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The biological and statistical significance of life-history invariants in walleye (*Sander vitreus*)

Craig F. Purchase,[1]* Jeffrey A. Hutchings[1] and George E. Morgan[2]

[1]*Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1*
and [2]*Cooperative Freshwater Ecology Unit, Department of Biology,*
Laurentian University, Sudbury, Ontario P3E 2C6, Canada

ABSTRACT

Questions: Do life-history invariants exist in walleye (*Sander vitreus*) and do they differ between the sexes? How does the probability of detecting life-history invariants vary with sample size? How much error is created if invariance is incorrectly assumed when using the relationships to predict one trait from another?

Data description: Sex-specific data, obtained from standardized research surveys, on growth, age and size at maturity, and mortality for 435 populations of walleye from Ontario, Canada.

Search method: Invariance in four life-history relationships (L_m/L_{inf}, M/k, $T_m \cdot M$ and T_m/L_m) was assessed using linear slopes. We examined sample and effect sizes to determine the extent to which life-history invariants are influenced by statistical power. Errors in estimating traits from predicted invariants were obtained from random samples of 50 populations.

Conclusions: Life-history invariants did not exist among populations of walleye. The value of each ratio and the extent of invariance differed between the sexes. The number of populations required to generate variance in L_m/L_{inf} was high for males (200) and females (41), suggesting that this potential life-history invariant may be statistically robust. However, none of the other ratios examined (M/k, $T_m \cdot M$ and T_m/L_m) was invariant at sample sizes of 10 or more populations for either sex. For walleye, L_m can be predicted from L_{inf} if comparisons are from populations ranging widely in L_{inf}. Estimates of either k or T_m are unlikely to yield reliable estimates of M; similarly, T_m cannot be reliably estimated from L_m.

Keywords: covariation, life-history invariants, inter-population, statistical power, walleye.

INTRODUCTION

The objective of most life-history research in fish is to test hypotheses of adaptive and non-adaptive variation to explain the extraordinary life-history variability expressed within and among species. An alternative approach has been to determine whether there is a constancy, or invariance, among life-history traits that may reflect adaptive life-history processes of

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* Author to whom all correspondence should be addressed. e-mail: purchasecraig@hotmail.com

a very broad and general nature. This search for constancy amidst diversity was very much evident when quantitative studies of patterns of growth, maturation and longevity in fishes first appeared in the late 1950s. Alm (1959), for example, sought patterns among growth rate, and age/size at maturity from experiments he had conducted on Swedish populations of brown trout (*Salmo trutta*). Using data primarily from commercially important marine species, Beverton and Holt (1959) investigated general associations among growth pattern (expressed by the von Bertalanffy growth parameter, k, and asymptotic length, L_{inf}), age (α) and length at maturity (L_{α}), natural mortality (M) and lifespan (proportional to M^{-1}).

There are several associations among life-history-related traits that appear to be common across many species, and among populations within species. The first of these relationships is the relative length at maturation, defined as the ratio of maturation length (common notation is L_{m}) over asymptotic length (L_{inf}; as determined from the von Bertalanffy growth equation), $L_{\text{m}}/L_{\text{inf}}$. The ratio tends to remain constant within taxa because L_{m} and L_{inf} are positively correlated. The second relationship is that between the Brody growth coefficient (k), estimated from the von Bertalanffy growth equation, and adult instantaneous natural mortality (M). These parameters are also positively related such that the ratio M/k has been reported to be relatively constant across populations. It was noted by Charnov and Berrigan (1991) that if the above two relationships are constant, the relationship between maturation age (T_{m}) and M, $T_{\text{m}} \cdot M$, should also be constant, thus generating a third life-history invariant.

A fourth invariant relationship, that between the von Bertalanffy parameters L_{inf} and k, has also been identified (Charnov, 1993, Jensen, 1997). The utility of this potential invariant is unclear, however, given that the same data are used to generate both parameters. As a consequence, we have excluded this ratio from our analysis of walleye life-history variation. However, we do explore the potential invariance associated with the relationship $T_{\text{m}}/L_{\text{m}}$, given its potential utility in estimating age at maturity from the more commonly available data on length at maturity. This relationship has been described as a reaction norm between size and age at maturation (Stearns and Koella, 1986).

The evolutionary basis of the dimensionless relationships M/k, $L_{\text{m}}/L_{\text{inf}}$ and T_{m}/M has been discussed by Charnov and Berrigan (1991) and by Charnov (1993). Jensen (1996) showed that the relationships could result from a trade-off between survival and fecundity, such that maturation occurs at an age when reproductive output from a cohort is maximized. More specific values of these ratios have been made recently for a variety of taxa [27 orders (Froese and Binohlan, 2000)] and for elasmobranch fishes (Frisk *et al.*, 2001). Within species, the most comprehensive studies addressing life-history invariants have been conducted on 29 populations of brown trout (Vøllestad *et al.*, 1993), on 44 comparisons from 37 populations of Arctic char, *Salvelinus alpinus* (Vøllestad and L'Abée-lund, 1994), and on 75 populations of Eurasian perch, *Perca fluviatilis* (Heibo and Vøllestad, 2005). Invariance was not evident among the trout populations, whereas evidence of invariant ratios was reported in char and perch. Largely due to sample size problems, no study to date has examined life-history invariants by sex.

The walleye (*Sander vitreus*) is a relatively large freshwater percid species found throughout much of North America. Being commercially important and a highly prized sportfish, data on life histories are more readily available for numerous populations than for most other species. However, unlike many fishes, previous work has suggested that walleye do not exhibit consistency in the life-history invariants (Beverton, 1987; Charnov, 1993). Based on data for walleye populations extending from Ontario to Texas (Colby *et al.*, 1979; Colby and Nepszy, 1981), Beverton (1987) found M/k and $L_{\mathrm{m}}/L_{\mathrm{inf}}$ not to be constant, although $T_{\mathrm{m}} \cdot M$ was invariant over the geographical range of the species. Beverton (1987) hypothesized that the lack of consistency was related to temperature. The ratio $L_{\mathrm{m}}/L_{\mathrm{inf}}$ was variable because L_{m} remained relatively constant, whereas L_{inf} decreased with increasing temperature. Although growth rate (k) and M both increased with temperature, he argued further that k did so at a faster rate.

Previous life-history invariant work is unusual in that support for the predictions of interest comes from failure to reject a null hypothesis (the slope of the relationship between two variables is 1.0). The primary goal of the present study was to use an extensive database on 435 populations of walleye to address questions related to statistical and biological invariance in the invariant relationships. The general hypothesis tested was that each of the four associations under consideration remains constant across a range of trait values – that is, the functional slope of a log-log plot is 1.0 (or −1.0 for $T_{\mathrm{m}} \cdot M$). Specifically, our objectives were as follows. First, we examined whether the relationships among the aforementioned life-history traits are invariant, and whether there are differences between the sexes. We then examined two power-related processes: the relationship between sample size and the probability of detecting statistically significant variation, and the extent to which trait values would need to change to make relationships constant (the effect size). Finally, we examined the amount of error created if invariance is incorrectly assumed when using the relationships to predict one trait from another.

METHODS

Data collection

Walleye sampling was conducted by the Cooperative Freshwater Ecology Unit (Laurentian University, Sudbury, Ontario) in conjunction with the Ontario Ministry of Natural Resources (OMNR), Canada. Details of sampling techniques have been documented by Morgan (2002). Briefly, multiple-mesh size, sinking gill nets were set at random locations in lakes perpendicular to the shore at two depth strata (2–5 m, 5–15 m), the number of sets being proportional to lake surface area. All lakes were sampled in an identical manner over a period of 10 years, when surface water temperatures were between 10 and 15°C (sampling started in the north and ran from late September to mid-November across Ontario). Ages were determined primarily from otoliths, and occasionally from dorsal spines, opercula bones or scales. Measurements of individual fish (length, maturity, sex, age) were used to calculate mean sex-specific life-history traits for each population. Environmental data (surface area, depth, etc.) were also available for the various lakes from the OMNR Aquatic Habitat Inventory Database.

Parameter estimation

L_{inf} *and k*

Lifetime growth rate was modelled using the von Bertalanffy growth equation

$$L_t = L_{\mathrm{inf}}(1 - \mathrm{e}^{-k(t - t_0)})$$

where L_t is total length (mm) at age t, L_{inf} is asymptotic length, k is the Brody growth coefficient, and t_0 incorporates a non-zero length at hatch (set as −1.0). Asymptotic length was also set empirically. For sex-specific sample sizes of less than 500 fish, the geometric mean of the largest five fish was used to estimate L_{inf}. Whenever the total number of fish aged was greater than 500, L_{inf} was calculated as the geometric mean length (L_g) of the largest p% of the sample ($p = 1\%$). Both estimates were multiplied by a correction factor to make the estimates more comparable with previous work:

$$L_{\mathrm{inf}} = L_g\,(1.0732 + 0.0223p - 0.0006p^2)$$

where p was 1% of $n > 500$ and was calculated for individual populations and sexes in other cases (Morgan, 2002).

Maturation age and size

By early autumn, gonadal tissue of individual walleye that are preparing to spawn in spring has begun differentiation. Visual examination of gonads in autumn samples was used to identify maturing fish (Morgan, 2002). The age (T_m, years) and total length (L_m, mm) at which 50% of the population was mature was determined using logistic regression. This analysis incorporates the assumption that fish spawn annually after the first reproductive season.

Mortality

Total adult instantaneous mortality (Z) was estimated from catch curves, using the Robson and Chapman estimator for fish at least 5 years of age (Robson and Chapman, 1961; Ricker, 1975). Mortality is expressed as the percentage of fish that die in one year. We could not directly determine natural mortality (M) and thus use Z, which incorporates both M and fishing mortality (F). Other studies on life-history invariants have also used Z instead of M (e.g. Vøllestad *et al.*, 1993; Vøllestad and L'Abée-lund, 1994). The use of Z incorporates the assumption that F is independent of the parameters with which mortality is being compared. Only fish aged 5 years and older were used in the mortality estimate, which minimized any bias attributed to size-specific differences in catchability. For consistency with other studies on life-history invariants, we present Z as M hereafter.

Statistical analyses

Data from a total of 435 populations (we assume that each lake comprises a separate population) are included in the analyses, with some lakes being sampled in more than one year. We have taken the mean life-history statistic from multiple years when this occurred. Note also that the number of degrees of freedom reported in our statistical analyses varies among parameters because data were not available for all variables from all populations.

Invariant relationships

We transformed our data to natural logarithms before the analyses of invariance. The question of whether the relationship between Y and X remains constant is independent of the intercept (determines value of the relationship but not whether the ratio holds constant). Slopes must not be significantly different from 1.0 (or −1.0 for $T_m \cdot M$) for invariance to occur. Since these are functional relationships, model II (reduced major axis) regressions were performed. Significance in deviations from unity was evaluated using 95% confidence intervals around the slopes (Zar, 1974).

Residual analyses

Regardless of whether the slope = 1.0, measurement error will create some scatter. We used the model II regression residuals around each relationship to determine if some of the observed variability could be explained. These residuals were calculated as

$$(Y - \hat{Y}) \cdot \cos \alpha$$

where $\alpha = \tan^{-1}$ of the function slope (W.G. Sprules, Professor of Biostatistics, University of Toronto at Mississauga, personal communication).

Beverton (1987) concluded that walleye did not show consistency in some relationships and suggested this was related to temperature. We tested this hypothesis by determining how much residual variation could be explained by growing degree days (≥ 5°C) and by M (for ratios that did not include M).

Sample size

Previous studies on life-history invariants in fishes have generally been based on fewer than 50 populations of a given species. Repeated random sampling (500 times) of our data set was used to determine sample sizes needed to generate statistical deviation from invariant relationships. Confidence intervals around model II slopes were determined (using model I outputs of standard errors) at each sample size to evaluate significant deviation from the expected 1.0 (or −1.0) slope.

How important is the deviation?

We evaluated how much change (on average) was required in Y or X to make a ratio statistically invariant. By way of example, our approach is described using the L_m/L_{inf} relationship. First, we predicted Y_1 (L_{inf}) from X (L_m) using the model II equation. Then, assuming the slope was actually equal to 1.0, we determined what the average intercept would be, given the mean observed L_m and L_{inf}. We then used this new equation (estimated intercept and $b = 1.0$) to predict Y_2 (L_{inf}). Lastly, the absolute percent change from Y_1 to Y_2 was calculated for each population, and the mean change determined.

An important use of the invariant relationships has been to predict more difficult-to-measure traits, such as mortality, from other more easily measured traits, such as growth. For each relationship, we randomly selected 50 populations from the data set and calculated the value of the ratio. We then used this value to predict Y in the remaining populations. Predicted and observed values of Y were compared to evaluate statistical versus biological importance of deviations from a truly invariant relationship. The deviation was calculated as

$$\Sigma \sqrt{\left(\frac{(Y - \hat{Y})^2}{(\hat{Y})^2}\right)} \cdot n^{-1} \cdot 100\%$$

where n is the number of populations where Y was predicted.

RESULTS

Life-history invariants for walleye were generally slightly lower than those reported for other species (Table 1). To some extent, this can be attributed to the somewhat different

Table 1. Mean invariant relationships from studies of among-population variation within a species of fish

Species	Source	L_m/L_{inf}	M/k	$T_m \cdot M$
Walleye ($n = 435$)	This study	$M = 0.562$ $F = 0.600$	$M = 1.68$ $F = 1.84$	$M = 0.95$ $F = 1.34$
Brown trout ($n = 29$)	Vøllestad *et al.* (1993)	0.599	1.92	3.14
Arctic char ($n = 37$)	Vøllestad and L'Abée-lund (1994)	0.728	1.97	3.19
Atlantic cod ($n = 16$)	Beverton (1992)	0.61		0.29
Atlantic herring ($n = 11$)	Beverton (1992)	0.61		0.22
Theory	Jensen (1996)	0.66	1.50	1.65

Note: Walleye M has been converted to proportion (from percentage) for comparison purposes. Cod and herring data were taken from Figure 1 and Figure 3 in Beverton (1992), where M is T_{max}^{-1}.

means by which the parameters were estimated; thus, values will not be directly comparable across species, regardless of whether there are meaningful underlying differences. The 95% confidence intervals associated with the model II regressions indicated that slopes for all walleye relationships differed between males and females.

L_m/L_{inf}

The mean value of the L_m/L_{inf} ratio was 0.562 for males (range 0.350–0.770, coefficient of variation [CV] = 0.106) and 0.600 for females (range 0.380–0.820, CV = 0.117). Only 14% (males) and 13% (females) of the variation in L_m was explained by L_{inf} (Fig. 1). Among males, 4% of the residual variation (scatter around the line) was explained by growing degree days ($F_{1,223} = 9.75$, $P = 0.002$), while M accounted for 5% of the variation ($F_{1,213} = 10.46$, $P = 0.001$). Among females, < 1% of the residual variability was explained by growing degree days ($F_{1,212} = 0.52$, $P = 0.473$); 20% of the variation was explained by variability in M ($F_{1,206} = 50.75$, $P < 0.001$). The ratio increased with L_m and decreased with L_{inf} (Fig. 2).

Pooling data from all populations, both males ($n = 226$, slope = 0.951, 95% confidence interval [CI] = 0.9508–0.9512) and females ($n = 215$, slope = 0.772, 95% CI = 0.7719–0.7721) had slopes significantly less than 1.0, indicating that the relationships were not invariant. Nevertheless, very large sample sizes (200 populations for males, 41 populations for females) would be required to reject the null hypothesis that postulated invariance, although a very small change in L_{inf} or L_m would make the ratio constant (Table 2). (Note that a percentage change will have different effects on the absolute values of the variables, such that a change in either variable can potentially affect both the slope and the intercept of the regressions.) Observed values of L_m differed from those estimated from L_{inf} by only 9% (Table 2). This deviation appears to be residual variation around the fitted regression with no systematic bias across a range of trait values (Fig. 3).

M/k

Across all populations, the M/k ratio averaged 1.68 (range 0.71–4.44, CV = 0.333) for males ($n = 231$) and 1.84 (range 0.60–4.17, CV = 0.337) for females ($n = 225$). K explained 25%

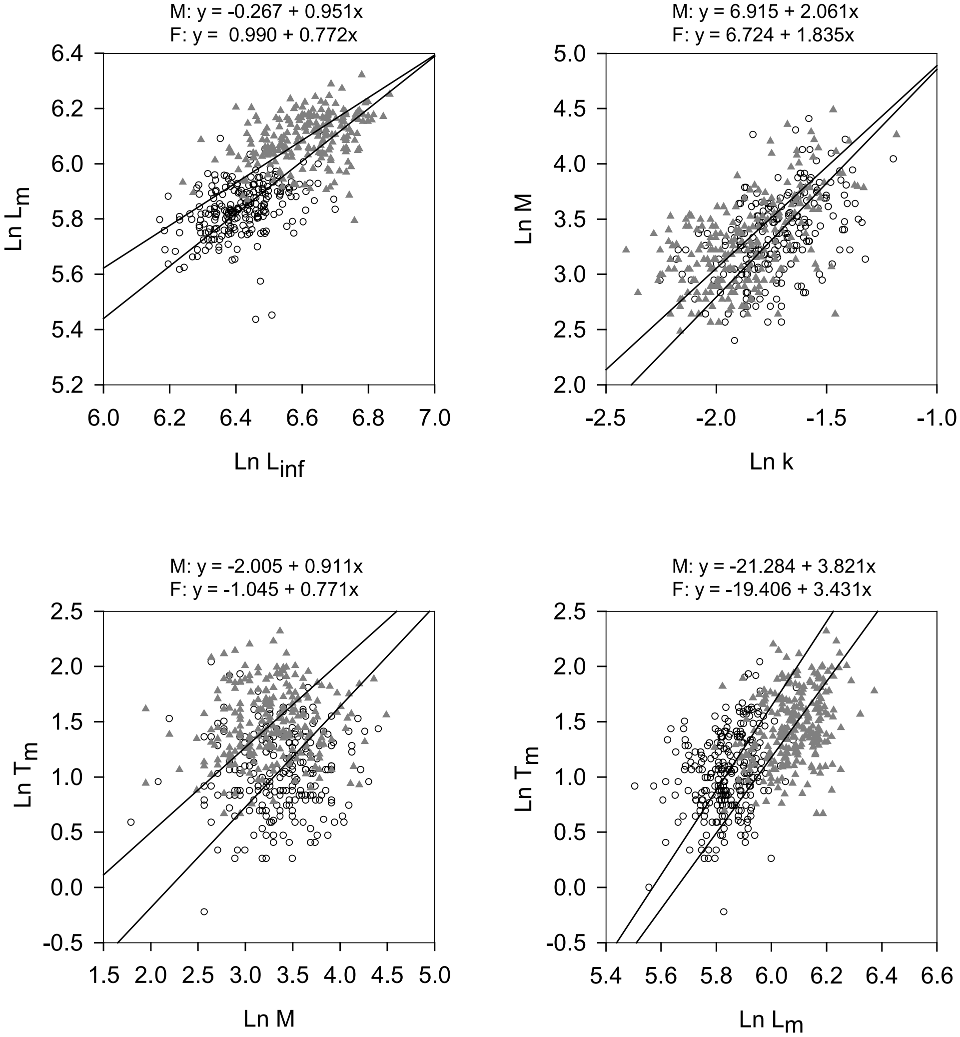

Fig. 1. Walleye life-history invariant relationships. Lines represent model II regressions. Each data point represents a different population. Circles are males, triangles are females.

(males) and 31% (females) of the variability in M (Fig. 1). Little of the residual variation in M was explained by growing degree days (males: 1%, $F_{1,228} = 2.00$, $P = 0.159$; females: 4%, $F_{1,222} = 8.26$, $P = 0.004$).

The M/k ratio was statistically variable (males: slope = 2.061, 95% CI = 2.053–2.069; females: slope = 1.835, 95% CI = 1.827–1.843). The ratio itself was not related to variability in k, but was strongly positively related to M (Fig. 2). Fewer than 10 populations were required to reject the null hypothesis of unity (Table 2), but only an approximately 5% change in either M or k would result in a constant ratio. Observed values of M deviated from those predicted from k by about 28% (Table 2). There was systematic bias in this error; observed estimates of M were more often than not lower than those predicted at low M and substantially above those predicted at high M (Fig. 4a).

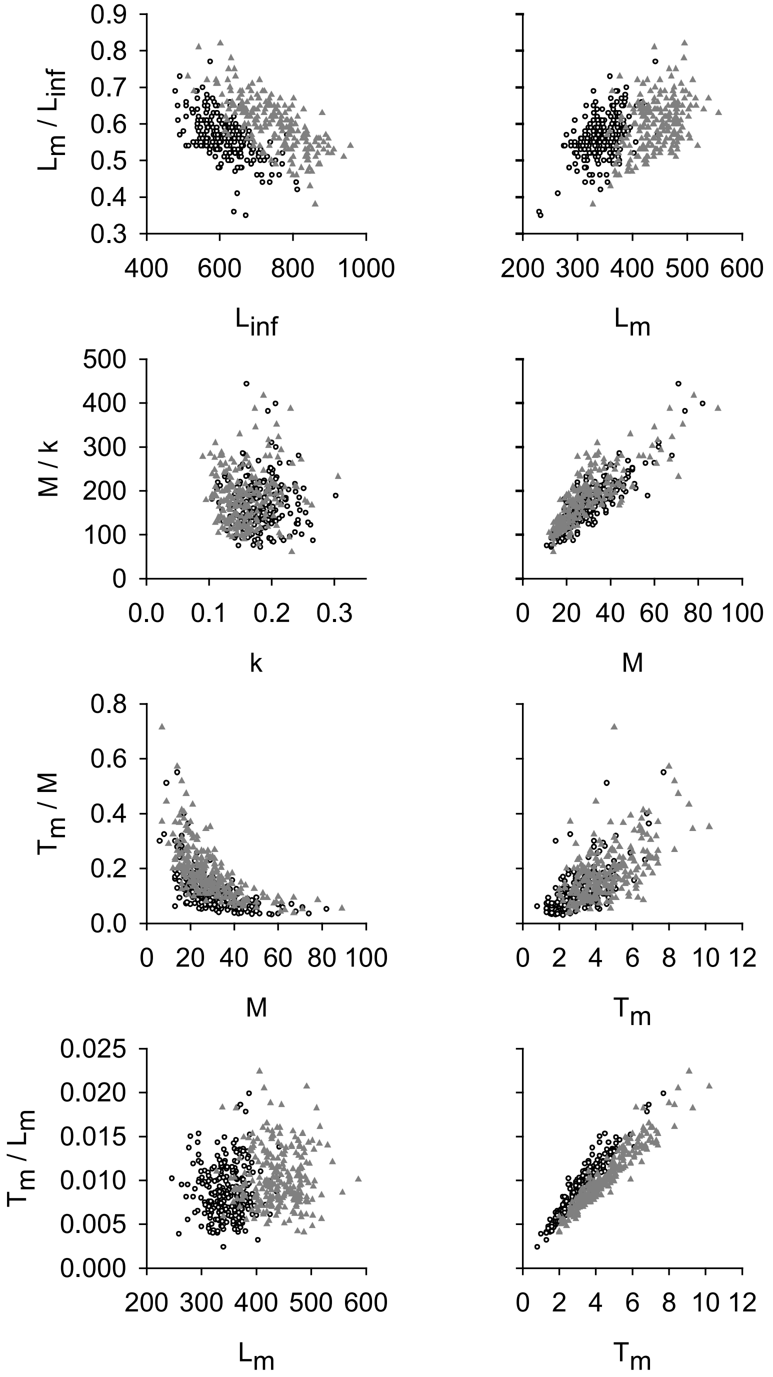

Fig. 2. Relationship between 'invariant ratio' and the value of *X* and *Y*. Each data point represents a different population. Circles are males, triangles are females.

Table 2. Results of analyses evaluating statistical versus biological deviation from constant relationships

Relationship	Analysis	Males	Females
L_m/L_{inf}	# of populations for variance	200	41
	% change in Y for invariance	< 1	< 1
	% change in X for invariance	< 1	< 1
	% deviation in predicted values	8	10
M/k	# of populations for variance	8	9
	% change in Y for invariance	4	4
	% change in X for invariance	7	7
	% deviation in predicted values	26	29
$T_m \cdot M$	# of populations for variance	—	—
	% change in Y for invariance	17	17
	% change in X for invariance	44	32
	% deviation in predicted values	43	43
T_m/L_m	# of populations for variance	4	4
	% change in Y for invariance	16	11
	% change in X for invariance	3	3
	% deviation in predicted values	28	26

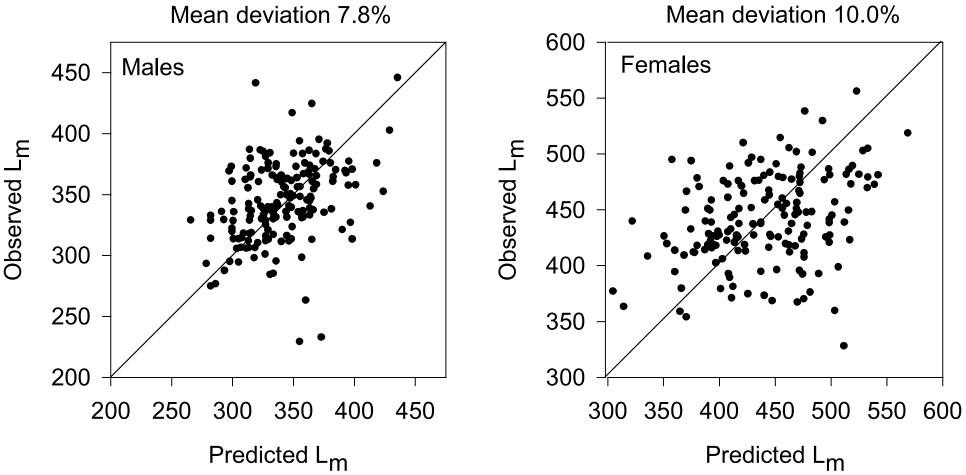

Fig. 3. Observed versus predicted L_m of walleye. Fifty randomly selected populations were used to generate a mean invariant ratio of L_m/L_{inf} to predict L_m in the remaining populations. The 1 : 1 line is shown.

$T_m \cdot M$

Among all populations, the mean value of the $T_m \cdot M$ relationship was 0.95 (range 0.10–3.44, CV = 0.557) for males ($n = 230$) and 1.33 (range 0.18–5.14, CV = 0.550) for females ($n = 236$). The T_m/M relationship increased linearly with T_m, and decreased in a concave

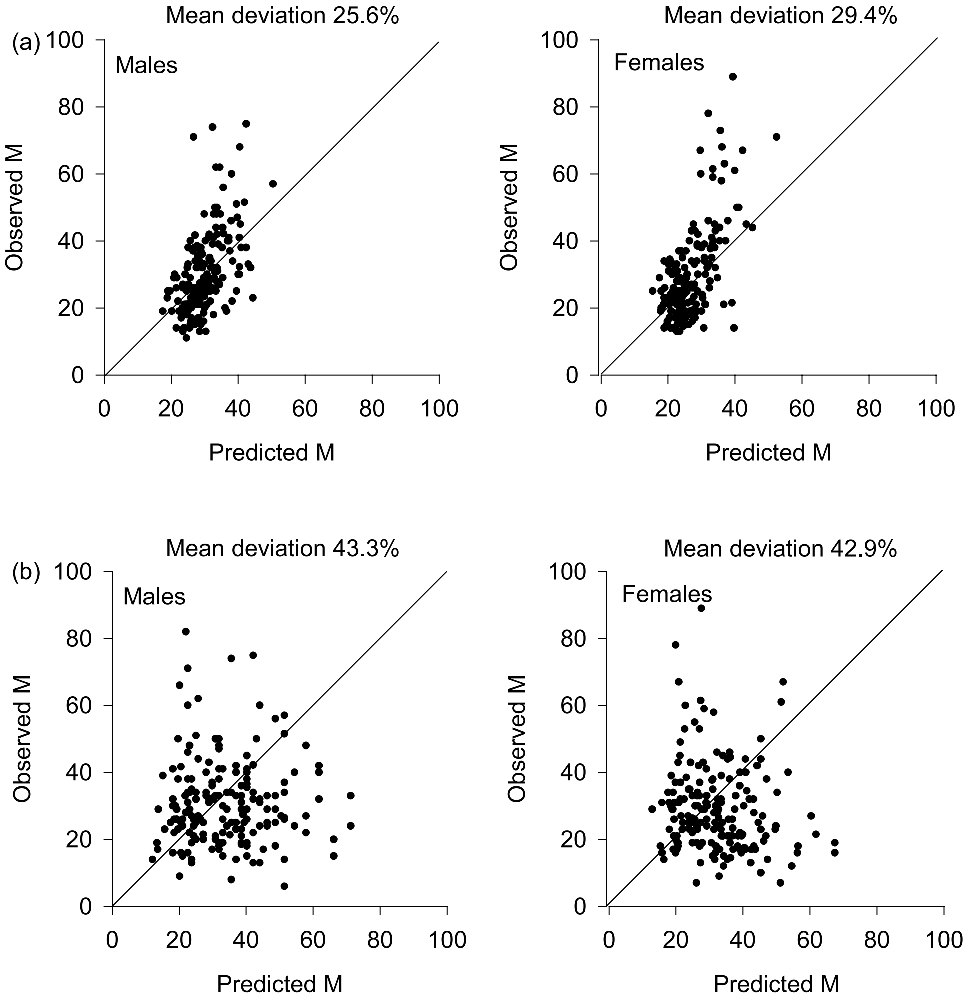

Fig. 4. Observed versus predicted M of walleye. Fifty randomly selected populations were used to generate a mean invariant ratio of (a) M/k and (b) T_m/M to predict M in the remaining populations. The 1 : 1 line is shown.

fashion with M (Fig. 2). This relationship had a high degree of scatter, with M explaining < 1% of the variability in T_m for males and females (Fig. 1). A comparatively high amount of the residual variation was explained by growing degree days in males (12%; $F_{1,227} = 30.32$, $P < 0.001$) and females (11%; $F_{1,233} = 28.47$, $P < 0.001$).

Although the expected slope for the $T_m \cdot M$ relationship is negative, the actual slope was positive (Fig. 1). It is important to note that there is very little difference in the square of the total residuals if the model II slope is positive or negative, as the model I regression was flat ($P > 0.15$). In other words, the amount of explained variation is very similar for either a positive or negative slope. Although this is a statistical reflection of the scatter, it does complicate one's interpretation of the data. For example, it was impossible to evaluate sample size requirements for invariance. To make the $T_m \cdot M$ relationship invariant (i.e. to achieve a slope of −1.0), changes of 17% and 38% were required in M and T_m, respectively (Table 2). Observed M deviated from the predicted M by an average of 43% (Table 2). Although most of this deviation could be attributed to a high degree of scatter in the data, there was some systematic bias (Fig. 4b), such that observed M tended to be larger than that predicted at low M and smaller than that predicted at high M.

T_m/L_m

The mean T_m/L_m ratio was 0.009 (range 0.002–0.020, CV = 0.345) for males ($n = 264$) and 0.010 (range 0.002–0.022, CV = 0.315) for females ($n = 254$). Maturation size accounted for only 10% and 9% of the variation in T_m for males and females, respectively (Fig. 1). Eight percent of the residual variation was explained by growing degree days for males ($F_{1,261} = 21.68$, $P < 0.001$) and for females ($F_{1,251} = 21.39$, $P < 0.001$). Little variation was explained by M for males (4%; $F_{1,228} = 7.79$, $P = 0.006$) or for females (1%; $F_{1,234} = 2.85$, $P = 0.093$).

The T_m/L_m relationship was not constant for either males (slope = 3.82, 95% CI = 3.819–3.824) or females (slope = 3.43, 95% CI = 3.429–3.433). Within a sex, the actual ratio was strongly positively correlated with T_m, and not correlated with L_m (Fig. 2). Only four populations were required to conclude that the ratio was not constant; changes of 3% in L_m or about 14% in T_m were required to make the ratio statistically invariant (Table 2). Observed T_m deviated from the predicted T_m by an average of 27% (Table 2). The range of predicted T_m is much narrower than that observed (Fig. 5).

DISCUSSION

Studies of life-history invariants are unusual in that failure to reject a null hypothesis (that the slope of the relationship between two variables is 1.0) constitutes support for the predic-

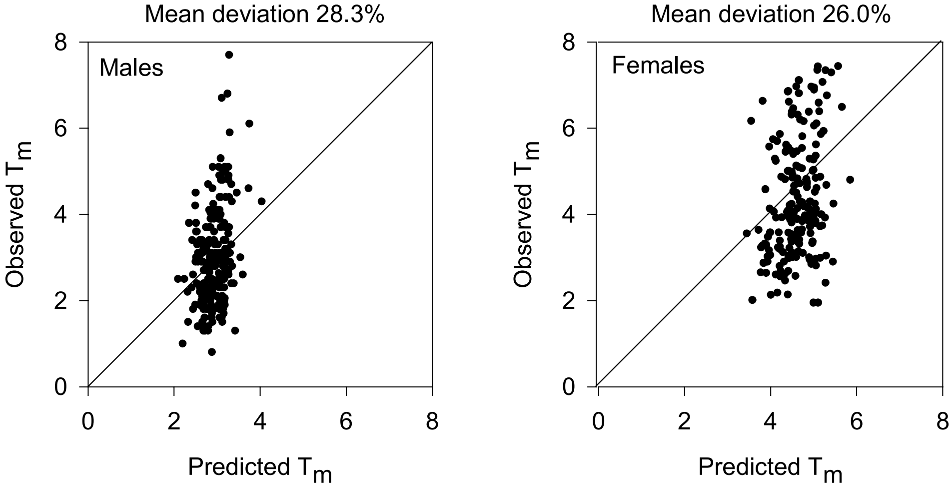

Fig. 5. Observed versus predicted T_m of walleye. Fifty randomly selected populations were used to generate a mean invariant ratio of T_m/L_m to predict T_m in the remaining populations. The 1 : 1 line is shown.

tions of interest. Analyses based on small samples sizes that normally invoke critique are ignored because they do not result in statistical conclusions of lack of consistency. Ecological relationships are often variable and thus one strives to achieve samples sizes as large as possible to provide reasonable statistical power to detect differences. The question thus arises as to whether under desirable statistical power life-history invariants exist at all? Based on one of the most extensive population data sets available for any fish species, our primary goal was to explore a set of circumstances that might result in life-history relationships being interpreted as invariant or not.

The L_m/L_{inf} value of 0.6 documented here for walleye is invariant unless large sample sizes are available; under full sample size little change was required in either parameter to make the relationship constant. The relationship contains a high degree of scatter, however, which may simply be due to error in parameter estimates. Thus, predicting L_m from L_{inf} may not be problematic if used to examine populations with large deviations in L_{inf}, but may be a problem if questions are related to single populations or those of similar L_{inf}. Purchase *et al.* (2005b) have shown how using different L_m/L_{inf} relationships to predict life-history traits can affect estimates of maximum sustainable harvest rates in walleye.

The relationship between M and k was statistically variable for walleye at sample sizes typical of most studies. A change in k of 7% or in M of 4% is required to make the relationship invariant. It is likely that most of the ~28% deviation in observed versus predicted M is simple scatter, perhaps a problem of measurement error.

Although the functional slope of the relationship between T_m and M averages 0.8 (predicted to be −1.0), the association is not significant and the least-squares slope is flat. The $T_m \cdot M$ relationship can, therefore, be interpreted as truly not constant. The average value between the sexes required to make the relationship invariant is a change of 17% in M or of 38% in T_m. A change of this magnitude in these traits would presumably result in tremendous differences in individual fitness and population growth and are thus difficult to accept as a possibility. It is also unlikely that such large deviations are caused by error in parameter estimates. Using this relationship for predicting M in walleye should, therefore, be avoided.

The relationship between maturation age and size, uncommonly referred to as a reaction norm (Stearns and Koella, 1986), is not constant in walleye. On average, L_m would have to change 3% or T_m 13% for the relationship to conform to unity. Given that selection likely acts more strongly on T_m than L_m (Roff, 2002), the smaller change in L_m is much more likely. Observed T_m is much more variable than that predicted, with the mean deviation being 27%. Since a lake with predicted T_m of 4.5 years can actually have a T_m from 2 to over 7.5 years, the utility of this relationship would appear to be quite limited.

Values of life-history traits differed between males and females. Our analyses also indicated differences between the sexes in the slopes of how traits covaried. This dichotomy in slopes suggests that male and female walleye might respond in a different manner to pressures that select for changes in life-history traits. Work by Purchase *et al.* (2005a) suggests that this may also happen in the closely related yellow perch (*Perca flavescens*).

All of the four relationships were highly variable. We tested the hypothesis of Beverton (1987) that temperature differences across populations of walleye explained variability in the ratios. Relatively little of the variation in residuals around the invariant relationships was explained by growing degree days, and thus the hypothesis is not supported. Perhaps the next most likely factor is M, but this did not explain much of the variation either.

Although it was not our purpose to examine possible causes for lack of consistency in relationships, some comment appears warranted. Associations involving mortality (M/k, $T_m \cdot M$) were not constant and a common phenomenon may explain both. Mortality was measured as total mortality instead of natural mortality. In general, we feel that this is not likely to cause a problem, although estimates of M based only on fish age 5 years or older fish could be problematic. It was not possible for us to obtain an accurate measure of mortality on younger fish. It is very likely that, on average, fishing mortality has increased steadily and substantially on Ontario walleye populations in recent years. However, it is also likely that the change in F has not been uniform across all regions (lakes). An increase in Z in recent years can explain lack of invariance in both relationships.

The relationship between M and k can arise in two ways. Within populations, increased mortality may decrease density, reducing competition, and resulting in a phenotypic response of increased growth. Alternatively, faster growing individuals may experience higher M through metabolic damage and/or increased predation. If Z has recently increased, there may not have been enough time for density changes to cascade through the ecosystem and cause increased growth. For the latter explanation, changes in Z have no feedback on k, and thus the ratio will have to change.

There are also two explanations for the association between T_m and M. Within populations, increases in M likely increase individual growth through density-dependent effects, and T_m generally decreases under faster growth through an individual plastic response. Alternatively, under higher M, later maturing genotypes are more likely to die before first reproduction and thus the population will evolve to a younger T_m. Recent increases in Z over 1–3 walleye generations may not have had enough time to express plastic responses of T_m to changes in growth, or evolved responses to selection.

In summary, our results suggest that life-history invariants do not exist in walleye. None of the associations exhibited a high degree of explained variation, nor did they show the expected relationship of ratios remaining relatively constant across the range of trait values. However, there is no persuasive support for the suggestion that walleye are somehow different from other species, as large numbers of populations may be required to reject the null hypothesis of invariance in many species where it has been supported. It is important to examine species-specific relationships carefully when using life-history invariants for predicting life-history traits.

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