



Does condition of Lake Whitefish spawners affect physiological condition of juveniles?

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ABSTRACT

Recent declines in growth and condition of several Great Lakes lake whitefish populations have raised concerns over potential impacts on juvenile physiological condition and ultimately recruitment. To test whether the condition of spawning adults influences juvenile condition via energy allocation dynamics, we partitioned the variation in age 0 juvenile physiological condition (i.e., growth in length and weight, whole-body moisture content, energy density, and protein content) among adult male and female (i.e., body condition, muscle moisture content, energy density, and protein content) and egg (i.e., wet and dry weight, moisture content, energy density, energy content per egg, and protein content) effects using redundancy analysis. Overall, a model that included sampling site, female condition, and egg quality explained 39% of the variation in juvenile physiological condition. After partitioning out the effects of females and eggs, site explained the most variation (23%). When other factors were accounted for, neither females (1.4%) nor eggs (2.7%) explained much variation in juvenile physiological condition. Of the variables studied, female muscle energy density, muscle moisture content, and egg moisture content were most closely associated with juvenile physiological condition. Our results suggest that parental effects, such as size, age, body condition, or body composition, may not be as important as extrinsic site-related effects or density-dependent effects in determining juvenile physiological condition.

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Introduction

Lake whitefish *Coregonus clupeaformis* support some of the largest and most valuable commercial fisheries in the Laurentian Great Lakes (Madenjian et al., 2002; Modeling Subcommittee, 2002; Mohr and Nalepa, 2005). During the 1990s, declines in length at age ranging from 4% to 7% and in weight at age ranging from 36% to 47% were associated with large (34–40%) declines in body condition of this species in northern Lake Michigan (Pothoven et al., 2001; Madenjian et al., 2002; Schneeberger et al., 2005). Similar declines have also been reported for lake whitefish from lakes Huron and Ontario (Hoyle, 2005; Modeling Subcommittee, 2005; Lumb et al., 2007). By contrast,

growth and condition of lake whitefish in lakes Erie and Superior have been stable over the past several decades (Cook et al., 2005; Kratzer et al., 2007). Reduced growth and condition have been attributed to high lake whitefish density coupled with bottom-up trophic restructuring and subsequent food habit shifts (e.g., increase in dreissenid mussels and decrease in *Diporeia* spp.; Pothoven, 2005; McNickle et al., 2006). These declines in lake whitefish growth and condition have led to concerns among managers regarding potential impacts on reproduction and subsequently on juvenile physiological condition.

In several fishes, including lake whitefish, size at hatch, growth, and survival of larvae and/or juveniles have been linked to parental traits such as age, body size, body condition, and energetic resources (reviewed by Kamler, 2005). This *parental effects hypothesis* holds that the condition of spawning adults drives energy allocation dynamics that lead to physiological consequences for their offspring. This hypothesis predicts that reduced maternal and paternal condition will result in reduced egg quality and subsequent reductions in juvenile physiological condition. Brown and Taylor's (1992) research provided support for the parental effects hypothesis by demonstrating that lake

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whitefish larvae produced from eggs with high energy density had higher percent lipid content, resulting in larvae that had more endogenous energy reserves. Larvae hatching from eggs with higher lipid content hatched at a slightly smaller average size but were able to compensate through accelerated endogenous growth (Brown and Taylor, 1992). In addition, researchers have noted a positive relationship between size at hatch, which may be linked to parental attributes, and early growth and survival of lake whitefish (Teska and Behmer, 1981; Miller et al., 1988; Freeberg et al., 1990).

Juvenile physiological condition may influence recruitment success, which is largely driven by early life stage mortality (Wootton, 1998). Survival is often size dependent, with larger individuals having a competitive advantage over smaller individuals (Miller et al., 1988). For example, larger larvae have been shown to have a higher resistance to starvation (Miller et al., 1988; Ludsins and DeVries, 1997; Trippel et al., 1997; Keckeis et al., 2000), greater ability to ingest larger prey (Teska and Behmer, 1981; Miller et al., 1988; Freeberg et al., 1990), increased growth rates (Gutreuter and Anderson, 1985; Hurst and Conover, 1998), reduced predation rates (Cushing, 1982; Miller et al., 1988), and increased winter survival (Rice et al., 1987; Pangle et al., 2004). Hurst and Conover (1998) also proposed that mortality from energy depletion is higher among smaller individuals due to the allometrics of energy storage and metabolism. Taken together, these studies support the hypothesis that larger, more energy-dense lake whitefish larvae will more successfully transition from endogenous to exogenous food resources, resulting in enhanced juvenile physiological condition.

Given the physiological link between parental condition and juvenile growth and survival in fishes, we sought to examine the relationship between spawning adult condition and juvenile physiological condition in lake whitefish. The specific objectives of our study were (1) to assess the role of adult male and female lake whitefish condition and egg quality in determining age 0 juvenile physiological condition (i.e., parental effects hypothesis) and (2) to

determine which physiological indicators associated with spawning male and female condition and egg quality were most closely associated with juvenile physiological condition. Reducing uncertainties related to growth- and condition-mediated parental effects on juvenile condition will improve our understanding of the early life history dynamics of lake whitefish and may allow us to hypothesize potential impacts of reduced spawner condition on recruitment potential in the Laurentian Great Lakes.

Methods

Fish collections

Adult male, female, eggs, and age 0 juvenile lake whitefish were collected from six sites in Lake Michigan and one site in Lake Superior between 2004 and 2006 (Fig. 1). Mature adults were collected on the spawning shoals during the fall of 2004 and 2005 using commercial gill nets and trap nets. Upon capture, adults were examined to determine their gender and reproductive state. From each site, 30 mature males and 30 mature females, which were staging to spawn but had not yet released their gametes (i.e., not freely expelling gametes when pressure was applied to the abdomen), were placed live in a 100-L holding tank and transported to shore where total length (± 1.0 mm) and wet weight (± 0.05 g) were recorded for each individual. Ten scales were collected from the area below the middle of the dorsal fin but above the lateral line for aging. Two skinless, dorsal muscle plugs were collected from the region anterior to the dorsal fin and stored in a 100-ml centrifuge tube on wet ice. A 100-g sample of eggs was extracted from each female and stored in a centrifuge tube on wet ice. After transport to Purdue University, samples were kept at -20 °C prior to laboratory analysis.

Age 0 juveniles were collected using a 50-m long \times 1.5-m deep seine with 3.2-mm stretch mesh, which was deployed in nearshore

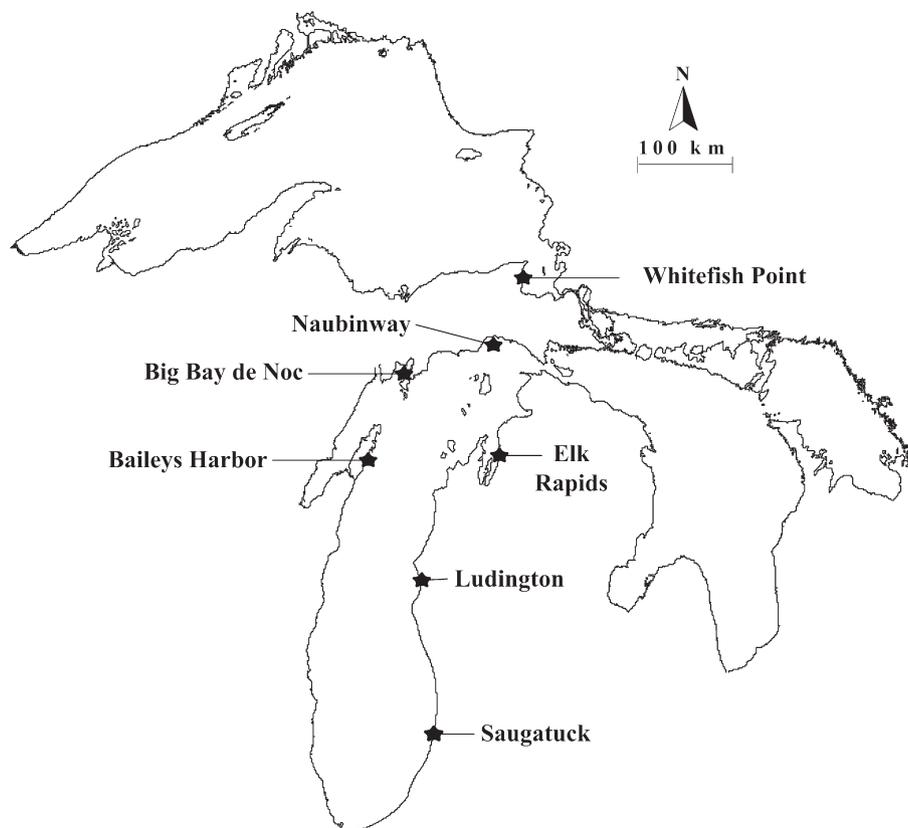


Fig. 1. Sampling sites for lake whitefish in lakes Michigan and Superior.

sandy beach habitats adjacent to shoals where spawning adults were sampled during the previous year. Sampling was conducted during the spring and summer of 2005 and 2006 because lake whitefish spawn in the fall and the larvae emerge during the following spring. We assumed that the juveniles that we collected adjacent to spawning shoals were the progeny of the adults that we sampled from that shoal during the previous fall because of the low dispersal abilities of lake whitefish larvae and their requirement for specific nearshore nursery habitats (Hoagman, 1973; Frederick, 1982). Upon capture, total length (± 1.0 mm) and wet weight (± 0.05 g) were recorded for each individual. Whole fish were stored in vials on wet ice and transported to Purdue University and stored in a -20 °C deep-freeze prior to laboratory analysis.

Age and growth

Adult lake whitefish age was estimated by scale-acetate impressions. Acetate impressions were prepared by rolling a subsample of three nonresorptive scales of similar shape and size onto acetate sheets using a jeweler's press (Wildlife Supply Company, Buffalo, NY). Impressions were viewed and interpreted using a Micron 370 microfiche reader under transmitted light ($10\times$ magnification; Muir et al., 2008).

Age 0 juvenile lake whitefish age was estimated by examining sagittal otolith microstructure (Campana, 1992). One otolith from an individual was mounted, sulcus side down, on a glass microscope slide (76×25 mm) using Buehler thermoplastic cement heated to 275 °C (Buehler, Lake Bluff, IL). Aluminum oxide 261X metallurgical dry-lapping film (3 M; St. Paul, MN) in 30-, 12-, 9-, 5-, 3-, and $0.3\text{-}\mu\text{m}$ grades was temporarily fixed to a scratch-free piece of Plexiglas® by adhesion with 10% acetate solution to create a polishing surface. Polishing times varied depending on thickness of the otolith and the grit of the lapping film required. Polishing was ceased just short of the increment plane, the microscope slide was heated to 275 °C, and the otolith was flipped so that the other side was exposed for polishing. Increment microstructure was interpreted directly through a compound microscope ($40\text{--}1000\times$ magnification; Nikon, Tokyo, Japan) under transmitted light. True daily increments were distinguished from false increments on age 0 juvenile otoliths based on visual appearance and were identifiable by focusing in and out of the increment plane. In general, we observed two prominent growth checks in the otoliths of lake whitefish from all sites. The first check occurred between 10 and 12 days and was interpreted as the "hatching check". This check encircled 10–12 narrowly spaced, well-defined, concentric rings that extended outward from the foci and could only be resolved under $1000\times$ magnification. Post-hatch, there were approximately another 10–12 rings of varying widths, after which growth bands became widely spaced and irregular and sub-daily increments became apparent. The growth increments between 10 and 24 d may have represented a transition period during which fish began consuming exogenous prey. The 24-day check was interpreted as the time of complete transition to exogenous food sources. Subsequent to collecting our aging data, this assumption was corroborated by Oyadomari and Auer (2007). These authors reported that a prominent check formed on the otoliths of laboratory-reared larval cisco *Coregonus artedii* otoliths at around 28 days post-hatch, which was shown to correspond with the timing of yolk-sac absorption. We also observed the formation of prominent growth checks on the otoliths of laboratory-reared lake whitefish between 24 and 28 days post-hatch (A. Muir, unpublished data). These two checks provided useful benchmarks for verifying otolith increment counts. As a crude measure, age 0 juvenile daily growth in length (mm/day) and weight (mg/day) were calculated by dividing the total length or wet weight of each fish at capture by its age (days).

Body condition and composition

Body condition of adults was quantified using relative condition ($K_n = W_w / W_l$), where W_w is the wet weight and W_l is the length-specific mean weight for a fish predicted by a weight-length regression relationship for all of the fish in our study (Anderson and Neumann, 1996). The weight-length relationship for males and females combined ($n = 849$) from all sites examined in our study was $\log_{10} W_l = 3.282 \times (\log_{10} \text{length}) - 5.81$ ($r^2 = 0.89$, $F_{1,847} = 6504.28$, $P < 0.001$; Muir, 2008). Relative condition (K_n) was not calculated for the age 0 juvenile life stage because the assumptions of isometric growth and a cubic relationship between weight and length are not typically valid for this life stage (Wootton, 1998).

Moisture content, energy density, and protein content of adults, eggs, and juveniles were estimated following standard Association of Official Analytical Chemists procedures (Helrich, 1990). Moisture content was calculated as ((wet weight – dry weight) / wet weight) $\times 100$, where the wet weight was recorded using an M-310 balance (Denver Instrument Company, Denver, CO). Dry weight was recorded to the nearest 0.0001 g after drying in an oven (Precision & Napco, Winchester, VA) at 100 °C for 24 h (Helrich, 1990; Pangle et al., 2004). To facilitate calculation of egg properties on a per-egg basis, a subsample ($n = \sim 60$ eggs) was extracted from the 100-g sample for each individual and processed according to the methods described below. Mean wet weight (g) of individual eggs was determined by dividing the wet weight of the subsample by the number of eggs in that subsample. The total weight of the entire 100-g egg sample collected from each individual was divided by the mean wet weight per egg to estimate the total number of eggs contained in the sample. Finally, the dry weight of the entire sample was divided by the estimated number of eggs to obtain the mean dry weight for individual eggs, and the energy content per egg was calculated by multiplying the energy density (J/g) of the entire sample by the mean dry weight (g) of the eggs in that sample. Dehydrated muscle and egg samples were individually homogenized using a commercial 1.0-L laboratory blender (Waring Laboratory, Torrington, CT). Because 1 g of dried tissue homogenate was required for energy density and protein content analysis, age 0 juvenile samples were pooled when necessary. For example, within a site, individuals were randomly selected and pooled until dry weight > 1 g. The energy density and the protein content for the pooled sample were assumed to represent the average for all individuals that were included in the pooled sample.

Energy density of 0.5-g adult, egg, and juvenile tissue homogenates was measured using a Parr Isoperibol Oxygen Combustion Bomb Calorimeter (Parr Instruments, Moline, IL; Pierce et al., 1980). Homogenates were compacted using a Parr pellet press. The enthalpy of hydrocarbon fuel combustion ± 0.0001 °C was measured as J/g dry matter. A CNS-2000 Elemental Analyzer (LECO Corporation, St. Joseph, MI) was used to combust 0.2-g homogenates to estimate muscle nitrogen content. These data were converted to protein equivalents using percentage protein = average percent nitrogen of dry matter $\times 6.25$, where 6.25 is a conventional multiplication factor for conversion of nitrogen into protein because the nitrogen fraction of protein is assumed to be 0.16 (AOAC, 1990; Kamler, 1992).

Statistical methods

To achieve our first objective, we partitioned the variation in lake whitefish juvenile physiological condition among maternal, paternal, and egg effects using redundancy analysis (RDA; Legendre and Legendre, 1998; Peres-Neto et al., 2006). In general, RDA is an extension of multiple regression (i.e., a single response variable y and multiple predictors x), which involves a matrix of multiple response variables Y and one or more matrices of explanatory variables X_1, X_2, \dots, X_n . In our analysis, Y consisted of a matrix containing five juvenile physiological condition variables: (1) growth in length (mm/day);

(2) growth in weight (wet weight mg/day); (3) whole-body muscle moisture content (%); (4) energy density (J/g whole-body dry matter); and (5) protein content (%N whole-body dry matter). Matrices X_F and X_M consisted of the full sets of female and male predictor variables, respectively: (1) size [total length (mm)]; (2) age (years); (3) body condition (K_n); (4) muscle moisture content (%); (5) energy density (J/g dry muscle tissue); and (6) protein content (%N dry muscle tissue). Matrix X_E consisted of the full set of egg predictor variables: (1) size (mg/egg dry matter); (2) moisture content (%); (3) energy density (J/g dry matter); (4) energy content (J/ egg dry matter); and (5) protein content (%N dry matter).

These 11 variables are relevant indices of reproductive investment because they are indicative of overall physiological condition, relate to reproductive physiology, and have been linked to juvenile growth and survival in several fishes, including *Coregonus* spp. (reviewed by Kamler, 2005). Sample site (matrix X_S) was dummy coded and used as a factor in the analysis because we were interested in whether some of the residual variation in juvenile physiological condition could be attributed to variation among sites. The percentage of variation in Y explained by the X_S was measured by the redundancy statistic ($R_{Y|X_n}^2$), which represents the canonical equivalent of the regression coefficient of determination R^2 (Legendre and Legendre, 1998). Therefore, the simultaneous analysis of multiple response variables associated with energy transfer among life stages allowed us to test predictions of the parental effects hypothesis.

In addition to the aforementioned variables, we quantified the following fatty acids from freeze-dried dorsal muscle tissue measured as micrograms of fatty acid methyl ester per milligrams of dry weight of tissue extracted: (1) α -linolenic acid (ALA; C18:3n3); (2) arachidonic acid (ARA; C20:3n3); (3) eicosapentaenoic acid (EPA; C20:5n3); and (4) docosahexaenoic acid (DHA; C22:6n3; Michael Arts, Environment Canada, unpublished data). We incorporated the ratio of EPA:ARA, ALA, EPA, and DHA as predictor variables for females, males, and eggs in each of the models described below and found that the addition of these variables

($n=12$ in total) only explained 2% more variation in juvenile physiological condition; therefore, we elected not to include these data in the current study.

For the RDA, we randomly re-sampled our data without replacement to create four balanced matrices containing the variables of interest (Table 1). Data were pooled across years to maximize sample size and to create balanced data matrices that were not missing any data. Thirty sub-samples were randomly drawn from each site ($n=7$) for females (X_F), males (X_M), eggs (X_E), and juveniles (Y) resulting in a total sample size of 210 individuals for each of the four matrices. With the exception of juvenile muscle energy density ($t_{615} = -3.65$, $P < 0.001$), there were no significant differences between the reduced and the complete data set for any of the 22 variables; therefore, the re-sampling routine did not bias our results. To achieve dimensional homogeneity, all data matrices were standardized to zero mean and unit variance (i.e., z-scores; Legendre and Legendre, 1998); however, unstandardized data are reported in Table 1.

The R function *varpart* (vegan library, www.r-project.org) was used to decompose the total variation in juvenile physiological condition into three fractions according to the methods described by Peres-Neto et al., (2006): (1) variation contributed by the combined effects of each set of explanatory variables; (2) unique variation contributed by each set of explanatory variables (i.e., X_F , X_M , X_E , X_S); and (3) residual variation not accounted for by the sets of variables we measured. Therefore, the total contribution to variation in juvenile physiological condition was divided into eight parts—7 canonical analyses and 10 subtraction equations were used to estimate the 8 fractions. The significant contribution to explaining variation in juvenile physiological condition for parts obtained by canonical analyses was tested by an F -ratio according to $F(X_n) = ([R_{Y|X_n}^2 X_n] / (\text{residuals } df_{[X_n + h]})) / (h / (n - 1 - df_{[h]}))$, where $R_{Y|X_n}^2$ is the redundancy statistic for a given explanatory matrix X_n (e.g., $X_1 = \text{females}$), $h = R_{Y|X_n}^2$ residuals, and df is the degrees of freedom (Oksanen, 2008). Using this method, the following four models were fit to the reduced data set: (1) $Y = X_S + X_F + X_M + \epsilon_i$; (2) $Y = X_S + X_F + X_E + \epsilon_i$; (3) $Y =$

Table 1

Mean total length (L; mm), relative condition (K_n), age (years), moisture content (%M), energy density (J/g), total protein (%N), daily growth in length (GL; mm/day), growth in weight (GW; mg/day), egg dry weight (DW; mg/egg), and energy content (EPE; J/egg) \pm SE for Naubinway (NB), Big Bay de Noc (BBN), Elk Rapids (ER), Baileys Harbor (BH), Ludington (LD), Saugatuck (SA), and Whitefish Point (WP) adult female (♀), male (♂), egg (E), and age 0 juvenile (J) lake whitefish; $n = 30$ individuals/life stage/gender randomly subsampled per site from entire data set.

Stock	Gender	L	K_n	Age	%M	J/g	%N	GL	GW	DW	EPE
NB	♀	485.47 ± 4.71	96.56 ± 1.12	6.63 ± 0.18	76.81 ± 0.30	1317.49 ± 20.97	91.15 ± 0.82	—	—	—	—
	♂	488.03 ± 5.81	91.69 ± 1.69	7.50 ± 0.21	76.61 ± 0.19	1308.9 ± 10.16	91.78 ± 1.05	—	—	—	—
	E	—	—	—	63.74 ± 0.28	1566.27 ± 18.02	61.51 ± 0.46	—	—	3.05 ± 0.11	4.76 ± 0.16
	J	—	—	—	74.16 ± 1.20	1158.04 ± 3.31	80.60 ± 0.18	0.57 ± 0.02	4.96 ± 0.97	—	—
BBN	♀	519.30 ± 6.09	98.67 ± 1.59	7.43 ± 0.21	76.50 ± 0.28	1322.82 ± 14.51	89.00 ± 1.04	—	—	—	—
	♂	508.63 ± 3.75	92.61 ± 1.75	6.90 ± 0.26	75.11 ± 0.24	1314.78 ± 17.1	89.37 ± 1.00	—	—	—	—
	E	—	—	—	62.75 ± 0.19	1465.68 ± 13.7	62.57 ± 0.34	—	—	3.14 ± 0.09	4.62 ± 0.15
	J	—	—	—	75.83 ± 0.65	1197.46 ± 0.37	83.55 ± 0.02	0.60 ± 0.02	3.15 ± 0.28	—	—
ER	♀	500.73 ± 6.86	103.35 ± 1.41	7.90 ± 0.32	75.99 ± 0.43	1289.18 ± 13.24	84.70 ± 1.08	—	—	—	—
	♂	491.50 ± 7.49	100.92 ± 5.78	8.23 ± 0.27	76.30 ± 0.32	1288.65 ± 13.49	84.67 ± 1.13	—	—	—	—
	E	—	—	—	62.70 ± 0.26	1531.14 ± 13.93	63.20 ± 0.77	—	—	2.93 ± 0.08	4.47 ± 0.12
	J	—	—	—	79.14 ± 0.45	1199.88 ± 4.01	83.08 ± 0.66	0.63 ± 0.01	5.16 ± 0.27	—	—
BH	♀	553.83 ± 6.50	102.42 ± 1.74	7.50 ± 0.21	77.45 ± 0.21	1325.96 ± 2.58	87.05 ± 1.03	—	—	—	—
	♂	561.87 ± 6.10	92.80 ± 1.50	7.73 ± 0.24	76.71 ± 0.20	1295.98 ± 7.79	87.05 ± 1.03	—	—	—	—
	E	—	—	—	65.51 ± 0.41	1544.23 ± 13.52	62.81 ± 0.49	—	—	2.87 ± 0.06	4.43 ± 0.09
	J	—	—	—	79.91 ± 0.53	1063.19 ± 0.08	83.04 ± 0.35	0.62 ± 0.01	8.07 ± 1.10	—	—
LD	♀	542.80 ± 5.27	111.26 ± 1.30	7.20 ± 0.20	76.95 ± 0.29	1315.68 ± 11.76	85.33 ± 0.91	—	—	—	—
	♂	513.40 ± 4.64	105.01 ± 1.14	6.37 ± 0.16	81.01 ± 1.18	1343.4 ± 10.61	81.01 ± 1.18	—	—	—	—
	E	—	—	—	63.19 ± 0.22	1544.9 ± 14.97	61.33 ± 0.95	—	—	2.56 ± 0.10	3.95 ± 0.15
	J	—	—	—	79.74 ± 0.33	1210.29 ± 2.82	81.61 ± 0.46	0.62 ± 0.02	8.05 ± 1.11	—	—
SA	♀	528.37 ± 5.42	110.95 ± 1.69	7.03 ± 0.20	77.69 ± 0.36	1359.82 ± 21.32	85.38 ± 1.13	—	—	—	—
	♂	508.33 ± 6.27	98.86 ± 1.42	6.40 ± 0.17	77.27 ± 0.24	1302.04 ± 9.87	87.67 ± 0.86	—	—	—	—
	E	—	—	—	67.54 ± 0.54	1521.95 ± 13.7	63.91 ± 0.73	—	—	3.01 ± 0.10	4.59 ± 0.16
	J	—	—	—	76.39 ± 1.51	1151.12 ± 4.14	81.36 ± 0.40	0.78 ± 0.02	11.79 ± 0.49	—	—
WP	♀	585.37 ± 11.67	110.65 ± 1.81	7.07 ± 0.36	81.57 ± 1.37	1367.32 ± 19.08	81.57 ± 1.37	—	—	—	—
	♂	535.07 ± 8.52	101.91 ± 1.90	5.57 ± 0.23	73.39 ± 0.38	1399.75 ± 21.16	79.91 ± 1.44	—	—	—	—
	E	—	—	—	61.73 ± 0.43	1572.78 ± 8.43	60.42 ± 0.57	—	—	3.15 ± 0.09	4.8 ± 0.2
	J	—	—	—	76.76 ± 0.86	1203.16 ± 3.95	79.85 ± 0.28	0.61 ± 0.02	4.44 ± 0.67	—	—

$X_S + X_M + X_E + \epsilon_i$; and (4) $Y = X_F + X_M + X_E + \epsilon_i$. The “best” model was defined as the one with the lowest residual variation (ϵ_i).

To accomplish our second objective, we conducted a correlation analysis to determine which female attributes or egg properties were most closely associated with juvenile physiological condition. Adult males were excluded from this analysis because they did not contribute significantly to explaining variation in juvenile physiological condition (see Results). All statistical analyses (significance level was set at $\alpha = 0.05$) were conducted using R 2.6.1 (www.r-project.org) and SPSS 14.0 (SPSS Inc., Chicago, IL).

Results

Objective 1

Of the four variance partitioning models, model 2 site (X_S) + female (X_F) + egg (X_E) + ϵ_i explained the most variation in juvenile physiological condition (i.e., had the lowest residual variation; Fig. 2). Overall, this model explained 39% of the variation in juvenile physiological condition (Table 2). After partitioning out the effects of females and eggs, site (fraction a in Table 2) explained the most significant proportion of variation (23%; $F = 10.11$; $P < 0.001$) in juvenile physiological condition. When other factors were accounted for, neither females (1.4%) nor egg quality (2.7%) explained a significant amount of variation in juvenile physiological condition. There appeared to be a female \times site (fraction d) and egg \times site (fraction f) interaction, which explained 4.5% and 4.1% of the variation, respectively; however, these fractions were not testable because they were obtained by subtraction (Legendre and Legendre, 1998). Males contributed little to explaining variation in juveniles for any of the models tested; therefore, results of models which included males are not reported herein. Sixty-one percent of the variation in juvenile physiological condition was unaccounted for by the intrinsic biotic variables that we measured.

Objective 2

In general, there were no strong correlations between juvenile physiological condition and female or egg attributes (all $r < 0.36$). Of the variables that we examined, juvenile physiological condition was

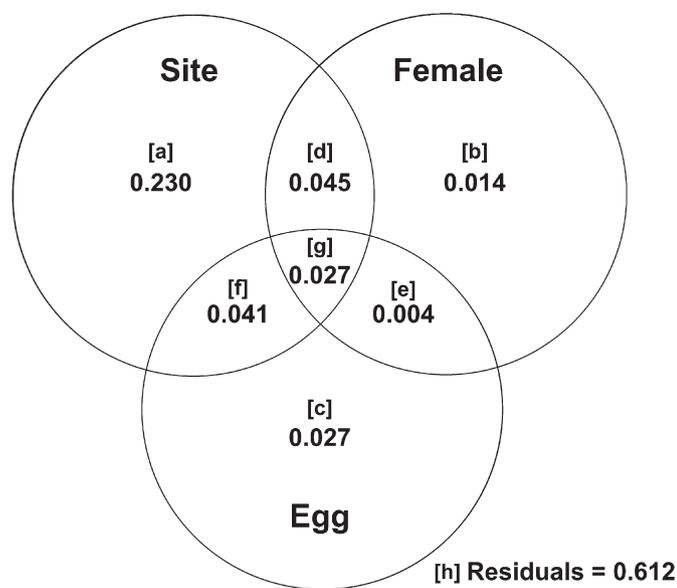


Fig. 2. Partitioning of variation in lake whitefish juvenile physiological condition among three sets of explanatory variables: sampling site, female condition, and egg quality. The outer rectangle represents the total variation in juvenile physiological condition.

Table 2

Variation partitioning of juvenile physiological condition among three sets of explanatory variables: sampling site, female condition, and egg quality.

	Fractions	df	Adjusted R^2	F	P
Site	[a + d + f + g]	6	0.34	17.63	<0.001
Female	[b + d + e + g]	5	0.09	3.98	0.002
Egg	[c + e + f + g]	6	0.10	3.70	0.002
Site + female	[a + b + d + e + f + g]	11	0.36	10.13	<0.001
site + egg	[a + c + d + e + f + g]	12	0.37	9.79	<0.001
Female + egg	[b + c + d + e + f + g]	11	0.16	3.37	<0.001
All	[a + b + c + d + e + f + g]	17	0.39	7.15	<0.001
Site egg	[a + d]	6	0.27	12.82	<0.001
Site female	[a + f]	6	0.27	12.59	<0.001
Female egg	[b + d]	5	0.06	2.55	0.030
Female site	[b + e]	5	0.02	0.73	0.600
Egg site	[c + e]	6	0.03	1.08	0.376
Egg female	[c + f]	6	0.07	2.49	0.024
Site female + egg	[a]	6	0.23	10.11	<0.001
Female site + egg	[b]	5	0.01	0.59	0.711
Egg site + female	[c]	6	0.03	0.95	0.457

Fractions d, e, f, g, and h are not provided because they are calculated via subtraction and therefore not testable (letters refer to Fig. 2). The vertical bar separating two variables represents the first term controlled for the second term.

most closely associated with female muscle energy density and muscle moisture content and egg protein and moisture content (Table 3). For example, juvenile protein content was negatively correlated with female K_n ($r = -0.16$) and positively associated with female age ($r = 0.21$) and egg protein content ($r = 0.30$). Juvenile energy density was negatively correlated with female muscle protein ($r = -0.16$) and moisture ($r = -0.30$) content as well as egg moisture content ($r = -0.36$). Juvenile moisture content was positively correlated with female length ($r = 0.21$) and energy density ($r = 0.23$). Juvenile growth in length was negatively associated with female muscle protein content ($r = -0.14$) and positively with female muscle energy density ($r = 0.16$) and moisture content ($r = 0.34$), whereas juvenile growth in weight was positively correlated with female muscle energy density ($r = 0.16$), moisture content ($r = 0.30$), egg protein ($r = 0.20$), and egg moisture content ($r = 0.31$). Most of the other correlations were weak (i.e., $r < 0.10$; Table 3). Surprisingly, none of the juvenile physiological condition variables that we measured were correlated to egg energy density, energy content per egg, or egg dry weight (all $r < 0.10$).

Table 3

Pearson correlation analyses identifying associations between juvenile growth in length (mm/day) and weight (g/day), whole-body moisture content (%), energy density (J/g), and protein content (%N) and female total length (mm), relative condition (K_n), muscle protein content (%N), muscle energy density (J/g), muscle moisture content (%), age (years) and egg protein content (%N), energy density (J/g), moisture content (%), dry weight (g), and energy content per egg (J/egg).

	Variable	Juvenile				
		Protein content	Energy density	Moisture content	Growth in length	Growth in weight
Female	Length	-0.04	-0.01	0.21**	0.11	0.07
	K_n	-0.16*	0.02	0.08	0.10	0.13
	Protein	0.10	-0.16*	-0.09	-0.14*	0.03
	Energy	-0.10	0.02	0.23**	0.16*	0.16**
	Moisture	0.11	-0.30**	0.11	0.12	0.30**
Egg	Age	0.21**	0.04	0.08	0.09	0.03
	Protein	0.30**	-0.05	0.08	0.11	0.20**
	Energy	-0.05	0.06	-0.01	-0.02	0.06
	Moisture	-0.05	-0.36**	-0.04	0.34**	0.31**
	Dry weight	0.03	-0.10	0.09	0.02	-0.02
weight	Energy content	0.01	-0.08	0.09	0.02	0.00

** Correlation is significant at the 0.01 level (two-tailed).

* Correlation is significant at the 0.05 level (two-tailed).

Discussion

Our first objective was to assess the role of adult male and female lake whitefish condition and egg quality in age 0 juvenile physiological condition, within the context of the parental effects hypothesis. Our results refute the prediction that parental condition and egg quality explain significant variation in juvenile physiological condition. Sampling site alone explained 23% of the variation in juvenile physiological condition, while 61% of the variation was unaccounted for by the intrinsic biotic variables that we quantified (Fig. 2). We suggest that this finding is consistent with lake whitefish life history and recruitment dynamics. For instance, lake whitefish are “periodic strategists” (Winemiller and Rose, 1992), whereby they exhibit delayed sexual maturation, iteroparity, relatively high fecundity (range = 10,000–30,000 eggs/kg flesh; Hart, 1930; Christie, 1963; Cucin and Regier, 1966; Bidgood, 1974; Ihssen et al., 1981), and attain a large size and relatively old age. This species is a non-guarding benthic spawner (Balon, 1975), which exhibits indirect ontogeny (i.e., a larval life stage is present). Spawning occurs during late fall on rocky nearshore shoals, embryos incubate over the winter in the interstitial spaces of the substrate, and temperature-dependent larval emergence occurs during the spring (i.e., April–May in the Great Lakes). Upon emergence, larvae disperse to productive nearshore nursery habitats (Faber, 1970; Reckahn, 1970; Hoagman, 1973; Frederick, 1982). During dispersal, larvae rely on endogenous (i.e., yolk) energy reserves for nutrition; the transition from endogenous to exogenous feeding is a critical period that is characterized by high mortality (Hjort, 1914). Large numbers of relatively small eggs are produced as a compensatory mechanism to offset the low survival of larvae (Crawford and Balon, 1996). This strategy is likely adaptive for population persistence in variable environments such as the Laurentian Great Lakes. Based on simulation models, Winemiller and Rose (1993) reported that investing in large numbers of smaller eggs was an evolutionarily superior reproductive strategy when resources were patchy on a relatively large spatial scale, as is the case in the Laurentian Great Lakes (Makarewicz et al., 1995).

In a study of the reproductive life history strategies of lake whitefish, Muir (2008), found support for the hypothesis that female lake whitefish maintain a degree of quality control over their gametes through trade-offs between their body condition, egg size, number, and composition and that those dynamic processes may buffer the effects of changes in energy availability on recruitment potential. This reproductive strategy is consistent with a “periodic” life history, in which large numbers of relatively small eggs are produced and early life history mortality is high during hatching, dispersal, and the transition to exogenous feeding. The fact that little of the variation in juvenile physiological condition could be attributed to the combination of parental and egg variables measured in the current study suggests that in addition to female reproductive trade-offs, extrinsic factors and/or density-dependent factors may also play an important role in driving variation in juvenile condition, survival, and potentially recruitment among stocks. The interactions between female and egg variables further suggest that there was a geographic trend in energy allocation to reproduction. Although conclusive elimination of the parental effects hypothesis requires controlled laboratory experiments to quantify embryonic and larval survival in relation to parental effects, our study suggests that an alternative hypothesis may be required to explain variation in juvenile lake whitefish physiological condition.

We offer two alternative hypotheses to explain variation in juvenile physiological condition, both of which require further study. First, the *extrinsic recruitment regulation hypothesis* predicts that extrinsic abiotic factors, such as temperature, and biotic factors, such as zooplankton quantity and quality, drive variation in juvenile lake whitefish physiological condition. Of the factors previously studied, temperature and juvenile prey availability appear to be two

important extrinsic influences on juvenile lake whitefish growth, survival, and ultimately recruitment. For example, Christie (1963) and Lawler (1965) reported that a cold November (spawning) followed by a warm April (hatching) tended to produce large year classes of lake whitefish due to increased growth and survival in Lakes Ontario and Erie, respectively. Further, cold winter temperatures produce ice, which suppresses wind-driven currents and may reduce physical damage and prevent embryos from being swept off the spawning shoals (Taylor et al., 1987; Freeberg et al., 1990; Brown et al., 1993).

A second alternative to the parental effects hypothesis is the *post-embryonic density dependence hypothesis*, which holds that larval/juvenile physiological condition is a function of density-dependent effects such as intraspecific competition for prey. Evidence of competition comes from Hoagman (1974), who demonstrated that lake whitefish larvae require continuous nutritional input and suggested a minimum daily ration of 10–20 copepods per individual. A later study suggested that this ration may be closer to 32 prey per individual, below which growth in length and weight was suppressed and mortality increased dramatically (Taylor and Freeberg, 1984). Similarly, Brown and Taylor (1992) linked exogenous growth and survival of lake whitefish larvae to feeding ration in laboratory experiments.

Our second objective was to determine which physiological indicators associated with spawning male and female condition and egg quality were most closely associated with juvenile physiological condition. Of the explanatory variables that we quantified, female muscle energy density, female muscle moisture content, and egg moisture and protein content were most closely correlated with juvenile physiological condition. Some of the correlations that we observed were broadly consistent with what is known about the bioenergetics of early growth in fishes; however, others were not. For example, juvenile energy density was negatively related to female muscle protein and moisture content and egg moisture content, which is what we would expect given that moisture content is generally negatively related to energy density in fishes (Kamler, 2005).

By contrast, the positive correlation between juvenile moisture content and female energy density that we observed was unexpected and could reflect a reproductive trade-off. This result is opposite of what would be expected if females were in poor condition and had little energy available to invest in reproduction. Relative condition is considered a surrogate for physiological condition in fishes; thus, high K_n of maternal females should indicate greater whole-body energy reserves and potentially more resources available for reproduction. Lipids and proteins stored in the body tissues during active feeding yield energy for growth and reproduction in coregonids (Dabrowski, 1982, 1983). The lipid content of biological tissues is often inversely related to percent moisture content, with higher moisture values being indicative of lower K_n (Brown and Murphy, 1994; Sutton and Ney, 2001; Pangle et al., 2004). It seems reasonable to suppose that females with low muscle moisture and high muscle energy density should produce embryos with higher quality yolk and larvae with higher growth rates. However, reproductive trade-offs may buffer maternal effects on egg quality; therefore, reduced female K_n may be the consequence of making a greater reproductive investment, during a time when the prey base is declining. These types of trade-offs may explain why none of the juvenile physiological condition variables that we measured were strongly correlated with female K_n but were correlated to female energy density in unexpected ways.

The association between juvenile growth in length and weight and egg moisture content was also counterintuitive and suggests that eggs with high moisture content experienced poor overwinter survival. One explanation may be that poor quality eggs result in greater embryo mortality but enhanced growth and survival at the juvenile life stage due to reduced density-dependent competition for resources. Juvenile growth in weight was also positively related to female moisture content, which makes sense if females are making

high reproductive investments and are less fit as a consequence (i.e., poor female K_n is a consequence of allocating greater energetic resources to their eggs). Brown and Taylor (1992) reported that lake whitefish larvae produced from eggs with high energy density had higher percent lipid content, resulting in larvae that had more endogenous energy reserves. Larvae hatching from eggs with higher lipid content hatched at a slightly smaller average size but were able to compensate through accelerated endogenous growth (Brown and Taylor, 1992). Resolving the mechanism underlying the positive relationship between juvenile growth and egg moisture content will require controlled laboratory experiments; therefore, egg moisture content cannot be considered a reliable indicator of juvenile lake whitefish physiological condition at this time.

In general, juvenile lake whitefish with the highest whole-body moisture content (i.e., poorest condition) were produced from females with the greatest mean age, highest muscle energy density, and highest muscle moisture content. The effect of adult age on juvenile moisture content is likely manifest indirectly through egg quality. As fish mature, there is an increased energy demand for reproduction. For example, Craig (1977) reported an increase in recruitment of energy to support reproduction at the expense of somatic growth in European perch *Perca fluviatilis* of increasing age. Egg dry weight and moisture content have a curvilinear association with parental age in several species (Nikolskij, 1974, cited in Kamler, 1992). Taken together, these results suggest that aging populations of lake whitefish may be in poorer physiological condition, therefore producing juveniles with poorer body composition; however, this pattern was not evident across all sites and was not strongly supported by our statistical analyses.

One caveat to our study was that we assumed that the juveniles that we collected were the progeny of the spawning adults that we sampled from the adjacent shoals during the previous fall. Lake whitefish larvae have low dispersal ability and require specific nearshore nursery habitats (Frederick, 1982). The spawning shoals that we sampled are within close geographic proximity to known larval and juvenile nursery habitat. Lake whitefish spawning grounds (Goodyear et al., 1982), nursery habitats, and the ecology of embryo and age 0 juvenile lake whitefish are well known (Cucin and Regier, 1966; Faber, 1970; Reckahn, 1970; Hogman, 1971; Loftus, 1977; Loftus, 1979; Frederick, 1982; Cucin and Faber, 1985). To our knowledge, there is no evidence to suggest that our study design invalidates the assumption that the juveniles sampled represent a random sample of progeny from a given spawning stock.

In summary, we found little evidence to suggest that parental effects, such as size, age, K_n , or body composition, are critical drivers of lake whitefish juvenile physiological condition. It is likely that maternal effects do occur at the individual level, particularly in terms of reproductive trade-offs, but at the stock level, these effects may be overridden by density-dependent competition or by extrinsic environmental effects. If the physiological variables that we measured in juveniles are suitable indicators of fish health and are linked to survival, then declines in adult growth and condition observed within the Laurentian Great Lakes may not be as important as other factors, such as larval/juvenile density or environmental change, on the early life history and recruitment dynamics of lake whitefish. Although we found no single variables that were strong predictors of juvenile physiological condition, female muscle moisture content and egg moisture content may be suitable candidate proxies for maternal reproductive investment. These variables are easy to measure, are correlated with important physiological measures of condition, such as muscle energy density, and are correlated with some juvenile attributes that have been linked to overwinter survival and recruitment potential. However, as previously discussed, controlled laboratory studies may be required to conclusively determine the effects of these variables and their correlates on juvenile lake whitefish physiological condition.

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