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ARTICLE

Condition Indices as Surrogates of Energy Density and Lipid Content in Juveniles of Three Fish Species

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Abstract

To guide the selection of condition indices for juvenile fishes, we compared the ability of several indirect condition indices (those based on length–mass relationships, the hepatosomatic index, and relative lipid estimates from the Distell fish fatmeter) to assess energy density and lipid content of Summer Flounder *Paralichthys dentatus*, Striped Bass *Morone saxatilis*, and Atlantic Croakers *Micropogonias undulatus*. These species use estuarine areas as nurseries, but they have different life history strategies and ecological niches that affect their energy storage strategies. We tested hypotheses that differences in the distribution and role of lipids as energy stores among species would influence the suitability of condition indices for estimating energy and lipid content. Length-based indices were most suitable for estimating energy and lipid content of juvenile Summer Flounder and Striped Bass, suggesting that length-based indices may be appropriate for juveniles that store energy as proteins (i.e., juveniles with low lipid content). The fatmeter suitably predicted energy and lipid content of Atlantic Croakers, indicating its potential for assessing condition of juveniles that store lipids for migration and that display a high range of observed lipid content. Even though a small size range was examined, fish length improved predictions of energy and lipid content for some of the indirect condition indices for Atlantic Croakers and Summer Flounder, suggesting that fish length should be considered when developing relationships among measures of condition. The selection of condition indices should be tailored to the life stage and species of interest based on the energy and lipid storage strategies used by the fish.

Condition is often used to describe the general health and nutritional status of individual fish and fish populations (Bolger and Connolly 1989; Goede and Barton 1990; Brown and Murphy 2004; Lloret et al. 2014). Indices of condition have been associated with growth (Adams and McLean 1985; Gabelhouse 1991), swimming performance (Kolok 1992; Martinez et al. 2003), and other measures of fitness. These associations are based on the premise that the condition of an individual is correlated with its energy or lipid stores, yet this assumption is not routinely examined among species, particularly for juvenile stages. In addition to fitness, the energy density and lipid content of an individual are related to its survival. In both laboratory and wild settings, higher lipid content is associated with improved survival of larval (Lochmann et al. 1995; Booth and Alquezar 2002) and juvenile (Gardiner and Geddes 1980; Thompson et al. 1991; Booth and Hixon 1999; Simpkins et al. 2003) fishes. Individuals in relatively higher condition may represent a small segment of the population, but because they tend to have an increased probability of survival, these individuals may ultimately drive population-level effects (Crowder et al. 1992; Stevenson and Woods 2006). As a result, fisheries scientists seek appropriate means of identifying well-conditioned individuals to investigate population-level measures

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of fitness and survival. Unfortunately, the relationships among condition indices and energy and lipid content are seldom compared among species with different ecological niches and life history strategies to assess the versatility of condition indices (but see Copeland et al. 2008).

Energy density and lipid content (hereafter, "direct condition indices") are typically measured using bomb calorimetry and proximate composition analysis. Proximate composition analysis provides an estimate of the proportion of organic (e.g., lipid, protein, and carbohydrate) and inorganic (e.g., water and ash) compounds in the tissues of an individual fish (Stansby 1976; Shearer 1994). Bomb calorimetry directly estimates the energy density of individuals by measuring the amount of heat released during combustion of dried tissue (Cummins and Wuycheck 1971; Glover et al. 2010). Proximate composition analysis and bomb calorimetry are time-consuming and lethal methods that are costly when applied to large numbers of individuals. Therefore, these methods have limited utility in large-scale or long-term studies of fish condition.

Indirect indices of fish condition can be used to quickly estimate energy or lipid content and can be applied at lower cost; some indirect indices are nonlethal. Indirect indices are often based on easily measured features (e.g., morphometrics), which may reflect energy or lipid content, although justification for use of these indices is often lacking (Stevenson and Woods 2006). Many indirect indices of fish condition may be broadly described as indices based on fish length–mass relationships (hereafter, length-based indices), organ mass (i.e., organosomatic indices), or tissue properties. Fulton's condition factor (K), a length-based index, is a measure of individual fish robustness because greater body mass at a given length corresponds to better condition (Ricker 1975). However, Fulton's K may be correlated with body size for some species (Cone 1989; Sutton et al. 2000); therefore, when used to compare groups, Fulton's K should be measured using fish of similar lengths (Bolger and Connolly 1989; Anderson and Neumann 1996). Relative condition factor (K_n) can compensate for size-dependent changes in condition (Le Cren 1951); however, K_n can be compared only among populations that share a common allometric growth relationship (Anderson and Neumann 1996).

Organosomatic indices use the mass of the liver, gonads, or other viscera and express condition as the proportion of mass that is attributable to a particular organ. The hepatosomatic index (HSI) is believed to be a good measure of condition because some fish species store lipids in the liver (Jensen 1979; Lambert and Dutil 1997) and because the liver is sensitive to feeding history (Heidinger and Crawford 1977; Foster et al. 1993). However, in species that do not use the liver as a significant storage organ, HSI may be poorly correlated with whole-fish lipid content (Peters et al. 2007).

Indirect condition indices may also be derived from tissue properties. Using the Distell fish fatmeter (hereafter, "fatmeter"), the transmission of low-power microwaves through tissues can be used to estimate lipid content (Kent 1990). The fatmeter measures the water content of the tissues beneath the skin, which relates to the amount of lipid stored in subdermal reserves and associated peripheral muscle tissues (hereafter, subdermal lipids). For many species, measures of subdermal lipid content from the fatmeter are well correlated with whole-fish or fillet lipid content measured by proximate composition analysis ($0.58 \leq r^2 \leq 0.87$; Vogt et al. 2002; Hendry and Beall 2004; Bransden et al. 2007; Kaga et al. 2009; Saillant et al. 2009; Van Sang et al. 2009; Caldwell et al. 2013; Mesa and Rose 2015), but these relationships have often been developed for adult fish only, and the species investigated thus far are those that are likely to accumulate large lipid stores as adults. Only one study explicitly examined the lipid content of juvenile fish with the fatmeter (Hanson et al. 2010), and this was for salmonids. The utility of this technique may differ among life history stages and species with different body distributions of proteins and lipids (Lloret et al. 2014), but these potential limitations have not been studied to date.

The objective of this study was to assess the ability of various condition indices to predict energy density and lipid content in juvenile (age < 1 year) fishes. We focused on juvenile fish because energy storage at this life stage is not influenced by reproductive cycles. Juveniles of three mid-Atlantic estuarine fishes were examined: the Summer Flounder *Paralichthys dentatus*, Striped Bass *Morone saxatilis*, and Atlantic Croaker *Micropogonias undulatus*. These species were selected because they have different life history strategies and occupy different ecological niches that affect their energy storage strategies. For example, juvenile Summer Flounder and Atlantic Croakers may store energy in preparation for migration, whereas juvenile Striped Bass store energy for estuarine residence during winter (Schloesser and Fabrizio 2016). These strategies may influence the distribution and role of lipids as energy stores among species and thus may affect the suitability of condition indices for estimating energy and lipid content. Juvenile Summer Flounder have significantly lower lipid content than juvenile Striped Bass and Atlantic Croakers (Schloesser and Fabrizio 2015); therefore, we hypothesized that length-based indices would have a higher correlation with energy and lipid content of Summer Flounder than indices that reflect energy storage (i.e., HSI or relative subdermal lipid estimates from the fatmeter). As they grow, juvenile Atlantic Croakers and Striped Bass accumulate lipids more rapidly than Summer Flounder (Schloesser and Fabrizio 2015), suggesting a greater degree of lipid storage. Because adult Striped Bass store lipids primarily in the viscera (Jacobs et al. 2013), we suspected that organs in the coelom may reflect lipid storage, and therefore we hypothesized that the relationship between HSI values and energy and lipid content in Striped Bass would be stronger than those for subdermal lipids or length-based indices. Finally, because the majority of juvenile Atlantic Croakers move offshore to the continental shelf during the fall (Miller et al. 2003) and subdermal lipid reserves support migration in some species (Leonard and

McCormick 1999), we expected the relative strength of the relationships for juvenile Atlantic Croakers to be higher for subdermal lipids than for HSI values or length-based indices.

To assess the relative strength of the relationships among indirect condition indices and energy and lipid content for juveniles of these species, several length-based indices, the HSI, and relative lipid estimates from the fatmeter were compared with the total body energy density and lipid content of the same individuals. Because individuals of many fish species show an increase in energy density and lipid content with body size (Shearer 1994; Brown and Murphy 2004; Wuenschel et al. 2006) and because energy storage strategies differ as fish grow (Lloret et al. 2014), we also hypothesized that fish length and interactions between length and the indirect condition indices could influence relationships among condition indices.

METHODS

All animal collection, handling, care, and experimental protocols complied with relevant laws and guidelines of the United States and were approved by the College of William and Mary's Institutional Animal Care and Use Committee (Protocol Number IACUC-2010-07-20-6788-mcfabr). Juvenile fish were euthanized in an ice slurry, as recommended by Blessing et al. (2010).

Field collections.—Juvenile Summer Flounder, Striped Bass, and Atlantic Croakers were sampled monthly between August 2010 and August 2013 from Virginia's estuaries (Figure 1). Most samples were obtained according to a random stratified design using a 9.14-m otter trawl, as described by Tuckey and Fabrizio (2013). A 4.88-m otter trawl was used to collect Summer Flounder and Atlantic Croakers from coastal lagoons along the eastern shore of Virginia. Although individuals were sampled in all seasons, more individuals were collected at times when they were readily available to the sampling gear (e.g., Striped Bass during winter). Monthly length thresholds were used to identify young-of-the-year fish (Tuckey and Fabrizio 2016). After capture, individuals were immediately euthanized and returned to the laboratory, where they were measured for length to the nearest millimeter and for relative lipid content by using the fatmeter (Distell Model FFM-992). Body mass was measured with a Mettler Toledo XA204 balance (accurate to 0.1 mg); fish were then frozen for later processing (HSI and direct condition indices).

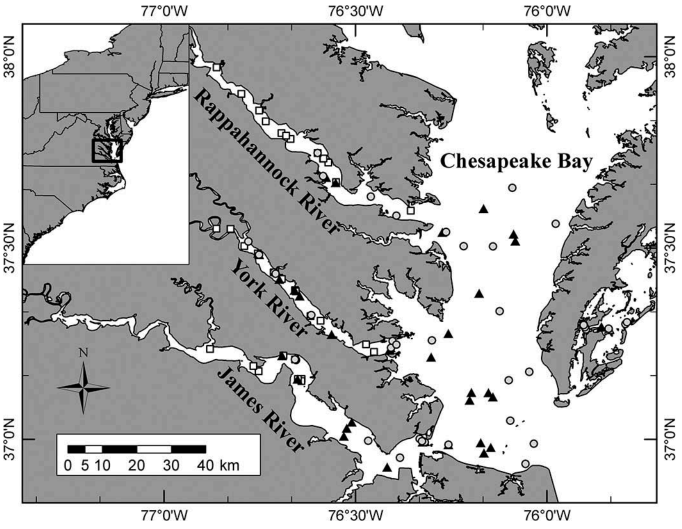

FIGURE 1. Spatial extent of sampling in Virginia estuaries for Summer Flounder (circles; $n = 73$), Striped Bass (squares; $n = 66$), and Atlantic Croakers (triangle; $n = 72$) used in comparisons of direct and indirect condition indices.

Laboratory specimens.—Because only a low percentage of wild fish may be in poor condition (Selleslagh and Amara 2013), individuals from a food-deprivation experiment were opportunistically used to increase the observed range of energy and lipid content for Summer Flounder and Striped Bass. The range of observed energy and lipid content for wild-caught Atlantic Croakers was acceptably broad such that food deprivation would not have appreciably increased the observed range. Live Summer Flounder and Striped Bass were collected in October 2010 and were maintained in recirculating (300-L) aquaria with filtered York River water at a temperature of 12–17°C and salinity of about 24‰. Three times per week, fish were offered Zeigler Finfish G prepared diets; however, some individuals refused to feed and exhibited a continuous decline in condition. Individuals that refused to feed were euthanized 2–5 months after collection and were examined here to extend the range of observed condition (n = 14 for Summer Flounder; n = 2 for Striped Bass). Individuals that fed were not used for condition index comparisons because differences in energy storage strategies between laboratory held and wild specimens might influence the relationships among condition indices.

Condition indices.—Length-based indices, the HSI, and the measurements from the fatmeter were evaluated for their ability to reflect lipid content and energy density of juvenile Summer Flounder, Striped Bass, and Atlantic Croakers. Analyses were focused on young-of-the-year individuals that were large enough to maintain contact between the fish and the fatmeter sensor for condition assessment. We examined Summer Flounder between 156 and 289 mm TL (n = 73), Striped Bass between 117 and 193 mm FL (n = 66), and Atlantic Croakers between 118 and 214 mm TL (n = 72).

In fish, the fat content often decreases from the head to the tail, and large amounts of fat may be stored beneath the skin around the lateral line (Stansby 1976). Therefore, we selected a location immediately behind the operculum and parallel to the lateral line as the site at which to estimate lipid content with the fatmeter. Because Summer Flounder store excess lipids in the fin ray musculature (Gaylord et al. 2003), this area was evaluated as a potential measurement site; however, this site was eliminated from further consideration due to inconsistent fatmeter measurements. Individual fish were measured with the fatmeter four times on each side of the body.

The side of the fish that produced fatmeter measurements with the highest r^2 for the relationships with energy and lipid content was identified for each species and was used in subsequent analyses. The ability of the fatmeter to estimate the lipid content of a fish varies and depends on the lipid content of the sample: accuracy is reported as ±1.5% when lipid content is between 2% and 15%; ±2.5% when lipid content is between 16% and 30%; and ±4% when lipid content is over 31% (Distell 2010).

Fulton's K was calculated as

$$K = \left(W/L^3\right) \times 10^N, \tag{1}$$

where W is wet body mass (g), L is length (mm), and N is an integer to bring the value of K near 1 (Ricker 1975). The relative condition factor (K_n) was calculated as

$$K_n = W/\left(aL^b\right), \tag{2}$$

where a and b are constants describing the allometric relationship for fish in a given population (Le Cren 1951). Constants were estimated using nonlinear regression based on lengths and masses from 2,291 Summer Flounder, 624 Striped Bass, and 3,798 Atlantic Croakers collected from Virginia estuaries between 2010 and 2012 (Schloesser 2015). Nonlinear least-squares estimation was conducted using the NLIN procedure in SAS version 9.3 (SAS Institute, Cary, North Carolina). The species-specific relationships were

$$Mass_{SummerFlounder} = (1.30 \times 10^{-6} \pm 0.10 \times 10^{-6}) \cdot \mathrm{TL}^{3.3588 \pm 0.0135}, \tag{3}$$

$$Mass_{StripedBass} = (4.59 \times 10^{-6} \pm 0.77 \times 10^{-6}) \cdot \mathrm{FL}^{3.1931 \pm 0.0328}, \tag{4}$$

and

$$Mass_{AtlanticCroaker} = (1.65 \times 10^{-6} \pm 0.16 \times 10^{-6}) \cdot \mathrm{TL}^{3.3715 \pm 0.0192}. \tag{5}$$

Deviations between the observed mass and the mass expected from these nonlinear regressions were calculated as

$$\text{Length–mass deviation} = Mass_{Observed} – Mass_{Expected}, \tag{6}$$

where $Mass_{Expected}$ is the expected mass based on equations (3)–(5). These length–mass deviations, or residual indices from the regression of wet mass on fish length (i.e., residualized wet weight index; Sutton et al. 2000), were also assessed for their ability to reflect lipid content and energy density.

For all individuals, the liver was extracted in a manner that minimized loss of body fluids (this was necessary to preserve the accuracy of proximate composition analysis). Liver mass was measured to calculate the HSI as

$$\mathrm{HSI} = 100 \times (W_{liver}/W), \tag{7}$$

where W_{liver} is the wet mass of the liver (g) and W is wet body mass (Jensen 1979; Lambert and Dutil 1997).

After liver extraction, gut contents were removed in preparation for bomb calorimetry and proximate composition analysis. Whole fish, excluding the gut contents but including the liver, were homogenized in a blender and dried at 55°C for 4–7 d in a drying oven. Dried tissues were pulverized with a mortar and pestle and were partitioned into two samples: one for bomb calorimetry and the other for proximate composition analysis. Dried tissue samples were combusted in a Parr 6300 bomb calorimeter to determine energy density in calories per gram of dry fish tissue, which was then converted to energy density per gram of wet body mass (kJ/g). The bomb calorimeter was calibrated using a benzoic acid standard, and the calibration was checked every 10 measurements (mean difference ± SE = 0.035 ± 0.035 kJ/g; t-test: $t_{26} = 1.0$, $P = 0.32$; this mean difference corresponds to a 0.13% error). Dried tissues for proximate composition analysis (to assess lipid content) were shipped to the Department of Zoology, Southern Illinois University, Carbondale, a laboratory certified in performing these analyses. More specifically, lipid content was determined using a modified Folch extraction technique (a chloroform–methanol mixture was used as the solvent) and was reported as percentage of wet body mass because these units are used in bioenergetics models (Hartman and Brandt 1995).

Statistical analyses.—The relationships among indirect and direct condition indices were examined with general linear models to determine whether the suitability of condition indices differed among species with different energy storage strategies. The hypothesis that fish length is an important predictor of energy density and lipid content was tested by including fish length as a predictor in the models, and the hypothesis that the relationship between direct and indirect condition indices varies with fish size was tested by including interactions between length and the indirect condition indices. The global model used to examine relationships between indirect and direct condition indices was

$$Y_i = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \beta_3 X_{i3} + \varepsilon_i, \tag{8}$$

where Y_i is the $\log_e$ transformed energy density or lipid content of the ith individual as measured by bomb calorimetry or Folch extraction; β_0 is the intercept, representing the overall mean energy or lipid content of individuals; β_1 is the slope for the partial regression of energy or lipid content on the indirect condition index (X_{i1}; as measured by length-based indices, HSI, or the fatmeter), with length and the length × indirect index interaction held constant; β_2 is the slope for the partial regression of energy or lipid content on fish length (X_{i2}), with the indirect condition index and the length × indirect index interaction held constant; β_3 is the slope for the partial regression of energy or lipid content on the interaction (X_{i3}) between fish length and the indirect condition index (as measured by length-based indices, HSI, or the fatmeter), with the indirect condition index and length held constant; and ε_i is the random unexplained error, which is assumed to be independent and normally distributed.

The indirect condition indices, fish length, and their interaction were considered fixed effects. Because inclusion of the interaction terms resulted in collinearity, all predictors were centered to remove these effects (Table 1; Quinn and Keough 2002). Energy and lipid content data were $\log_e$ transformed to improve normality and homogeneity of variance, which are necessary assumptions of these linear models. Fatmeter measurements were $\log_e$ transformed because this transformation provides the best linear relationship with lipid content (Colt and Shearer 2001; Crossin and Hinch 2005; Hanson et al. 2010). For model selection purposes, general linear models were fitted with the MIXED procedure in SAS version 9.3 using restricted maximum likelihood (REML) for parameter estimation. For each indirect condition index, Akaike's information criterion corrected for small sample size (AIC$_c$; Burnham and Anderson 2002) was used to determine whether fish length and the length × indirect index interaction explained additional variation in energy or lipid content. The AIC$_c$ was then compared among those models to identify the "best" indirect condition index for estimating energy or lipid content for each species. Models that had AIC$_c$ values within 2 units were considered to have a similar ability to account for variation in energy or lipid content (Burnham and Anderson 2002). When the best models included multiple predictors, partial regressions were used to examine the relationship between indirect and direct condition indices (Quinn and Keough 2002). The proportion of the total variation in energy and lipid content explained by the indirect condition indices was determined by using an REML-based estimate of r^2 (i.e., r^2_{REML}), as discussed by Singer (1998). For ease of comparing our results with previously published data, r^2 values are also provided for all condition index comparisons, with significance assessed at $\alpha = 0.05$.

TABLE 1. Descriptive statistics for direct and indirect condition indices (Fulton's *K* = Fulton's condition factor; K_n = relative condition factor; *L–M* = length–mass; HSI = hepatosomatic index) measured from the same Summer Flounder ($n = 73$), Striped Bass ($n = 66$), and Atlantic Croakers ($n = 72$). The *L–M* deviations are the deviations from nonlinear regression models for fish length (mm) and mass (g) given by equations (3)–(5). Due to collinearity among predictors, the means of the raw indirect condition data were subtracted from individual observations of condition to estimate relationships between indirect condition indices and energy density (kJ/g of wet mass) or lipid content (g/g of wet mass).

Condition index	Mean	SD	Minimum	Maximum
Summer Flounder				
Energy density	4.137	0.538	2.718	5.308
Lipid content	1.861	0.986	0.562	4.715
TL	223.9	34.6	156	289
Fulton's *K*	0.900	0.109	0.601	1.103
K_n	0.999	0.129	0.625	1.247
L–M deviation	–2.290	15.039	–66.375	21.226
HSI	0.788	0.421	0.230	2.030
$\log_e$(fatmeter)	0.826	1.374	–2.303	2.639
Striped Bass				
Energy density	5.032	0.658	3.441	6.869
Lipid content	3.930	1.429	1.262	7.828
FL	143.4	17.6	117	193
Fulton's *K*	1.169	0.075	1.025	1.407
K_n	0.977	0.064	0.832	1.157
L–M deviation	–1.030	2.699	–11.801	8.362
HSI	1.876	0.650	0.656	3.516
$\log_e$(fatmeter)	3.310	0.249	2.464	3.843
Atlantic Croaker				
Energy density	4.700	1.018	2.985	7.530
Lipid content	3.880	2.295	0.811	10.302
TL	160.8	22.7	118	214
Fulton's *K*	1.053	0.081	0.895	1.221
K_n	0.970	0.065	0.835	1.177
L–M deviation	–1.715	3.343	–13.203	4.738
HSI	1.256	0.602	0.429	2.770
$\log_e$(fatmeter)	3.210	0.435	2.059	3.925

RESULTS

The midline of the body was a feasible fatmeter measurement site for juvenile fish of all three species. At that location, the left side of Striped Bass and an average of measurements from both sides of Atlantic Croakers provided the highest r^2 values with energy and lipid content (Table 2). Results are reported from fatmeter measurements on the non-eyed side of Summer Flounder (Table 2).

The relative ability of indirect condition indices to estimate energy or lipid content varied depending on species, and not all of the indirect condition indices were suitable surrogates. As hypothesized, the length-based condition index, Fulton's *K*, best explained energy and lipid content for Summer Flounder, resulting in models with lower AIC$_c$ values than those with condition indices associated with lipid storage (HSI values or relative lipid estimates from the fatmeter; Table 3). Food deprivation greatly extended the range of observed energy density and lipid content for juvenile Summer Flounder and improved our ability to detect linear relationships between Fulton's *K* and energy and lipid content (Figure 2A, B). For juvenile Striped Bass, length-based condition indices (Fulton's *K* and K_n) also outperformed the models that included HSI values and fatmeter measurements (Table 3; Figure 2A, B), so our hypothesis that HSI values would be more suitable was not supported. For Striped Bass, Fulton's *K* and K_n showed a similar ability to account for variation in energy density. As hypothesized, relative lipid estimates from the fatmeter were reliable predictors of energy and lipid content for juvenile Atlantic Croakers (Table 3; Figure 2B, C). The HSI and deviations from the length–mass regression were generally unsuitable for assessing energy and lipid content of these juvenile fishes. Note that values of r^2_{REML} were higher than the r^2 values (Table 2) when AIC_c indicated that additional predictors (e.g., length) helped to explain variation in energy or lipid content.

Even though juvenile fish were from a relatively small size range, energy density and lipid content increased with fish size, and length remained an important predictor in some models for juvenile Summer Flounder and Atlantic Croakers (Table 3). Notably, predictions of Summer Flounder energy density and lipid content improved when K_n was adjusted for the effects of length. Length was included in all models estimating lipid content of Atlantic Croakers except for Fulton's *K* and relative lipid from the fatmeter; length was included in all models estimating energy density of Atlantic Croakers except for Fulton's *K* and HSI values. The length × indirect index interaction had a negative effect on lipid content when estimated with length–mass deviations and had a positive effect on estimates of energy density with fatmeter measurements, suggesting that mass is less reflective of lipid content in Atlantic Croakers as they grow because subdermal lipid reserves are more important energy stores for larger Atlantic Croakers. Length did not improve predictions of energy or lipid content for Striped Bass, regardless of the condition index investigated (Table 3).

DISCUSSION

Results from this study suggest that the energy and lipid storage strategies used by juvenile fish ultimately influence the utility of condition indices for predicting energy or lipid content. The relative ability of indirect condition indices to estimate energy or lipid content was highest for species displaying a wide range in condition, notably the Atlantic Croaker; furthermore, relationships developed from a limited range of condition often predicted direct metrics with some uncertainty ($r^2 < 0.50$). The importance of size for estimating energy and lipid content differed among species and depended on the condition index evaluated.

Due to the significantly lower lipid storage of juvenile Summer Flounder relative to juvenile Striped Bass and Atlantic Croakers (Schloesser and Fabrizio 2015), we expected that length-based indices would be suitable metrics of condition for this species. Flatfishes generally have a relatively low fat content (often ~1%) and a relatively high protein content (~20%) (Stansby 1976), and stored proteins may supplement energy needs in some flatfishes during adverse circumstances (e.g., food deprivation; Jobling 1980; Maddock and Burton 1994). Juvenile Summer Flounder likely also use this strategy given that they store a higher percentage of total energy as proteins compared with juvenile Striped Bass and Atlantic Croakers (Schloesser and Fabrizio 2015). Consistent with that expectation, energy content and lipid content of Summer Flounder were best estimated from Fulton's *K*. However, the suitability of Fulton's *K* as an estimator of condition varies among species. For juveniles of some fish species, r^2 values for the relationship between Fulton's *K* and energy density or lipid content range from 0.55 to 0.80 (Costopoulos and Fonds 1989; Pangle and Sutton 2005; Hanson et al. 2010), but for other species, the r^2 values are less than 0.25 (Trudel et al. 2005; Peters et al. 2007; Davidson and Marshall 2010). Fulton's *K* is useful for examining changes in condition of

TABLE 2. Values of r^2 between indirect condition indices (Fulton's K = Fulton's condition factor; K_n = relative condition factor; $L–M$ = length–mass; HSI = hepatosomatic index) and $\log_e$ transformed energy density (kJ/g of wet mass) and lipid content (g/g of wet mass) for juvenile Summer Flounder, Striped Bass, and Atlantic Croakers. Relative estimates of lipid content measured with the fatmeter were taken from both sides of each individual (Fatmeter_{Mean} represents the average) and $\log_e$ transformed to identify the "best" location for assessing lipid content. An asterisk denotes the fatmeter location used for index comparisons. All values were significant ($P < 0.05$) unless indicated by footnotes.

Indirect condition index	Lipid	Energy
Summer Flounder		
Fulton's *K*	0.39	0.46
K_n	0.19	0.32
L–M deviation	0.27	0.38
HSI	0.26	0.45
Fatmeter_{Eyed}	0.39	0.33
$\text{Fatmeter}_{Noneyed}$*	0.40	0.44
Fatmeter_{Mean}	0.41	0.41
Striped Bass		
Fulton's *K*	0.30	0.31
K_n	0.25	0.32
L–M deviation	0.23	0.29
HSI	0.21	0.33
Fatmeter_{Left}*	0.22	0.12
Fatmeter_{Right}	0.07	0.02[a]
Fatmeter_{Mean}	0.14	0.06[a]
Atlantic Croaker		
Fulton's *K*	0.53	0.48
K_n	0.22	0.23
L–M deviation	0.08	0.08
HSI	0.27	0.31
Fatmeter_{Left}	0.64	0.58
Fatmeter_{Right}	0.66	0.61
Fatmeter_{Mean}*	0.68	0.62

[a] $P > 0.05$.

TABLE 3. General linear models used to predict energy density (kJ/g of wet mass) and lipid content (g/g of wet mass) with indirect condition indices (Fulton's K = Fulton's condition factor; K_n = relative condition factor; L–M = length–mass; HSI = hepatosomatic index) and fish length for Summer Flounder (n = 73), Striped Bass (n = 66), and Atlantic Croakers (n = 72). Predictors were centered about their means (Table 1), and Akaike's information criterion corrected for small sample size (AIC$_c$) was used for final model selection (ΔAIC$_c$ = difference in AIC$_c$ value between the given model and the best-performing model). Parameter estimates for final models are presented with 95% confidence intervals. The proportion of the total variation in energy density and lipid content explained by the indirect condition indices was determined by using a restricted maximum likelihood (REML)-based r^2 estimate (r^2_{REML}).

Direct	Indirect	Model	AIC$_c$	ΔAIC$_c$	r^2_{REML}
		Summer Flounder			
Energy	Fulton's K	$\log_e(\text{Energy}) = (1.411 \pm 0.023) + (0.830 \pm 0.211)\cdot K$	–121.6	0.0	0.46
	K_n	$\log_e(\text{Energy}) = (1.411 \pm 0.023) + (0.733 \pm 0.195)\cdot K_n + (0.002 \pm 0.001)\cdot \text{TL}$	–106.6	15.0	0.44
	L–M deviation	$\log_e(\text{Energy}) = (1.411 \pm 0.025) + (0.006 \pm 0.002)\cdot \text{Deviation}$	–102.0	19.6	0.38
	HSI	$\log_e(\text{Energy}) = (1.411 \pm 0.023) + (0.213 \pm 0.056)\cdot \text{HSI}$	–117.1	4.5	0.44
	Fatmeter	$\log_e(\text{Energy}) = (1.411 \pm 0.024) + (0.064 \pm 0.017)\cdot \log_e(\text{Fatmeter})$	–113.3	8.3	0.43
Lipid	Fulton's K	$\log_e(\text{Lipid}) = (0.475 \pm 0.104) + (3.194 \pm 0.953)\cdot K$	92.3	0.0	0.38
	K_n	$\log_e(\text{Lipid}) = (0.475 \pm 0.101) + (2.723 \pm 0.848)\cdot K_n + (0.008 \pm 0.003)\cdot \text{TL}$	99.4	7.1	0.41
	L–M deviation	$\log_e(\text{Lipid}) = (0.475 \pm 0.099) + (0.024 \pm 0.007)\cdot \text{Deviation} + (0.007 \pm 0.003)\cdot \text{TL}$	105.2	12.9	0.44
	HSI	$\log_e(\text{Lipid}) = (0.475 \pm 0.114) + (0.683 \pm 0.272)\cdot \text{HSI}$	108.2	15.9	0.25
	Fatmeter	$\log_e(\text{Lipid}) = (0.475 \pm 0.103) + (0.258 \pm 0.075)\cdot \log_e(\text{Fatmeter})$	95.9	3.6	0.39
		Striped Bass			
Energy	Fulton's K	$\log_e(\text{Energy}) = (1.606 \pm 0.028) + (0.997 \pm 0.369)\cdot K$	–93.0	0.7	0.30
	K_n	$\log_e(\text{Energy}) = (1.606 \pm 0.028) + (1.180 \pm 0.432)\cdot K_n$	–93.7	0.0	0.31
	L–M deviation	$\log_e(\text{Energy}) = (1.606 \pm 0.028) + (0.027 \pm 0.011)\cdot \text{Deviation}$	–83.4	10.3	0.28
	HSI	$\log_e(\text{Energy}) = (1.606 \pm 0.027) + (0.119 \pm 0.042)\cdot \text{HSI}$	–90.1	3.6	0.32
	Fatmeter	$\log_e(\text{Energy}) = (1.606 \pm 0.031) + (0.185 \pm 0.063)\cdot \log_e(\text{Fatmeter})$	–74.5	19.2	0.10
Lipid	Fulton's K	$\log_e(\text{Lipid}) = (1.297 \pm 0.082) + (2.891 \pm 1.101)\cdot K$	47.0	0.0	0.29
	K_n	$\log_e(\text{Lipid}) = (1.297 \pm 0.086) + (3.073 \pm 1.343)\cdot K_n$	51.5	4.5	0.23
	L–M deviation	$\log_e(\text{Lipid}) = (1.297 \pm 0.087) + (0.070 \pm 0.032)\cdot \text{Deviation}$	60.6	13.6	0.22
	HSI	$\log_e(\text{Lipid}) = (1.297 \pm 0.088) + (0.282 \pm 0.136)\cdot \text{HSI}$	58.9	11.9	0.20
	Fatmeter	$\log_e(\text{Lipid}) = (1.297 \pm 0.087) + (0.752 \pm 0.352)\cdot \log_e(\text{Fatmeter})$	56.3	9.3	0.21
		Atlantic Croaker			
Energy	Fulton's K	$\log_e(\text{Energy}) = (1.525 \pm 0.036) + (1.811 \pm 0.449)\cdot K$	–58.4	26.6	0.47
	K_n	$\log_e(\text{Energy}) = (1.525 \pm 0.036) + (1.858 \pm 0.558)\cdot K_n + (0.005 \pm 0.002)\cdot \text{TL}$	–49.2	35.8	0.49
	L–M deviation	$\log_e(\text{Energy}) = (1.525 \pm 0.039) + (0.033 \pm 0.013)\cdot \text{Deviation} + (0.006 \pm 0.002)\cdot \text{TL}$	–30.5	54.5	0.40
	HSI	$\log_e(\text{Energy}) = (1.525 \pm 0.041) + (0.196 \pm 0.069)\cdot \text{HSI}$	–34.7	50.3	0.30
	Fatmeter	$\log_e(\text{Energy}) = (1.477 \pm 0.029) + (0.490 \pm 0.076)\cdot \log_e(\text{Fatmeter}) - (0.001 \pm 0.001)\cdot \text{TL} + (0.010 \pm 0.003)\cdot [\log_e(\text{Fatmeter}) \times \text{TL}]$	–85.0	0.0	0.75
Lipid	Fulton's K	$\log_e(\text{Lipid}) = (1.172 \pm 0.103) + (5.728 \pm 1.288)\cdot K$	89.2	22.6	0.52
	K_n	$\log_e(\text{Lipid}) = (1.172 \pm 0.102) + (5.630 \pm 1.601)\cdot K_n + (0.016 \pm 0.005)\cdot \text{TL}$	96.3	29.7	0.53
	L–M deviation	$\log_e(\text{Lipid}) = (1.099 \pm 0.107) + (0.139 \pm 0.037)\cdot \text{Deviation} + (0.019 \pm 0.005)\cdot \text{TL} - (0.003 \pm 0.001)\cdot (\text{Deviation} \times \text{TL})$	113.2	46.6	0.55
	HSI	$\log_e(\text{Lipid}) = (1.172 \pm 0.119) + (0.440 \pm 0.210)\cdot \text{HSI} + (0.010 \pm 0.006)\cdot \text{TL}$	122.3	55.7	0.36
	Fatmeter	$\log_e(\text{Lipid}) = (1.172 \pm 0.086) + (1.204 \pm 0.199)\cdot \log_e(\text{Fatmeter})$	66.6	0.0	0.67

fish among seasons (Heincke 1908; cited in Froese 2006); the specimens examined here were collected throughout the year and exhibited intra-annual dynamics in condition indices (Schloesser and Fabrizio 2016), which helped to provide sufficient contrast in the data to permit description of the relationship between Fulton's K and energy and lipid content. The additional use of food-deprived individuals furthered the observed contrast in Fulton's K with energy and lipid content of Summer Flounder. Fulton's K is also more reliable for predicting lipid content in temperate

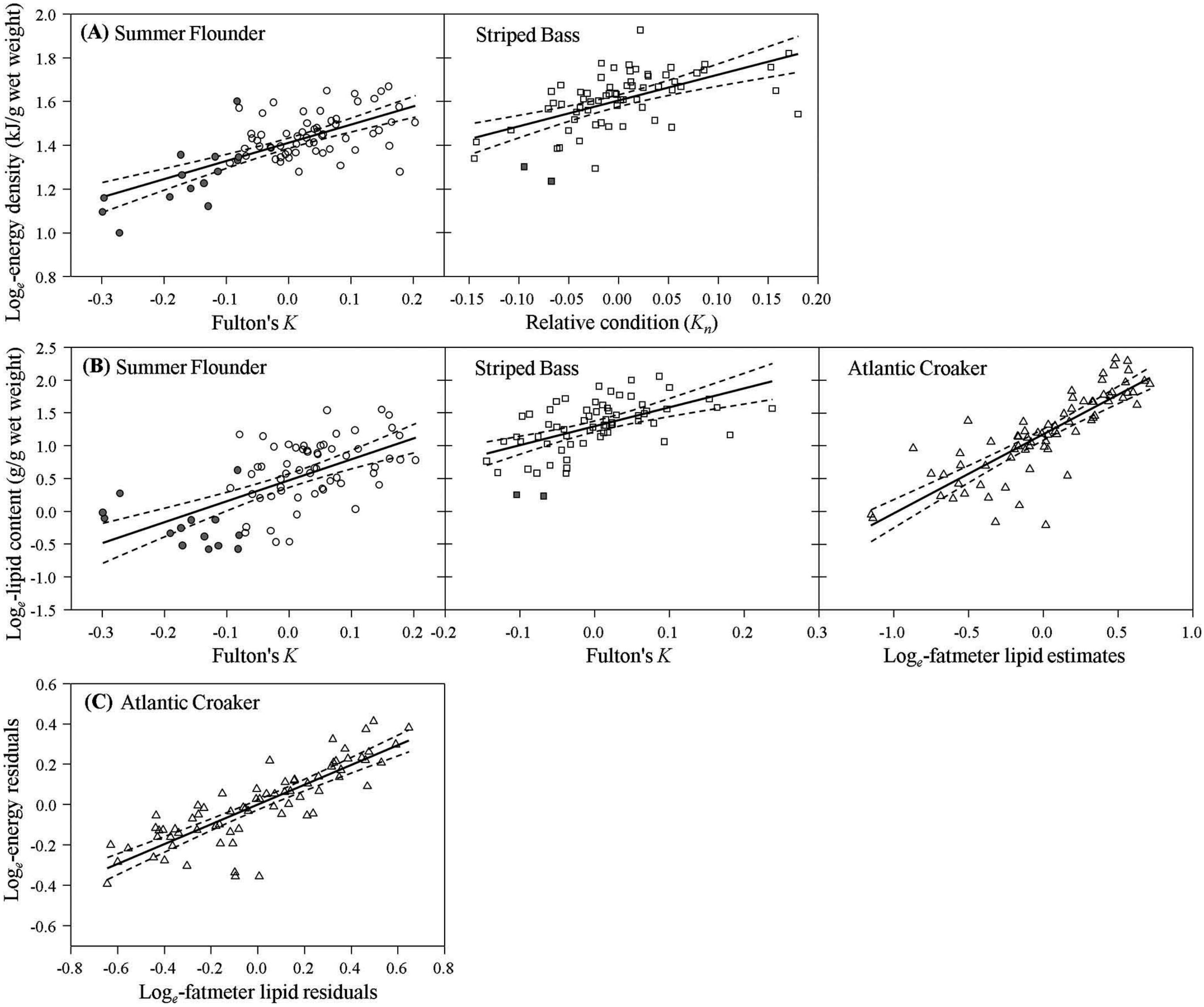

FIGURE 2. **(A)** Linear regressions (solid lines) of energy density and selected indirect condition indices for Summer Flounder and Striped Bass; **(B)** regressions of lipid content and selected indirect indices for all three species; and **(C)** partial regression plot used to assess the relationship between relative lipid estimates measured with the fatmeter and energy density for Atlantic Croakers. The indices shown are those selected from the general linear models based on the lowest Akaike's information criterion corrected for small sample size (Table 3; Fulton's K = Fulton's condition factor). The solid symbols indicate laboratory-held individuals; the dashed lines denote 95% confidence intervals around the equations used to predict log$_e$ transformed energy and lipid content (see Table 3).

freshwater fishes that exhibit greater and more variable lipid storage (Mozsár et al. 2015). However, intra-annual dynamics in the energy storage strategies of juveniles of the three species we examined (Schloesser and Fabrizio 2016) along with the broad spatial domain of the samples may have also introduced uncertainty into the relationships, thus limiting the amounts of the total variability in energy or lipid content that were explained (<50%).

Although we hypothesized that HSI values of juvenile Striped Bass would best estimate energy and lipid content, these variables were better estimated by length-based indices. In fact, the HSI was not a good predictor of energy or lipid content for any of the juvenile fishes examined here. The liver may not be a primary storage organ for lipids in juveniles (Litvin et al. 2011), which allocate proportionally more energy to growth rather than storage (Hurst and Conover 2003). The allocation of energy to growth (i.e., body mass) will result in less energy storage, and condition indices that reflect lipid storage may be less suitable for estimating energy density than those based on length–mass relationships. Alternatively, condition indices such as HSI that reflect lipid storage may only be suitable if examined during specific time periods when storage may be beneficial to juvenile survival (e.g., during winter instead of throughout the year). Finally, juvenile fish may also store energy as constituents other than lipids, and not all lipids function to store energy. The use of multiple lipid classes and energy storage compounds by individuals may result in weak relationships among indirect and direct condition indices. For example, fish that store energy as protein (instead of lipid) would not only exhibit lower lipid content but also lower energy density because protein contains less energy by mass than lipid. Under these circumstances, establishing a strong relationship between the HSI and lipid content or energy density is difficult due to the low and potentially limited range of observed lipid values (Weisberg 2014). The juvenile Striped Bass examined here had protein contents similar to those observed in juvenile Summer Flounder (Schloesser and Fabrizio 2015), suggesting that length-based indices may outperform the HSI for individuals with high protein contents.

The utility of the fatmeter for estimating direct condition indices appears to be related to the degree of subdermal lipid storage. As hypothesized, the fatmeter provided better estimates of condition for juvenile Atlantic Croakers than did length-based indices or the HSI. Among the species examined, Atlantic Croakers exhibited a wider range of energy and lipid content (Figure 2B; Schloesser and Fabrizio 2015), which was reflected in subdermal lipids. However, the fatmeter may have limited utility for predicting whole-body energy or lipid content for species that display low lipid content, like juvenile Summer Flounder. Although the accuracy of the fatmeter is high (±1.5%) for low-lipid-content individuals (Distell 2010), the degree of accuracy may limit applicability of fatmeter-based metrics for low-lipid-content species, particularly in combination with a limited observed range of subdermal lipid stores. Juvenile Atlantic Croakers exhibit a wide range in lipid content because individuals dramatically increase their subdermal lipid stores in preparation for fall migrations from Chesapeake Bay to the coastal ocean (Schloesser and Fabrizio 2016). Because migration may be supported by subdermal lipid reserves (Leonard and McCormick 1999), the fatmeter may be particularly useful for application to species with a migratory life history strategy involving the juvenile stage. The fatmeter may not be effective for species that are nonmigratory as juveniles or that do not readily utilize subdermal lipid stores, such as Striped Bass (Schloesser and Fabrizio 2016). Because the fatmeter measures water content in tissues near the skin, visceral lipid stores are often beyond the measurement area (Davidson and Marshall 2010) and therefore would not influence fatmeter measurements.

Lipid storage locations are particularly important to consider when applying condition indices to laboratory-held fish. Relationships between energy and lipid content and indirect approaches based on tissue properties (e.g., the fatmeter) are rarely developed for juvenile fishes, and the few studies that are reported in the literature often used laboratory-held specimens to extend the range of observed energy or lipid content. For juvenile Rainbow Trout *Oncorhynchus mykiss* obtained from a hatchery, a low r^2 value was found between lipid from proximate composition analysis and fatmeter estimates (Hanson et al. 2010). Similar issues were noted by Garner et al. (2012) for juvenile Atlantic Croakers when the condition of laboratory-held individuals was examined with bioelectric impedance analysis (BIA), which assesses similar lipid reserves as the fatmeter (Hanson et al. 2010). Condition measurements from BIA suggested a loss in condition of laboratory-held individuals despite increases in relative condition and energy density (Garner et al. 2012). Correlations among BIA measures and energy density were particularly low for fish that were fed (Garner et al. 2012). The differences in composition among wild and laboratory-held specimens are likely to be pronounced when fish are fed to satiation due to differences in energy storage tissues, nutritional value of food resources, and higher activity levels of wild fish. Differences in proximate components have been documented between wild and laboratory-held individuals in several studies, including the quantity and composition of fatty acids (Alasalvar et al. 2002), temporal patterns in lipid content (Thompson et al. 1991), HSI values (Grant et al. 1998), and variations in lipid: protein ratios in muscle tissue (McDonald et al. 1998; Morley et al. 2012). These observations indicate that feeding fish in a laboratory setting may lead to different tissue-specific distributions of proximate components compared with their wild conspecifics. However, if laboratory-held individuals are deprived of food, body composition may be similar to that of wild specimens that do not feed successfully. Because comparisons of individuals from wild and laboratory settings may not be physiologically meaningful (Copeland and Carline 2004), condition indices developed with fish fed in a laboratory should not be applied to wild populations unless it can be shown that the composition, distribution, and temporal patterns of proximate components are similar between wild and laboratory-held fish.

The importance of fish length for estimating energy and lipid content varied among species and among indices. Fish length did not improve model fit for any condition index evaluated for Striped Bass, potentially due to the examination of fish from a relatively restricted size range (i.e., juveniles). The size range of juvenile Striped Bass examined here was narrower than the size ranges observed for juvenile Summer Flounder and Atlantic Croakers; fish length improved model fit for some of the length-based indices applied to Summer Flounder and the majority of the indirect condition indices for Atlantic Croakers. The importance of fish length for describing energy and lipid content of Atlantic Croakers suggests that lipid storage co-occurs with growth. For juvenile Atlantic Croakers and other high-lipid, migratory species, maximal survival may require an energy allocation strategy that balances growth and storage (Post and Parkinson 2001).

Interestingly, Fulton's K did not require adjustments for size to predict energy or lipid content of the species examined, but estimation of energy and lipid content with K_n (a length-independent index) improved by including fish length. The appropriateness of Fulton's *K* as a measure of energy or lipid content has been questioned because *K* may be correlated with body size in species exhibiting allometric growth, such as Summer Flounder and Atlantic Croakers (the exponent in the allometric relationship [*b*] ± 95% confidence interval was 3.36 ± 0.01 and 3.37 ± 0.02, respectively). Because Fulton's *K* is calculated using the length of the individual and thus is not completely independent of length, the effect of size on energy storage capacity may be reasonably reflected in this index, and model fits were not improved by including fish size. Perhaps unsurprisingly, because K_n is independent of length, fish size improved prediction of energy and lipid content, despite the relatively narrow size range investigated here. Although K_n is more suitable than Fulton's *K* for comparing condition among individuals from a population exhibiting allometric growth, K_n may not be as beneficial for estimating energy or lipid content of individual fish unless fish size is explicitly incorporated into the models. Similarly, several models estimating energy and lipid content with deviations from a length–mass regression were improved by inclusion of fish length; however, deviations from a length–mass regression were generally unsuitable surrogates for energy and lipid content of juvenile fishes. Deviations from a regression model are less commonly used to investigate fish condition, and this may be due to the inability to meet key assumptions of the length–mass model (e.g., residuals are independent of body size; Garcia-Berthou 2001; Green 2001; but see Schulte-Hostedde et al. 2005). Further investigation into relationships among indirect and direct condition indices should explicitly consider fish size.

In conclusion, the species-specific distribution of proximate constituents, notably lipid, throughout the body may influence the utility of some indirect techniques for assessing energy or lipid content in juvenile fish. Food deprivation may increase the observed range of energy and lipid content and improve the detectability of relationships among measures of condition, but researchers should be cautious about feeding practices that may alter the distribution of energy storage compounds. Length-based measures of condition seem appropriate for species or life stages that have minimal lipid stores or that rely on protein as an energy source (e.g., Summer Flounder). Relative lipid measurements from the fatmeter are appropriate if subdermal lipids are a significant storage depot or if those stores change proportionately with other storage strategies (e.g., Atlantic Croaker). For these and similar species, the energy storage strategies used by fishes with different life history traits and ecological niches can be used to inform the selection of indirect condition indices that may be useful for assessing individual fitness and understanding factors that influence survival. Ultimately, only a comparison of indirect indices to energy or lipid content can determine whether an indirect index will be useful for assessing condition for a given species and life stage.

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