

Sex-based trade-offs among growth, mortality, and maturation in Great Lakes yellow perch stocks

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Abstract: Trade-offs among growth, mortality, and reproduction form the basis of life history theory but may vary among populations owing to local ecological conditions. We examined life history trade-offs driving variation in maturation among 13 yellow perch (*Perca flavescens*) stocks in the Great Lakes using sex-specific age and length at 50% maturity (A_{50} and L_{50} , respectively) and probabilistic maturation reaction norm midpoints ($Lp_{50,a}$). Both sexes exhibited positive correlations between growth and mortality, and faster-growing stocks were mature at younger ages but larger sizes. Male and female A_{50} and L_{50} were positively correlated among stocks, but $Lp_{50,a}$ estimates were negatively correlated among stocks, indicating stocks that matured at large sizes for a given age in females matured at smaller age-specific sizes in males. Female $Lp_{50,a}$ estimates were negatively related to growth and mortality, while male $Lp_{50,a}$ estimates were positively related to growth. These results suggest that (i) sex-based life history trade-offs sometimes act to differentially structure maturation schedules in males and females and (ii) males may be less responsive to changes in mortality than females.

Résumé : Si les compromis entre la croissance, la mortalité et la reproduction forment la base de la théorie du cycle biologique, ils pourraient varier entre populations en raison de conditions écologiques locales. Nous avons examiné les compromis associés au cycle biologique à l'origine de différences sur le plan de la maturation entre 13 stocks de perchaudes (*Perca flavescens*) dans les Grands Lacs en utilisant l'âge et la longueur selon le sexe à 50 % de la maturité (A_{50} et L_{50} , respectivement) et les valeurs médianes de la norme de réaction de maturation probabiliste ($Lp_{50,a}$). Les deux sexes présentent des corrélations positives entre la croissance et la mortalité, et les stocks à croissance plus rapide atteignent la maturité à de plus bas âges, mais des tailles plus grandes. Les A_{50} et L_{50} des mâles et des femelles sont positivement corrélés entre les stocks, mais les estimations des $Lp_{50,a}$ sont négativement corrélées entre les stocks, ce qui indique que les stocks caractérisés par l'atteinte de la maturité à des tailles plus grandes pour un âge donné chez les femelles sont caractérisés par la maturité à des tailles plus petites pour un âge donné chez les mâles. Les estimations des $Lp_{50,a}$ des femelles sont négativement reliées à la croissance et à la mortalité, alors que les estimations des $Lp_{50,a}$ des mâles sont positivement reliées à la croissance. Ces résultats donnent à penser que (i) les compromis associés au cycle biologique basés sur le sexe se traduisent parfois par des structures distinctes des calendriers de maturation entre les mâles et les femelles et (ii) les mâles pourraient réagir moins fortement aux variations de la mortalité que les femelles. [Traduit par la Rédaction]

Introduction

The process of maturation and resultant reallocation of energetic resources to gonadal development are subject to significant trade-offs with future growth, mortality, and reproductive potential (Stearns and Koella 1986; Stearns 1989; Roff 1992; Roff et al. 2006; Lee et al. 2013), with important implications for population demographics and resiliency to environmental and anthropogenic stressors (Dunlop et al. 2007; Kuparinen and Hutchings 2012; Neubauer et al. 2013). Variation in growth rates may alter the cost of current reproduction to future growth, thereby driving

differences in maturation schedules among populations experiencing fast or slow juvenile growth rates (Stearns 1989; Wang et al. 2008). Variation in mortality rates, alternatively, may alter the fitness of younger- or older-maturing individuals, often selecting for early maturation in populations with high mortality rates either post maturation (i.e., adult fish) or in older, larger fish regardless of reproductive status (Haugen 2000). The relative importance of growth and mortality to variation in maturation schedules remains unclear for many exploited species, as differences in predation pressure, fishing pressure, and resource availability, among other

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factors, interact to determine the structure of correlations between growth and mortality (Köster et al. 2001; Morita and Nagasawa 2010; Jørgensen and Holt 2013). Quantifying among-population variation in growth, mortality, and maturation, including their respective relationships among populations, can help generate and evaluate hypotheses for trait change in response to future disturbances, in addition to elucidating stock structure and informing stock management (Barot et al. 2004; Wright et al. 2011).

Most fisheries management has focused largely on the importance of females for reproductive success (Hixon et al. 2013) or assumed that both sexes should vary in maturation similarly over time or among populations (van Walraven et al. 2010). However, sexual differences in growth, mortality, and maturation schedules have been observed in many fish species, usually with males exhibiting smaller ultimate sizes, higher mortality rates, and maturation at smaller sizes and younger ages compared with females (Parker 1992; Henderson et al. 2003; Feiner et al. 2015). In some fishes, the sexes also differ in foraging and exploratory behavior (Horppila et al. 2011; Thompson and Simon 2014; Estlander et al. 2015), spawning phenology (Morgan and Trippel 1996), susceptibility to and recovery from fisheries capture (Lauer et al. 2008; Donaldson et al. 2014), and even the importance of maternal effects to an individual phenotype (Kruuk et al. 2015). Proposed mechanisms for these differences largely focus on the relative differences in energy allocation required for successful reproduction between sexes (e.g., Merrill and Collins 2015). Variation in environmental conditions, resulting in variation in mortality and growth rates among sexes and populations (e.g., Horppila et al. 2011), may differentially influence variation in male and female maturation schedules owing to the unique trade-offs each sex must balance among these vital rates. For example, some studies have shown that male maturation schedules appear relatively less sensitive to stressors such as fisheries exploitation than female maturation schedules (Devine et al. 2012; Feiner et al. 2015). Understanding variation in male maturation and the trade-offs among male vital rates, especially if they should exhibit different patterns than those found in females, represents a major gap in our understanding of life history variation. Exploring these sex-based trade-offs could yield novel insights into the mechanisms driving observed differences in the responses of males and females to ecosystem stress.

The interplay of growth and mortality is particularly relevant to fish stocks experiencing heavy anthropogenic pressures, as anthropogenic stressors may have a far greater impact on rapid phenotypic change in populations than natural processes (Hendry et al. 2008; Darimont et al. 2009; Palkovacs et al. 2012). In the Great Lakes, fisheries exploitation, invasive species, nutrient loading, and climate warming have all been shown to influence population characteristics of fish stocks (Madenjian et al. 1996; Dettmers et al. 2003; Marsden and Robillard 2004; Dobiesz et al. 2005; Allan et al. 2005, 2013; Fielder et al. 2007). Specifically, yellow perch (*Perca flavescens*) stocks have experienced pronounced changes in environmental conditions (Tyson and Knight 2001), harvest rates (Irwin et al. 2008), mortality rates (Fielder 2008; Fielder and Thomas 2014), stock abundances (Marsden and Robillard 2004), and recruitment levels (e.g., Redman et al. 2011) throughout the Great Lakes. Yellow perch is an iteroparous species that exhibits life history traits and trade-offs similar to those of many exploited freshwater and marine species (e.g., determinate spawning, no parental care of offspring, trade-offs between fecundity and egg size, and density-dependent growth; Henderson et al. 2000; Lauer et al. 2005; Headley and Lauer 2008). Thus, disentangling the respective importance of growth and mortality rates to broad-scale variation in maturation schedules in yellow perch could provide useful insights into the impact of stressors on fish life history traits in general. The specific objectives of this study were to (i) quantify variation in growth, mortality, and maturation schedules of male and female yellow perch among 13 Great Lakes stocks

in recent time (since 2000), (ii) quantify trade-offs among growth, mortality, and maturation between males and females, and (iii) determine the importance of variation in growth and mortality rates to among-stock variation in maturation schedules in both male and female yellow perch.

Methods

Yellow perch data

Data on yellow perch sex, length, age, and maturation status (reproductively active or immature) were provided by collaborating universities and natural resource agencies from 13 spatially distinct stocks throughout the Great Lakes: Green Bay, the southern basin of Lake Michigan, Les Cheneaux Islands, St. Marys River, North Channel, Georgian Bay, Saginaw Bay, the southeastern main basin of Lake Huron, Lake St. Clair, the western and central basins of Lake Erie, the Bay of Quinte, and the Kingston Basin in eastern Lake Ontario (Fig. 1). These stocks are spatially distinct with differing genetic structure and population dynamics (Todd and Hatcher 1993; Miller 2003; Sepulveda-Villet et al. 2009). Fish were collected using a number of different gear types, including mono- and multifilament gill nets, fyke nets, and bottom trawls (Table 1). When sampling was conducted over multiple months, data were first analyzed monthly, and months that did not significantly differ in age or length at 50% maturity were grouped together to maximize annual sample sizes (Table 1). Although there was some change in age-specific mean total fish length among months in each data set (likely indicating growth throughout the year), which could bias estimates of age or length at maturation, mean length at age of sampled fish did not significantly vary with sampling month and therefore was assumed to introduce little bias in our maturity estimates.

Cohorts (determined as the year of birth) were defined by subtracting the age of each fish from the year it was captured. Because fish from all stocks other than Green Bay were sampled after the spawning period (i.e., May–November), and gonadal development in yellow perch takes place throughout the summer and fall (Henderson et al. 2000), identification of individual reproductive status in those months indicated whether the fish would spawn the following spring. Therefore, one was added to the age of each fish to reflect that it would have increased in age by the next spawning season. Because the reproductive status of Green Bay fish was determined during the spawning season (i.e., April), the observed ages reported were used.

Length data were usually reported as total length (mm TL). However, for some stocks in Lakes Huron and Ontario, a combination of total and fork length (mm FL) was reported. When this occurred, a linear regression of fork length and total length (Lake Huron: $TL = 1.034 \times FL + 3.017$, $R^2 = 0.998$; Lake Ontario: $TL = 1.041 \times FL + 1.353$, $R^2 = 0.995$) was used to estimate total lengths where only fork lengths were given.

Quantifying maturation

We used three metrics in an attempt to unravel plastic and adaptive variation in maturation schedules across stocks of yellow perch for which the ability to account for plasticity induced by differences in growth and mortality varies: age and length at 50% maturity (A_{50} and L_{50} ; the age or length, respectively, at which 50% of individuals are mature) and length-based probabilistic maturation reaction norms (i.e., PMRNs estimated using the demographic method, defined as the region in age–length space where an individual will first become mature; Heino et al. 2002; Barot et al. 2004a). The metrics A_{50} and L_{50} are commonly used life history parameters and appear to be strongly influenced by plasticity in maturity caused by changes in growth, but they can also be sensitive to differences in sampling gear or the methods agencies use to identify reproductive status of individuals (Wang et al. 2008, 2009). In contrast, PMRNs appear to be robust to these types

Fig. 1. Great Lakes yellow perch stocks included in the maturation study (see Table 1 for contributing agency information).

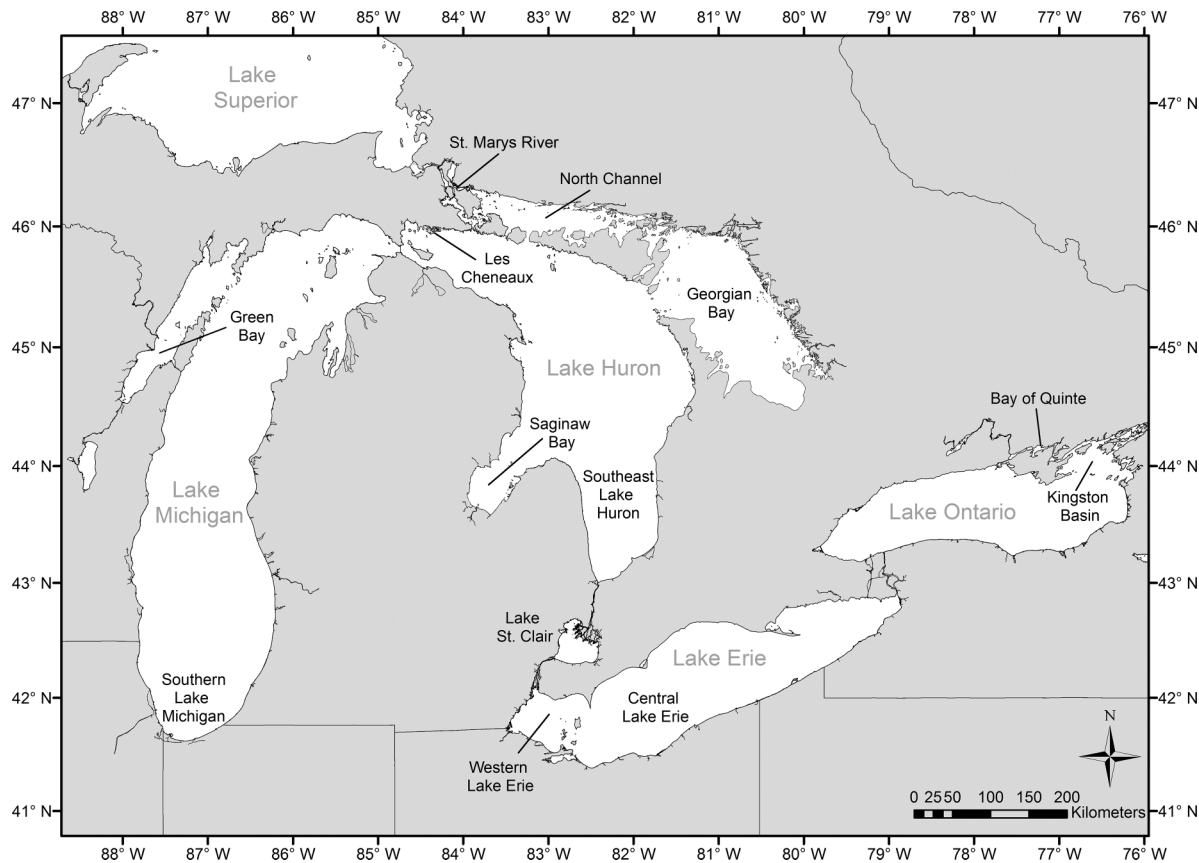


Table 1. Data-contributing agency, gear type, sample months, sample years, cohorts, and sample size (N) for yellow perch maturation data included in this study.

Stock	Agency	Gear	Months	Years	Cohorts	Female N	Male N
Green Bay	WI DNR	Fyke net	April	2003–2011	2000–2010	2 340	—
Southern Michigan	BSU	Trawl	June–Aug.	2001–2007	2000–2006	1 382	791
Les Cheneaux	MI DNR	Gill net	Oct.	2001–2009	2001–2008	1 246	1 058
St. Marys River	MI DNR	Gill net	Aug.	2002, 2006	2000–2006	917	708
North Channel	OMNRF	Gill net	July–Aug.	2001–2009	2000–2008	1 398	613
Georgian Bay	OMNRF	Gill net	July–Nov.	2003–2009	2001–2008	256	86
Southeast Huron	OMNRF	Gill net	June–Oct.	2001–2009	2000–2008	1 578	2 619
Saginaw Bay	MI DNR	Trawl	Sept.	2001–2005	2000–2005	297	375
Lake St. Clair	MI DNR	Trawl	May–Sept.	2002–2009	2000–2008	764	614
Western Erie	OH DNR	Trawl	Sept.–Oct.	2001–2011	2000–2010	1 670	2 274
Central Erie	OH DNR	Trawl	July–Oct.	2001–2009	2000–2008	10 088	10 450
Eastern Ontario	OMNRF	Gill net	June–July	2001–2011	2000–2009	866	247
Bay of Quinte	OMNRF	Gill net	July–Aug.	2002–2011	2000–2009	644	259

Note: See Fig. 1 for geographic locations of stocks. Agencies include Wisconsin Department of Natural Resources (WI DNR), Ball State University (BSU), Michigan Department of Natural Resources (MI DNR), Ontario Ministry of Natural Resources and Forestry (OMNRF), and Ohio Department of Natural Resources (OH DNR).

of biases. Furthermore, because they account for the influences of changing growth rates on maturation (Barot et al. 2004a; Wang et al. 2009), PMRNs have been used as an indicator of adaptive variation in maturation schedules across a range of fish stocks (Barot et al. 2004b; Sharpe and Hendry 2009; Wright et al. 2011; Devine et al. 2012). Conventionally, PMRNs are described in terms of their midpoints (the $L_{p_{50,a}}$, defined as the age-specific length at which a random individual from the stock has a 50% probability of becoming mature; Barot et al. 2004b). This metric of PMRN estimation assumes that there is no skipped spawning, that there is unbiased sampling of immature and mature fish, that sex and maturity status are assessed accurately, and that immature and mature individuals within an age class do not differ in growth

and mortality rates; however, sensitivity analyses have shown PMRN estimates to be robust to violations of these assumptions (Barot et al. 2004a). Because PMRN analyses require large sample sizes (>100 of both immature and mature individuals per age class; Barot et al. 2004a), all data for cohorts after 2000 were aggregated for analysis of maturation schedules for each stock, thus providing a relatively current perspective on the status of life history traits across these stocks and allowing for the inclusion and comparison of a maximum number of different stocks from 2000 to 2011 (Table 1). This data aggregation approach assumed that temporal changes in life history traits were relatively small compared with interpopulation differences. An earlier examination of decadal changes in

maturation found that population identity accounted for 70% to 80% of the variation in A_{50} (Feiner et al. 2015), and a preliminary analysis of data used in this project revealed that more than 65% of the variation in $L_{p_{50,a}}$ estimates was explained by population identity, while temporal variation accounted for less than 5%. Therefore, interpopulation variation in life history traits appears to be much larger than temporal variation, and our analytical approach should still be able to detect broad-scale interpopulation variation in these traits, as temporal variation may be comparatively minor within the time period studied.

Age and length at 50% maturity were determined via sex- and stock-specific logistic regressions using maturity status (0 = immature, 1 = mature) as the dependent variable and age or length as the independent variable. The respective A_{50} or L_{50} was calculated as the negative intercept divided by the slope of the regression. The PMRN, described as the probability of first maturing at age a and size s , is determined through the calculations of the probability of being mature at the current age and size ($o(a, s)$, the maturation ogive) and the probability of being mature at the age and size in the previous time step, $o(a - 1, s - \Delta s)$, where Δs is the increase in size from age $a - 1$ to age a (Barot et al. 2004b):

$$m(a, s) = \frac{o(a, s) - o(a - 1, s - \Delta s)}{1 - o(a - 1, s - \Delta s)}$$

Stock- and age-specific Bayesian logistic regression was used to model the maturation ogives, and a stock-specific von Bertalanffy model was used to estimate growth increments (Supplementary Tables S1 and S2¹). Both models were run for a 5000 iteration burn-in period followed by an additional 5000 iterations, storing every fifth sample. The probability of becoming mature at age a and size s ($m(a, s)$) was then calculated from 1000 posterior estimates of $o(a, s)$ and $o(a - 1, s - \Delta s)$ (Wright et al. 2011; Feiner et al. 2015). We used Spearman correlations on each set of posterior draws for each maturation metric to evaluate whether metrics of maturation were correlated (e.g., A_{50} and L_{50}) and whether male and female metrics were correlated among stocks.

Sex- and stock-specific A_{50} , L_{50} , and $L_{p_{50,a}}$ for this time period were determined using Bayesian methods in JAGS with R version 3.1.2 through the package “rjags” (Plummer 2003, 2013; McCarthy 2007; Kruschke 2010; R Core Team 2014). Bayesian inference provided a straightforward way to evaluate differences in parameter values within and among stocks through the sampling of posterior distributions using Markov chain Monte Carlo sampling methods and estimation of 95% credible intervals (CIs) based upon posterior distributions (McCarthy 2007; Kruschke 2010; Wright et al. 2011). Bayesian P values were also computed as the proportion of the posterior distribution that did not overlap zero (i.e., the probability that a random draw from the posterior of an estimated parameter with a positive or negative mean would also be respectively positive or negative).

Relating variation in maturation to growth and mortality

To address the question of how A_{50} , L_{50} , and $L_{p_{50,a}}$ are structured by among-population variation in growth, we also used Bayesian methods to estimate the sex- and stock-specific mean length of age-2 fish to quantify uncertainty and generate posterior distributions for further analyses (see below). Yellow perch growth rates in early life are strongly influenced by biotic and abiotic factors (Hokanson 1977; Kitchell et al. 1977; Graeb et al. 2004; Headley and Lauer 2008), potentially making length at age 2 a multivariate indicator of environmental growth conditions among stocks. One thousand samples from the posterior of each metric were kept to evaluate differences in growth over time as well as

relationships between growth and maturation within and among stocks.

Sex-specific annual instantaneous total mortality rates (Z) were estimated within a similar Bayesian framework. Instantaneous total mortality was determined for each sex and stock via age-based catch curve analysis (Quinn and Deriso 1999). After initial visualization, all catches from 2000 and later were pooled for analysis and all ages 1 year past the peak catch at age were included for each stock to limit data to those ages fully recruited to the gear. Total mortality was then estimated using a weighted linear regression with age as the independent variable and $\ln(\text{proportion of total catch})$ as the dependent variable, where each data point was weighted by the natural log of the total catch of that age class. The negative slope of this relationship represents the estimate of Z . Each catch curve model was initialized and thinned similarly to the maturation models, resulting in 1000 posterior estimates of Z for each sex and stock (Supplementary Tables S1 and S2¹). We examined potential trade-offs between growth and mortality by correlating sex-specific length at age 2 and Z among stocks on each posterior draw. We also used Spearman correlations to determine whether growth or mortality were correlated between sexes.

To evaluate relationships between growth and mortality rates and variation in maturation schedules, we linearly regressed 1000 posterior estimates of A_{50} , L_{50} , and $L_{p_{50,a}}$ at ages 3 and 4 ($L_{p_{50,3}}$ and $L_{p_{50,4}}$, the two ages with the most precise estimates across the most stocks) against 1000 posterior estimates of length at age 2 and Z , resulting in 1000 estimates for the slope and intercept of each relationship. Performing regressions across the posteriors of both maturation and mortality or length at age 2 estimates allowed us to incorporate uncertainty in the estimation of both metrics into the regression analysis to produce a more conservative estimate of the relationship strength than simply assuming the predictor variables (length at age 2 and Z) were measured without error. Use of this method produced 1000 posterior estimates for the intercept and slope of the relationship between a respective maturation index and either mortality or length at age 2. Nonzero slopes and intercepts were identified via estimation of 95% CIs and calculation of Bayesian P values.

Results

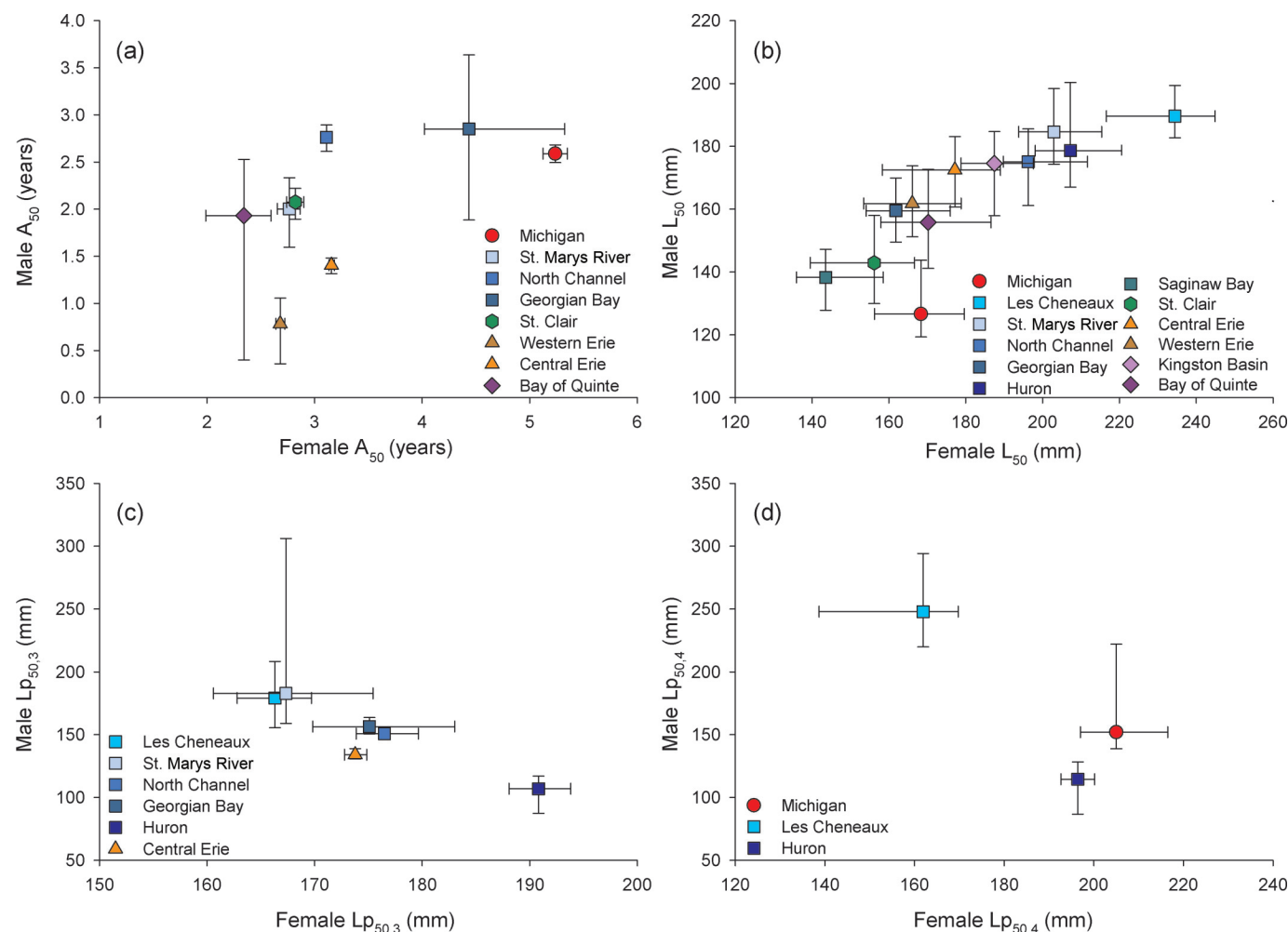
Variation in maturation schedules

Female A_{50} varied substantially among stocks, with estimates ranging from 5.2 years in southern Lake Michigan to as young as 1.9 years in Green Bay (Supplementary Table S1¹; Fig. 2). Southern Lake Michigan and Georgian Bay females reached 50% maturity older than all other stocks, whereas Green Bay females reached 50% maturity younger than all other stocks. Within this range, most stocks reached 50% maturity at either about 3 years (central and western Erie, Lake St. Clair, St. Marys River, and North Channel ranged from 2.7 to 3.2 years) or 2 years (Bay of Quinte, Kingston Basin, Saginaw Bay, and Les Cheneaux ranged from 2.0 to 2.3 years). Males reached 50% maturity at younger ages than females across all stocks (Supplementary Table S2¹; Fig. 2). Male stocks could be sectioned into stocks that reached 50% maturity at 2.5 to 3 years of age (Georgian Bay, North Channel, and southern Lake Michigan; 2.6 to 3.0 years) and about 2 years of age (Lake St. Clair, St. Marys River, and Bay of Quinte; 1.8 to 2.1 years). Males in the basins of Lake Erie reached 50% maturity at the youngest ages (central Erie, 1.4; western Erie, 0.8).

Estimates of female L_{50} also varied among stocks, ranging from 233 mm in Lake Michigan to 144 mm in Saginaw Bay, with most stocks reaching 50% maturity from 160 to 200 mm. There was less spatial variation in male L_{50} , with estimates ranging from 190 mm

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0173>.

Fig. 2. Biplots showing correlations between female (x axes) and male (y axes) estimates of age at 50% maturity, A_{50} (a); length at 50% maturity, L_{50} (b); probabilistic maturation reaction norm (PMRN) midpoint at age 3, $Lp_{50,3}$ (c); and PMRN midpoint at age 4, $Lp_{50,4}$ (d). Different colors and symbols represent different stocks, and error bars are 95% credible intervals for each estimate. [Color online.]



in Les Cheneaux to 128 mm in southern Lake Michigan. Similar to females, most males reached 50% maturity between 160 and 200 mm, although within stocks, males consistently reached 50% maturity at smaller sizes than females (Supplementary Tables S1 and S2¹; Fig. 2).

Probabilistic maturation reaction norms could be reliably estimated for at least one age class of females in 11 of the 13 stocks (PMRNs for Bay of Quinte and Kingston Basin could not be estimated owing to insufficient sample sizes). On average, stocks in southern Lake Michigan, southeastern Lake Huron, and Georgian Bay matured at larger sizes at a given age than the other stocks, while those in North Channel, Les Cheneaux, and the central and western basins of Lake Erie were intermediate and fish in Green Bay matured at much smaller sizes for a given age than any other stock (Fig. 3a). Estimates were limited to age-3 fish for western Lake Erie, Green Bay, and Saginaw Bay because there were few immature fish in older age classes. The slopes of PMRNs in females were generally flat (estimates did not differ among ages within a stock), with the exception of a slight negative slope in southern Lake Michigan.

Because early maturation of males in many stocks led to few immature males in many age classes, PMRNs were reliably estimated in only 8 of 13 stocks for males, and even these estimates tended to be fairly uncertain (i.e., large CIs around each estimate). Thus, there were few probable differences among stocks in male PMRNs (Fig. 3b). Males in Les Cheneaux, St. Marys River, Georgian

Bay, and North Channel all tended to mature at larger sizes at a given age than those in Bay of Quinte, central Erie, southern Lake Michigan, or southeastern Lake Huron. Where multiple ages were estimated, PMRN slopes again tended to be flat, with the exception of a positive slope in Lake Michigan males.

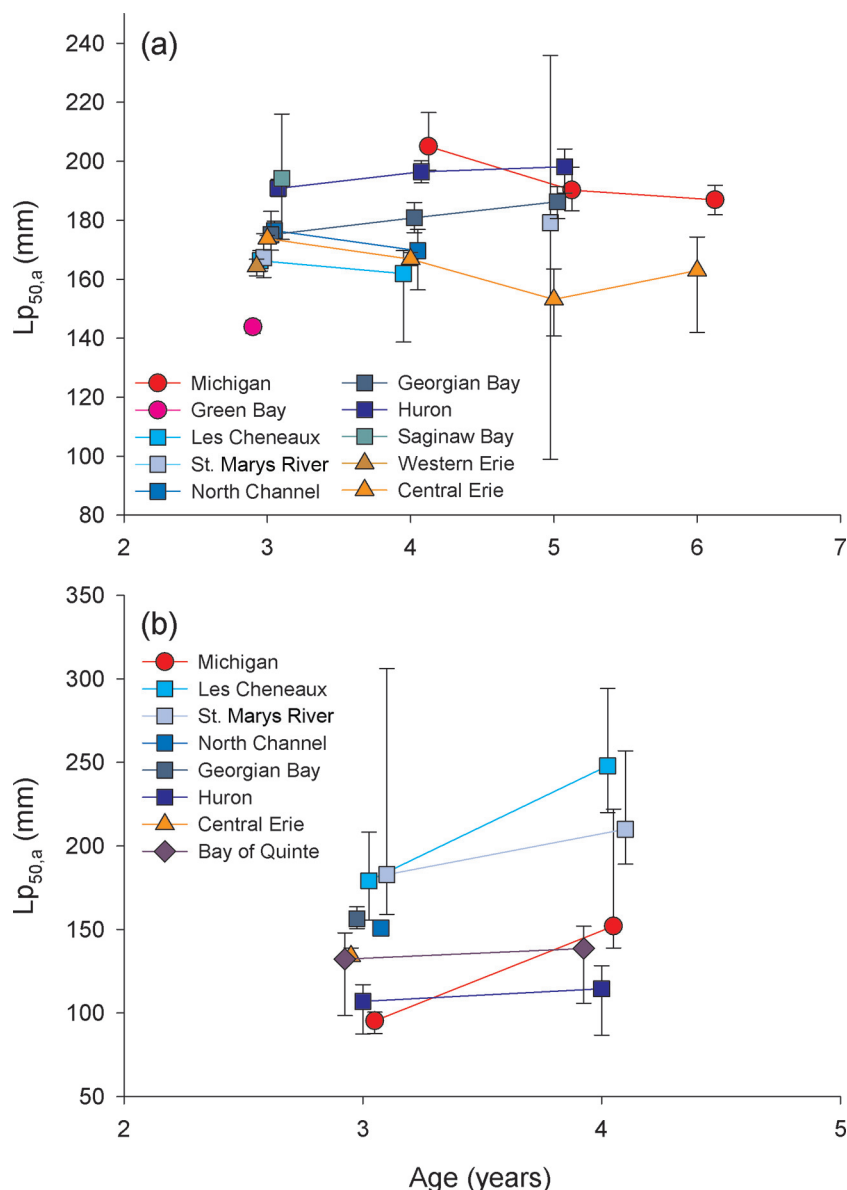
Correlations between estimates of A_{50} and L_{50} were low for both females (mean $r = -0.18$, 95% CI: $-0.34, 0.07$) and males (mean $r = -0.18$, 95% CI: $-0.46, 0.16$), meaning stocks that matured at older ages did not necessarily also mature at larger sizes. However, there were strong correlations between male and female estimates of A_{50} (mean $r = 0.56$, 95% CI: $0.33, 0.71$) and L_{50} (mean $r = 0.69$, 95% CI: $-0.03, 0.88$), meaning stocks that matured older or larger tended to do so in both sexes (Figs. 2a, 2b).

Counter to correlations between A_{50} and L_{50} within sexes, there were strong negative correlations between male and female estimates of $Lp_{50,3}$ (mean $r = -0.84$, 95% CI: $-0.96, -0.31$) and the same trend was present for estimates of $Lp_{50,4}$ ($r = -0.84$, 95% CI: $-0.98, -0.47$), although only three stocks had reliable estimates of $Lp_{50,4}$ in both sexes. These results indicate that stocks with females that matured at large sizes at a given age tended to also have males that matured at small sizes in those age classes (Figs. 2c, 2d).

Correlations between growth and mortality

Estimates of mean length at age 2 ($r = 0.95$, 95% CI: $0.84, 0.99$) and total mortality ($r = 0.58$, 95% CI: $0.15, 0.90$) were strongly positively correlated between sexes among stocks, indicating that

Fig. 3. Sex-specific probabilistic maturation reaction norms (PMRNs) for (a) female and (b) male yellow perch among Laurentian Great Lakes stocks (different colors and symbols; Lake Michigan stocks in red shades, Lake Huron stocks in blue shades, Lake Erie stocks in orange shades, and Lake Ontario stocks in purple shades) for all cohorts born after 2000. Error bars represent 95% credible intervals for each estimate, and stocks are offset along the x axis by 0.025 year for improved clarity. [Color online.]



there are consistent among-stock patterns in growth and mortality in both sexes. On average, positive correlations within sexes were also observed between Z and length at age 2 ($r = 0.21$, 95% CI: $-0.11, 0.48$ in females and $r = 0.35$, 95% CI: $-0.03, 0.65$ in males), but 95% CIs overlapped zero in both cases, suggesting only a weak trade-off between mortality and growth rate, which was slightly stronger in females than in males.

Relationship of maturation to growth and mortality

Female A_{50} was negatively related to both mean length at age 2 and total mortality across stocks. However, many of those relationships were strongly driven by the very small size at age 2, low mortality, and late maturity of the Lake Michigan and Georgian Bay stocks; after removing these stocks, only negative relationships between A_{50} and length at age 2 remained (Table 2; Figs. 4a, 4c). Male A_{50} was also negatively related to mean length at age 2, but

not Z . The relationship between A_{50} and length at age 2 was strongly influenced by very small size at age 2 of the Lake Michigan and Lake St. Clair stocks and weakened with the removal of these data points (Table 3; Figs. 4b, 4d). In contrast with A_{50} , estimates of L_{50} were positively related to length at age 2 in males and females, both including and excluding the presence of highly influential stocks in Lake Michigan and Lake St. Clair (Table 2; Figs. 5a, 5b). Male L_{50} also positively related to Z but this relationship was not present in females (Fig. 5).

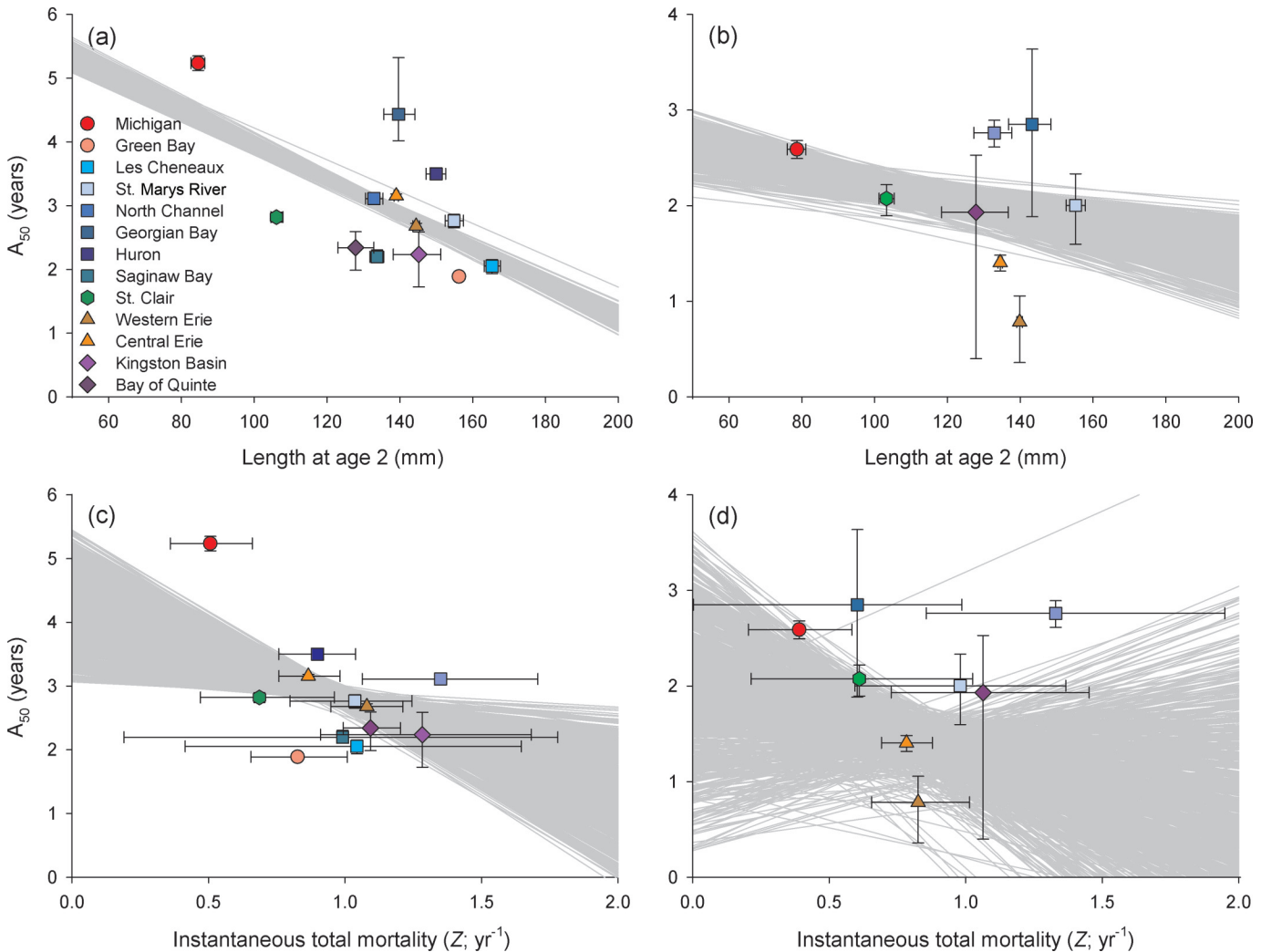
Estimates of $Lp_{50,3}$ and $Lp_{50,4}$ were strongly negatively related to mean length at age 2 in females, although this relationship weakened for $Lp_{50,4}$ upon removal of the influential Lake Michigan stock (Table 2; Figs. 6a, 6c). Female $Lp_{50,3}$ was not related to Z , while female $Lp_{50,4}$ estimates exhibited a strong negative relationship to total mortality both including and excluding the Lake Michigan stock (Figs. 7a, 7c). In strong contrast with estimates for

Table 2. Estimates of the intercept and slope for regressions among maturation metrics, mean length at age 2 (Length, mm), and instantaneous total mortality (Z , year⁻¹) for female Great Lakes yellow perch, both including all data points and excluding noted highly influential stocks.

Relationship	Including all data		Without influential stocks		Stocks removed
	Intercept	Slope	Intercept	Slope	
$A_{50} \sim \text{Length}$	6.70 (6.36, 7.05)	-0.03 (-0.03, -0.02)	3.77 (3.34, 4.16)	-0.008 (-0.011, -0.005)	Michigan, Georgian Bay
$L_{50} \sim \text{Length}$	91.30 (33.55, 143.87)	0.65 (0.23, 1.15)	-34.57 (-179.28, 138.89)	1.52 (0.27, 2.50)	Michigan, St. Clair
$Lp_{50,3} \sim \text{Length}$	278.23 (229.51, 327.59)	-0.72 (-1.05, -0.41)	—	—	
$Lp_{50,4} \sim \text{Length}$	238.66 (219.78, 269.33)	-0.43 (-0.67, -0.30)	193.27 (136.58, 293.28)	-0.13 (-0.83, 0.26)	Michigan
$A_{50} \sim Z$	4.38 (3.06, 5.45)	-1.60 (-2.66, -0.23)	2.73 (2.00, 3.58)	-0.12 (-0.92, 0.65)	Michigan, Georgian Bay
$L_{50} \sim Z$	155.41 (111.63, 206.86)	27.96 (-25.82, 74.41)	—	—	
$Lp_{50,3} \sim Z$	162.73 (123.54, 207.15)	8.95 (-33.65, 50.05)	—	—	
$Lp_{50,4} \sim Z$	218.62 (185.22, 249.62)	-41.20 (-76.64, -6.22)	194.88 (149.75, 242.91)	-19.85 (-72.97, 23.82)	Michigan

Note: Maturation metrics are as follows: age (years) at 50% maturity, A_{50} ; length (mm) at 50% maturity, L_{50} ; and probabilistic maturation reaction norm midpoint estimates (mm) at age 3, $Lp_{50,3}$, and age 4, $Lp_{50,4}$. The median and limits of the 95% credible interval for each estimate are provided. Relationships where 95% of posterior draws for the slope were different from zero (i.e., $P(\text{slope} > 0)$ for positive slopes and $P(\text{slope} < 0)$ for negative slopes ≥ 0.95) are shown in bold.

Fig. 4. Relationships between A_{50} and estimates of juvenile growth (mean length at age 2; top two panels) or instantaneous total mortality (Z ; bottom two panels) for female (a, c) and male (b, d) yellow perch across Laurentian Great Lakes stocks. Different stocks are indicated by different colors and symbols (see legend in panel a) and error bars are 95% credible intervals for each estimate. Each gray line represents a single regression of a single posterior draw of the respective A_{50} and growth or mortality estimate. All regressions that fell within the 95% credible interval of the slope are shown in each plot. [Color online.]



females, male $Lp_{50,3}$ and $Lp_{50,4}$ were positively related to length at age 2, and these relationships persisted when influential Lake Michigan data were excluded (Figs. 6b, 6d). In addition, there were no relationships between male $Lp_{50,3}$ and $Lp_{50,4}$ estimates and mortality (Table 3; Figs. 7b, 7d).

Discussion

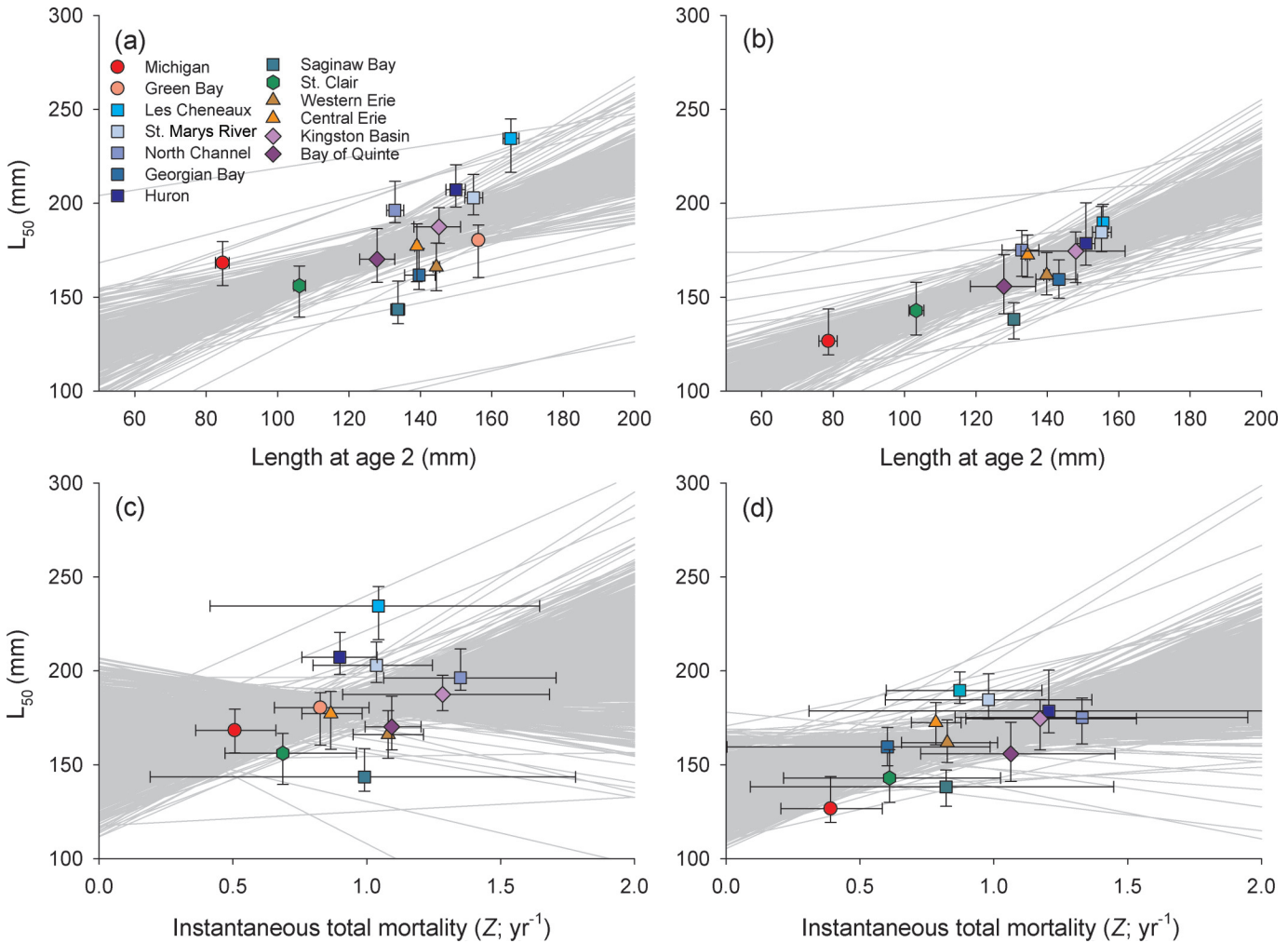
Trade-offs among growth, mortality, and reproduction form the basis of life history theory (Stearns 1989; Roff 1992). We observed some classically expected trade-offs (e.g., between age at maturation and growth rates) but also substantial differentiation in the

Table 3. Estimates of the intercept and slope for regressions among maturation metrics, mean length at age 2 (Length, mm), and instantaneous total mortality (Z , year⁻¹) for male Great Lakes yellow perch, both including all data points and excluding noted highly influential stocks.

Relationship	Including all data		Without influential stocks		
	Intercept	Slope	Intercept	Slope	Stocks removed
$A_{50} \sim \text{Length}$	3.01 (2.48, 3.54)	-0.01 (-0.01, 0.00)	1.42 (-3.90, 4.93)	0.00 (-0.02, 0.04)	Michigan, St. Clair
$L_{50} \sim \text{Length}$	65.20 (9.88, 171.02)	0.74 (0.02, 1.17)	19.70 (-197.12, 152.05)	1.05 (0.19, 2.60)	Michigan, St. Clair
$Lp_{50,3} \sim \text{Length}$	23.16 (-51.13, 62.86)	0.88 (0.53, 1.56)	-5.23 (-336.12, 215.39)	1.08 (-0.55, 3.54)	Michigan, St. Clair
$Lp_{50,4} \sim \text{Length}$	86.78 (23.03, 230.83)	0.63 (-0.29, 1.19)	-221.46 (-663.53, -7.22)	2.71 (1.29, 5.71)	Michigan, St. Clair
$A_{50} \sim Z$	2.14 (1.50, 2.97)	-0.12 (-1.26, 0.55)	—	—	
$L_{50} \sim Z$	135.82 (105.40, 177.97)	31.32 (-11.67, 63.58)	—	—	
$Lp_{50,3} \sim Z$	127.18 (83.56, 169.16)	16.94 (-25.17, 72.03)	—	—	
$Lp_{50,4} \sim Z$	197.63 (90.93, 293.95)	-27.19 (-116.09, 106.23)	—	—	

Note: Maturation metrics are as follows: age (years) at 50% maturity, A_{50} ; length (mm) at 50% maturity, L_{50} ; and probabilistic maturation reaction norm midpoint estimates (mm) at age 3, $Lp_{50,3}$, and age 4, $Lp_{50,4}$. The median and limits of the 95% credible interval for each estimate are provided. Relationships where 95% of posterior draws for the slope were different from zero (i.e., $P(\text{slope} > 0)$ for positive slopes and $P(\text{slope} < 0)$ for negative slopes ≥ 0.95) are shown in bold.

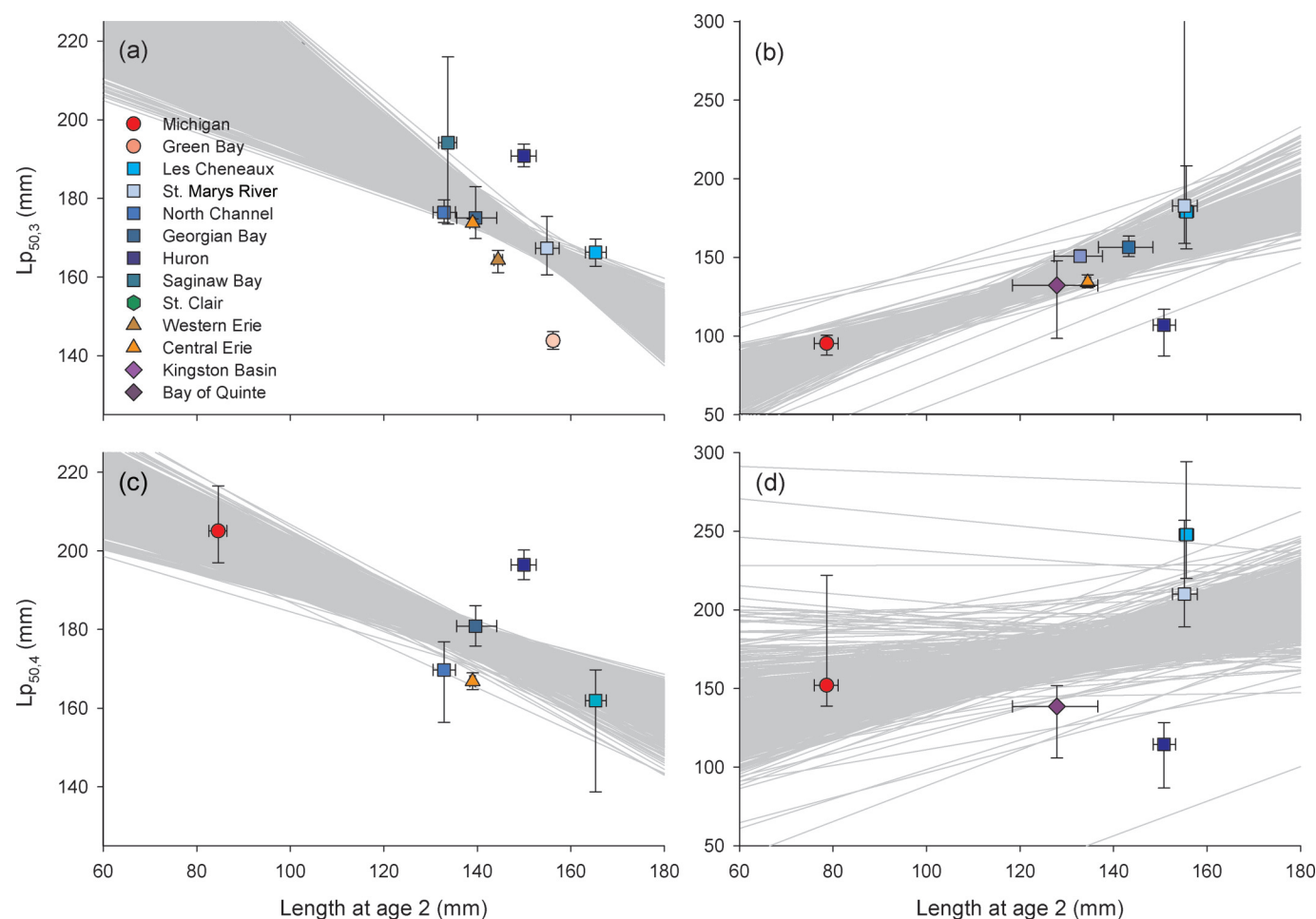
Fig. 5. Relationships between L_{50} and estimates of juvenile growth (mean length at age 2; top two panels) or instantaneous total mortality (Z ; bottom two panels) for female (a, c) and male (b, d) yellow perch across Laurentian Great Lakes stocks. Different stocks are indicated by different colors and symbols (see legend in panel a) and error bars are 95% credible intervals for each estimate. Each gray line represents a single regression of a single posterior draw of the respective L_{50} and growth or mortality estimate. All regressions that fell within the 95% credible interval of the slope are shown in each plot. [Color online.]



strength and even direction of some of these relationships between sexes in an iteroparous fish. Moreover, the trade-offs between maturation and mortality exhibited age-dependent dynamics in females. Accounting for these sex- and age-dependent trade-offs among vital rates could improve our understanding of the mechanisms driving life history trait variation in fishes and improve predictions of future

life history trait shifts in response to ecological or anthropogenic stress. Growth and mortality rates play a vital role in the evolution of maturation schedules (Shuter et al. 2005; Marty et al. 2011). However, the relative strengths and directions of trade-offs between these rates may vary among stocks with changes in, for example,

Fig. 6. Relationships between juvenile growth (mean length at age 2) and estimates of $L_{p_{50,3}}$ (a, b) and $L_{p_{50,4}}$ (c, d) in female (a, c) and male (b, d) yellow perch across Laurentian Great Lakes stocks. Different stocks are indicated by different colors and symbols (see legend in panel a) and error bars are 95% credible intervals for each estimate. Each gray line represents a single regression of a single posterior draw of the respective $L_{p_{50,a}}$ and growth estimates. All regressions that fell within the 95% credible interval of the slope are shown in each plot. [Color online.]



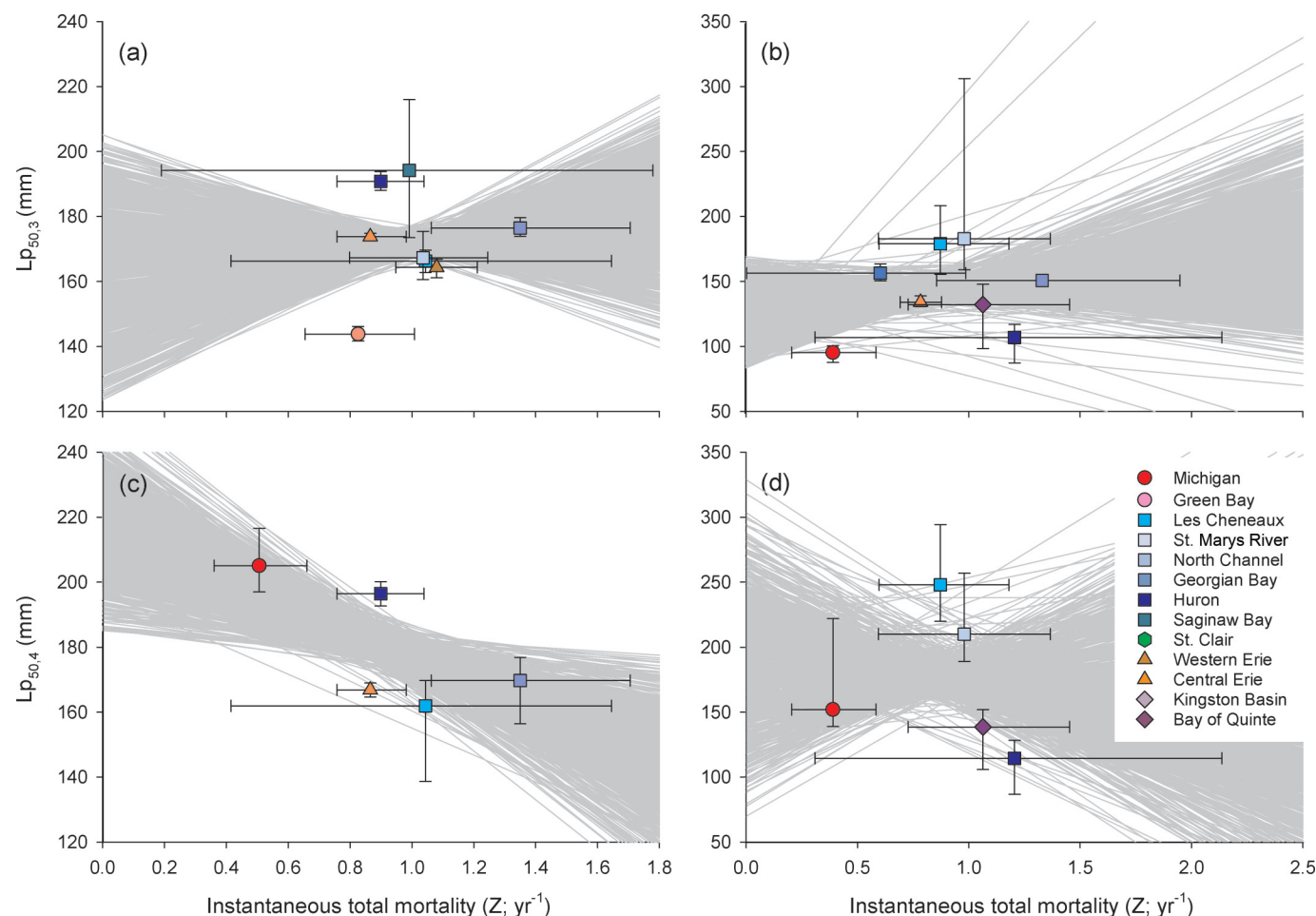
predation risk and resource availability (Jørgensen and Holt 2013). Growth and mortality were weakly positively correlated among stocks, offering some support for the “live fast, die young” life history observed in many species. The weakness of these correlations may stem from shifts in the relationship between mortality and growth throughout ontogeny. Mortality during early life in fish is often negatively related with size or growth, owing to strong size-specific mortality caused by predation or starvation (Anderson 1988; Roswell et al. 2014). In contrast, adult mortality is often positively related to growth rate owing to increased metabolic costs and differences in energy allocation and is often lower in adults than juveniles (Post and Lee 1996; Shuter et al. 2005). Size-selective harvest, which occurs to some extent in all of the yellow perch stocks considered, may also mediate the relationship between growth and survival in adults (Edeline et al. 2007). Such age- or stage-specific changes in this trade-off have been difficult to elucidate in the wild (Anderson 1988) but may serve as an important source of selection for the evolution of life histories (Sharpe and Hendry 2009; Marty et al. 2011; Jørgensen and Holt 2013).

We observed negative relationships between A_{50} and growth and mortality in females and between A_{50} and growth in males across stocks, consistent with life history theory (Roff et al. 2006). In fish, large body size increases the reproductive potential of individuals through increases in fecundity, egg size, and, poten-

tially, offspring survival (Heyer et al. 2001; Lauer et al. 2005). Thus, stocks that grow faster can mature earlier in life while mitigating potential costs to reproductive output. Moreover, high mortality rates reduce the chance that late-maturing individuals will survive to reproduce, therefore increasing the fitness of early-maturing individuals (Stearns 1989; Roff et al. 2006). High growth rates in early life may also reflect improved foraging conditions and body condition, which may increase surplus energy reserves and promote maturation of younger and smaller individuals (Henderson and Morgan 2002). These relationships fit the hypothesis that shifts in age at maturation caused by changing growth and mortality regimes will generally oppose the direction of the growth–mortality correlation (Marty et al. 2011), and they suggest that a combination of plastic and adaptive responses to variation in growth rates drive spatial variation in yellow perch maturation schedules.

Similar to the patterns observed in A_{50} , female $L_{p_{50,a}}$ estimates were strongly negatively related to length at age 2. However, a link between PMRNs and mortality was observed only for age-4 fish and not for age-3 individuals. This may represent an age-dependent trade-off reflecting the shifting costs of growth and mortality to reproductive output. At younger ages, only the largest individuals with sufficient surplus energy are likely to mature, as reallocation of energy to reproduction will hinder future growth and thus reproductive potential (Henderson and Morgan

Fig. 7. Relationships between estimates of $L_{P_{50,3}}$ (a, b) and $L_{P_{50,4}}$ (c, d) and instantaneous total mortality (Z) for female (a, c) and male (b, d) yellow perch across Laurentian Great Lakes stocks. Different stocks are indicated by different colors and symbols (see legend in panel d) and error bars are 95% credible intervals for each estimate. Each gray line represents a single regression of a single posterior draw of the respective $L_{P_{50,a}}$ and Z . All regressions that fell within the 95% credible interval of the slope are shown in each plot. [Color online.]



2002; Jonsson et al. 2013; Folkvord et al. 2014). As individuals age, the cost of delaying maturation becomes too great as the chance of mortality or senescence increases, and therefore adult mortality rates may have stronger influences on the maturation of old individuals (Tatar and Carey 1995). This shifting trade-off also explains why many expected and empirically observed two-dimensional (age and length) PMRNs have negative slopes — fish must be very large and in good condition to spawn early in life, but later in life individuals may mature regardless of individual body condition or size (Heino and Dieckmann 2008; Marty et al. 2011).

Size at maturation in fish has often presented a more complicated picture of life history adaptation than age at maturation. With variation in growth, some species correspondingly vary in size at maturation while others appear relatively invariant. Responses may depend on available food resources or predation pressure (Köster et al. 2001; Jørgensen and Holt 2013), as size at maturation can be controlled both through the timing of maturation (e.g., maturing earlier or later in life) and through individual growth rates. In yellow perch, both sexes exhibited positive relationships between growth and L_{50} across stocks. Thus, increased growth rates may allow individuals to compensate for maturing at younger ages, following the patterns of maturation at early life and large sizes observed with high growth and production in Atlantic cod (*Gadus morhua*; Köster et al. 2001). Length at maturity also exhibited relatively less variation among stocks than did age at maturity — most stocks matured within a 40 mm window

(160 to 200 mm TL) while age at maturity varied by almost 4.5 years in females. This, in addition to the generally flat to slightly negative PMRN slopes among stocks, could suggest that shifts toward earlier maturation are driven by faster growth (e.g., the observed negative relationship between A_{50} and length at age 2 in both sexes) while length at maturation is relatively constant owing to physiological constraints on the minimum size for successful reproduction, meaning the growth and mortality costs of early maturation are compensated for with increased body size (Marty et al. 2011; Kuparinen and Hutchings 2012).

Sex-based differences in life history traits are a common phenomenon in fish and other taxa and may represent differing trade-offs among growth, mortality, and reproduction. We observed strong differences in both male and female maturation schedules within stocks (males matured smaller and younger than females), among stocks (strong negative correlations between $L_{P_{50,a}}$ estimates of each sex), and with variation in growth and mortality rates (negative relationships in females, positive in males). This striking lack of concordance between sexes suggests that male and female maturation schedules are responding differentially to local environmental conditions that may be driving growth and mortality rates. This is in contrast with the conclusions of van Walraven et al. (2010), who suggested male and female responses to fishing and ecological change would be consistent in European plaice (*Pleuronectes platessa*), and those of Devine et al. (2012), who found similar changes in male and female

maturation schedules with changes in fishing pressure across several marine stocks. Male yellow perch may experience reduced costs of reproduction on future mortality and growth, as they invest less energy toward development in gonads than females (Henderson et al. 2000) and thus mature near a minimum age or size physiologically possible (i.e., age 1 to 2), much younger than most larger-bodied marine species (Devine et al. 2012). Increases in growth, then, increase size at maturation without coincident decreases in age at maturation. As growth and mortality were more strongly positively correlated in male yellow perch, this may also have driven the positive relationship between mortality and length at maturity observed in males but not in females. In contrast, females likely experience heavier costs of reproduction to future growth and mortality, which would select for delayed maturation (Kuparinen et al. 2012). Increased mortality rates have also been shown to increase reproductive investment in fish — such a reallocation of energy to reproduction likely reduces growth rates and may reduce age-specific size at maturation in females but not males (Heino and Kaitala 1999; Folkvord et al. 2014; Merrill and Collins 2015). Thus, sex-specific trade-offs in the costs of growth and reproduction may lead to strong differences in the responses of males and females to changes in ecological conditions or mortality rates.

Different maturation indices revealed opposing patterns in yellow perch maturation. A_{50} and L_{50} were positively correlated between sexes, while $L_{p50,3}$ and $L_{p50,4}$ were negatively correlated between sexes. Age and length at 50% maturation are highly sensitive to changes in growth rates and analytical methods, and as growth was positively correlated between sexes, it could be expected that A_{50} and L_{50} would covary similarly. In contrast, PMRNs largely account for differences in growth rates among populations (Barot et al. 2004a, 2004b). Accounting for growth allowed us to observe that stocks with larger-maturing females at a given age often contained smaller-maturing males, an important distinction illustrating potential adaptive differences in the trade-offs between size and reproductive success between sexes. In populations experiencing slow growth or limited resources, only the largest females in a given age class may be able to sufficiently provision offspring and successfully reproduce (Olin et al. 2012), while males, facing fewer energetic costs of reproduction (Henderson et al. 2000), simply mature at smaller sizes for a given age. Although we only measured phenotypic variation in maturation schedules, these results may suggest some genetic control of maturation timing between sexes. Unfortunately, the genetic bases of maturation in most fishes, including yellow perch, are relatively unknown. Recent research in Atlantic salmon (*Salmo salar*) and ninespine stickleback (*Pungitius pungitius*) has provided some evidence for sex-specific genes for maturation timing (Ghani et al. 2013; Debes et al. 2014). Future studies elucidating the genetic mechanisms controlling maturation in both sexes could lead to further insights into the basis of sexually dimorphic maturation and other life history traits. In sum, differences in the relationships between metrics indicate that managers should consider accounting for differences in the effects of growth rates on maturation between sexes. Female maturation, and therefore stock productivity (Kuparinen and Hutchings 2012), may be more sensitive to variation in growth rates, and changes in $L_{p50,4}$ may be a stronger indicator of current maturation patterns than highly plastic indices such as A_{50} and L_{50} .

An earlier study including some of the same yellow perch stocks found rapid changes in maturation rates in response to changes in fisheries harvest following a commercial moratorium in Lake Michigan (Feiner et al. 2015). However, those responses were largely sex-specific and limited to females, similar to findings across many exploited marine species (Devine et al. 2012). Our results may suggest a mechanism for these differences. Mortality was only associated with spatial variation of female maturation schedules, while male maturation schedules varied primarily with growth.

Most fisheries management seeks to shift harvest toward larger, older individuals through minimum size or slot limits (Gwinn et al. 2015). Likely, this type of size selection tends to affect larger population members, which are often female (Lauer et al. 2008), and may select against later-maturing phenotypes. These results support the contention that it is selection on females that drives previously observed divergence of maturation schedules, while males are unresponsive (Wang and Höök 2009; Ghani et al. 2013).

Temperature, body condition, and other variables all may significantly influence maturation schedules of other species and likely vary among our study stocks, which could influence observed relationships between vital rates (Kuparinen et al. 2008; Wright et al. 2011; Uusi-Heikkilä et al. 2011). For instance, many of the stocks that matured youngest and smallest, while exhibiting high mortality and large size at age, inhabit generally warmer, more productive regions of the Great Lakes, such as Green Bay, Saginaw Bay, Les Cheneaux, and eastern Lake Ontario. Additionally, stock exploitation history may have influenced the relationships between life history traits. Lake Michigan was a consistent outlier in many of the relationships, exhibiting very low mortality, small size at age 2, and maturation both later in life and at larger age-specific sizes. As mentioned, the Lake Michigan yellow perch stock was severely overfished in the late 20th century to the point of collapse, experiencing sex ratios skewed toward males, truncated length distributions, and reduced age-specific size at maturation (Lauer et al. 2008; Feiner et al. 2015). A closure of the commercial fishery and reduction in recreational fishing pressure in the late 1990s resulted in rapid increases in size structure, increased age and size at maturation, and an increased abundance of large females within the next decade (Lauer et al. 2008; Feiner et al. 2015). This is in sharp contrast with exploitation of yellow perch in, for example, Lake Erie, where a robust commercial and recreational fishery provides the majority of commercially harvested yellow perch from the Great Lakes (Kinnunen 2003) and represents a population with a relatively faster life history (higher mortality and growth, earlier and smaller maturation). Intensive size-selective harvest has often been related to reduced size and age at maturation and reduced growth in marine species, changes which may signal an imminent stock collapse (Trippel 1995; Post 2013; Neubauer et al. 2013). Generally, the fisheries from the study stocks have been closely regulated for multiple decades (Fielder 2008; Irwin et al. 2008; Yellow Perch Task Group 2014) and therefore may exhibit lessened effects of fishing exploitation. However, historical harvest has been sufficiently intense to collapse the stocks of several species in the Great Lakes during the early and mid-20th century (Smith 1968; Allan et al. 2005), and other stressors, such as changes in resource availability due to species invasions, have been shown to influence maturation schedules in other species (e.g., Wang et al. 2008). Thus, environmental and anthropogenic forces may have significant effects on life history traits and trade-offs among populations and these differences should be accounted for when examining variation in population dynamics of different fish stocks.

The approaches used to quantify trade-offs among growth, mortality, and maturation in this study required certain assumptions. First, measures of L_{50} and A_{50} may be biased owing to gear or other sampling effects (Wang et al. 2009), making comparisons among samples collected using different gears difficult. We attempted to account for this by removing highly influential data points from analyses to examine whether overall trends remained. Variation in life history traits did not appear to trend with gear — for example, southern Lake Michigan and Saginaw Bay samples were both collected using trawls but exhibited highly distinct patterns of maturation, growth, and mortality — suggesting that among-stock variance was stronger than any gear- or sampling-related biases. In addition, most of the relationships we observed between traits were in the theorized direction (e.g., positive correlations between mortality and growth, negative relationships between A_{50}

and growth), strengthening support for our general conclusions. Second, we made the assumption that these metrics of growth rate, mortality, and maturation did not trend within our study stocks over the years we examined, as previous analyses suggested interpopulation differences in traits were much greater than temporal variation within populations (Feiner et al. 2015). Changing maturation rates and growth and mortality rates within a population over time could confound our ability to detect relationships. Given this limitation, we believe that our findings are conservative in that if we can detect and quantify these relationships over the noise of within-stock variation, then we likely are detecting true differences and interactions.

In conclusion, we have elucidated several important trade-offs shaping the maturation schedules of Great Lakes yellow perch stocks inhabiting a range of environments. Variability in growth conditions was highly influential in shaping the maturation schedules of these stocks in both sexes, whereas mortality rates were more important in shaping maturation patterns in females than in males. Moreover, while females largely met expectations delineated by life history theory (negative relationships between maturation and growth and mortality), there were significant sexual differences not only in the timing of maturation but also in how male and female maturation schedules varied among stocks in response to these trade-offs. In sum, accounting for interstock and sexual variation in maturation schedules not only provided additional support for the importance of life history trade-offs in structuring the vital rates of stocks, but a complete elucidation of their respective mechanisms could significantly improve models seeking to predict how these stocks may respond to future environmental change.

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