003). Thus, the lipid content of a fish indicates the surplus energy available for future maintenance, growth, and reproduction. Lipid content is a good index of future survival in some species (Simpkins et al. 2003) and a strong indicator of reproductive potential in some fish stocks (Marshall et al. 1999). It is often assumed or implied that body condition indices are good indicators of the lipid status and, hence, energetic status of fish. Though several studies have quantified the relationships between condition indices and fish proximate composition (Lambert and Dutil 1997; Sutton et al. 2000; Simpkins et al. 2003; Brown and Murphy 2004; Copeland and Carline 2004; Pangle and Sutton 2005), relatively few have examined adult life stages, and fewer have compared the relationships between sexes or among populations that may store or use nutrient reserves in different manners. Further research is required to assess both the strength and the generality of relationships between condition indices and body composition in fish.

The objective of this study was to examine the relationships between a variety of condition indices and measures of proximate body composition, particularly lipid, in a freshwater fish, the walleye *Sander vitreus*. Our prediction was that if these indices truly reflect energetic status, then adult walleyes of higher condition should have proximate body compositions that are relatively high in energy-dense constituents, namely lipids, and relatively low in energy-poor constituents, such as water. We examined the generality of these relationships in several ways. First, we used a variety of condition indices that differed in data requirements and derivation. Second, we used data from both male

and female walleyes from a range of populations differing greatly in body composition. Finally, we examined the condition versus composition question at two spatial scales: among populations and among individuals within populations.

Methods

Field sampling.—Mature walleyes were sampled from nine diverse populations across Canada. We selected populations across wide gradients of both climate and exploitation history (Table 1) in an attempt to maximize the observed variation in growth, body condition, and lipid content. To reduce seasonal variation, all sampling was carried out on spawning aggregations of adults over a short period in the spring (early April in the south to late May in the far north). Most populations were sampled immediately before or during the spawn, such that most females had fully developed but unovulated gonads. However, two populations (Tathlina and Orange lakes) could only be sampled immediately after the spawn when all females were spent. Fish were captured using dip nets, trap nets, or gill nets. Roughly equal numbers of mature males and females were selected impartially, except with respect to body size; for each population, we deliberately attempted to obtain a wide length range for both sexes. All individuals were killed by a blow to the head and packed on ice or frozen before transport to the laboratory.

Laboratory analyses.—Each individual was weighed (wet mass; ± 10 g) and measured (fork length [FL]; mm). Testes were removed, weighed wet (± 0.1 g), and frozen at -20°C in a small plastic bag. Ovaries were removed and weighed whole (g wet weight); then a subsample (~ 30 g) of ovary was removed from the midregion, weighed wet (± 0.1 g), placed in a small plastic bag, and frozen at -20°C . For both sexes, the carcass was then weighed wet without gonads (somatic mass; ± 10 g wet weight); the liver was then removed, weighed wet (± 0.1 g), placed in a small plastic bag, and frozen at -20°C . Most fish had empty stomachs at capture. However, if stomach contents were evident, these were removed, weighed wet (g), and the mass was subtracted from the total and somatic mass measurements. The carcass was weighed wet a final time following the removal of all remaining viscera except the heart and kidneys (eviscerated mass; ± 10 g). A subsample of skinless muscle (~ 30 g) was removed from alongside the first dorsal fin just above the lateral line, weighed wet (± 0.1 g), placed in a small plastic bag, and frozen at -20°C . Sagittal otoliths were removed, rubbed clean, then placed into 5-mL plastic vials and allowed to air dry. Opercle bones were removed and frozen. The remaining carcass was then

TABLE 1.—Descriptive data for nine diverse walleye populations sampled across Canada. Populations are listed from north to south. Climate was expressed as mean annual growing degree-days (GDD) above 5°C over the period 1971–2000 (data from Environment Canada). Recent exploitation history was categorized as high or low based on observations of regional fishery managers.

Population (lake)	Coordinates	GDD	Exploitation history	Year(s) sampled	Number sampled	
					Females	Males
1. Trout	60°30', 121°30'	1,225	Low	2002–2003	78	64
2. Tathlina	60°30', 117°55'	1,225	High	2003	16	6
3. Winefred	55°20', 110°40'	1,365	High	2004	39	41
4. Orange	51°14', 94°32'	1,532	Low	2004	21	30
5. Winnipeg	51°01', 96°53'	1,551	High	2002–2004	82	97
6. Lake of the Woods	49°00', 95°00'	1,711	High	2004	40	16
7. Beauchêne	46°30', 78°45'	1,642	Low	2002	40	40
8. Nipissing	46°12', 79°24'	1,682	High	2002–2005	74	88
9. Ontario	44°00', 76°40'	2,145	High	2002–2005	112	80

placed in a large plastic bag with the viscera except the liver, and frozen at -20°C .

All fish tissues underwent further processing before total lipid analyses. Carcasses with their viscera were thawed, cut coarsely into pieces, and homogenized by passing three times through a commercial stainless steel meat grinder. A subsample (~ 25 g) of the homogenate was weighed wet (± 0.1 g), placed in a glass vial, and frozen at -20°C . Ovary, testis, liver, muscle, and carcass homogenate samples were all freeze-dried for 7 d and reweighed dry (± 0.1 g) to estimate water content. All freeze-dried tissues were then reduced to a coarse powder in a ball mill (Retsch MM301).

The total lipid content of the freeze-dried tissues was determined gravimetrically using a chloroform : methanol extraction procedure modified from earlier studies (Folch et al. 1957; Herbes and Allen 1983). An aliquot of the powdered tissue (~ 0.20 g) was weighed (± 0.0001 g) into a 15-mL glass centrifuge tube to which 5 mL of chloroform–methanol solvent (2:1 by volume) was added to the tissue; the tube was sealed with a Teflon-lined cap. After soaking overnight (> 12 h) the mixture was centrifuged (10 min at $1,000 \times$ gravity). The supernatant was transferred to a second centrifuge tube (hereafter, the supernatant tube) by glass pipette, and 1 mL of chloroform–methanol solvent was then rinsed through the pipette into the supernatant tube. The residue in the first centrifuge tube received an additional 3 mL of chloroform–methanol and was centrifuged again. The resulting supernatant was added to the supernatant tube followed by another 1 mL of solvent for rinsing the pipette (total supernatant volume, ~ 10 mL). The solvent and lipid mixture was washed by adding 2.5 mL of 0.88% KCl (0.88 g KCl in 100 mL distilled water) solution to the supernatant tube, agitating on a wrist-action shaker (15 min), then centrifuging (10 min at $1,000 \times$ gravity).

After drawing off and discarding the upper aqueous layer, the lower solvent layer was transferred by glass pipette to a preweighed (± 0.0001 g) aluminum pan, and the pipette was rinsed twice (1 mL solvent each) into the pan. Pans were placed in a fume hood at room temperature for about 1 h to allow the solvent to evaporate, transferred to a desiccator for about 1 h, and then weighed (± 0.0001 g) to determine lipid mass. Two extractions were performed for all samples, and a third was carried out if the coefficient of variation for the first two exceeded 10%.

The water and lipid contents of each fish were estimated at four levels: whole body, soma (body minus gonads), liver, and muscle. Lipid content was estimated on a dry-mass basis ($100 \cdot \text{lipid [g]}/\text{dry tissue [g]}$) and then converted to a wet-mass basis ($100 \cdot \text{lipid}/\text{wet tissue}$) using the corresponding water content. The whole-body and somatic water and lipid contents were reconstructed from the masses and the water and lipid contents of the component tissue samples.

Ages were primarily determined by counting annuli on sagittal otoliths. Dried otoliths were set in epoxy, and transverse 360- μm (SD, 30) sections were cut through the nucleus using a Buehler Isomet low-speed saw. These sections or acetate replicas of these sections were interpreted following standard procedures (i.e., techniques already validated with known-age walleyes extant in natural environments for 2–8 years; Casselman 1987; Casselman and Gunn 1992). Where ages could not be determined from otoliths (< 10 fish), annuli were read from opercle bones. Opercles were soaked in hot water to remove all flesh, air-dried, and read under a dissecting microscope with reflected light. When counting annuli, the outer edge of the otolith or opercle was always counted as a complete annulus because individuals were collected at spawning time (i.e., near their birthdates). One of our sample populations, Lake Winnipeg, contained both normal

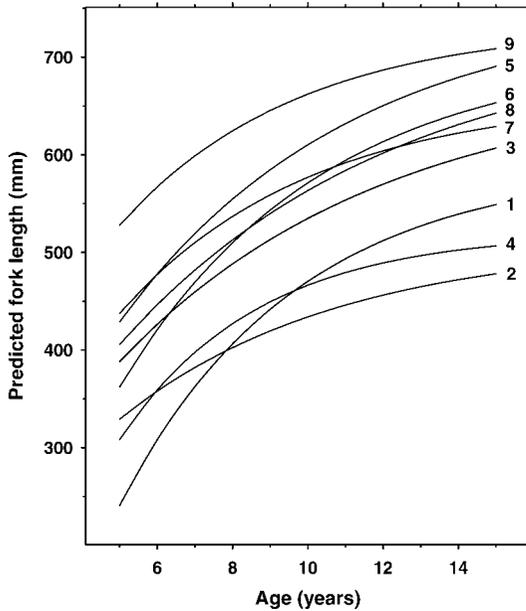


FIGURE 1.—Predicted fork-length-at-age relationships from a von Bertalanffy growth model for female walleyes from nine populations across Canada (Table 1).

and slow-growing (dwarf) walleye morphotypes (W. Lysack, Manitoba Conservation, Winnipeg, unpublished data). For the purposes of this study, we restricted our analyses to the normal form. Normal fish were separated from dwarf fish based on size-at-age criteria (Moles 2006).

Statistical analyses.—We examined fork-length-at-age relationships using the von Bertalanffy growth model (Ricker 1975) fitted by nonlinear least-squares (NLIN procedure; SAS Institute 1999). For analyses of mass we used somatic mass (m_s [total body mass minus gonad mass]). This closely corresponds to body mass in the immediate postspawn period for both sexes. The mass-length relationship in fish is log-linear. Consistencies in the relation of $\log_e(m_s)$ versus $\log_e(\text{FL})$ between sexes and among populations were examined via analyses of covariance (ANCOVA). These results were used to determine the level at which the data could be pooled in subsequent analyses.

We evaluated several different indices of condition that varied in the complexity of their data requirements. Our primary condition index, residual $\log_e(m_s)$, was estimated from the least-squares-fitted relation of $\log_e(m_s)$ to $\log_e(\text{FL})$. Because it is a residual, this index of condition is not correlated with body size (i.e., with $\log_e[\text{FL}]$). We also evaluated three other commonly used condition indices derived from mass and length data, namely, relative condition, relative weight

(W_r), and Fulton's K . Relative condition was estimated as the ratio of observed $\log_e(m_s)$ to predicted $\log_e(m_s)$ as estimated from the fitted relation of $\log_e(m_s)$ to $\log_e(\text{FL})$. Thus, both residual $\log_e(m_s)$ and relative condition were calculated from the same observed and predicted mass values. Relative weight was estimated as the ratio of observed m_s to predicted m_s , where the latter was estimated from a mass-length relationship developed from multiple walleye populations (Murphy et al. 1990). Fulton's K was calculated as the ratio of m_s to the cube of fork length (g/cm^3). Several alternate indices of condition were derived from body processing and proximate composition data. Because walleye store much of their lipids as visceral fat (Henderson et al. 1996) an index of visceral mass may prove to be a useful measure of condition for this species (Henderson and Morgan 2002). We estimated the visceral-somatic index (VSI), as the ratio of viscera mass (m_s minus eviscerated mass) to m_s expressed as a percentage. We also examined the usefulness of the hepatosomatic index (HSI; ratio of liver mass to m_s), liver lipid content, and muscle lipid content as indices of somatic body composition.

The relationships between the condition indices and body lipid and water contents were examined using multiple regression analyses (REG procedure; SAS Institute 1999). Residual somatic mass and relative condition were always calculated using mass-length relationships at the appropriate spatial scale (within or among sexes and populations) for the particular analysis. The relative strengths of the relationships between the condition indices and lipid and water contents were assessed using partial R^2 -values.

Results

A total of 964 mature walleyes were sampled during spring from the nine populations (Table 1). Mature males averaged 454 mm FL; females were 561 mm. Four of the nine populations were sampled in multiple years, and data were pooled across years within each of these populations. Thermal inputs (growing degree-days of $>5^\circ\text{C}$) to the water bodies inhabited by these populations declined by more than 50% from south to north, and the recent exploitation pressure on these populations ranged from negligible (Orange Lake) to heavy (Lake Winnipeg; Table 1). Across these gradients, the walleye populations varied substantially in growth (Figure 1) and body lipid content (Figure 2). In general, growth rates declined from south to north, but there was considerable variation (Figure 1). Body lipid content did not appear to be strongly related to latitude or climate but to exploitation; heavily exploited populations tended to have higher body lipid content

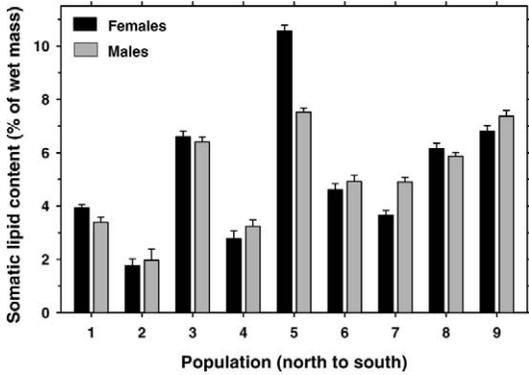


FIGURE 2.—Mean + SE somatic lipid content for male and female walleyes from nine populations across Canada (Table 1).

than lightly exploited populations, although Tathlina Lake walleyes did not conform to this trend (Figure 2).

The slopes of the relation of $\log_e(m_s)$ to $\log_e(FL)$ did not differ significantly between males and females in any of the nine populations examined (ANCOVA, heterogeneity of slopes: $F < 2.7, P > 0.09$), but elevations of these relationships did differ significantly between sexes in three of the nine populations (ANCOVA: $F > 9, P < 0.001$). In all three cases, males had higher somatic mass at length than females. All subsequent analyses were conducted separately for the two sexes.

Among-population relationships between mean somatic lipid and water content and mean condition expressed as residual $\log_e(m_s)$ supported our predictions. Residual $\log_e(m_s)$ was positively correlated with somatic lipid content in both females ($r = 0.85, N = 9, P = 0.0040$; Figure 3) and males ($r = 0.91, N = 9, P < 0.001$) and was negatively correlated with somatic water content in both females ($r = -0.78, N = 9, P = 0.014$) and males ($r = -0.88, N = 9, P = 0.0019$). Overall, walleye populations with higher mean mass at length tended to have both higher mean lipid content and lower mean water content.

We next examined the relative importance of water and lipid contents to the variation in condition at the gender \times population level. In multiple regression analyses, body lipid content explained greater amounts of variation in residual $\log_e(m_s)$ than did body water content, and this was fairly consistent among populations (Table 2). Relationships between condition and body lipid were slightly more consistent in females than in males; condition was significantly related to body lipid content in eight of nine populations for females but in only five of nine populations for males. Where the relationship was significant, it was always positive. In contrast, body water content rarely

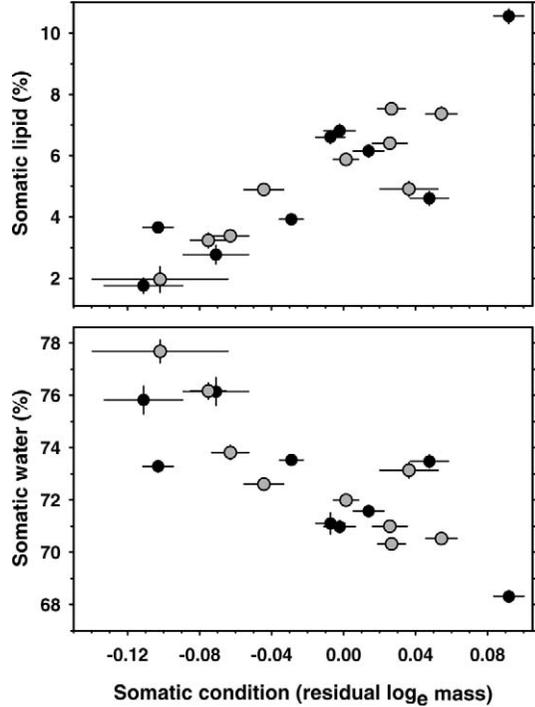


FIGURE 3.—Scatterplots of somatic lipid content and somatic water content versus somatic condition (mean \pm SE) for male (grey circles) and female walleyes (black circles) from nine populations across Canada. Somatic condition is expressed in terms of the residuals from a regression of $\log_e(\text{somatic mass})$ on $\log_e(\text{fork length})$ with pooled data.

accounted for any significant amount of the remaining variation in residual $\log_e(m_s)$, and the nature of the relationship was variable. There was no indication that either the strength or nature of these relationships was related to the growth characteristics or lipid status of the populations.

We examined the robustness of the observed relationships with respect to changes in the calculation of the condition index and body proximate composition. First, we recalculated the residual condition index and body lipid content on a whole-body rather than a somatic basis. Total body mass was substantially larger ($>5\%$) than somatic mass only for prespawm, unovulated females, and thus we limited our comparison to this group of fish. For the seven of nine populations with sufficient sample sizes of unovulated females, there was no marked difference in the outcomes of the multiple regression analyses between somatic-based and whole-body-based measurements (Table 3). We used somatic-based measures for all subsequent analyses.

The observed relationships between mass-at-length

TABLE 2.—Results of multiple regression of somatic condition (residual \log_e [somatic mass]) on both percent water and percent lipid (wet mass basis) in the soma for adult walleyes from each of nine populations. Condition indices were calculated at the population \times gender level. Regression coefficient signs indicate the slope or nature of the relationships, and the partial R^2 values indicate the percent of the variance explained for each of the independent variables. Significant coefficients (partial- F test; $P < 0.05$) are indicated by asterisks.

Population	Females				Males			
	Water		Lipid		Water		Lipid	
	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2
1. Trout	–	1.5	+	9.9*	–	0.9	+	38.0*
2. Tathlina	–	2.7	+	13.7	+	8.8	+	2.8
3. Winefred	+	1.7	+	18.6*	+	3.5	+	4.4
4. Orange	–	0.0	+	24.6*	+	0.2	+	9.8
5. Winnipeg	–	0.0	+	23.2*	+	0.3	+	38.0*
6. Lake of the Woods	+	1.9	+	12.2*	–	6.0	–	21.4
7. Beauchêne	+	0.3	+	28.9*	+	0.0	+	25.6*
8. Nipissing	–	0.0	+	11.6*	–	1.0	+	30.0*
9. Ontario	+	0.8	+	4.8*	+	4.1*	+	41.0*

condition indices and proximate composition were not strongly influenced by the choice of index. Condition expressed as relative weight was significantly and positively related to somatic lipid content in six of nine populations for females and in five of nine populations for males (Table 4). These results did not differ greatly from those observed for residual somatic mass (see Tables 2 and 4). Similarly, when either relative condition or Fulton's K were used as the condition index the outcomes of multiple regression analyses were nearly identical to those obtained for residual somatic mass for all sex \times population combinations.

The VSI was significantly and positively related to somatic lipid content in seven of nine populations for both males and females (Table 5). As with residual condition, somatic water content did not account for significant amounts of the remaining variation in VSI in females. However, somatic water content did account for significant remaining variation in VSI in

two of nine populations of males. The relationships between somatic proximate composition and VSI appeared to be stronger (based on partial R^2) than those for residual condition in some populations (Lake of the Woods, Winefred) but weaker in others (Beauchêne; see Tables 2, 5). As an index of somatic lipid content, VSI appeared to work equally well for both sexes (Table 5). In contrast, the relationships between HSI and somatic lipid content were more consistently positive and significant for females but not for males (Table 6). There was no clear indication that either the strength or nature of these relationships was related to the growth characteristics or lipid status of the populations.

The lipid content of liver and muscle tissues varied in their value as measures of condition. Liver lipid content appeared to be a poor index of body condition. The only observed significant relationships (partial F -test; $P < 0.05$) between liver lipid content and somatic

TABLE 3.—Results of regression analyses for condition, estimated as residual \log_e (mass), as a function of water and lipid concentrations. As only prespaw, unovulated females were used in this analysis, no data are available for Tathlina or Orange lakes). Condition indices were calculated at the population level. See Table 2 for additional details.

Population	Somatic condition				Whole-body condition			
	Water		Lipid		Water		Lipid	
	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2
1. Trout	+	0.0	+	3.4	+	0.0	+	6.0
2. Tathlina								
3. Winefred	+	2.2	+	19.1*	+	5.0	+	28.0*
4. Orange								
5. Winnipeg	–	0.2	+	20.9*	+	0.2	+	15.7*
6. Lake of the Woods	+	1.0	+	12.7*	+	3.9	+	17.3*
7. Beauchêne	+	0.0	+	23.8*	–	0.1	+	25.5*
8. Nipissing	+	1.4	+	22.4*	+	2.2	+	16.4*
9. Ontario	–	0.0	–	1.1	–	1.4	–	3.0

TABLE 4.—Results of multiple regression of relative weight (W_r) on percent water and percent lipid (wet mass basis) in the soma for adult walleyes from nine populations across Canada. See Table 2 for additional details.

Population	Females				Males			
	Water		Lipid		Water		Lipid	
	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2
1. Trout	–	1.9	+	19.0*	–	0.2	+	44.8*
2. Tathlina	–	5.2	+	20.4	+	4.3	+	29.1
3. Winefred	+	1.8	+	18.3*	+	0.8	+	4.0
4. Orange	+	0.3	+	16.1	+	0.5	+	5.8
5. Winnipeg	–	0.4	+	20.5*	–	0.2	+	20.8*
6. Lake of the Woods	+	3.1	+	8.9	–	21.7	–	7.0
7. Beauchêne	+	2.8	+	33.3*	+	0.2	+	18.8*
8. Nipissing	+	0.0	+	11.2*	–	0.7	+	29.4*
9. Ontario	+	0.7	+	10.3*	+	4.4*	+	41.8*

proximate composition were with somatic water content in Lake Winnipeg males and females and with somatic water content in Lake Ontario females. Relationships between liver and somatic lipid contents were weak and nonsignificant (partial F -test; $P > 0.05$) for both sexes in all populations. In contrast, muscle lipid content was a much better index of somatic proximate composition. For females, muscle lipid content was significantly and positively related to somatic lipid content in all nine populations, somatic water content accounting for a significant part of the remaining variation in only one of these populations (Table 7). For males, muscle lipid content was significantly and positively related to somatic lipid content in six of nine populations and significantly and negatively related to somatic water content in the remaining three populations. Total variance explained by proximate composition was generally higher for muscle lipid content than for residual somatic condition (see Tables 2 and 7), and this trend was most pronounced in populations with low somatic lipid content (Tathlina, Orange, and Beauchêne).

Discussion

Condition indices derived from mass and length data provide a simple index of the relative tissue mass carried by an organism of a given size. The interpretation of differences in condition indices depends, in part, on how biochemical composition varies between high and low mass at length. If concentrations of high energy constituents, namely lipid, are positively related to mass at length and (or) concentrations of low energy constituents, such as water, are negatively related to mass at length, then the condition index will reflect differences in energetic status. In contrast, if tissue proximate composition does not vary with mass at length, the condition index will reflect differences in body form more than in energetic status. However, given two individuals of equal length and identical proximate composition, the heavier individual will have greater energy reserves, simply by virtue of its larger absolute mass. Nevertheless, the strength of relationships between condition indices and proximate composition can indicate the relative importance of energy storage to differences in mass at length.

TABLE 5.—Results of multiple regression of the visceral somatic index on percent water and percent lipid (wet mass basis) in the soma for adult walleyes from nine populations across Canada. See Table 2 for additional details.

Population	Females				Males			
	Water		Lipid		Water		Lipid	
	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2
1. Trout	–	1.1	+	16.8*	+	3.7	+	33.6*
2. Tathlina	–	0.0	+	14.3	+	54.5	+	1.6
3. Winefred	+	5.1	+	46.6*	+	8.6*	+	37.5*
4. Orange	+	0.2	+	22.3*	+	1.1	+	30.6*
5. Winnipeg	–	0.0	+	56.2*	–	1.4	+	31.0*
6. Lake of the Woods	+	4.8	+	50.6*	–	0.1	+	36.9*
7. Beauchêne	+	0.1	+	4.3	+	4.9	+	4.5
8. Nipissing	–	0.3	+	50.6*	+	8.1*	+	20.1*
9. Ontario	+	1.8	+	27.6*	+	1.6	+	32.2*

TABLE 6.—Results of multiple regression of the hepatosomatic index on percent water and percent lipid (wet mass basis) in the soma for adult walleyes from nine populations across Canada. See Table 2 for additional details.

Population	Females				Males			
	Water		Lipid		Water		Lipid	
	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2
1. Trout	+	2.4	+	8.3*	-	0.2	+	40.9*
2. Tathlina	-	10.0	-	5.2	+	5.6	+	83.8*
3. Winefred	+	0.0	+	2.5	+	8.8	+	5.8
4. Orange	-	0.1	+	24.1*	-	9.5	+	0.3
5. Winnipeg	-	0.0	+	8.9*	+	1.7	+	0.6
6. Lake of the Woods	+	0.3	+	17.4*	-	11.7	-	0.2
7. Beauchêne	+	1.6	+	23.6*	-	1.4	-	0.2
8. Nipissing	+	0.1	+	18.5*	+	3.0	+	4.9*
9. Ontario	+	0.2	+	6.4*	+	1.5	+	7.1*

We found that simple condition indices derived from mass and length data were significantly related to the proximate composition of adult walleyes at two spatial scales. Among populations, mean somatic lipid content increased and mean somatic water content decreased with increasing body condition. Thus, differences in condition among walleye populations are related, at least in part, to the energetic status of the fish; high-condition walleye populations contain energetically richer fish. These trends were also evident among individuals within populations, though the strengths of the relationships varied somewhat between sexes and among the populations. Our analyses indicated that where both water and lipid contents were regressed against condition, only one of these usually accounted for significant variance in condition; in most cases, lipid content accounted for the greatest variation. The well-documented negative relationship between lipid and water contents assumes that lipid and water are interchangeable in the cell, dependent on the energetic state of the fish (Idler and Bitners 1959; Love 1970), and thus tissue water content has been used as a surrogate for lipid or energy content in a variety of fish

species (Lambert and Dutil 1997; Plante et al. 2005; Trudel et al. 2005).

Previous research into the relationships between body condition indices and proximate composition has demonstrated considerable interspecific variation. In juvenile walleyes, the relationship between mass-at-length condition indices and body lipid content was found to be positive but weak (Copeland and Carline 2004). Proximate composition related well to Fulton's K in overwintering juvenile cisco *Coregonus artedii* (Pangle and Sutton 2005) and in northern pike *Esox lucius* (Salam and Davies 1994). In contrast, condition indices were considered poor predictors of body lipid content in fasting juvenile rainbow trout *Oncorhynchus mykiss* (Simpkins et al. 2003) and in juvenile Pacific salmon (Trudel et al. 2005). This variability suggests that energy storage strategies may differ among fish species. Energy storage strategies may also differ ontogenetically as energy allocation shifts from growth to reproduction. Many of these earlier studies focused on juvenile life stages. The current study is one of the few to examine relationships between condition and proximate composition in a range of adult populations.

TABLE 7.—Results of multiple regression of percent lipid (wet mass basis) in muscle on percent water and percent lipid (wet mass basis) in the soma for adult walleyes from nine populations across Canada. See Table 2 for additional details.

Population	Females				Males			
	Water		Lipid		Water		Lipid	
	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2	Sign	Partial R^2
1. Trout	+	0.5	+	50.6*	-	2.1	+	14.2*
2. Tathlina	+	0.1	+	67.3*	+	5.3	+	84.0*
3. Winefred	+	0.3	+	14.3*	-	0.1	+	27.8*
4. Orange	+	5.5	+	39.9*	-	1.3	+	71.6*
5. Winnipeg	-	0.1	+	18.8*	-	15.5*	+	1.2
6. Lake of the Woods	+	17.4*	+	13.0*	-	29.6*	+	1.2
7. Beauchêne	+	0.5	+	39.8*	+	0.7	+	29.4*
8. Nipissing	-	0.9	+	11.0*	-	0.7	+	23.6*
9. Ontario	-	0.8	+	16.6*	-	18.0*	-	2.4

We conducted our analyses separately for each of the sexes and populations to assess patterns in variability of the observed relationships. Previous research on juvenile walleyes had indicated considerable variation in these relationships among populations (Copeland and Carline 2004). We found that the strengths of the relationships between condition and proximate composition of adult walleyes were highly variable for both sexes but, particularly for males. There was no clear indication that the relationships were stronger for one sex than the other. Our expectation was that the strength of the relationship between condition and lipid content would vary with the overall lipid status of the population because of relative differences in the anabolism and catabolism of various body constituents for fish with high and low body reserves. Though we sampled walleye populations that varied widely in overall proximate composition, we found no evidence that this may have influenced the strength of condition versus proximate composition relationships within the populations.

Mass-at-length condition indices are popular in fisheries research because they are easy to measure and do not require lethal sampling. They also allow comparisons of condition over longer time scales because historical data sets usually contain mass and length data but lack proximate composition data. However, not all mass-at-length condition indices may be related to body composition or energetic status in the same manner. For example, in juvenile muskellunge *Esox masquinongy*, energy density related equally well to Fulton's K and relative weight (Jonas et al. 1996), whereas in juvenile Atlantic salmon *Salmo salar*, residualized fat weight correlated well with relative condition factor but not with Fulton's K (Sutton et al. 2000). We found that the relationships between mass-at-length condition indices and body proximate composition in adult walleyes were not greatly influenced by our choice of mass-at-length index. Residual somatic mass, relative condition, relative weight, and Fulton's K were all related to proximate composition in a similar manner. This similarity may be because the slope of the relation of $\log_e(\text{mass})$ to $\log_e(\text{length})$ in most of our study populations was similar to the fixed-slope values used to estimate relative weight ($b = 3.18$) and Fulton's K ($b = 3$). In situations where the fitted slope deviates greatly from the fixed slope value used in the condition index denominator, the condition index will be correlated with body size. This potential correlation of relative weight or Fulton's K with body size could confound its relationship with body proximate composition because proximate composition can vary with

body size alone in some species (Salam and Davies 1994; Brown and Murphy 2004).

Other nonlethal body measurement techniques have been employed to assess body composition in fish. Linear body measurements related well to lipid content in young Arctic char *Salvelinus alpinus*, but the relationship varied considerably among populations (Rikardsen and Johansen 2003). Fitzgerald et al. (2002) used truss (shape) analysis to assess condition of yellow perch *Perca flavescens*. Newer, nonlethal techniques for assessing the proximate composition or energy content of fish include bioelectrical impedance analysis (Cox and Hartman 2005) and microwave energy measurement (Crossin and Hinch 2005). Both techniques have been applied on salmonids and the latter technique appears to provide very consistent estimates of energy content among stocks and sampling years (Crossin and Hinch 2005). It is unknown if the utility of these techniques will differ among species that have different body distributions of the proximate constituents.

We compared our results from analyses with nonlethal, mass-at-length condition indices with those of indices requiring lethal sampling and greater tissue processing. The strength of the relationships between these indices and body proximate composition must be put in perspective with the extra effort required to derive them. We found that VSI and muscle lipid content exhibited relationships with adult walleye proximate composition that were comparable to or slightly stronger than those observed with mass-at-length condition indices for both sexes. In contrast, HSI was a reasonable predictor of overall proximate composition for females only, and liver lipid content was a very poor predictor for both sexes. The relatively strong predictive power of VSI is not surprising because walleyes store much of their lipids in the viscera (Henderson and Morgan 2002). Similarly, the weak predictive power of liver lipid content was also not surprising because these lipid stores have been shown to be highly transitory in other species (Sheridan et al. 1983; Plante et al. 2005). In contrast, the strong relationships observed between muscle lipid content and body proximate composition were somewhat surprising because the muscle has not been previously recognized as a major lipid storage depot in this species. It is likely that the usefulness of VSI, HSI, liver lipid, and muscle lipid as indices of condition will vary among fish species in accordance with their particular lipid storage strategies.

We have demonstrated that a variety of measures of body condition are related to somatic proximate composition in diverse populations of adult walleyes. However, the strengths of these empirical relationships

vary somewhat among indices and among populations, and caution should be exercised in extrapolating results from one population to another. In general, variation in nonlethal mass-at-length condition indices was strongly related to body proximate composition. Some indices requiring more laborious derivations, such as VSI or muscle lipid content, may be marginally better predictors of body proximate composition in some populations. We conclude that mass-at-length condition indices can serve as useful indices of proximate composition and energetic status in many adult walleye populations, but the relationship may need to be calibrated on a population-by-population basis.

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