Variation in the Condition of Northern Pike, *Esox lucius*¹

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The relationship between condition and latitude, temperature, and sex of northern pike (*Esox lucius*) was examined by regression analysis of 5210 published observations drawn from more than 38 populations. Most populations showed nearly isometric growth, but the overall exponent of the power function relationship between total body length and body weight was slightly less than 3 (p < 0.01). Multiple regression analysis showed that females weighed about 9% more than males of equal length, that body weight for fish of equal length increased about 5% for every 10° increase in north latitude and increased about 4% for every 10°C decrease in mean annual air temperature, and that fish in European and Asian populations attained about 13% greater weight for a given length than their North American counterparts.

On a étudié la relation entre la condition et la latitude, la température et le sexe du grand brochet (*Esox lucius*) à l'aide de l'analyse de régression de 5 210 données publiées, tirées de plus de 38 populations. La majorité des populations de brochets démontrent une croissance quasi isométrique quoique l'exposant de la relation entre la longueur totale et le poids corporel, pour tous les brochets, soit de façon significative (p < 0.01) légèrement inférieur à 3. L'analyse de régression multiple révèle que les femelles pèsent environ 9 % de plus que les mâles de longueur identique, que le poids corporel des poissons d'une même longueur augmente d'environ 5 % pour une augmentation de 10° de latitude nord et de 4 % pour toute baisse de 10°C de température moyenne annuelle de l'air, et que, pour les brochets d'une longueur donnée, les poissons européens et asiatiques atteignent un poids qui est d'environ 13 % supérieur à celui des brochets d'Amérique du Nord.

Received November 13, 1986
Accepted November 2, 1987

¹Publication of the Groupe d'écologie des eaux douces of l'Université de Montréal.
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The northern pike (*Esox lucius*) is a fish of economic and ecological importance in North America, Europe, and Asia. In the United States, northern pike is one of the top five sportfish species (U.S. Fish and Wildlife Service 1977). The economic value derived from the northern pike makes it a major focus of fisheries management organizations. The northern pike is a voracious predator (Kipling 1984), often found near the margins of productive weed beds in lakes, ponds, and rivers (Carlander 1969; Scott and Crossman 1973). *Esox lucius* thrives in several types of habitats including reservoirs (Kupchinskaya 1985), large lakes (Kipling 1983a, 1983b; Kipling and Frost 1970), small lakes (Van Engel 1940), ponds (McCarrather 1957), rivers (Holland and Huston 1984), and streams (Le Louarn and Baglinière 1985). Young-of-the-year grow rapidly eating large quantities of large invertebrates such as amphipods, isopods, and insect larvae but graduate rapidly to a diet composed mainly of small fishes (Holland and Huston 1984). *Esox lucius* is the ubiquitous top carnivore in many aquatic ecosystems; thus, factors regulating its growth and success are of interest to the management of prey species.

Many factors influence the growth and condition of fish species. The optimality of their growth conditions is often thought to be reflected by the relative weight of fish at a given length.

Fish living under marginal environmental conditions will theoretically weigh less at any particular body length than those living under more luxurious circumstances. *Esox lucius* has been called a northern species (Scott and Crossman 1973); thus, one might expect greater body condition at high latitudes and low temperatures. Females often show greater body condition than males because of the large mass of eggs produced during the year (e.g. Brown and Clark 1965; Johnson 1966). Body condition might also vary between geographically isolated stocks due to genetic inequality of stocks or geographic variations in living conditions. European pike, for example, have long been thought to grow more rapidly than North American pike (Scott and Crossman 1973). The purpose of this research was to test the hypotheses that body condition in *Esox lucius* varies systematically on a large scale with latitude, temperature, and sex and that there are systematic differences in the condition of European, Asian, and North American populations.

Methods

The relative weight of fish of similar lengths has been referred to as their condition (Ricker 1975) or ponderal index (Lagler et al. 1977). The measurement of the condition of fish is a standard component of most fisheries curricula (Lagler et al. 1977; Weatherly and Rogers 1978), and the morphological measurement of the condition of fishes has not changed materially in over 80 yr (cf. Fulton 1902; Buck and Hooe 1986). Fulton (1902) observed that the mass of fishes rose approxi-
mately as the cube of the body length and therefore laid the
intuitive foundation for the coefficient of condition, $k$:

$$k = W/L^3$$

where $W$ is body mass (grams) and $L$ is body length (millimetres). Calculation of $k$ assumes that $W$ rises exactly as the cube of $L$, or that growth is isometric.

Not all fish growth is isometric. Fulton (1902, p. 334) himself observed that "The curves do not everywhere agree with the rule that in similarly-shaped bodies the masses vary as the cubes of the dimensions; the proportions appear to change somewhat with growth." If fish growth is allometric and equation 1 is used as an index of condition, then there will be an artifactual systematic variation in "condition" with body length (reviewed by Carlander 1969, 1977). To avoid these difficulties, Le Cren (1951) advanced a relative or allometric (Ricker 1975) condition factor:

$$k_* = W/L^b$$

where $b$ is the population-fitted exponent of the power relationship between $L$ and $W$. $k_*$ is perfectly correlated with the predictions of $L$ and $W$. $k_*$ is perfectly correlated with the residuals of a log $W$- log $L$ regression.

In our analyses, published data were collected on total fish length ($L$, millimetres) and fresh weight of individual animals ($W$, grams) from several populations of *Esox lucius*. Most length and weight data were read from tables, but some data were extracted from graphs using digital measurement of photographic enlargements (Table 1). Data were also collected on the sex of specimens and the latitude and the mean annual air temperature in the geographic area in which they were collected. Latitudes were taken from publications or estimated from maps, while temperatures were estimated as the long-term annual average from the nearest reporting station (Wernstedt 1972). Information on air temperature was used instead of water temperature because it was more readily available. Some data were included from unspecified water bodies within large geographical areas (e.g. Michigan, Minnesota, Sweden) and therefore could not be paired accurately with exact latitudes or precise temperatures. For these data, prevailing latitudes and temperatures were calculated as the average of all latitudes listed for the specific political unit by Wernstedt (1972). Fractional latitudes were truncated to whole degrees.

Data on more than 5200 northern pike from more than 38 populations were collected from the published literature (Table 1). Lengths of fish ranged from 68 to 1170 mm and weights from 1.1 to 8200 g. Data on populations living between 41 and 65° north latitude were collected. This covers much of the circumpolar geographic distribution of *Esox lucius* (Scott and Crossman 1973). Mean annual ambient air temperatures varied between $-4.3$ and $10.4$°C. Although some gravid individuals are included in the sample, no systematic correlation exists between temperature and the collection of spawning individuals. Fewer observations (11%) were collected for European than North American fish.

After the data were collected, $L$ and $W$ data were analyzed statistically. First, the $b$ value (equation 2) was estimated for each of the $i$ populations by least squares regression:

$$\log W = a + b \log L$$

where $a$ and $b$ are fitted constants (Nie et al. 1975). Confidence intervals for $b$ were computed and comparisons were made visually. Second, an overall $b$ value was calculated using pooled data from all populations, and this was compared with the theoretical value of 3 using a $t$-test. Conclusions are compared with those obtained using geometric regression (Ricker 1973). Third, we fitted the multiple regression

$$\log W = a + b \log L + cL_t + dT + eS + fE + g$$

where $L_t$ is latitude, $T$ is air temperature, $S$ is sex (male or unspecified = 0; female = 1), $E$ is a dummy variable (Gujarati 1978) indicating whether the population was European or Asian ($E = 1$) or from North America ($E = 0$), and $a$–$f$ are constants fitted by least squares multiple regression. The fit of the model was verified using standard residual analysis (Draper and Smith 1981). The significance of the effect of each variable was inferred by the partial significance of its effect on log $W$. No variables were retained in the regression that did not have a highly significant ($p < 0.01$) effect on body mass.

### Results and Discussion

#### Length–Weight Relationships

Individual populations showed only a narrow range of fitted $b$ values (Fig. 1). Length–weight exponents for individual populations ranged between 1.62 and 3.8 but the 95% confidence intervals of most overlapped $b = 3$ (Fig. 1). This analysis agrees with Carlander (1969) in that the analysis of individual populations shows little evidence of allometric growth. The fact that $b$ is generally similar in different populations shows little evidence of allometric growth. The fact that $b$ is generally similar in different populations shows little evidence of allometric growth. The fact that $b$ is generally similar in different populations shows little evidence of allometric growth. The fact that $b$ is generally similar in different populations shows little evidence of allometric growth. The fact that $b$ is generally similar in different populations shows little evidence of allometric growth.

For the analysis of all populations together, we fitted the multiple regression

$$\log W = a + b \log L + cL_t + dT + eS + fE$$

where $n = 5210$, $r^2 = 0.99$, and $p = 0.0001$. The exponent in this equation is highly suggestive of isometric growth even though a $t$-test ($t = 10.6; p < 0.001$) shows a significant difference from $b = 3$. The slope of the geometric regression ($b_g = 2.97$; Ricker 1973) also indicates allometric growth, but no technique exists for testing whether the slope of the geometric regression is different from 3 (Prepas 1984). Our results indicate that the body form of *Esox lucius* becomes slightly more fusiform with increasing size or the specific gravity decreases slightly.

#### Sex, Geographic Location, and Climate

The multiple regression analysis indicates that sex, geographic location, and climate (in order of significance of partial

Table 1. Data sources on length and weight of Esox lucius. Lt is the latitude (°N), T is the mean annual air temperature (°C), and n is the number of fish sampled.

<table>
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<tr>
<th>Site</th>
<th>Country</th>
<th>n</th>
<th>Lt</th>
<th>T</th>
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*Length and weight data taken from graph.

*Latitude and air temperature calculated as the state average of reporting stations.

Effects; Table 2) all significantly affect fish condition. After the significant effect of body length on weight, sex was the variable having the most significant effect on W. The regression coefficient for S indicates that, on average, females weigh 5% more than the average for males and animals for which sex is not specified. In the male and unspecified category were 415 males and 4423 for which sex is not specified. Assuming that the sex ratio in Esox lucius is 1:1 (Kipling and Frost 1970), our results suggest that females are about 9% heavier than males. Analyses presented by Johnson (1966) showed that females were between 8 and 35% heavier than males and that this percentage increased with increased body length. Brown and Clark (1965) found differences of 7% to 86% between males and females of similar length in a spawning population. The allometric equation presented by Blueweiss et al. (1978) suggests that clutch mass in fish in general varies between 14 and 20% of body weight for animals between 100 g and 6 kg. The discrepancy between these values and the general regression coefficient for the partial effect of sex on body mass at length probably stems from two factors: (1) our analyses were necessarily performed on data collected at different times of the year and thus contain females of varying degrees of gravidity and (2) the regression coefficient S in Table 2 pools the effect of sex on mass for mature and immature pike. Our analyses, however, provide evidence for the generality of superior weights of female pike, although not perfectly, negatively correlated. The regression coefficient for the effect of latitude shows that, on average, females weigh 5% more than the average for males and animals for which sex is not specified. In the male and unspecified category were 415 males and 4423 for which sex was not specified. Assuming that the sex ratio in Esox lucius is 1:1 (Kipling and Frost 1970), our analyses were necessarily performed on data collected at different times of the year and thus contain females of varying degrees of gravidity and (2) the regression coefficient S in Table 2 pools the effect of sex on mass for mature and immature pike. Our analyses, however, provide evidence for the generality of superior weights of female pike, although the number of fish for which sex was not determined and the variety of seasons represented in the data set make interpretation of this difference difficult.

Geographic location was the third most important variable. Table 2 shows that European and Asian pike are 13% heavier at a given length than North American pike. This may reflect genetic differences between stocks of Esox lucius or generally better growth conditions in European and Asian habitats. Our analyses cannot distinguish between these hypotheses.

Latitude and temperature had a highly significant effect on fish condition. Table 2 shows that pike condition increases at a given length than North American pike. This may reflect geographic location was the third most important variable. Table 2 shows that European and Asian pike are 13% heavier at a given length than North American pike. This may reflect genetic differences between stocks of Esox lucius or generally better growth conditions in European and Asian habitats. Our analyses cannot distinguish between these hypotheses.
length increases by about 5% for every increase of 10°C. In addition, weight tends to decrease by about 4% for every 10°C increase in mean annual air temperature. This suggests that the mass of a male pike of 80 cm would be 3310 g near the southern limit of its North American distribution (e.g. central Missouri) and 3970 g near Yellowknife, N.W.T. Seasonal variation, impossible to quantify here, may yield even greater differences at certain times of year. Latitude and temperature can thus lead to up to 20% differences in body weight for fish of equivalent length when effects of season are ignored. The analysis suggests that northern climates represent optimal living conditions for \textit{Esox lucius}.

\textit{Esox lucius} has been labelled a northern species (Scott and Crossman 1973) and this appellation is supported by our results. Body condition is highest at high latitudes and low temperatures. This variation may be linked to season length and the physiological need for greater energy storage where summer seasons are short. The systematic difference in condition between North American and European/Asian populations suggests that North American populations may either be physiologically less efficient or live in less affluent environments. If the latter is true, then comparison of living conditions experienced by northern pike in Europe, Asia, and North America may yield clues to successful habitat management strategies for this important fish species.

Acknowledgments

We gratefully acknowledge the financial support of the Natural Sciences and Engineering Research Council of Canada and the Minister of Education of the Province of Quebec (FCAR). We also thank two anonymous reviewers for comments on an earlier draft of this manuscript and Duane Shodeen for practical discussions.

References


