

Relative Weight (W_r) as a Field Assessment Tool: Relationships with Growth, Prey Biomass, and Environmental Conditions

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Abstract.—We evaluated the relative weight (W_r) condition index as a field assessment tool with pumpkinseed *Lepomis gibbosus* and golden shiner *Notemigonus crysoleucas*, focusing on sources of variability and potential of W_r as a predictor of growth, prey availability, and environmental conditions in 10 southern Quebec lakes over 2 years. To allow calculation of W_r , we developed standard weight (W_s) equations for both species, using the regression-line-percentile (RLP) technique. The proposed W_s equation in metric units (grams wet weight and millimeters total length, TL) for pumpkinseed is $\log_{10}W_s = -5.179 + 3.237 \log_{10}TL$; for golden shiner it is $\log_{10}W_s = -5.593 + 3.302 \log_{10}TL$. Spatial and temporal variation in W_r was highly significant and largely asynchronous in both species, although spring values were lowest in most lakes. The W_r index frequently varied with length, prompting us to examine relationships in stock and quality length fish separately. We found little evidence for a relationship between W_r and growth in either species. Pumpkinseed W_r s were positively correlated with total benthic invertebrate biomass; stock length W_r was positively correlated with chironomid biomass, and quality length W_r was positively correlated with gastropod biomass. The relative weight of quality length golden shiners was positively correlated with chironomid biomass. Our results and those of other studies suggest that the common assumption of a relationship between W_r and growth in field populations should be reconsidered, but that W_r could be cautiously used as a working index of prey availability. We recommend empirical or experimental verification when W_r is used as an assessment tool in field populations.

Condition indices are widely used in assessing freshwater fish populations (Nielsen and Johnson 1983; Schreck and Moyle 1990; Murphy et al. 1991; Kohler and Hubert 1993). Condition indices measure the “plumpness” or “robustness” of fish, and are easily calculated from routinely collected length–weight data. Condition is frequently assumed to reflect not only characteristics of fish, such as health, “well-being,” reproductive state, and growth, but also characteristics of the environment, such as habitat quality, water quality, and

prey availability (Anderson and Gutreuter 1983; Busacker et al. 1990; Ney 1993).

There has been much debate concerning the use of condition indices in recent literature, centering largely around methodological issues such as the appropriateness of various indices (Bolger and Connolly 1989; Cone 1989; Springer et al. 1990). Recently, the relative weight (W_r) condition index (Wege and Anderson 1978) has become popular, prompting discussion regarding the various methods for generating the necessary standard weight (W_s) equations (Murphy et al. 1990, 1991). A more fundamental issue regarding the use of condition indices remains unresolved, however, and that is how to interpret condition of fish in natural populations. What does condition predict? Evidence for relationships with growth and other characteristics mentioned earlier is scattered throughout the literature on condition but is largely anecdotal. We are aware of no previous uses of spatially and tem-

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porally replicated sampling designs to evaluate W_r as a tool for predicting growth, prey availability, and other factors in field populations.

The primary purpose of this study was to evaluate W_r as a tool for assessing freshwater fish populations. To do this, we took advantage of a concurrent study of littoral fish communities, invertebrate prey availability, limnological conditions, and growth of two fish species in 10 lakes in southern Quebec (Pierce et al. 1994). First, we developed standard weight (W_s) equations for two of the dominant species in these lakes, pumpkinseed *Lepomis gibbosus* and golden shiner *Notemigonus crysoleucas*. Then, using these equations to calculate W_r , we analyzed sources and patterns of variation in W_r and explored relationships of W_r with growth, fish biomass, prey biomass, and limnological variables. Results of this evaluation illustrate strengths and weaknesses of W_r as an assessment tool for fish populations in nature and will help guide the use of W_r for other species.

Methods

Study lakes and species.—Evaluation of W_r was conducted in 10 lakes in the Eastern Townships region of southern Quebec, Canada. Locations, littoral fish communities, and other characteristics of these lakes were recently described by Pierce et al. (1994). Pumpkinseeds and golden shiners are common and widely distributed littoral zone fishes in North America (Scott and Crossman 1973; Lee et al. 1980). Together, they account for 30% of the fish biomass of the littoral zone and are among the most abundant littoral species in these lakes (Pierce et al. 1994).

Development of standard weight equations.—We obtained weight-length data from 302 pumpkinseed populations representing 11 states and provinces and 285 golden shiner populations representing 9 states and provinces (Liao 1994) to develop standard weight (W_s) equations for each species. The data were of two general types: weights and lengths of individual fish, or regressions describing weight-length relationships of populations. Individual weights and lengths were provided by management and research personnel, along with site names, locations, and occasionally additional descriptive information. Most of these data sets contained no information regarding age, growth, or sex. Weight was either reported as or converted to the nearest 0.1 g (wet) and total length (TL) to the nearest millimeter. Eight or more individual fish and $r^2 > 0.80$ for the regression of weight (\log_{10}) on length (\log_{10}) were minimum

criteria for including populations in the development of W_s equations. Regressions describing weight-length relationships of many additional populations were taken from published studies, agency reports, and data compilations. When known, the same inclusion criteria as just described were used for these regressions. Regressions reported without sample size and r^2 (5% of pumpkinseed populations, <1% of golden shiner populations) were assumed to be valid and included.

Standard weight equations for pumpkinseeds and golden shiners were developed with the regression-line-percentile (RLP) technique (Murphy et al. 1990). The RLP technique is currently favored for developing W_s equations because it weights each population equally and produces W_r estimates of low variance and free of length bias (Murphy et al. 1991). For each population, we computed a linear regression of weight (\log_{10}) on length (\log_{10}) or used the existing one. We established 50 mm and 300 mm as minimum and maximum points of the length range. At the midpoint of each 1-cm length interval within this range (i.e., 55 mm, 65 mm, 75 mm, etc.), we calculated a predicted \log_{10} weight using the weight-length regression and then back-transformed these values to predicted arithmetic weights. For each length interval, the 75th percentile was then calculated from the predicted weights of all the populations in the data set. Finally, the 75th percentile weights were \log_{10} -transformed and regressed against the corresponding \log_{10} -transformed midpoint lengths, yielding the \log_{10} - \log_{10} version of the W_s equation. Further details and rationale for the RLP technique were given by Murphy et al. (1990).

Fish sampling for evaluating W_r .—Using beach seines as described by Pierce et al. (1990), we sampled pumpkinseeds and golden shiners in each of the 10 lakes once in early summer (hereafter referred to as "early") and once in late summer (hereafter referred to as "late") during 1987 and 1988. The early summer period was from 18 June to 26 June in 1987 and from 4 July to 15 July in 1988. The late summer period was from 24 August to 17 September in 1987 and from 8 September to 22 September in 1988. Details of the early and late sampling were presented by Pierce et al. (1994). Additional samples of both species were obtained from 9 May to 20 May 1988 and are hereafter referred to as "spring" samples.

Captured fish were anesthetized immediately in 2-phenoxyethanol, put on ice, and frozen within a few hours. In the laboratory, a length-stratified

random subsample of at least 50 fish (>50 mm TL) of each species from each combination of lake and sampling date was weighed (wet) to the nearest 0.01 g on an electronic balance and measured to the nearest millimeter (TL). A few subsamples contained fewer than 50 fish, reflecting low abundance on the corresponding sampling date. Scale samples for age and growth analysis were collected from each fish in spring and late 1988 subsamples. Pumpkinseed scales were taken at the tip of the depressed left pectoral fin; golden shiner scales were taken above the lateral line dorsal to the tip of the depressed left pectoral fin. Sex was determined for the spring subsamples only.

Determination of size-classes for test populations.—We used the length categorization system of Gabelhouse (1984) to establish meaningful lengths for comparisons of W_r and to examine relationships of W_r with growth and other variables. These descriptive categories were chosen because of their frequent use in fisheries studies and their intuitive appeal. Minimum "stock" and "quality" lengths of 80 mm and 150 mm, respectively, were used for pumpkinseeds (Gabelhouse 1984). Using the rationale of Gabelhouse (1984) and 305 mm as an estimate of maximum length (Becker 1983), we set minimum "stock" length as 70 mm (23% of maximum) and "quality" length as 120 mm (39% of maximum) for golden shiners. Although Gabelhouse's system includes three larger size-classes (preferred, memorable, trophy), very few fish of these sizes were caught. Therefore, our size-specific analyses of W_r were restricted to stock and quality lengths.

Condition of test populations.—The W_r index was calculated for all fish with the equation

$$W_r = 100 \cdot W/W_s \quad (1)$$

(Wege and Anderson 1978); W is the wet weight of the fish and W_s is the length-specific standard weight predicted from the appropriate W_s equation described above. These individual W_r values were used to explore sources of variation in W_r and the relationship with growth of individuals as described below.

For each subsample (i.e., for each combination of species, lake, and sampling date), W_r was regressed against total length. If the regression was significant (slope significantly different from zero at $\alpha = 0.05$), it was used to generate size-specific (stock and quality) W_r estimates for that subsample. If the regression was not significant, the subsample mean W_r was used to represent W_r for all sizes in that subsample. Neither regressions nor

subsample means were extrapolated beyond the ranges of fish sizes in subsamples; this resulted in no W_r estimates for some size-classes on some sampling dates.

For comparing W_r with growth and food availability across lakes, size-specific estimates from the early and late subsamples from both years were averaged by species and lake. This produced size-specific "average" estimates of W_r for each species in the 10 lakes and prevented unequal weighting of sampling periods due to variable numbers of fish in subsamples.

Growth of test populations.—We estimated growth rates of individual fish by aging and back-calculating lengths at previous ages using scales (Busacker et al. 1990). Ten or more scales per fish were cleaned and mounted between glass slides; large, opaque scales were impressed on acetate slides. All scales on slides were viewed when ages were assigned to fish, and a single reader did all aging. Scales from 30 fish of both species were viewed by a second reader, and age assignments were in 100% agreement. Ages assigned by reading scales corresponded well with length-frequency distributions.

Radii and interannular distances on 10 scales per fish were measured with a dissecting microscope (25 \times magnification), drawing tube, and computerized digitizing tablet as described by Frie (1982). Regenerated or otherwise distorted scales were not digitized, resulting in fewer than 10 replicate scales measured for some fish. Replicate measurements were then averaged for each fish, providing precise estimates of scale growth increments for back-calculations (Newman and Weisberg 1987).

We used the Fraser-Lee technique (Busacker et al. 1990) for back-calculation of lengths at previous ages based on scale growth increments. Intercepts (a) for back-calculation were generated from regressions of fish length on scale radius from 1,095 pumpkinseeds and 1,127 golden shiners distributed approximately equally among all 10 study lakes. Whereas all fish from spring and late 1988 subsamples were used in generating body-scale relationships, fish older than 5 years were omitted from back-calculations to avoid potential errors from incorrect aging of older fish. Pumpkinseed and golden shiner back-calculations were based on averages of 81 and 104 fish per lake, respectively.

Using the back-calculated lengths at previous ages and differences between successive lengths as estimates of annual growth increments, we regressed annual growth increments against length

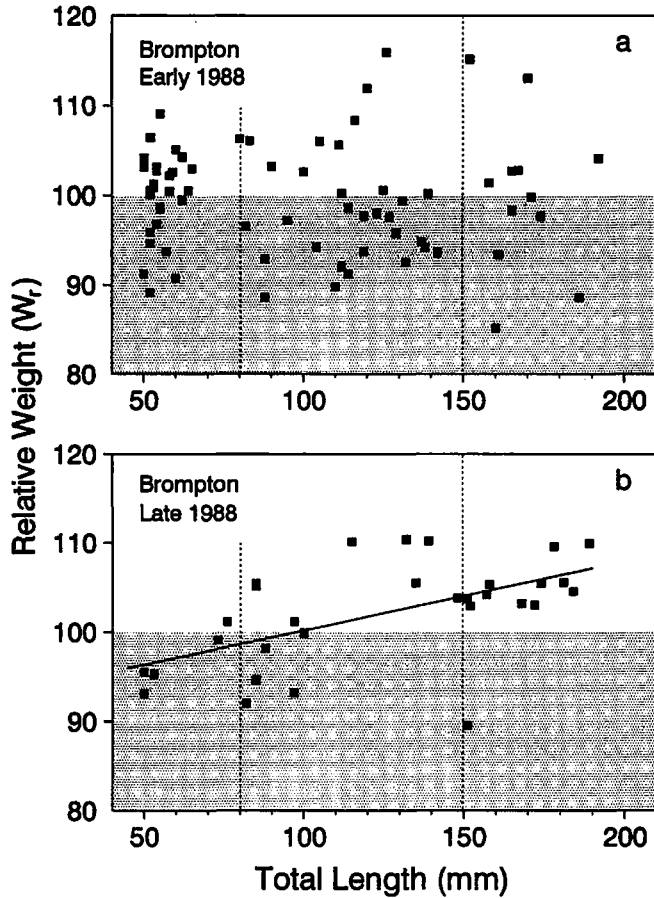


FIGURE 1.—Example of variation in relative weight (W_r) among individual pumpkinseeds and relationships with fish length. Data points represent individual fish from Lake Brompton collected in (a) early 1988 and (b) late 1988. Vertical dashed lines indicate minimum stock (80 mm) and quality (150 mm) lengths. Shaded areas indicate W_r less than 100. Among-fish variation was similar in other lakes and for golden shiner. When no significant relationship with total length existed, as in panel a, W_r for both length-classes was represented by the mean W_r for that date (99.5 in this case). When a significant relationship with total length existed, as in panel b, W_r was estimated by solving the W_r -total length regression for stock and quality lengths (98.7 and 104.0, respectively, in this case).

at the start of the growing season for each species in each lake. All regressions had negative slopes, indicating decreasing annual growth with increasing size. Growth rates of young-of-year fish were simply estimated as lengths at first annulus and were not included in regressions, because initial length was length at hatching and was essentially the same for all fish. Quadratic regressions were used to improve fit when both linear and quadratic terms were significant ($\alpha = 0.05$). These size-specific growth regressions explained averages of 51% and 60% of the variation in annual growth of pumpkinseed and golden shiner populations, respectively, and allowed estimation of "average" growth of a population at stock and quality lengths,

similar to the way in which size-specific W_r estimates were obtained, as described earlier. Expressing growth as a function of fish size has several advantages over the more traditional age-specific approach, especially when one is comparing growth among populations (Gutreuter 1987; Osenberg et al. 1988).

Using fish from late 1988 subsamples only, we estimated recent growth of individual fish as the difference between length at capture and back-calculated length at the last annulus. These recent growth increments were then regressed against length at last annulus for each species in each lake, similar to the procedure described earlier. Residuals from these regressions were used as length-

corrected estimates of recent growth and were examined for each species within each lake for correlation with W_r .

Fish biomass, prey biomass, and limnological variables in study lakes.—Biomass of pumpkinseeds, golden shiners, and the total littoral fish community was estimated from the early and late samples described earlier. Detailed descriptions of the procedures and analysis of these samples were presented by Pierce et al. (1990, 1994).

Invertebrate prey and limnological variables were sampled several times from May through September 1987 and 1988. Littoral sediment-dwelling and epiphytic macroinvertebrate prey were sampled as described by Rasmussen (1988). Organisms were identified, counted, and measured for conversion to biomass with length–mass regressions (Smock 1980; C. W. Osenberg, University of California–Berkeley, unpublished data; J. B. Rasmussen, unpublished data).

Littoral zooplankton prey were sampled at 0700 hours by triplicate bottom-to-surface vertical hauls with a 30.5-cm-diameter, 75- μ m-mesh net. Depths were recorded to the nearest 0.1 m, and were generally near 3 m. A filtering efficiency of 46%, estimated by several calibrations with pooled Schindler–Patalas trap samples taken at 1-m intervals, was applied as a correction factor in biomass calculations. Samples were preserved in a sucrose–formalin solution (Haney and Hall 1973). Organisms in subsamples (usually 10% of sample) were identified and counted, and at least 30 individuals of each taxon were measured for conversion to biomass with length–mass regressions (Dumont et al. 1975; Culver et al. 1985).

Water temperatures were estimated with a combination of littoral and pelagic temperature profiles at 1-m depth intervals. Littoral temperature profiles were recorded near fish sampling areas from the surface to the bottom (~3 m). Pelagic profiles were recorded at offshore locations from the surface to a depth of 3 m. Temperatures from individual profiles were averaged across depths, and these values were then averaged over the 2 years of sampling for each lake. Chlorophyll-*a* concentrations were determined from integrated epilimnetic water samples obtained from offshore locations with a tube sampler; triplicate 500-mL subsamples were vacuum-filtered (65- μ m pores), frozen in the field, and extracted in the laboratory (Strickland and Parsons 1968). We sampled submerged littoral macrophyte biomass and fish concurrently as described by Pierce et al. (1990).

Statistical analyses.—We analyzed data using

TABLE 1.—Summary of ANOVAs testing the effects of lake, year, and season on W_r of pumpkinseeds and golden shiners in 10 southern Quebec lakes. Data are from the early and late summer samples, 1987 and 1988. Sums of squares are type III (SAS Institute 1985).

Source of variation	df	Sum of squares	F	P
Pumpkinseed				
Lake (L)	9	16,837.6	28.56	0.0001
Year (Y)	1	21.8	0.33	0.56
Season (S)	1	767.2	11.71	0.0006
L \times Y	9	5,797.9	9.84	0.0001
L \times S	9	8,047.1	13.65	0.0001
Y \times S	1	3,606.2	55.06	0.0001
L \times Y \times S	9	2,351.9	3.99	0.0001
Error	2,495	163,421.1		
Golden shiner				
Lake	9	19,215.6	29.41	0.0001
Year	1	1,854.8	25.54	0.0001
Season	1	724.3	9.98	0.0016
L \times Y	9	5,021.1	7.68	0.0001
L \times S	9	10,444.7	15.98	0.0001
Y \times S	1	11,060.8	152.33	0.0001
L \times Y \times S	9	12,154.5	20.92	0.0001
Error	2,565	186,241.8		

linear regression, quadratic regression, analysis of variance (ANOVA), and correlation analysis. Linear regressions of \log_{10} -transformed length and weight data were performed to generate W_s equations with the RLP method as described earlier. Lake, yearly, and seasonal variation in W_r of both species was evaluated with 3-way ANOVAs with interactions, and sex and lake variation was evaluated with 2-way ANOVAs with interactions. Data for relative weight were analyzed untransformed. Relationships of W_r with growth and other variables were examined by regression and correlation analysis. Growth data were analyzed untransformed; other variables were transformed as described by Pierce et al. (1994). All analyses were performed with the CORR, GLM, REG, and UNIVARIATE procedures of SAS (SAS Institute 1988).

Results

Standard Weight Equations

The proposed standard weight (W_s) equation for pumpkinseed is

$$\log_{10}W_s = -5.179 + 3.237 \cdot \log_{10}TL; \quad (2)$$

for golden shiner it is

$$\log_{10}W_s = -5.593 + 3.302 \cdot \log_{10}TL; \quad (3)$$

W_s is standard weight in grams and TL is total length in millimeters. These W_s equations were

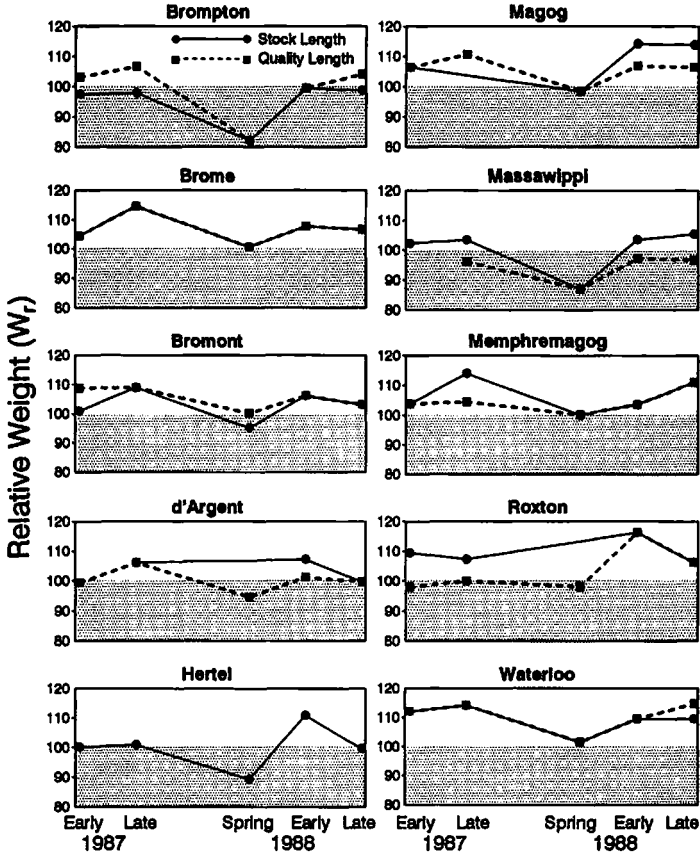


FIGURE 2.—Temporal changes in relative weight (W_r) of stock length (80 mm, solid lines) and quality length (150 mm, dashed lines) pumpkinseeds in southern Quebec lakes. Overlapping data points indicate a nonsignificant regression of W_r on fish length and are represented by the mean W_r for that date. Nonoverlapping data points represent size-specific W_r estimates from a significant regression of W_r on fish length for that date. Missing data points indicate that no fish of that size were sampled on that date. Shaded areas indicated W_r less than 100.

used to calculate W_r of individual fish from test populations.

Influence of Fish Length on W_r

Plots of W_r of individual fish showed variable relationships with fish length, depending on species, lake, and sampling date (e.g., Figure 1). Regressions of W_r on length were significant ($\alpha = 0.05$) in 40% of the pumpkinseed subsamples and 33% of the golden shiner subsamples (early and late subsamples only). In both species, 31% of the significant regressions had positive slopes, and 69% had negative slopes. Significant regressions for a given species and lake were usually all either positive or negative, although there were both positive and negative regressions for golden shiner in two lakes (Brompton and d'Argent). There was no case of significant regressions occurring in all sub-

samples of a given species and lake, but it was common for at least one subsample to have a significant regression. The examples in Figure 1 are representative of the overall pattern of relationships of W_r with length; correlations were ephemeral, perhaps reflecting changing relative ecological conditions for fish of different sizes over time.

Spatial and Temporal Variation in W_r

The W_r of both species varied significantly and asynchronously among lakes, years, and seasons (Table 1; Figures 2, 3). Interactions of all variables were highly significant (ANOVA) for both species (Table 1), making interpretations difficult. These tests of the effects of lake, year, and season can be considered conservative, because variation due to length was contained in the error sums of squares. Figures 2 and 3 illustrate this,

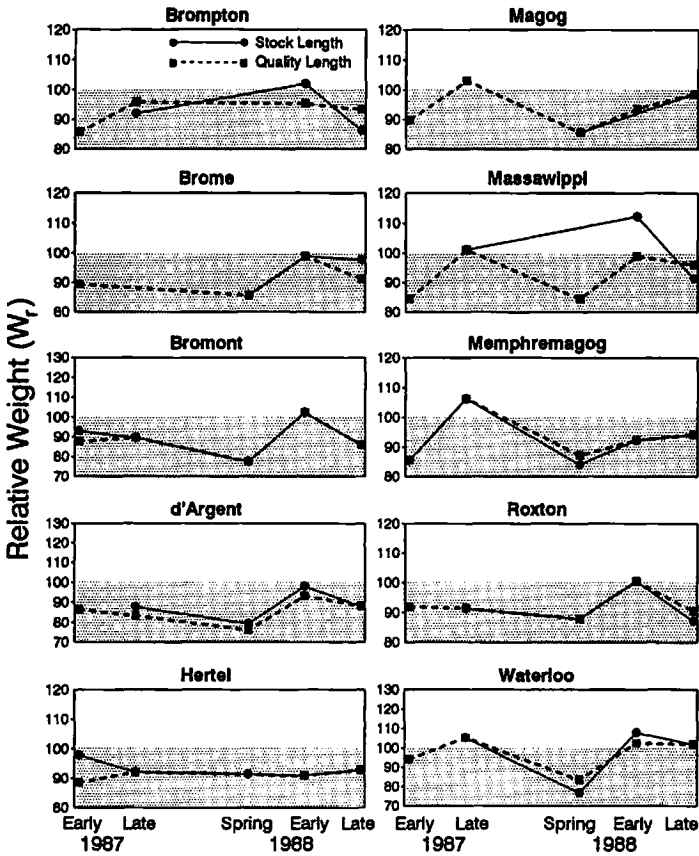


FIGURE 3.—Temporal changes in relative weight (W_r) of stock length (70 mm, solid lines) and quality length (120 mm, dashed lines) golden shiners in southern Quebec lakes. Details are the same as those for Figure 2.

showing that although W_r tended to be higher in some lakes and lower in others, the temporal patterns differed considerably among lakes. Early W_r was higher than late W_r in some lakes, whereas the reverse was true in others. In some lakes, early W_r was higher than late W_r in one year but lower in the other year. The only consistent pattern was that the lowest W_r s occurred in spring in most lakes.

Influence of Sex on W_r

There were no significant differences in W_r between males and females of either species in the spring subsamples (Table 2). The spring samples were collected from all lakes just before the beginning of the spawning seasons of both species, and thus at a time when sexual differences in W_r , if any, would likely be most evident. The highly significant lake effects (Table 2), here in the absence of interacting temporal effects, further sup-

port the previous inference of significant differences in W_r among lakes.

Intra- and Interspecific Relationships in W_r Among Lakes

Intraspecific correlations of W_r of stock and quality length fish among lakes showed mixed results. The W_r estimates of stock length pumpkinseeds were not significantly correlated with W_r estimates of quality length pumpkinseeds among the 10 lakes ($r = 0.65, P = 0.059$). In contrast, the corresponding correlation for golden shiners was significant ($r = 0.83, P = 0.003$). These results suggest greater among-lake independence of factors related to pumpkinseed W_r across length than of those related to golden shiner W_r .

Interspecific correlations of W_r estimates of both stock and quality length fish among lakes were nonsignificant (stock length: $r = 0.42, P = 0.227$; quality length: $r = 0.50, P = 0.167$), suggesting

TABLE 2.—Summary of ANOVAs testing the effects of lake and sex on W_r of pumpkinseeds and golden shiners in 10 southern Quebec lakes. Data are from the spring samples, 1988. Sums of squares are type III (SAS Institute 1988).

Source of variation	df	Sum of squares	F	P
Pumpkinseed				
Lake (L)	9	13,769.4	27.65	0.0001
Sex (S)	1	13.8	0.25	0.62
L × S	9	355.3	0.71	0.70
Error	461	25,510.7		
Golden shiner				
Lake	9	6,191.0	18.10	0.0001
Sex	1	13.6	0.32	0.57
L × S	9	422.1	1.41	0.20
Error	413	17,690.7		

that W_r responses of the two species to environmental conditions in lakes differed.

Relationship of W_r with Growth

We found little evidence for a relationship between W_r and growth. There were no significant correlations of size-specific W_r estimates with corresponding size-specific growth estimates among lakes (Table 3). Although these results suggest a general lack of relationship, they are based on lake means of seasonally and annually varying W_r estimates and therefore could potentially contain confounding individual and temporal variation. As a test of the relationship of W_r and growth among individual fish, we examined correlations of growth residuals (length-corrected estimates of recent growth) with W_r in each subsample (e.g., Figure 4). These correlations compared late summer W_r s with growth during that summer among individual fish in subsamples. Eighty percent of these correlations for both species were nonsignificant ($P > 0.05$; e.g., Figure 4c). Three of the four significant ($P < 0.05$) correlations were negative (e.g., Figure 4d), contrary to the a priori expectation of a positive relationship.

Relationships of W_r with Fish Biomass, Prey Biomass, and Limnological Variables

We found no evidence of density dependence in W_r estimates among lakes for either species (Table 3). Neither total fish biomass nor conspecific biomass were significantly correlated with W_r .

The strongest relationships in our data set were between W_r estimates and biomass estimates of benthic prey among lakes, especially for pumpkinseeds (Table 3). The W_r of both stock and qual-

TABLE 3.—Correlations of relative weight (W_r) of pumpkinseeds and golden shiners with growth, fish biomass, and prey biomass in 10 southern Quebec lakes; P values are given in parentheses. All data used in correlations are lake averages; fish and prey biomass data are from Pierce et al. (1994). Spring 1988 W_r data were not included in calculation of lake averages.

Variable	Pumpkinseed		Golden shiner	
	Stock length	Quality length	Stock length	Quality length
Growth ^a	0.41 (0.242)	-0.24 (0.539)	0.37 (0.291)	0.51 (0.129)
Littoral fish biomass				
Total	0.38 (0.283)	0.07 (0.864)	0.51 (0.133)	0.59 (0.072)
Conspecific	0.28 (0.440)	0.28 (0.461)	-0.31 (0.389)	-0.01 (0.989)
Littoral benthos biomass				
Total	0.69 (0.027)	0.90 (0.001)	0.12 (0.739)	0.41 (0.244)
Gastropods	0.53 (0.115)	0.84 (0.004)	-0.03 (0.929)	0.26 (0.467)
Chironomids	0.72 (0.018)	0.58 (0.098)	0.61 (0.063)	0.72 (0.019)
Littoral zooplankton biomass	0.22 (0.538)	0.19 (0.626)	0.44 (0.202)	0.41 (0.242)

^a Appropriate size-specific growth estimates were used for comparison with W_r (i.e., growth of stock length fish compared with W_r of stock length fish, growth of quality length fish compared with W_r of quality length fish).

ity length pumpkinseeds was positively correlated with total benthos biomass; the quality length relationship was particularly strong (Table 3). The W_r of stock length pumpkinseeds was positively correlated with chironomid biomass (Figure 5a), and W_r of quality length pumpkinseeds was positively correlated with gastropod biomass (Figure 5b). The W_r of quality length golden shiners was positively correlated with chironomid biomass (Table 3). We found no significant correlations between W_r of either species and littoral zooplankton biomass (Table 3).

Chlorophyll *a* was the only limnological variable significantly correlated with W_r , and only for pumpkinseeds. Correlations of pumpkinseed W_r with chlorophyll *a* were positive (stock length: $r = 0.67$, $P = 0.035$; quality length: $r = 0.75$, $P = 0.019$). All correlations of W_r with temperature and macrophyte biomass were nonsignificant ($P > 0.05$).

Discussion

Our W_s equations are the first formally proposed standard weight equations for pumpkinseed and golden shiner, thus allowing calculation of W_r for these species. Standard weight equations have

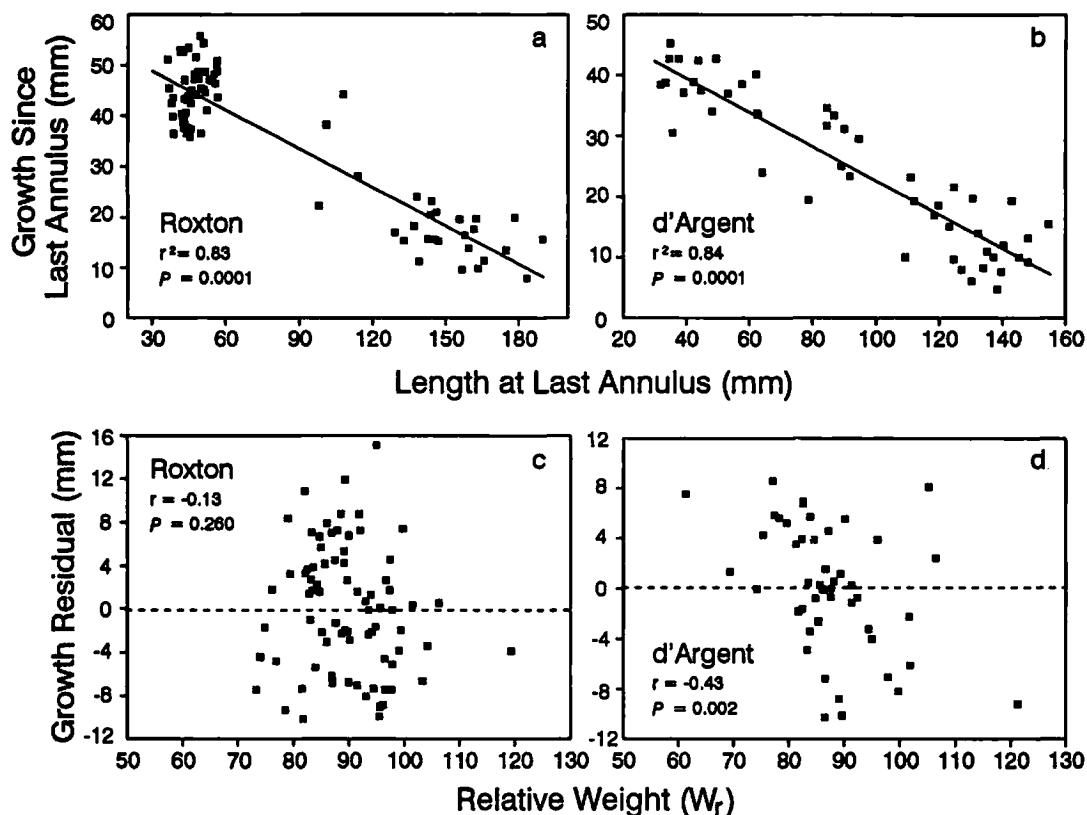


FIGURE 4.—Example of relationships of recent growth increments with length (a, b) and of growth residuals with relative weight (W_r) (c, d) for individual golden shiners collected in 1988 from Roxton Pond and Lac d'Argent, Quebec. Lengths at last annuli and recent growth increments since last annuli were estimated by back-calculation. Growth residuals are residual variation in growth not explained by regressions of growth increments on length (panels a and b), and thus represent length-corrected estimates of growth of individual fish since the last annulus. These length-corrected growth estimates of individual fish were then examined for correlation with W_r (panels c and d) for each species in each lake.

been proposed for over 30 species and are used by at least 19 state fisheries management agencies for calculating W_r (Murphy et al. 1991). Although W_r has become the favored index for expressing condition in fish, it still must be used and interpreted with care. We agree with Springer and Murphy (Springer et al. 1990) that W_s more properly represents a benchmark for comparison than a goal for management. Furthermore, we believe that it is important to clearly distinguish between the issue of how best to calculate condition, and once an appropriate condition index is selected, what information it provides about fish and their environment. Our intention was neither to contribute to the debate (Bolger and Connolly 1989; Cone 1989; Springer et al. 1990) over W_s methodology, nor to give explicit support for the RLP technique; thus, we have not provided exhaustive documen-

tation of the performance of our W_s equations. Several recent studies (Murphy et al. 1990; Brown and Murphy 1991; Neumann and Murphy 1991; Willis et al. 1991) with other species demonstrate that the RLP technique produces acceptable equations. In particular, this technique produces W_r estimates free of length bias, allowing changes in W_r with length in a population to be interpreted as real phenomena rather than methodological artifacts. We believe that our proposed W_s equations will provide useful standards for calculating and comparing W_r for pumpkinseeds and golden shiners and have been valuable in enabling us to evaluate the predictive utility of W_r with data from these species.

We found significant relationships of W_r with length, both positive and negative, in many of our subsamples of each species. Roughly similar pat-

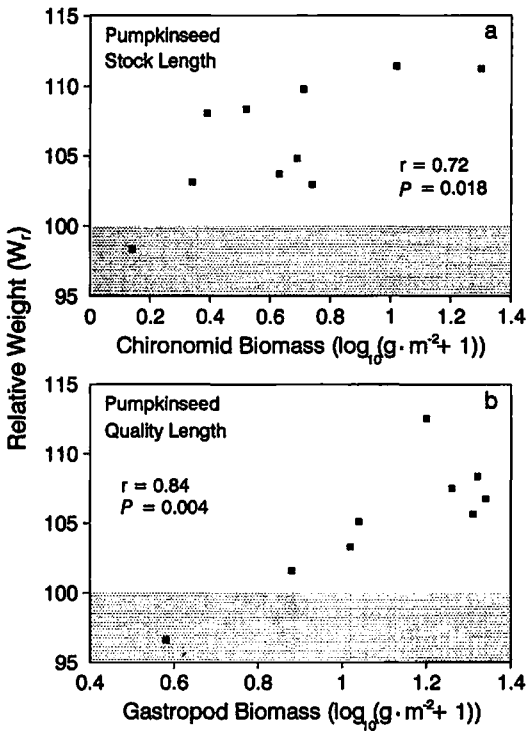


FIGURE 5.—Relationships of relative weight (W_r) of (a) stock length (80 mm) pumpkinseeds with chironomid biomass and (b) quality length (150 mm) pumpkinseeds with gastropod biomass in southern Quebec lakes. Data points represent lake averages; prey data are from Pierce et al. (1994). Spring 1988 W_r data were not included in calculation of lake averages. Shaded areas indicate W_r less than 100.

terns have been shown for walleye *Stizostedion vitreum* (Murphy et al. 1990), yellow perch *Perca flavescens* (Willis et al. 1991), white crappie *Pomoxis annularis* and black crappie *P. nigromaculatus* (Neumann and Murphy 1991), and striped bass *Morone saxatilis* and palmetto bass *M. chrysops* ♀ × *M. saxatilis* ♂ (Brown and Murphy 1991). A significant change in W_r with length might be expected in cases in which species undergo size-related changes in resource needs, and resources required or preferred by different size-classes vary. Size-related (or ontogenetic) prey and habitat switching is well known for many fish species (Zaret 1980; Mittelbach 1981; Keast 1985), including the species mentioned above. Pumpkinseeds, for example, undergo pronounced dietary shifts from zooplankton to small littoral invertebrates to gastropods as they grow (Sadziowski and Wallace 1976; Keast 1978; Mittelbach 1984; Osenberg and Mittelbach 1989). Prey abun-

dance varies widely among lakes and other aquatic systems (Hanson and Peters 1984; Rasmussen 1988), and it is reasonable to assume that different prey types will often vary independently. Therefore, we believe that the general agreement of our results with those of previous work showing a mixture of positive, negative, and nonsignificant relationships of W_r with length is consistent with present knowledge of the resource ecology of fishes. Because of the variable nature of this relationship, use of mean W_r for summarizing condition of fish populations should be avoided unless a lack of relationship with length is demonstrated. Again, pumpkinseeds provide a good example. The W_r of stock and quality length pumpkinseeds was not significantly correlated across our set of 10 lakes, reflecting different W_r -length relationships among lakes. Comparing these populations by mean W_r would obscure potentially important size-related phenomena.

The W_r of pumpkinseeds and golden shiners varied both spatially (across 10 lakes) and temporally (between early and late summer and over 2 years of sampling). Furthermore, spatial and temporal patterns of variation in W_r among lakes were inconsistent over time and vice versa. Temporal variation in condition has been reported in previous studies of yellow perch (Le Cren 1951; Guy and Willis 1991), burbot *Lota lota* (Pulliainen and Korhonen 1990), black crappie (Gabelhouse 1991; Guy and Willis 1991), and northern pike *Esox lucius* and walleye (Guy and Willis 1991), but these studies were all limited to single systems. With the exception of the study of Gutreuter and Childress (1990), we are aware of no previous studies designed to simultaneously quantify and compare both temporal and spatial variation. The previous studies of temporal variation in condition (and probably many unpublished data) have resulted in the common practice of sampling during "standard" seasons for assessing condition and other parameters (Gabelhouse 1991). The temporal asynchrony of our results suggest that so-called "standard" time periods might not be as comparable among lakes as previously believed.

In contrast to the pattern of temporal asynchrony we observed in summer, the spring subsamples had the lowest W_r values in most of our lakes, a pattern similar to that documented by Le Cren (1951) for yellow perch. Our spring subsamples were taken before the fish spawned and presumably reflect coincident declines in condition due to overwintering in cold Canadian lakes rather than direct spawning activities.

Contrary to results of some previous studies and common expectations, we found scant evidence for a relationship of W_r with growth. The first paper proposing W_r as a condition index reported a positive correlation between W_r and growth of largemouth bass *Micropterus salmoides* (Wege and Anderson 1978). Likewise, positive relationships have been shown for northern pike (Willis 1989), yellow perch (Willis et al. 1991), and juvenile striped and palmetto basses (Brown and Murphy 1991). These empirical results have apparently led to the common notion that W_r and other condition indices can be used as indicators of growth; poor condition indicates poor growth and vice versa. Despite recent contradictory evidence (Gutreuter and Childress 1990; Gabelhouse 1991), this notion now appears in the general methodological literature (e.g., Busacker et al. 1990; Ney 1993). We do not dispute previous results showing positive relationships between W_r (or other condition indices) and growth. Rather, we believe that the collective evidence to date suggests that the assumption of condition mirroring growth should not be made uncritically. Perhaps cautious use of W_r as an indicator of growth could be justified in limited situations in which an appropriate empirical or experimental basis exists.

Another factor commonly linked with W_r in the methodological literature is prey availability (Anderson and Gutreuter 1983; Busacker et al. 1990; Flickinger and Bulow 1993; Ney 1993). Low W_r values are assumed to reflect prey scarcity, whereas high values are assumed to reflect an abundance of prey. Our results provide some support for this relationship. Benthic invertebrates are known to be very important in the diets of pumpkinseeds (Scott and Crossman 1973; Sadzikowski and Wallace 1976; Keast 1978), and W_r of both stock and quality length pumpkinseeds was positively correlated with benthos biomass in our study lakes. Our results also corresponded well with the known dietary shift by pumpkinseeds; W_r of stock length fish was positively correlated with chironomid biomass, and W_r of quality length fish was positively correlated with gastropod biomass. These two prey taxa accounted for averages of 24% and 41% of the total littoral invertebrate biomass in these lakes, respectively (Pierce et al. 1994).

Relationships of golden shiner W_r with prey were less evident; the only statistically significant correlation was between W_r of quality length fish and chironomid biomass. Perhaps the lack of clear relationships between body condition of golden shiners and prey availability reflects their appar-

ently flexible and omnivorous diet. Golden shiners have been reported to use varying foraging behaviors (Ehlinger 1989) and to feed on zooplankton, soft-bodied macroinvertebrates, phytoplankton, and periphyton (Keast and Webb 1966; Scott and Crossman 1973; Hall et al. 1979). Alternatively, the lack of strong W_r -prey relationships for golden shiners could have other explanations, including failure to adequately quantify an important prey taxon, lack of food limitation, or existence of other controlling factors that mask potential food effects. Although our data provide better support for the use of W_r as an index of prey availability than of growth, the somewhat equivocal golden shiner results suggest that this relationship should be inferred cautiously for other species unless diets are known precisely and the relationship is empirically or experimentally verified.

Density-dependent interactions, both intra- and interspecific, have been well documented for a variety of species (Hanson and Leggett 1985; Mittelbach 1988; Persson and Greenberg 1990), typically resulting in reduced feeding success, growth, or altered habitat use. These effects are generally interpreted as exploitative competition for some limiting resource or possibly interference competition via behavioral interactions. Although not a direct test for their existence, we hypothesized that W_r might reflect such interactions, varying inversely with biomass of either conspecifics or the entire littoral community. Despite large variation of fish biomass across our lakes (Pierce et al. 1994), we found no evidence that W_r varied with biomass. These results may indicate a lack of competitive interactions involving these species (but see Hanson and Leggett 1985), but experiments would be required to test this interpretation. We speculate that W_r may have potential in assessing extremely intense competition, such as occurs in situations involving exotic species.

Of the limnological variables that we examined, only chlorophyll *a* was significantly correlated with W_r and only for pumpkinseeds. As a general index of water quality and lake productivity (Carlson 1977; Oglesby 1977), chlorophyll-*a* data are widely available and could also potentially be linked with fish condition. The positive correlations of W_r with chlorophyll *a* for both stock and quality length pumpkinseeds are consistent with the relationships of pumpkinseed W_r and benthos, assuming "bottom-up" control among trophic levels (McQueen et al. 1986). The lack of relationship of golden shiner W_r s with chlorophyll *a* is also consistent with the weaker W_r -prey relationships

for this species. We hesitate in making this interpretation, however, and believe that because of the necessary intermediate linkages required, inferring relationships between fish condition and limnological indices of lake productivity should probably be avoided.

Implications for W_r as an Assessment Tool

Relative weight will vary with fish length in some populations but not in others. Furthermore, the existence and even the sign of this relationship in a population might change over time. Use of mean W_r to characterize these populations will systematically overestimate condition of fish at one end of the length range and underestimate it at the other end. We urge biologists to test for length relationships before using mean population W_r . In addition to more accurately expressing condition, discovery of length-related changes in W_r may provide important additional information about the population and system, such as availability of different resources, size-structured interactions, and life-history phenomena.

Relative weight will generally vary temporally, but temporal variation may be asynchronous among populations. Thus, assessing W_r at one "standard" period (e.g., by fall electrofishing) for comparison among populations may not provide a true comparison; W_r of one population might be at its maximum, while others could be increasing or decreasing. We suggest that biologists measure W_r at different times in a coordinated fashion among populations to examine the pattern of temporal variation. If temporal variation is negligible or the pattern is consistent among populations, comparisons based on a standard sampling period are justified. Otherwise, comparisons of W_r among populations should probably be based on temporal averages.

The common assumption of a positive relationship between W_r and growth should be reconsidered. Relative weight may reflect growth of some species under certain circumstances, but this should be empirically or experimentally demonstrated before W_r is used as a predictor of growth. Uncritical use of W_r as a growth indicator could lead to substantial errors in field assessment of fish populations, and probably already has.

Relative weight may be a good predictor of prey availability, especially for species with relatively narrow or well-defined diets. We suggest that W_r could be used as a working index of prey availability but recommend verifying this relationship if possible.

Aquatic and fisheries ecology are rapidly developing and progressively intertwining fields (Kerfoot and Sih 1987; Carpenter 1988; Northcote 1988), and much of the excitement in these areas is sustained by new studies proposing opposing mechanisms, indirect effects, alternative pathways, and other ideas that complicate our models of how these systems work. Accordingly, we feel that the simplicity and historical inertia of field assessment tools such as W_r must be weighed against a healthy dose of caution regarding their interpretation. As a practical matter, we advocate testing for relationships before assuming their existence. With proper care and foresight, W_r and other field assessment indices can be important tools in both research and management.

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