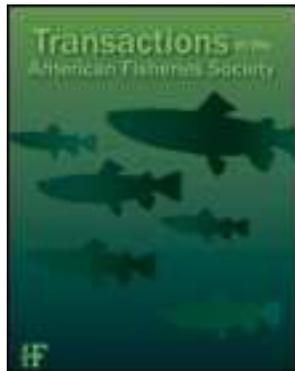


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Age-0 Yellow Perch Growth and Its Relationship to Temperature

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Abstract.—Temperature is known to be an important determinant of growth, but its influence on the growth of juvenile yellow perch *Perca flavescens* has not been unambiguously quantified. In this study, temperature data loggers were deployed in several northern Alberta lakes, and the data collected were used to compute the cumulative number of days for which water temperature exceeded the 13.5°C minimum temperature required for yellow perch growth. Tow-net and seine samples of young of the year (age-0 fish) were obtained to describe growth in fork length throughout the summer. Length and degree-day data were used to test the importance of temperature as a determinant of growth. A significant relationship was obtained and validated with data from previous studies of age-0 yellow perch in Manitoba. The importance of temperature was further assessed over a broader geographic range with the use of latitude as a surrogate for temperature and published data on end-of-season lengths. Though not the sole determinant of among-population variability, latitude was found to have a significant effect on growth. Collectively the results suggest that temperature has both a micro- and a macro-scale effect on determining age-0 yellow perch growth.

The ubiquity of yellow perch *Perca flavescens* in the ponds and lakes of temperate North America has made the species a favorite among investigators attempting to illuminate the important ecological factors affecting fish population size and structure. As a result, the relationship between growth of young-of-the-year (age-0) yellow perch and food supply has been well established (Noble 1975; Nakashima and Leggett 1978; Mills and Forney 1981; Confer and Lake 1987; Boisclair and Leggett 1989; Mills et al. 1989; Confer et al. 1990; Prout et al. 1990; and Letcher et al. 1996). The causes and effects of overwinter mortality (Post and Evans 1989; Johnson and Evans 1991), inter-specific competition (Roseman et al. 1996), predation effects on year-class strength or growth (Forney 1971; Post and Prankevicius 1987) and the patterns of first-year growth (Pycha and Smith 1955; Fortin and Magnin 1972; Ney and Smith 1975) are also now reasonably well understood.

The influence of temperature, however, is less certain. Although temperature is known to be an important ecological resource for fish (Magnuson et al. 1979) and to play a role in determining yellow

perch growth (Coble 1966; Barans and Tubb 1973; Ney and Smith 1975; Mills et al. 1989), the extent of its influence on yellow perch is debated, and quantification of the effect is rare. Clady (1976) demonstrated a positive correlation between early survival of age-0 yellow perch and temperature for Oneida Lake. Controlled laboratory experiments have shown temperature to be less important than photoperiod in growth determination when food intake is not limited (Huh et al. 1976). In the field, Coble (1966) demonstrated a significant relationship between length and mean water temperature at 6.5 m for female yellow perch sampled from South Bay, Manitoulin Island, but was unable to repeat the analysis for data obtained from studies by Pycha and Smith (1955). Barans and Tubb (1973) found seasonal differences in selected temperature preferences of age-0 fish and adults and suggested that age-related differences in temperature preferences varied in importance for defining thermal habitat requirements and consequent growth. Ney and Smith (1975) noted that high summer temperatures appeared to exert a positive influence on growth but did not quantify the relationship. A 2-year study of larval yellow perch growth in Lake Opeongo, Algonquin Park, indicated that the relative increase in length over a common period was higher in the year with the most accumulated degree-days (Cucin and Faber

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TABLE 1.—Lake morphological and limnological data. Measures for all but the West Blue Lake site were made in the summer of 1997. West Blue lake measurements were obtained from Kelso and Ward (1977). Values in parentheses are SEs; NA = not available.

Measurement	Lake			
	West Blue	Kimowin	Sucker	Mildred
pH	8.3	7.7 (0.2)	7.3 (0.1)	7.7 (0.3)
Conductivity ($\mu\text{S}/\text{cm}$)	NA	242.0 (1.4)	176.4 (1.5)	288.0 (1.5)
Total dissolved solids ($\mu\text{g}/\text{L}$)	185.3	179.0 (2.1)	137.5 (15.2)	199.3 (7.1)
Morphoedaphic index ^a	16.4	50.1	38.7	48.2
Chlorophyll <i>a</i> ($\mu\text{g}/\text{L}$)	3.8	9.8	13.8	13.0
Lake area (km^2)	1.6	4.5	0.6	1.7

^a Total dissolved solids/mean depth.

1985). Henderson (1985), however, rejected the hypothesis that temperature influenced Lake Huron yellow perch growth, based on a lack of correlation between size at age 1 and deviations in annual water temperatures and an inability to correlate instantaneous growth rates with cumulative degree-days above 14°C. In contrast, Mills et al. (1989) demonstrated that mean weight of age-0 yellow perch collected at weekly intervals from Lake Oneida, New York, increased steadily with cumulative water temperature measured in degree-days but remained variable from year to year.

In a study of among-population variability in yellow perch in southern Quebec, Boisclair and Leggett (1989) concluded that minor differences in temperature could not explain observed variations in growth in three yellow perch age-classes (age 1, age 2, and age 3) and that factors such as prey type, prey availability, and fish community descriptors were the most important determinants of among-population variability. In a similar study of age-0 yellow perch in Ontario lakes, Post and McQueen (1994) found that the addition of mean epilimnetic temperature or cumulative degree-days did not significantly add to the explanatory power of a multivariate zooplankton and benthic biomass model that was used to describe growth variability. Both studies agree with Schlesinger and Regier (1982), who raised doubts about whether regional analyses would show any discernable climatic effect, despite the importance of temperature as a predictor of fish production on a global scale. Nevertheless, Shuter et al. (1980) were able to use data for smallmouth bass *Micropterus dolomieu* from limited sites in southern Ontario to parameterize a model capable of assessing the effects on first-year survival of short-term and long-term fluctuations in temperature on a wider geographic scale.

Growth is the product of complex physiological and ecological processes. The physiological processes that affect growth include standard and active metabolism, food consumption and the energetic costs of food foraging, handling, digestion, and excretion. The ecological processes that affect growth include predator-prey relationships and the list of ecological and physical variables that define a species' niche. The complexity of growth and the adaptability of yellow perch to a wide variety of warm and cooler habitats suggests that conclusions concerning the influence of temperature on growth will vary, with temperature having its most pronounced influence toward the extremes of the geographic range. To test this hypothesis, we used measures of the in-situ habitat regime to determine the significance of temperature as a determinant of age-0 yellow perch growth in northern Alberta. Secondary objectives of the study included validation of our results with data from independently conducted research and the testing of the generality of temperature as an explanation of variability in age-0 yellow perch growth by using latitude as an index of temperature.

Methods

Temperature data.—Lake morphometry and limnological measures for each of the study sites are given in Table 1, and a map, showing the location of study sites is given in Figure 1. Submersible temperature loggers with $\pm 0.2^\circ\text{C}$ accuracy in the -5°C to 37°C temperature range (Optic StowAway by Onset Computer Corporation) were deployed in Kimowin ($56^\circ 12' \text{N}$, $110^\circ 07' \text{W}$), Mildred ($57^\circ 03' \text{N}$, $111^\circ 36' \text{W}$) and Sucker lakes ($56^\circ 25' \text{N}$, $110^\circ 52' \text{W}$) in late March 1997. Loggers were encased in galvanized-metal pipe and deployed under the ice by attaching the casing to a



FIGURE 1.—A map of the Canadian prairie provinces showing the location of the 1997 study sites and West Blue Lake, where the validation data set was collected in 1969.

float system suspended below the bottom ice surface at a depth of approximately 1 m. At the first opportunity in the open-water season, the logger was resuspended from an anchored surface float to ensure that a constant depth of 1 m would be maintained. Temperature ($^{\circ}\text{C}$) was recorded every 3 h from deployment until recovery in late September or early October of the same year. Ice action resulted in the loss of the Sucker Lake logger, necessitating the deployment of a second logger on June 28, 1997.

Data gathered from the loggers were used to model seasonal temperature profiles for each of the study sites and to compute all degree-day measures used in study regressions. Seasonal temperature (T) profiles were modeled as a function of day of year (D) using the following nonlinear model:

$$T (^{\circ}\text{C}) = aD^b e^{-cD}. \quad (1)$$

The specified model is flexible and nonsymmetric, having a single maximum and two inflection points. The statistical estimation properties are close-to-linear (Ratkowsky 1990). Accordingly, the model can be linearized as follows:

$$\log_e(T, ^{\circ}\text{C}) = \log_e(a) + b \log_e(D) - cD, \quad (2)$$

where \log_e defines the natural logarithm of the specified parameter or variable and the transfor-

mation is used to facilitate estimation of the parameters (a , b and c) and confidence intervals.

Differences in mean seasonal lake temperature provide an integrated measure of water temperatures experienced by fish over a growing season (Boisclair and Leggett 1989) and one means of assessing the possible influences of temperature on growth. Mean seasonal temperatures, however, combine temperatures variably suited to growth. Some temperatures will be more optimal for growth than others, and it is the accumulation of the more favorable temperature periods that will be most closely correlated with growth (e.g., Conover 1990). To account for possible accumulation effects, data derived from the temperature loggers were used to define the number of degree-days for each lake exceeding 13.5°C , the minimum bound for growth in yellow perch (Le Cren 1958; Nakashima and Leggett 1975). This was done by computing the difference between daily mean temperature and 13.5°C and summing these differences over the season.

Where actual observations were not available, degree-days were estimated from the seasonal temperature profile models discussed above. This was necessary for Sucker Lake between May 30, when temperatures were predicted to have risen above the minimum temperature necessary for yellow perch growth, and June 28, when the second tem-

perature logger was deployed. Data from Kimowin Lake for April 1–June 28 were used to interpolate the missing Sucker Lake data points. This was accomplished by using average weekly lake temperature differences between June 29 and August 15 and knowledge of ice-out dates, where it was assumed minimal differences in water temperatures existed, to construct a data set profiling time-related differences in temperature between the lakes. The resulting data were used to model differences between the two lakes with a quadratic equation defined in terms of day of year (D) as follows:

$$\text{difference in } T = a_0 + a_1D + a_2D^2. \quad (3)$$

Because temperatures recorded above the optimum for yellow perch growth (22.5°C; Neill and Magnuson 1974) accounted for only 1.57% of all observations made and never exceeded 24.79°C, no specific adjustments for temperatures in excess of the optimum for growth were made.

Young-of-the-year data.—Young-of-the-year yellow perch were initially sampled with a 60-cm-diameter tow net constructed of 1-mm mesh pulled on 15–25 m of rope at varying speeds behind a boat. A 50-m-long, 4-m-deep seine with a 3-m bag constructed of 6.4-mm mesh was used for later samples. Tow and seine hauls were completed in a representative sampling of littoral zone habitats. All sampling was completed during daylight hours and occurred at intervals ranging from 3 to 4 weeks, as dictated by floatplane and helicopter schedules. All samples were collected between early June and the end of the first week of October, a period that encompasses the majority of the growing season for yellow perch (Coble 1966; Fortin and Magnin 1972; Ney and Smith 1975). A minimum of five samples were obtained for each lake, and each sample contained between 20 and 30 individuals. An exception was the August 25 sample at Kimowin Lake when a collecting accident resulted in the loss of all but eight of the sampled individuals.

A subsample of specimens were initially measured in the field and then preserved in 10% neutral buffered formalin. Field measurements were reassessed in the laboratory, and agreement between the pre- and postformalin preservation measurements was evaluated. Correspondence between the two measurements was good. Postpreservation measurements showed a minor increase in length (0.6%), with no statistically significant differences ($N = 61$, $P < 0.05$). As a result, all measurements

of length reported here are of preserved specimens. Measurements of 1-year-old fish captured in Sucker and Kimowin lakes in early June 1997 showed no statistically significant sex-related size dimorphism (Sucker Lake: $N = 43$ males, 41 females; Kimowin Lake: $N = 24$ males, 41 females). As a result, sex was omitted from further consideration in the study. All length measurements report fork lengths to the nearest millimeter.

Individual fork length observations were used to model growth as a function of day of year (D) using von Bertalanffy models of the form

$$\text{length (mm)} = L_{\text{Max}} [1.0 - \alpha \exp(-\beta D)], \quad (4)$$

where L_{Max} is the maximum attainable length in the first growing season, β is the growth coefficient relating day of year to length, and α is a scale constant. Parameter estimates were obtained by applying nonlinear regression techniques (e.g., Bates and Watts 1988) to available data. All estimated models were judged for statistical adequacy on the basis of an examination of model residuals, the proportion of explained variation, and parameter P -values. Tests of nonlinear model residuals included plots of the residuals against both fitted and regressor values and formalized serial correlation and normality testing (Bates and Watts 1988).

Temperature-based regressions and validation.—Average age-0 fork length measures for each sample date in each lake were regressed against cumulative degree-day measures estimated from the logger data using models of the form

$$\text{length (cm)} = b_0 + b_1\text{CD}, \quad (5)$$

where CD defines cumulative degree-days over 13.5°C, as computed above. Results were statistically validated by examining model residuals for evidence of serial correlation, heteroscedasticity, and normality. Serial correlation was examined by computing the sample autocorrelation function for regression residuals and comparing computed values to the critical limits defined by $\pm 2/\sqrt{n}$ (Wei 1990). The Goldfeld–Quandt test was used to test for heteroscedasticity (Koutsoyiannis 1977), and normality was tested with the Shapiro–Wilk W or its extensions (Dunn and Clark 1987).

To validate results obtained from the Alberta study, a data set available for West Blue Lake, Manitoba (51°36'N, 101°53'W), was obtained from Wong (1972). West Blue Lake is situated in the same boreal forest geographic zone as the Alberta sites. The data consisted of mean fork lengths

TABLE 2.—Lake names, latitude, end-of-growing-season lengths (mm), pH, and reference data used to estimate the latitudinal regression model (equation 8). Green Bay refers to Lake Michigan.

Lake	Latitude (°N)	End-of- season length (mm)	pH	Reference
Claytor	37°03'	75.62	8.2	Rosebery (1951)
Clear (Alberta)	54°14'	58.58	8.5	Norris (1984)
Clear (Iowa)	43°08'	69.80	8.6	Ridenhour (1960)
Clear (Ontario)	45°12'	53.20	6.0	Post and McQueen (1994)
Dickie	45°09'	57.04	6.0	Post and McQueen (1994)
Green Bay	45°50'	68.20	7.8	Joeris (1956)
Harp	45°23'	54.64	6.3	Post and McQueen (1994)
Heming	54°53'	53.33	6.8	Lawler (1953)
Lessard	53°57'	59.60	7.8	Norris (1984)
Kimowin	56°12'	63.56	7.7	This study (1997)
Mildred	57°03'	64.27	7.7	This study (1997)
Oahe	45°23'	66.26	8.2	Nelson and Walburg (1977)
Oneida	43°12'	68.80	8.3	Nielsen (1980)
Opinicon	44°33'	62.42	8.5	Keast (1977)
Pine	52°04'	65.68	8.4	Norris (1984)
Red	48°01'	66.00	8.5	Pycha and Smith (1955)
St. George	43°57'	60.29	7.4	Post and McQueen (1994)
Ste. Anne	53°42'	62.19	8.5	Norris (1984)
Sucker	56°25'	62.13	7.3	This study (1997)
West Blue	51°36'	63.61	8.3	Wong (1972)
Winnebago	43°46'	75.89	8.0	Weber and Les (1982)

for age-0 yellow perch sampled in 1969 as part of a study of diel migration and food consumption patterns. Daily surface water temperature readings allowed an exact replication of the methodology outlined above and estimation of the model defined by equation (5). A test for the equality of estimate model coefficients, Chow test (Chow 1960), was applied to the separately derived Alberta and West Blue Lake regression models to determine whether significant differences existed that might indicate varying ecological influences on the determination of growth.

Finally, the potential significance of temperature as a determinant of age-0 yellow perch growth on a larger geographic basis was assessed by looking for evidence of a latitudinal gradient. This was accomplished by combining data available from the literature on end-of-growing-season lengths with the 1997 field data to estimate a linear regression model relating latitude to end-of-season length. Data on end-of-growing-season lengths were obtained for 21 lakes separated by 20 degrees of latitude from the following sources: Rosebery (1951), Lawler (1953), Pycha and Smith (1955), Joeris (1956), Ridenhour (1960), Wong (1972), Nelson and Walburg (1977), Keast (1977), Nielsen (1980), Weber and Les (1982), Norris (1984), Post and McQueen (1994) and this study (1997). Lake names, latitudes, end-of-growing-season lengths

(mm), pH, and references for the data used to estimate the latitudinal model are given in Table 2.

Data sets were selected for use in the analysis based on the availability of associated limnological and water chemistry data and end-of-growing-season length measurements, or data suitable for the estimation of a von Bertalanffy model from which end-of-growing-season length could be reliably projected. Only fork length measurements (mm) were used. Where they were not available, total lengths were converted to fork lengths following Carlander (1950).

Where measures for multiple years were available (e.g., Pycha and Smith 1955), they were averaged. Where a range of values was given (e.g., Weber and Les 1982), the geometric mean of the range was used. For Lac Ste. Anne and Clear Lake, Alberta, (Norris 1984) and West Blue Lake, Manitoba (Wong 1972), end-of-growing-season lengths were estimated using a von Bertalanffy model ($r^2 = 0.898, 0.964, \text{ and } 0.926$, respectively). The value for Pine Lake, Alberta, was based on a back-calculated value estimated by Norris (1984). All other data were taken directly from the literature or our field studies and represent end-of-season values based on mid-September to mid-October sample dates.

Because reliable temperature data were not available for each of the literature studies, latitude

TABLE 3.—Estimated von Bertalanffy growth model parameters for 1997 Alberta study sites. Estimates were derived by using nonlinear regression methods. The 95% confidence intervals are in parentheses below each estimate.

Parameter or statistic	Lake		
	Kimowin	Mildred	Sucker
L_{Max}	72.45 (68.01–76.88)	79.53 (75.35–83.72)	74.87 (71.26–78.49)
α	18.54 (9.28–27.80)	8.21 (5.83–10.58)	7.25 (5.63–8.88)
β	0.018 (0.015–0.021)	0.014 (0.012–0.016)	0.013 (0.012–0.015)
P	≤ 0.002	≤ 0.001	≤ 0.001
r^2	0.943	0.952	0.985

was used as a surrogate measure. Temperature and latitude are known to be correlated. For example, the correlation between mean daily temperature and latitude equaled 0.963 for 85 randomly selected Quebec, Ontario, and Manitoba weather stations (data from Canadian climate normal tables, Environment Canada 1982).

To adjust for possible differences in trophic status and water chemistry, available limnological and water chemistry data were tested for inclusion in the linear model relating latitude to end-of-growing-season length. Variables considered were total dissolved solids, total phosphorous, total nitrogen, chlorophyll *a*, Secchi depth, pH, lake area and mean depth, and the morphoedaphic index (total dissolved solids/mean depth). We used *t*-

tests to judge the significance of variable inclusion at the $\alpha = 0.05$ level of significance (Dunn and Clark 1987). As elsewhere, model residuals were examined for statistical adequacy with appropriate tests.

Results

By late August and early September, age-0 yellow perch in the studied northern Alberta lakes have completed approximately 80% of their growth. This is lower than the 90% value given for yellow perch in southern Quebec (Fortin and Magnin 1972) and is in the lower end of the 72–97% range given for yellow perch in Minnesota lakes (Ney and Smith 1975). Table 3 presents estimated parameters, *P*-values, 95% confidence intervals, and proportion of explained variation measures for the von Bertalanffy growth models. Tests of model residuals conducted at the $\alpha = 0.05$ level of significance indicated residuals were independently and normally distributed. Figure 2 plots the estimated models for each of the study sites.

Although no major differences in growth patterns are evident, slight differences between sites exist at both the beginning and the end of the study period. Fish in Mildred and Sucker lakes showed the best initial growth. Although Mildred Lake fish maintained that advantage throughout the summer, growth of Sucker Lake fish slowed to the point where the initially smaller Kimowin Lake fish were able to catch and surpass Sucker Lake fish in length. Ney and Smith (1975) suggested that

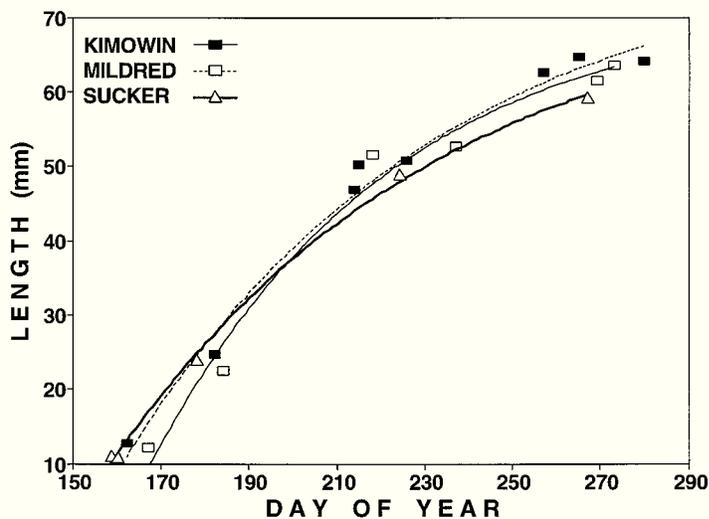


FIGURE 2.—Estimated von Bertalanffy growth models for the Alberta study sites. Lines plot the estimated models defined in Table 3. Symbols plot the length data used to estimate each model. No significant differences ($P > 0.05$) were found between the models.

growth rates were compensatory, being greater in years when mean lengths were less than 30 mm on July 1 and less when mean lengths were greater than 30 mm on that same date. Mean lengths in the studied lakes were all less than 30 mm on July 1 (Mildred Lake, 24.8 mm on July 1; Sucker Lake, 23.9 mm on June 27; Kimowin Lake, 22.5 mm on July 3). In addition, no pattern consistent with the compensation hypothesis and the observed early and end-of-season sizes was evident. Accordingly, compensation cannot explain the relative differences in growth rates in this instance.

Mean seasonal temperatures (June 1–September 21) showed only marginal differences (Mildred Lake, 18.11°C; Kimowin Lake, 18.47°C; Sucker Lake, 18.67°C) that did not explain the pattern of observed seasonal growth rates (Mildred, 0.437 mm/d; Sucker, 0.446 mm/d; Kimowin, 0.486 mm/d). The results here concur with those found in other studies (Boisclair and Leggett 1989; Post and McQueen 1994) that dismissed temperature as a significant explanation of observed differences in growth among studied yellow perch populations. Seasonal means, however, do not account for the many fluctuations in thermal habitat evident from seasonal profiles for study sites.

Figure 3 plots the seasonal temperature profiles, the estimated models, and associated 95% predictive confidence intervals for each of the study sites. Models were statistically validated by testing the residuals for serial correlation, heteroscedasticity, and normality at the $\alpha = 0.05$ level of significance. No violations of the basic assumptions required for linear regression were found. All parameter P -values were less than 0.001. The models for Kimowin, Mildred, and Sucker lakes explained 97.0, 98.1, and 90.3% of the observed variation in the available logger data, respectively. The quadratic corrective model (equation 3) used to interpolate temperature observations for Sucker Lake explained 86.4% of the variation in temperature differences between Sucker and Kimowin lakes. All parameter P -values were 0.002 or less, and residual tests confirmed the statistical sufficiency of the estimated model.

The high explanatory power and statistical adequacy of the seasonal temperature profile models allowed their use in estimating degree-days when actual temperature logger data were not available, as was the case for Sucker Lake from May 1 to June 27. Because the von Bertalanffy growth models for the Alberta lakes showed no significant differences among the lakes ($P > 0.05$), the Alberta length data were combined and regressed against

degree-day ($>13.5^\circ\text{C}$) data to obtain the following significant relationship:

$$\text{length (mm)} = 11.615 + 0.092 \text{ CD}, \quad (6)$$

where CD defines cumulative degree-days. All P -values were less than 0.001, and r^2 equaled 0.969. Residual serial correlation, homoscedasticity, and normality tests confirmed the statistical adequacy of the estimated model. Data used to estimate the regression line are plotted as solid squares in Figure 4, along with the estimated model and associated 95% predictive confidence intervals.

The West Blue Lake validation data set obtained from Wong (1972) resulted in the following regression relating length to cumulative degree-days:

$$\text{length (mm)} = 13.634 + 0.098 \text{ CD}, \quad (7)$$

where CD defines cumulative degree-days in excess of 13.5°C . All P -values were less than 0.001, and r^2 equaled 0.970. As elsewhere, tests of model residuals at the $\alpha = 0.05$ level of significance showed no indication of a violation of the assumptions required of linear regression methods. The data used to estimate the model are plotted as open squares in Figure 4, along with the estimated model (dotted line) and the data and results of the degree-day regression for the Alberta lakes (equation 6). Despite the apparent similarity of the models, a Chow test (1960) indicated that the estimated relationships differed significantly ($P < 0.05$), suggesting possible latitudinal or trophic factors in growth determination.

Regression of available end-of-season lengths obtained from the literature and field against latitude produced significant gradients that explained 16.9% of the observed variation for all lakes ($N = 21$, P -values ≤ 0.05) and 45.9% of the observed variation for all nonacidic lakes ($\text{pH} > 7.0$, $N = 17$, P -values < 0.05). The difference in the explanatory power of the two regressions suggests that lake acidity has an important direct or indirect effect on growth of age-0 fish. To adjust for possible acidity effects on growth, an indicator variable was included in the model. The variable was set equal to one if pH value was 7.0 or above and at zero otherwise, resulting in an improvement in model fit and the following parameter estimates:

$$\begin{aligned} \text{end-of-season length (mm)} \\ = 79.548 - 0.526 \text{ LAT} + 11.521 I, \end{aligned} \quad (8)$$

where LAT defines latitude ($^\circ\text{N}$), and I is the in-

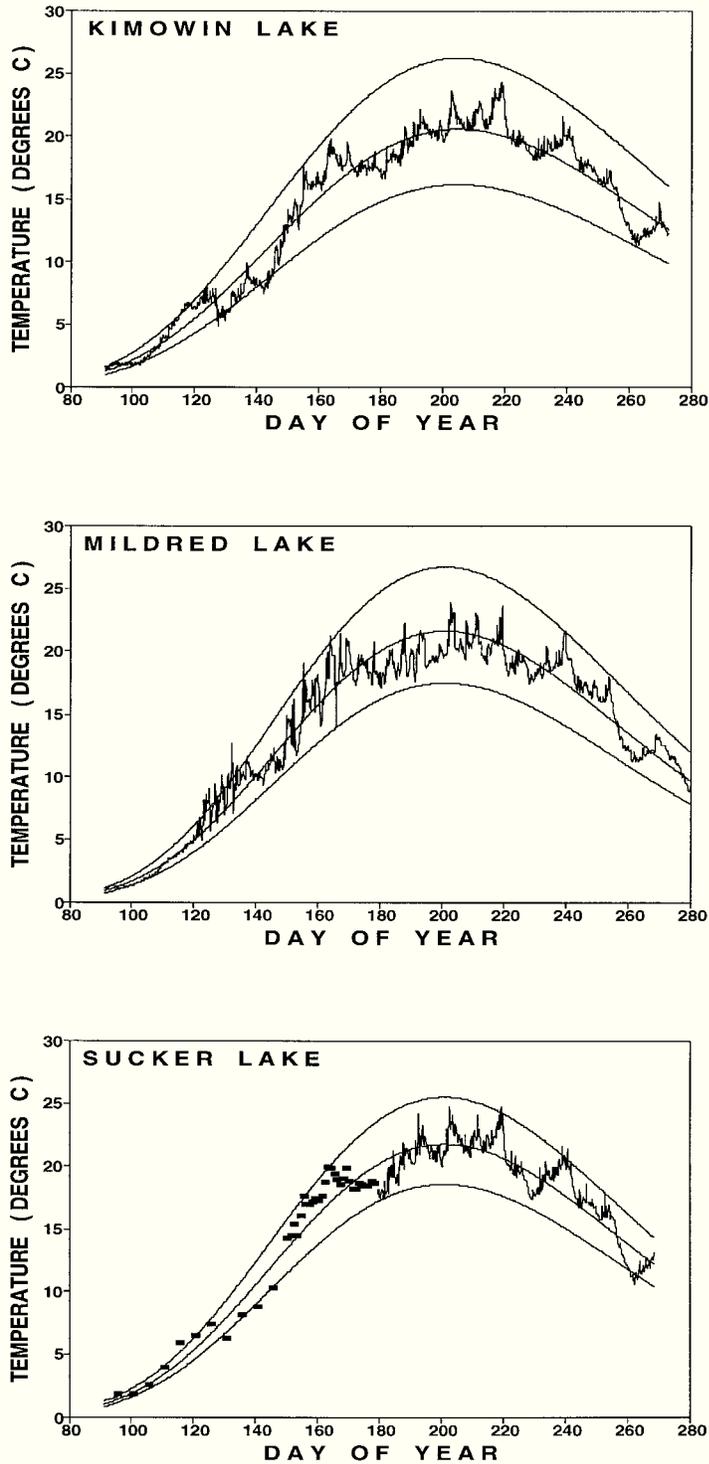


FIGURE 3.—The seasonal temperature profile (jagged line) and model estimate (center smooth line) with 95% confidence intervals (outer smooth lines) are plotted for each of the Alberta study sites. For Sucker Lake, estimated spring temperatures based on equation (3) are plotted as solid squares. The models for Kimowin, Mildred and Sucker lakes had r^2 values of 0.970, 0.981, and 0.903, respectively.

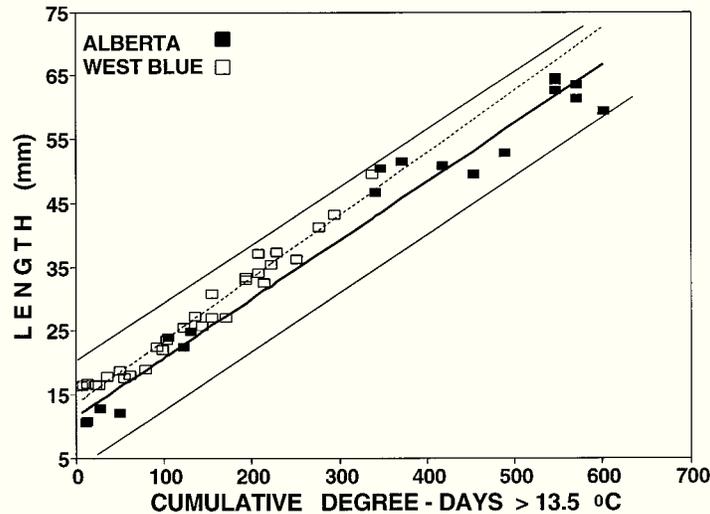


FIGURE 4.—Length–cumulative-degree-day models for the 1997 Alberta study and the West Blue Lake validation data set. Data from 1997 are plotted as solid squares. The estimated model for 1997 is plotted as a thick solid line, and 95% confidence intervals are given as solid lines. Data from West Blue Lake are plotted as open squares. The estimated West Blue Lake model is plotted as a broken line. Both models explain more than 96% of the observed variation in available data.

indicator variable. All P -values were 0.002 or less, and r^2 equaled 0.707. Tests of model residuals showed no evidence of autocorrelation, heteroscedasticity, or nonnormality (Dunn and Clark 1987). End-of-season lengths predicted by the latitudinal model (equation 8), actual end-of-season lengths, the perfect-fit 45° line, and the associated 95% confidence intervals for the regression, relating predicted to actual end-of-season lengths, are plotted in Figure 5. The plot shows good correspondence between actual and predicted lengths. The addition of total dissolved solids, total phosphorous, total nitrogen, chlorophyll a , Secchi depth, lake area and mean depth, and the morphoedaphic index did not add significantly to the explanatory power of the relationship ($P > 0.05$), either in conjunction with latitude, latitude and the indicator variable, or latitude and any considered combination of the candidate variables.

A similarly significant regression relationship, including pH in place of the indicator variable, was estimated. The model, however, did not improve the explanatory power of the length–latitude regression ($r^2 = 0.623$; P -values ≤ 0.009). A similar regression excluding all lakes with pH values less than 7.0 resulted in a nonsignificant pH parameter estimate (P -values > 0.05), suggesting that pH per se was not the dominant variable controlling observed among-lake variability in growth.

Discussion

The aim of this study was to assess the importance of temperature as a determinant of age-0 yellow perch growth in northern Alberta. Previous unsuccessful attempts to correlate growth with an integrated temperature measure (mean seasonal) led other investigators (e.g., Mills and Forney 1981; Boisclair and Leggett 1989; Post and McQueen 1994) to concentrate on the implications of diet and ration and to conclude that prey type and availability were the most important determinants of observed growth variability. For example, Post and McQueen (1994) concluded that a strong relationship between seasonally averaged growth and prey abundance implied that prey abundance dominated growth variation at the seasonal scale. On the basis of a similarly strong relationship between temperature, measured in terms of the cumulative degree-days, and length, this study concludes that temperature dominates growth determination at a seasonal scale in northern Alberta lakes.

The difference in study conclusions depends upon the interaction of the variables defining the hypervolumetric niche (Hutchinson 1957) for yellow perch and the associated difficulties posed for the interpretation of physical factor influences on growth. As Elliott (1994) has demonstrated, the energy budget for fish will depend on water tem-

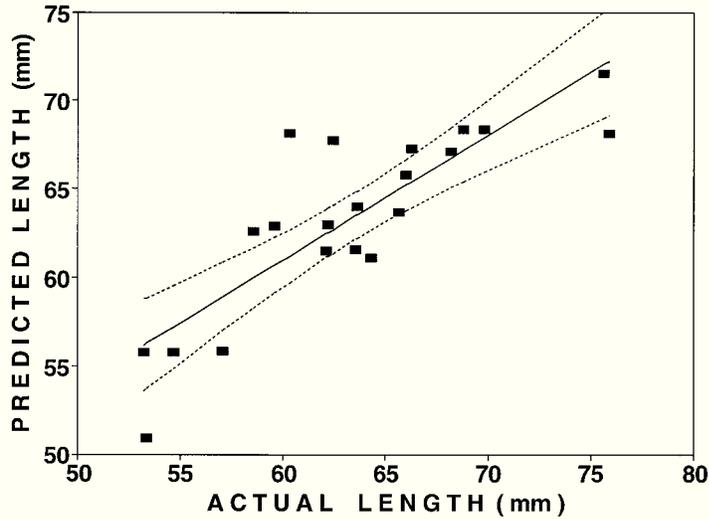


FIGURE 5.—Actual end-of-season lengths and those predicted from the regression model (equation 8), with latitude and an acidity indicator variable as the independent variables. The solid line is the perfect-fit 45° line. Broken lines plot the 95% confidence intervals for the regression relating predicted to actual end-of-season lengths. Latitude and acidity explain 70.7% of the variability in end-of-season lengths across 20 degrees of latitude.

perature, size, and the level of energy intake. Temperature, in particular, has a marked effect on both the maximum and the maintenance energy intakes for fish. The range between the two defines the scope for growth. In experiments with brown trout *Salmo trutta*, the scope for growth was found to increase toward the upper end of the preferred temperature range (18°C) before declining rapidly to zero at 19.5°C. Kitchell et al. (1977) describe a similar response pattern for yellow perch, noting that growth increased as temperature approached the optimum for growth (23°C) and declined sharply thereafter. Fluctuations in water temperature will, therefore, define cumulative differences in the scope for growth over the length of the growing season. Although heterogeneous thermal environments allow fish opportunities to compensate for temperature fluctuations by selecting for preferred temperatures, such opportunities will be limited in the portion of the geographic range where temperatures do not typically exceed those that define the optimum scope for growth. Unless temperatures increase above the point where the maximum scope for growth is realized, northern fish will be limited in their abilities to select for optimal growth temperatures and will, as a consequence, more strongly reflect the influence of temperature on growth than southern populations of the same species.

Conover (1990) has similarly postulated that the suitability of the thermal environment within the

growing season may differ with latitude. He argues that temperatures in southern lakes may be too high for growth to occur during substantial portions of the year, thus weakening the correlation between temperature and growth. Temperatures in northern lakes, on the other hand, may remain within the band of temperatures suited for growth for longer periods of time, thereby strengthening the correlations between temperature and growth.

Temperature is typically regarded as a factor affecting individual physiological and behavioral processes, but it is also a key characteristic of an organism's habitat. Hutchinson (1957) considered an animal's niche to be defined by the complete range of environmental variables to which it must be adapted for survival. Species will not compete along many of the niche axes defined by these variables (e.g., water quality, temperature, and illumination), but the variables nonetheless combine to determine the presence and success of a species in a particular locality by defining important aspects of the abiotic environment that may exceed tolerances. In turn, tolerances determine the geographic distribution of a species. At the fringes of the distributional range, abiotic niche axes variables are likely to exert a greater influence over the physiological responses (e.g., growth) of the species to its environment than elsewhere. Shuter et al. (1980) make a similar point when noting that if the northern edge of a species' distribution does reflect an ecological barrier then the variable rep-

resenting the barrier is most closely followed in determining the distribution. This relationship implies that growth rates and population dynamics of fish living at the limits of their distribution will usually differ from those of the same species living in the optimum temperature range (Elliott 1994), where interspecific competition along ecological niche axes are likely to predominate.

Replication of the results obtained from the Alberta sites with the data collected by Wong (1972) is interesting in light of the above discussion simply because the data were similarly collected at the fringe of the geographic distribution of yellow perch in North America. Fringe collection may also explain why Coble (1966) was able to obtain significant results for Lake Huron but unable to replicate the analysis for data obtained from other study sites.

Size-dependent physiological relationships may also explain the divergence in study results as a function of latitude. Fish have been shown to have growth sensitivities to changes in water temperatures that are negatively related to body size and weight (Elliott 1994). Thus growth in age-0 yellow perch will be much more susceptible to fluctuations in water temperatures than growth in older fish (Boisclair and Leggett 1989). Because of that sensitivity, age-0 fish are often selected for use in field studies (Post and McQueen 1994). The temperature sensitivity implies that continuous measures of temperature, and not mean seasonal measures, should be used to assess growth variability. Although favorable changes in the thermal habitat will accelerate growth, unfavorable changes halt, rather than reverse, growth (Conover 1990). The asymmetrical response of growth to changes in temperature implies that variables incorporating the accumulation of favorable changes in temperature (e.g., cumulative degree-days) will be more closely correlated with growth than variables based on integrated measures which average both favorable and unfavorable changes (e.g., mean seasonal temperature).

The results of this study indicate that temperature is capable of explaining observed growth variability on a variety of geographic scales. High correlations ($r^2 = 0.969$) between length and degree-days were obtained for a regional study of several highly productive northern Alberta lakes. Attempts to correlate end-of-season lengths across 20 degrees of latitude demonstrated that latitude was capable of explaining a statistically significant proportion of the observed variability in first-year growth on a larger geographic scale ($r^2 = 0.459$ for nonacidic lakes).

When adjusted for acidity, the explanatory power of the relationship rose to 70.7%. The relationship is a strong one, especially when it is recognized that latitude alone will not always be an adequate surrogate for temperature. Latitude will often fail to incorporate the cumulative differences in the thermal habitat that variations in local weather patterns, altitude, lake size and depth might induce. These factors will increase observed growth variability by increasing the range of environmental conditions in which yellow perch are found, thus reducing the overall explanatory power of latitude in comparison to the continuous thermal measures used to model regional responses in the studied Alberta lakes.

Inclusion of the indicator variable as a significant explanatory factor in the length–latitude regression points to the fact that other ecological variables are required to explain observed variability across the geographic range of the species. Acidity can directly affect plankton and benthic species composition and, in so doing, will affect both the quality and quantity of food available to age-0 yellow perch. Stokes (1986) noted significant effects on primary production resulting from changes in species richness and composition as pH decreased that had implications for both nutrient cycling and zooplankton forage bases. Harvey and McArdle (1986) associated reduced pH with declines in the abundance or absence of a number of important prey species for age-0 yellow perch, including amphipods, daphnids, and ephemeropterans. Frenette and Richard (1986) found that weight–length relationships of yellow perch inhabiting acid Quebec lakes showed poor condition compared with yellow perch in nonacid lakes (covariance analysis, $P < 0.001$).

Reductions in prey abundance or prey absence in acid lakes could act as a limiting factor, resulting in both decreased condition and growth of yellow perch. Therefore, regional studies showing a wider range of acidity measures might be expected to correlate observed growth variability with measures of prey abundance when including lakes with pH values above and below 7.0. For example, Post and McQueen (1994), whose pH measures ranged from 6.0 to 7.4, selected prey abundance over temperature as more important for explaining observed growth variability. Studies with a narrow range of pH values (e.g., 7.3–7.7 in the Alberta lakes) will control more for a common forage base and might be expected to correlate growth with variables other than prey abundance. This possibility would be especially true of lakes where age-0 yellow perch were not food limited, as is likely

in the highly productive mesotrophic and eutrophic lakes studied here (see Table 1).

Because of the implications of acidity for plankton and benthic community composition, prey availability and abundance will be among the suite of variables that could influence observed variability in age-0 yellow perch growth. Other complex factors such as density, predator-prey relationships and abiotic niche variables that could not be included or controlled for in our analysis will also possibly influence age-0 yellow perch growth. We, therefore, propose that additional field studies aimed at understanding variations in growth of age-0 yellow perch focus on interactions between temperature, prey availability, and density to explain observed variations in growth for the species.

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