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Sex-specific covariation among life-history traits of yellow perch (*Perca flavescens*)

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ABSTRACT

Questions: How do life-history traits covary among populations? Do two-trait models show different patterns of covariation than multi-trait models? Is covariation different for males and females? Is covariation among traits within populations (many generations) different to that among populations (one generation)?

Organism: A sexually dimorphic medium-sized freshwater fish, yellow perch (*Perca flavescens*).

Study system: Over 70 lakes in central North America.

Methods: Fish older than young-of-the-year were collected using standardized autumn surveys. Mean life-history traits were calculated for each population by sex.

Conclusions: Life-history traits generally covaried in the predicted manner among populations. Traditional two-trait comparisons resulted in similar conclusions as more complex models of covariation. Male and female patterns of covariation differed substantially for relationships between growth and age/size at maturation, moderately for lifespan and age at maturation, but were similar for size at maturation and maximum size. The relationships between female growth rate and maturation depended on the cause of variability in growth rates. Slow-growing populations matured young and small in warm lakes but old and large in cold lakes. Patterns of covariation in life-history traits were similar for temporal and spatial variability in traits.

Keywords: inter-population, intraspecific, life history, sexual dimorphism, yellow perch.

INTRODUCTION

Variable life histories can result from genetics, the environment (plasticity), or a combination of the two. Specific life-history traits do not vary at random but covary in a consistent manner that can be predicted in many species/populations. As an example, one of the main

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foci of life-history research has been the response of age and size at maturation to different growth and mortality rates (Roff, 1984; Stearns and Crandall, 1984; Stearns and Koella, 1986; Kozlowski and Wiegert, 1987; Kozlowski, 1992; Abrams *et al.*, 1996). These theoretical studies have generally concluded that faster growth or higher juvenile mortality reduce the age of maturation (but see Abrams and Rowe, 1996). Although there has been much empirical support for life-history theory, a major weakness of it and the theory itself has been the tendency to independently examine pairs of life-history traits. It is likely that many, if not all, life-history traits are interrelated to some extent (e.g. growth and life span may influence age at maturation, which may influence size at maturation and reproductive effort). The full extent of these interrelationships is not known, nor is the simpler question of how do relationships between pairs of life-history traits change, when other traits are also taken into consideration. Due to different selection pressures, relationships among life-history traits may also differ by sex.

To compare two-trait and multi-trait models, and sex differences in life-history covariation, we used among-population comparisons to examine within-population (among-individual) mechanisms. Despite life-history theory being based on predictions regarding selection acting on individuals (Roff, 1992; Stearns, 1992), a good deal of empirical work on life histories has consisted of comparisons among species. Much of our understanding of life-history variation among species has come from fisheries research (e.g. Beverton and Holt, 1959; Roff, 1982; Miller *et al.*, 1991; Rochet *et al.*, 2000; Frisk *et al.*, 2001), where extensive sampling has been supported through economically based management needs. However, relative to interspecific relationships, variation among populations of a single species is much less influenced by the confounding effect of phylogenetic differences, and can therefore be more revealing about selection pressures that have brought about that variation. Some of the most extensive work on life-history variation among populations also comes from fishes – for example, Atlantic salmon, *Salmo salar* (Schaffer and Elson 1975), brown trout, *Salmo trutta* (Vøllestad *et al.*, 1993; Mangel, 1996), Arctic char, *Salvelinus alpinus* (Vøllestad and L'Abée-lund, 1994), and lake trout, *Salvelinus namaycush* (Shuter *et al.*, 1998).

Although comparisons among populations are better than among species for testing life-history theory, studies comparing generations within a population are a further improvement. Virtually all tests of the theory on covariation in life-history traits have been made using spatial contrasts (e.g. among geographically separated populations). Temporal environmental heterogeneity may result in demographic differences among generations in a given population. The period over which such heterogeneity occurs may be short enough that significant genetic change is unlikely, and questions of life-history plasticity can be largely (although not completely) freed of the possibility of genetic variation.

Here we describe life histories of a sexually size-dimorphic species of fish, from a relatively large number of populations that exhibit a wide variation in growth and environmental conditions. There should therefore be a large plastic component to life-history differences, while the extent of a genetic influence is unknown. Our four objectives were to determine: if life-history traits covary among populations, whether two-trait models show different patterns than multi-trait models, whether males and females display differences in covariation among life-history traits, and whether the covariation of life-history traits among years within populations (temporal variability) is different from that among populations (spatial variability).

Based on theoretical and empirical work of others, we tested the following hypothesized relationships between pairs of life-history traits: (1) age at maturation decreases and (2) size at maturation increases under faster juvenile growth rates, (3) maximum size is positively

related to size at maturation, (4) age at maturation is older under longer life spans [~ lower mortality], and (5) reproductive investment is higher under faster juvenile growth and (6) younger ages at maturation. For multiple-trait comparisons, we hypothesized that (1) growth and life span act together on the age at maturation, (2) size at maturation is influenced by a combination of growth and age at maturation, (3) maximum size is a function of size of maturation and life span, (4) age at maturation and reproductive effort influence life span, and (5) reproductive investment is an outcome of the interaction between growth and age at maturation.

METHODS

Data collection

The study organism for this work was yellow perch (*Perca flavescens*), a medium-sized freshwater fish that occurs throughout much of North America. Data were obtained from yellow perch that were collected during standardized research surveys on various lakes. Multiple-mesh size sinking gillnets (19–152 mm stretched measure) were set at random locations perpendicular to the shore, at two depth strata (2–5 m and 5–15 m), with the number of nets sets being proportional to lake surface area. Sampling was conducted in autumn when water temperatures 1 m below the surface were between 10 and 15°C. Most samples for the 72 Ontario (Canada) lakes were collecting during a walleye (*Sander vitreus*) survey conducted by the Cooperative Freshwater Ecology Unit (Sudbury) in conjunction with the Ontario Ministry of Natural Resources. These data were supplemented with sampling by researchers using similar methods from the University of Toronto and Queen's University. The 72 populations served as a spatial comparison (hereafter referred to as the spatial lakes) of the covariation of life-history traits, and were sampled from 1995 to 2001. The location, environmental characteristics, years sampled and sampling agency of each of the lakes is presented elsewhere (Purchase *et al.*, in press).

A temporal analysis of the covariation of life-history traits was made using multi-year data collected from standardized research surveys by the Ontario Ministry of Natural Resources on Lake Erie and in South Bay (Lake Huron), and for Oneida Lake (New York) by the Cornell University Warmwater Fisheries Unit. Four time periods (see Appendix) encompassing 18 years in Lake Erie, and 27 years in South Bay, were used, together with two time periods spanning 20 years for Oneida Lake [adequate samples could not be obtained for four time periods for Oneida Lake (see Appendix)]. Data from adjacent years were pooled (e.g. for South Bay 1965 + 1966, 1983 + 1984) and the comparisons were spread over as much of a time period as possible to minimize measurement error in relation to true temporal variation in life-history parameters. The temporal and spatial data sets were generated in identical fashion.

Information on fork length (± 1.0 mm), whole body weight (± 0.01 g), gonad weight (± 0.01 g), sex, maturation status (maturing versus non-maturing) and oocyte counts was obtained for individual fish. Age was determined using otoliths, and all assigned ages were increased by one year to correct to the number of growing seasons. Data obtained from individual fish were used to calculate population mean life-history traits. Sample sizes for individual lakes ranged into the thousands, but few traits could be calculated for a population if samples comprised less than 100 individual fish (see Appendix).

Calculation of life-history traits

Growth rate

Fork length at age 2 was used as an index of early growth rate, as catches of young-of-the-year were too limited to be useful in most populations. A sex-specific sample size of at least four individuals was set as the minimum to calculate this trait for each population (sample size was much higher in most cases; mean = 45, median = 18). Even four fish provided a highly repeatable measure of mean fork length within a lake (Purchase *et al.*, in press). For the spatial lakes, when this sample size was not met, but other age classes were more abundant, the lake-specific mean fork length at age 2 was predicted using regression from the mean fork length at age 3 or 4 [mean $R^2 = 52.5\%$ with no systematic bias; equations based on among-population variation are presented in Purchase *et al.* (in press)]. Instances where fork length at age 2 was measured directly versus predicted from other age classes are distinguished in the Appendix.

Maximum body size was calculated as the mean fork length of the largest 5% of measured fish (sex-specific) when at least 50 individuals were sampled. Random sampling of Lake Nipissing data indicated that maximum size calculated in this manner did not increase (maximum size correlated with sample size) with the size of the data set (50, 100, 150, 200, 250, 300, 350 individuals) for males ($r = 0.384$, $P = 0.085$) or females ($r = 0.017$, $P = 0.941$).

Maturation

Age at maturation (years) and size at maturation (fork length, mm) were defined as the age and size when 50% of the population reached sexual maturation. This was primarily estimated using logistic regression, or if insufficient data were available, through a previously determined regression relationship across lakes between the percentage of fish mature in age and size classes with age and size at maturation, respectively [mean $R^2 = 82.2\%$ with no systematic bias; equations are presented in Purchase *et al.* (in press)]. Size and age at maturation estimated using the different methods are distinguished in the Appendix.

Reproductive investment

Yellow perch spawn in the spring, and a study of Lake Simcoe perch sampled in autumn (2000) and spring (2001) showed that relative fecundity estimates taken in the autumn are significantly higher than those immediately before spawning, but that the rate of increase in fecundity with body weight does not differ between seasons (Purchase, 2004). As only one lake was available to adjust intercepts based on season, no correction was made in our study. We attempted to collect ovaries from at least 30–40 mature fish in each lake during the autumn sampling. To obtain oocyte counts, ovaries were removed from preservative, blotted dry and weighed (± 0.001 g). Two sub-samples (~ 75 oocytes each) were removed from each ovary (anterior and posterior), weighed (± 0.0001 g), and then the number of maturing oocytes was counted using a dissecting microscope. The mean number of oocytes per gram of sub-sample was then multiplied by the weight of the entire ovary to obtain an estimate of the total number of maturing oocytes present in the ovary.

An index of relative female reproductive investment (RI) for each of the spatial lakes was calculated following procedures described by Reist (1986) [see Hendry and Taylor (2004) for an

example]. Both body weight and potential fecundity were log transformed and an analysis of covariance (ANCOVA) was performed with body weight as a covariate and lake as a factor. The interaction term was not significant ($P = 0.083$) and was removed, allowing estimation of the common within-group slope ($b = 0.9788$). This was used to standardize fecundity to the overall mean fish size (123.35 g) (see Hendry and Taylor, 2004).

Life span

To estimate life span, the mean age of the oldest 5% of fish (sex-specific) was calculated when at least 50 individuals were sampled. Thus, the estimated parameter is neither average adult life span, nor maximum adult life span, but can be interpreted as a life span index that should be useful for inter-population comparisons. Random sampling of Lake Nipissing data indicated that life span calculated in this manner did not increase (life span correlated with sample size) with the size of the data set (50, 100, 150, 200, 250, 300, 350 individuals) for males ($r = 0.081$, $P = 0.728$) or females ($r = -0.064$, $P = 0.782$).

Mortality

We could not estimate mortality rates in these populations, as no mark-recapture study and very little multi-year sampling were conducted. Many studies use proportional numbers of different age classes in nets as a means of estimating mortality in fishes (e.g. Vøllestad and L'Abée-lund, 1994). This technique cannot be used here, as it assumes equal recruitment among years, and it is widely known that yellow perch recruitment is highly variable (e.g. Pope *et al.*, 1996; Rudstam *et al.*, 1996).

Covariation of life-history traits

Correlation, linear regression and analysis of covariance were used to evaluate relationships among life-history traits for the spatial lakes (temporal comparisons of Lake Huron, Lake Erie and Oneida Lake are presented but not used in the statistical analyses, as the Great Lakes are fundamentally different systems and all necessary data were not available for Oneida Lake). Relationships between female growth rate and age/size at maturation violated an assumption of parametric statistics, as maturation schedules were much more variable at low versus high growth rates. These triangular distributions were quantified using quantile regressions, which are described in detail by Cade *et al.* (1999).

Two-trait and multi-trait comparisons are presented in Table 1 (and see Results). The first procedure in comparing multi-trait to two-trait models was to regress the response variable on the single predictor. The additional independent variables were then added in a stepwise fashion. Explained variation and the regression coefficients were then compared between the different models.

RESULTS

The calculated sex-specific life-history traits for each population are presented in the Appendix. The environmental characteristics of each of the 72 spatial lakes (Purchase *et al.*, in press) and plots of length at age (Purchase, 2004) are shown elsewhere.

Table 1. Relationships among life-history traits

Model	DV	IV(1)	IV(2)	IV(3)	Constant	IV(1)	IV(2)	IV(3)	Adjusted R^2 (%)	Significant
M1	**T_m**	**growth**			1.59 (0.39)	0.00 (0.00)			0.0	No
M2	**T_m**	**life span**			0.85 (0.35)	0.14 (0.05)			21.1	Yes
M3	**T_m**	**growth**	**life span**		0.79 (0.64)	0.00 (0.01)	0.14 (0.05)		17.8	2
M4	**T_m**	**growth**	**temp**		1.89 (0.52)	0.00 (0.00)	−0.00 (0.00)		0.0	No
M5	**T_m**	**growth**	**life span**	**temp**	1.12 (0.78)	0.00 (0.01)	0.14 (0.05)	−0.00 (0.00)	16.3	2
M6	T_m	temp			2.13 (0.42)	−0.00 (0.00)			0.0	No
M7	T_m	life span	temp		1.24 (0.68)	0.14 (0.05)	−0.00 (0.00)		19.4	1
M8	**L_m**	**growth**			60.50 (23.73)	0.21 (0.24)			0.0	No
M9	**L_m**	**growth**	**T_m**		−1.66 (20.34)	0.35 (0.18)	26.05 (5.57)		44.1	2
M10	**L_m**	**growth**	**temp**		69.95 (26.19)	0.34 (0.28)	−0.01 (0.02)		0.0	No
M11	**L_m**	**growth**	**T_m**	**temp**	0.43 (23.18)	0.37 (0.22)	25.84 (5.76)	−0.00 (0.01)	42.2	2
M12	L_m	T_m			32.15 (10.84)	26.91 (5.80)			39.1	Yes
M13	L_m	temp			86.90 (22.33)	−0.00 (0.01)			0.0	No
M14	L_m	T_m	temp		17.29 (21.72)	27.44 (5.87)	0.01 (0.01)		38.4	1
M15	**Max. size**	**L_m**			103.67 (25.68)	1.23 (0.32)			33.5	Yes
M16	**Max. size**	**L_m**	**life span**		73.74 (32.38)	0.91 (0.32)	8.21 (4.00)		39.4	1
M17	Max. size	life span			125.53 (23.33)	11.09 (3.34)			21.7	Yes
F1	**T_m**	**growth**			5.12 (0.50)	−0.02 (0.00)			23.4	Yes
F2	**T_m**	**life span**			2.05 (0.46)	0.10 (0.06)			4.5	No
F3	**T_m**	**growth**	**life span**		3.58 (0.65)	−0.02 (0.01)	0.12 (0.05)		21.3	1,2
F4	**T_m**	**growth**	**temp**		6.16 (0.54)	−0.02 (0.00)	−0.001 (0.000)		36.1	1,2
F5	**T_m**	**growth**	**life span**	**temp**	4.46 (0.66)	−0.01 (0.01)	0.13 (0.05)	−0.00 (0.00)	34.0	2,3

F6	T_m	temp			5.14 (0.46)	−0.001 (0.000)			26.3	Yes
F7	T_m	life span	temp		3.85 (0.61)	0.12 (0.05)	−0.00 (0.00)		29.0	1,2
F8	**L_m**	**growth**			101.55 (17.66)	0.36 (0.16)			6.1	Yes
F9	**L_m**	**growth**	**T_m**		−42.92 (17.83)	0.94 (0.11)	28.12 (2.77)		65.6	1,2
F10	**L_m**	**growth**	**temp**		130.83 (19.81)	0.52 (0.17)	−0.03 (0.01)		15.5	1,2
F11	**L_m**	**growth**	**T_m**	**temp**	−42.33 (22.93)	0.94 (0.12)	28.07 (3.08)	−0.00 (0.00)	65.0	1,2
F12	L_m	T_m			90.86 (10.73)	17.16 (3.54)			27.0	Yes
F13	L_m	temp			171.76 (17.25)	−0.02 (0.01)			3.5	No
F14	L_m	T_m	temp		77.61 (26.25)	18.37 (4.18)	0.01 (0.01)		26.1	1
F15	**Max. size**	**L_m**			101.96 (22.19)	1.06 (0.16)			46.6	Yes
F16	**Max. size**	**L_m**	**life span**		77.22 (25.39)	1.01 (0.17)	4.23 (2.51)		53.5	1
F17	Max. size	life span			166.23 (23.18)	10.51 (3.04)			19.6	Yes
F18	**Max. size**	**L_m**	**RI**		46.12 (27.32)	1.21 (0.14)	0.00 (0.00)		78.8	1
F19	**Max. size**	**L_m**	**life span**	**RI**	45.44 (31.77)	1.19 (0.17)	0.64 (3.29)	0.00 (0.00)	77.4	1
F20	Max. size	RI			239.32 (35.64)	0.00 (0.00)			0.0	No
F21	Max. size	life span	RI		144.85 (55.76)	12.22 (5.57)	0.00 (0.00)		13.0	1
F22	**Life span**	**T_m**			5.75 (1.11)	0.66 (0.38)			4.5	No
F23	**Life span**	**T_m**	**RI**		2.37 (1.30)	1.57 (0.28)	−0.00 (0.00)		62.7	1
F24	Life span	RI			7.97 (1.43)	−0.00 (0.00)			0.0	No
F25	**RI**	**T_m**			28864.8 (4826.2)	−1476.8 (1561.9)			0.0	No
F26	**RI**	**growth**			23177.5 (5023.5)	10.46 (45.25)			0.0	No
F27	**RI**	**T_m**	**growth**		29099.7 (9828.7)	−1498.3 (1774.0)	−1.59 (57.53)		0.0	No

Note: Models contain a dependent variable (DV) and up to three independent variables (IV), an abbreviation for sex (M or F) and temperature (temp); hypothesized relationships are in **bold**. Regression coefficients are given with their standard errors. Significance is indicated for models with one independent variable as 'yes' or 'no', and as the specific variable for those with multiple independent variables. T_m = age at maturation, L_m = size at maturation, RI = index of relative female reproductive investment.

Sex-specific two-trait comparisons among populations (spatial variation)

The complex relationship between growth rate and maturation

The age of maturation of males showed no relationship with early growth rate ($r = 0.193$, $P = 0.221$) (Fig. 1). The 80th and 20th quantile regressions had similar slopes ($F_{1,80} = 1.446$, $P = 0.233$), indicating no change in variability between fast- and slow-growing populations (Fig. 1). Females exhibited a completely different pattern that had a negative trend (Spearman rank order $r = -0.488$, $P < 0.001$). Relatively fast-growing populations matured at a young age, but under relatively slow growth (fork length < 100 mm) age at maturation was much more variable and was distributed over the complete range (2–5 years) (Fig. 1). The slopes of the 80th and 20th quantile regressions were significantly different ($F_{1,120} = 6.333$, $P = 0.013$), indicating a triangular relationship.

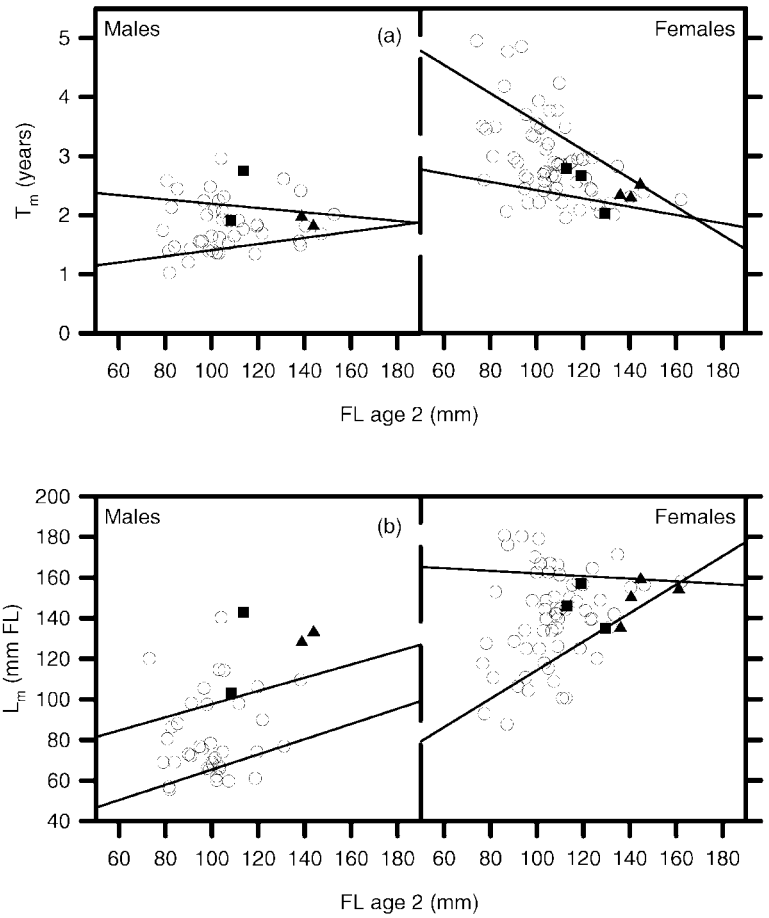

Fig. 1. Fork length (FL) at age 2 versus (a) age and (b) size at maturation (T_m and L_m, respectively) in yellow perch. Each data point represents a single population. Open circles are spatial lakes, triangles are Lake Erie, squares are South Bay (Lake Huron). Lines are 20th and 80th regression quantiles. Lake Erie and South Bay data were not used in the statistical analyses.

Size at maturation (Fig. 1) was positively but not significantly related to early growth rate in males ($r = 0.149$, $P = 0.378$), with no decrease in variability at faster growth rates, and thus no significant difference in the slopes of the 80th and 20th quantile regressions ($F_{1,72} = 0.004$, $P = 0.948$). In females, populations with relatively slow growth rates had more variable size at maturation than faster growing ones, and a positive trend is apparent (Spearman rank order $r = 0.232$, $0.050 < P < 0.100$). The slopes of the 80th and 20th quantile regressions were significantly different ($F_{1,122} = 6.985$, $P = 0.009$). The high variability in age at maturation of females did not result from differences in growth rates and a fixed size at maturation, or vice versa (Fig. 1). The variable maturation of slow-growing populations was not a result of populations with lower sample sizes, or differences in directly measured versus predicted traits, as indicated in the Appendix.

Other comparisons

The general linear relationship between size at maturation and maximum size that is seen in other species (see, for example, Vøllestad *et al.*, 1993; Vøllestad and L'Abée-lund, 1994; Shuter *et al.*, 1998) held true for both male and female yellow perch, and did not differ between the sexes (Fig. 2).

The association between age at maturation and life span differed in elevation between males and females, such that for a given life span, females matured at a later age (Fig. 3). Model I and model II slopes are shown, as the increasing variability in y with x in the female plot results in a different interpretation of the intercept differences (Fig. 3). Statistics are based on model I regressions (females have higher intercept), while the functional line (model II) indicates males have a higher intercept.

Unexpectedly, reproductive investment was not related to early growth rate ($r = 0.044$, $P = 0.819$) or age at maturation ($r = -0.186$, $P = 0.353$) (data not shown).

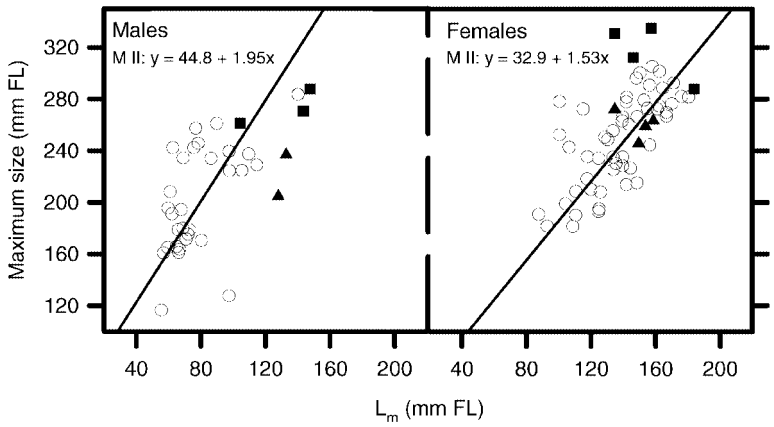

Fig. 2. Size at maturation (L_m) versus maximum size (mean of 5% of largest fish) of yellow perch. Open circles are from spatial lakes, triangles are Lake Erie, squares are South Bay (Lake Huron). Model II regressions of spatial lakes are shown; neither slopes (ANCOVA: $F_{1,77} = 0.06$, $P = 0.800$) nor intercepts (ANCOVA: $F_{1,78} = 2.70$, $P = 0.104$) differ significantly between males and females. Lake Erie and South Bay data were not used in the statistical analyses. FL = fork length.

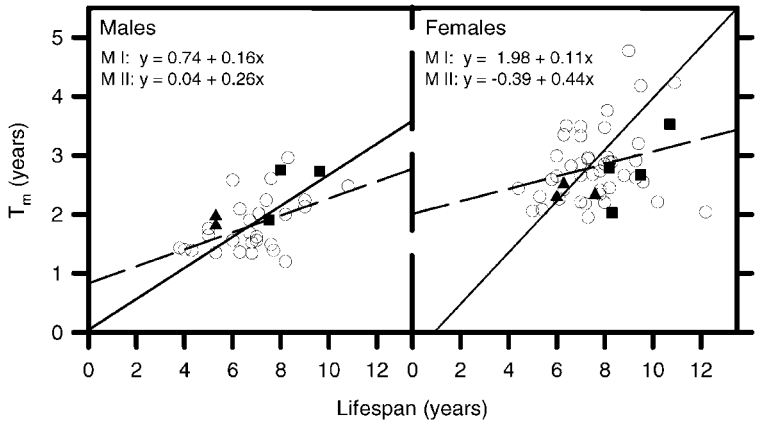

Fig. 3. Life span (oldest 5%) versus age at maturation (T_m) of yellow perch. Open circles are for spatial lakes, triangles are Lake Erie, squares are South Bay (Lake Huron). Model I regressions of spatial lakes are shown as dashed lines; the slopes do not differ (ANCOVA: $F_{1,65} = 0.39$, $P = 0.536$) but the intercepts do (ANCOVA: $F_{1,66} = 40.30$, $P < 0.001$) between males and females. Model II slopes are shown as solid lines. Lake Erie and South Bay data are were not used in the statistical analyses.

Sex-specific multi-trait comparisons among populations (spatial variation)

Models of two-trait and multi-trait relationships among life-history traits are described in Table 1. Hypothesized relationships among traits are indicated by bold text; others are presented to determine possible sources of relationships in the more extensive models. Although temperature is not a life-history trait, it has been included in the models for age and size at maturation because of an observed relationship (*post hoc*) explaining the triangular relationships between female maturation and growth rate.

The models were examined using linear regression and the results are summarized in Table 1. Of interest is whether explained variation, or the direction/magnitude of coefficients, changes in two-trait versus multi-trait models. In general, hypothesized multi-trait relationships showed little change from simpler models. There were no exceptions in males, but four cases of notable change in females. Although the coefficient for the relationship between maturation and growth rate remained the same, the explained variation was significantly increased with the addition of temperature for both maturation age (F4) and size (F10); the coefficient of the relationship between size at maturation and growth rate increased nearly threefold, and the explained variation by over tenfold with the addition of age at maturation (F9); and the relationship between life span and age at maturation becomes much stronger with the addition of the reproductive index (F23). For the latter, the observed change is due to the number of lakes changing from 43 to 20 with the addition of the reproductive index. The relationship with growth rate is strong in these 20 lakes regardless of whether the reproductive index is included in the model or not.

The complex pattern seen in the relationships between female early growth rate with size and age at maturity (Table 1, Fig. 1) was examined in more detail. Populations with the slowest growth rates matured at large sizes when at a late age and small sizes when at a young age (Fig. 4). The slowest growing populations also tended to mature at relatively old ages (Fig. 5) and large sizes in colder lakes, and at relatively young ages (Fig. 5) and small sizes in warmer lakes.

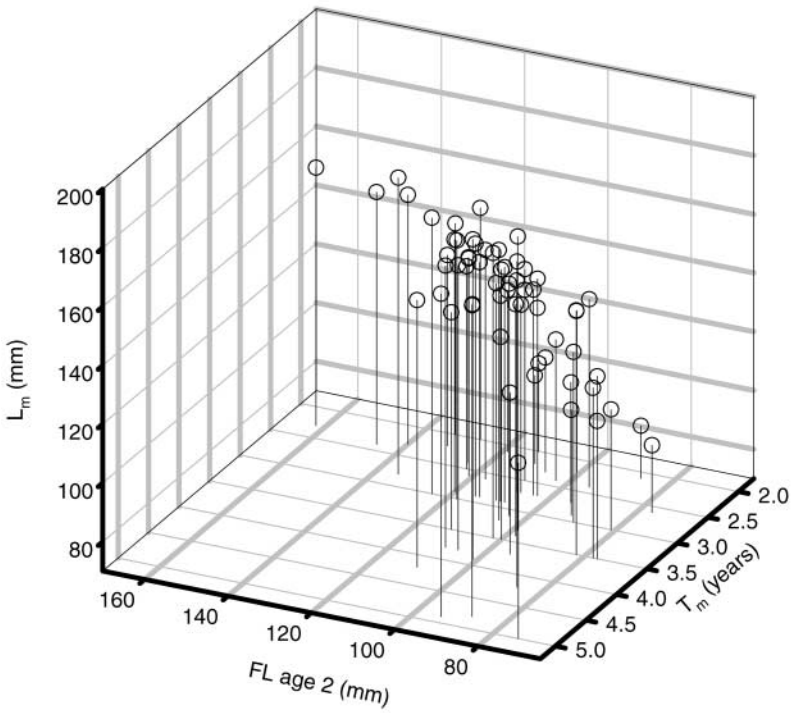

Fig. 4. Effect of early growth rate (FL) and age of maturation (T_m) on size of maturation (L_m) of female yellow perch. Both variables account for significant explained variation in a multiple regression (Table 1).

Temporal variation within populations

Both Lake Erie and South Bay life-history traits varied over the four time intervals. Multiple random samples ($n = 10$) of four of the 72 populations of spatial lakes were selected to determine mean coefficients of variation for the among-population life-history traits. In all cases, temporal variability was less than that present among the spatial lake populations (Table 2, Appendix). Measures of fork length at age 2, maximum size and life span of the Oneida Lake population were remarkably more consistent over the 20 year period in which these samples were taken than in the Lake Erie and South Bay (Lake Huron) samples (Table 2, Appendix A). Temporal covariation among life-history traits followed the same general pattern as that present spatially (Figs. 1, 2 and 3).

DISCUSSION

We have shown that covariation of life-history traits among many populations of yellow perch is, in general, similar using multi-trait and two-trait models. These relationships are very different between males and females for some combinations of traits, but not for others. It is also evident that the associations between age/size at maturity and growth rates depend on the causal factors underlying slow versus fast growth. In addition, temporal variation in the covariation of life histories within populations over several generations is not markedly different from that across populations.

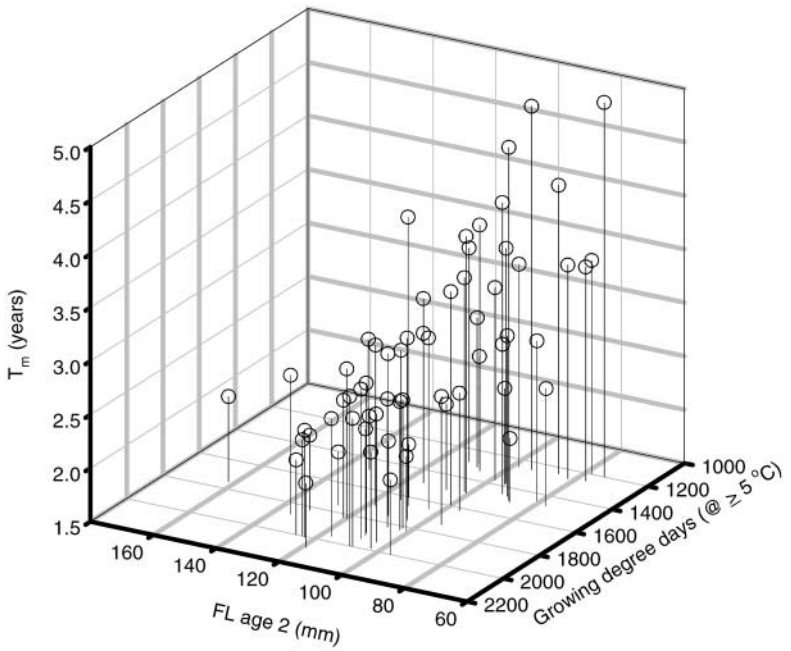

Fig. 5. Effect of early growth rate (FL) and temperature on age of maturation (T_m) of female yellow perch. Both variables account for significant explained variation in a multiple regression (Table 1).

Table 2. Comparison of the coefficients of variation for different life-history traits using spatial contrast (multiple random sampling of four populations from the 72 spatial lakes, see text), temporal contrast from Oneida Lake (Oneida, 2 years), Lake Erie (Erie, 4 years) and South Bay Lake Huron (SB, 4 years), and the temporal mean (Lake Erie and South Bay only)

	Males					Females				
Trait	Spatial mean	Oneida	Erie	SB	Temporal mean	Spatial mean	Oneida	Erie	SB	Temporal mean
FL age 2	12.4	0.0	6.5	13.7	10.1	11.7	0.0	6.5	13.7	7.3
T_m	22.8	N.A.	7.4	20.0	13.7	22.3	N.A.	7.4	20.0	13.6
L_m	20.6	N.A.	2.7	18.8	10.8	14.1	N.A.	2.7	18.8	10.2
Max. size	14.2	0.3	7.8	5.5	6.7	13.6	0.5	7.8	5.5	5.5
Life span	24.7	3.3	13.2	11.0	12.1	21.0	0.9	13.2	11.0	13.5

Note: Number of years in which each trait could be calculated for the Lake Erie and South Bay populations is given in the Appendix. FL = fork length, T_m = age at maturation, L_m = size at maturation.

The multi-trait models provided similar conclusions as two-trait models of how life-history traits covary. The four models where this was not the case do not provide any firm insight on life-history covariation as models F4 and F10 included temperature, which is not a life-history trait (implications are discussed below), and model F23 was a sampling artifact. The fourth model (F9) supports the intuitive result that under slow growth size at maturity is large when age at maturation is old, and small when age at maturation is young. We have not drawn any inferences from other models with non-significant but potentially

interesting changes because sample sizes decrease with the addition of extra variables (Appendix) and thus subtle differences may not be biological in nature. Our interpretation of these results is that the traditional paired-trait comparisons of life-history covariation adequately describe causal relationships among traits. Therefore, inferences drawn from previous empirical support of paired-trait comparisons should be reliable.

Covariation of life-history traits differed for males and females. If costs and benefits of large size are different between the sexes, selection could lead to sexual dimorphism in body size (Darwin, 1871). In most fishes, females gain fitness with increasing size through increased egg production. The extent to which males gain fitness with size depends on the mating system of the species (Magurran and Garcia, 2000). In species with relatively simple reproductive behaviour like yellow perch (no nest is built, no parental care of offspring), males usually grow slower than females after first reproduction and attain smaller maximum sizes (presumably because females gain more fitness benefits with size than males). One might expect sexual differences in the relative importance of selection acting on different life-history traits. Therefore, one would expect males and females to show similar patterns in the covariation among traits in certain cases, but dissimilar patterns in others. We found substantial differences between the sexes in the relationships of age and size at maturation with early growth rates, a minor difference between age at maturation and life span, but no difference in the relationship between size at maturation and maximum size.

One theoretical study that assumed that growth rate was totally environmentally determined (Stearns and Crandall, 1984) predicts fast growth should normally produce an early age at maturation and high reproductive investment after maturity. This association need not be present if growth rates can be varied depending on their fitness consequences (Abrams *et al.*, 1996). If varying foraging rates (growth) has different fitness consequences for males and females (C.F. Purchase and M.D. Rennie, unpublished), the sexes would be expected to show differences in patterns of covariation between growth rate and maturation. Our work supports this prediction.

Relatively fast growing populations of yellow perch did not produce earlier maturing males. Maturation was usually earlier in females (although some slow-growing populations matured just as early as the fastest growing populations), but reproductive investment did not increase with faster early growth rates. We measured relative reproductive investment in terms of potential numbers of eggs produced. Increased egg size may have been another means by which reproductive investment could have increased. This was impossible to measure, as differential oocyte size in the autumn can be due to differences in oocyte developmental stage, and not to differences in sizes of spawned eggs.

One of our more interesting findings was that the slowest growing populations had females with an average size and age at maturation that were highly variable, whereas fast-growing populations were relatively constant. Thus, the rule seems to be when growth conditions are 'good' perch mature early, but delaying maturation depends on why conditions are 'bad'. The different maturation ages under slow growth were related to temperature, as slow-growing populations from cold lakes tended to mature at a relatively large size and old age, while those from warm lakes matured at a small size and young age. The potential for future growth and survival provides a possible explanation for this pattern. Fish in cold lakes may grow slowly purely due to temperature constraints. Slow-growing populations in warm lakes (these tended to be small lakes) may be limited by food instead of temperature. By delaying maturation for an extra 2–3 years, fish in both warm and cold lakes could continue to grow (although slowly) and thus mature at a later

age and at a larger size. However, it is likely that mortality rates of young perch are higher in warmer lakes, as these generally have more species, higher densities of potential predators, and higher predator metabolic rates. Delaying maturation under slow growth in warm lakes would therefore not be adaptive if benefits of higher future reproductive effort are outweighed by a lower probability of survival to reproduction.

Due to genetic constraints, one might expect temporal relationships of covariation of life-history traits within populations to be 'tighter' than the covariation among populations. However, if phenotypic plasticity is only present in a subset of traits, it might be common to observe some traits to be constant over time while others vary. In our study, low sample sizes of populations with multiple years, and few sample years among populations, mean only large deviations from inter-population patterns can be detected. Temporal variation in life-history traits within a population was less than that present between spatially distinct populations. Covariation among traits expressed over several decades in two Great Lakes populations did not show substantial differences from spatial patterns present among 72 other populations, suggesting that the patterns reported among lakes from single-point-in-time sampling are likely to be representative and stable. However, the data were too limited in scope to define temporal trajectories, and this remains a challenge for the future.

In summary, increasing model complexity from the traditional two-trait models resulted in similar conclusions concerning the covariation among life-history traits. Our results illustrate the importance of separating the sexes when addressing questions arising from life-history theory, as different selection pressures can clearly lead to differences between males and females in the covariation among life-history traits. It is also evident that testing life-history theory using a small number of comparison units (e.g. populations) may not provide the same answers as those obtained using larger data sets. Here, as predicted from some other studies, female maturation occurred at a young age and large size when early growth rates were relatively fast; however, the maturation trajectory under slow growth appeared to depend upon the mechanisms affecting growth rates. Temporal patterns of the covariation in life-history traits were similar to those seen spatially across populations, but the magnitude of variation within populations across years (more than one generation) was less than that among populations at a single time (one generation).

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APPENDIX

Life-history traits of male and female yellow perch from 72 Ontario populations (spatial lakes), Lake Erie (over four time periods), Oneida Lake (over two time periods) and South Bay Lake Huron (SB, over four time periods). Column headings are sample size (*N*), fork length at age 2 (FL 2, mm), age at maturation (T_m), size at maturation (L_m), life span (years), maximum size (Max. size, mm), and relative reproductive investment (RI).

	Males						Females						
Lake	*N*	FL 2	T_m	L_m	Life span	Max. size	*N*	FL 2	T_m	L_m	Life span	Max. size	RI
Spatial lakes													
Agnew	66	147	1.7*			184	36	154					22044
Arthur	20	100					34	103					22927
Ashley	116	91	1.4	72	3.8	175	105	90	3.0	128	7.3	250	14302
Balsam	512	119	1.3*	61*	6.8	208	729	121	2.6	144	9.3	260	
Belmont	19	120	1.8*	74*			25	123	2.5	139		263	
Biscotasi	28	139	2.4*				83	133*	2.0	142		278	
Blue	88	103	1.4*	67*	5.3	164	146	113	2.0*	100	7.3	278	
Buckhorn	222	103	1.6*	66*	7.0	179	657	109	2.9	126	8.0	208	
Burntbush	22	107*					18	109*	3.8	166			
Cameron	20	105					43	110	2.9	144		227	
Cataract	5						24	112					25048
Chemong	138	101	2.1*	71*	6.3	171	311	103	2.4	118	7.8	235	
Chesley	19	118*					50	120*	2.9	156	7.3	244	26672
Corrallen	12						31	74*	5.0	130		249	
Crabstoe	29	99*					29	94*	4.9	180			
Crotch	55	122	1.7*	90	6.7	261	80	124	2.4	140	6.3	266	20420
Dalrymple	55	99	1.4*	65*	4.3	166	90	101	2.2	125	7.0	234	23827
Denbigh	68	98			5.0	124	116	111	2.2	100	10.2	252	
Desmilles	35	100	1.6*	69*			26		3.5	183			
Dog	16	141	1.8*				12	146	2.4*	156			27304
Elephant	136	102		60*	8.8	165	282	107	2.3	109	7.8	181	
FourMile	26	100					48	103	2.7	144			
French	110	92			6.0	175	130	95	2.7	111	7.0	208	19409

Howcum	39	73		120			35	78	3.5	128			
Jack	46	99*					102	107*	2.7	134	8.8	235	
Jowsey	67	96	1.6	76	7.0	242	58	99	3.3	170	7.0	276	19488
Kasshabog	118	104			9.8	197	115	109	2.5	142	8.2	214	
LaCave	28	120	1.8	106			38	118	3.0	158			23279
Lady Ruth	63	82	1.4	57	7.7	161	109	77	2.6	93	5.8	182	26052
Lower Paudash	83	107			9.3	217	128	127*	2.0*	149	12.2	266	
Madawaska	48	95	1.6*	77			89	96	2.2	104	8.0	199	
Makokibatan	49	99*					50	98*	3.4*	149	6.3	215	
Manitou	207	153	2.0*		7.1	261	188	162	2.3	158	6.1	305	35596
Margueratt	40	85*	2.4	88			80	88*	4.8	176	9.0	282	21832
Marian	31	109*				273	24	114*	2.9	150			
Mcfarlane	183	91		98*	6.0	128	305	97			4.8	166	
Melic	70	79	1.7	69		180	93	81	3.0	111	6.0	190	21270
Mindemoya	190	104	3.0	140	8.3	283	202	105	3.2	162	9.4	301	
Mink	35	105	2.3	114			197	117*	2.6	148	9.6	296	
Mississagagon	64	102	1.4*	62*	6.3	191	129	103	2.7	134	7.5	255	
Moira	109	107	1.5*	60	6.8	196	166	109	2.9	140	7.0	235	
Mountain	94	98	2.0	97	8.2	239	46	101	3.9	179			15830
Nagagami	22	107					7						
Nagagamisis	206	83	2.1	86	9.0	234	195	86	4.2	181	9.5	282	23097
Nippigon	24	108	1.9*				50	108	2.9	150	8.3	300	
Nippissing	372	100	2.5	78	10.8	246	437	110	4.2	161	10.9	272	24873
Ottawa	19	106					28	132	2.2*	135		230	20991
Pigeon	269	101			6.6	191	578	104	2.7	140	7.8	228	
Plastic	87	91*			5.8	179	211	93*			6.0	199	
Bay of Quinte (L. Ont.)	55	110	1.6*		5.0	163	221	126	2.2	120	7.2	210	
Ramsay	29	98*		66*		161	54	105*		115		272	
Rennie	17	103					54	112*	3.5*	144*			26380
Rice	543	114	1.8*		5.0	176	820	119	2.1	125	5.4	195	21317
Richard	19	100					30	96*	2.6*			201	
Round	196	103	2.2	115	7.4	229	119	102	3.5	167	8.0	267	
Saganash	118	97	2.2	105	9.0	225	139	106*	3.8	167	8.1	270	25807
Scolt	154	90	1.2	73	8.2	179	150	92	2.9	106	8.2	243	33177

APPENDIX—*continued*

	Males						Females						
Lake	*N*	FL 2	T_m	L_m	Life span	Max. size	*N*	FL 2	T_m	L_m	Life span	Max. size	RI
Shoe	103	117			5.2	185	177	124			4.3	210	
Simcoe	99	138	1.5	110	7.6	237	113	135	2.8	171	6.6	292	19488
Stormy	2						48	107				233	
Stumpy	65	112	1.9	98	6.7	224	45	115*	2.9	156	9.3	291	
Thistle	42	105	2.1*	74*			27	104*	3.1	149			23021
Trailer	71	82	1.0	56		117	138	87	2.1	88	5.0	191	37833
Vermillion	52	105	1.9			242	41	100	3.5	162		275	
Wabibigima	98	81	2.6	80	6.0	170	174	77	3.5	117	6.4	218	23904
Wakami	90	100	1.4*	68*	4.0	194	133	95	2.4	134	4.4	225	
White	53	138	1.6*		6.0	239	69	140	2.3	155	5.3	273	26474
Whitefish	239	131	2.6*	77	7.6	257	228	124	3.0	164	8.1	289	
Whitelilly	20	85*					78	95	3.7	125		193	
Wildgoose	54	84	1.5*	69*		234	76	82	3.5	153	7.0	279	35981
Wolfe	61	105			4.3	194	88	108	2.7	142	6.0	281	
Wowun	9	106*					24	109*	2.5*	135*			21809
Other lakes													
Erie 1978–1979	959	139	2.0	128	5.3	205	1218	141	2.3	150	6.0	246	
Erie 1982–1983	740	155			5.3	208	628	161		154	5.5	259	
Erie 1991–1992	722	133			6.8	236	1029	136	2.3	135	7.6	272	
Erie 1995–1996	2591	144	1.8	133	5.3	237	2979	145	2.5	159	6.3	263	
Oneida 1980–1983	426	149			8.8	280	442	148			7.6	291	
Oneida 1997–2000	190	149			8.4	281	136	148			7.7	289	
SB 1965–1966	1116		2.7	148	9.6	288	942		3.5	184	10.7	288	
SB 1974–1976	261	139			8.0	294	357	130	2.0	135	8.3	331	
SB 1983–1984	399	114	2.8	143	8.0	271	395	119	2.7	157	9.5	335	
SB 1991–1992	359	108	1.9	103	7.5	261	480	113	2.8	146	8.2	312	

* Fork length age 2 predicted from FL age 3 and 4, T_m from % mature at age, and L_m from % mature at size (see text).