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Rapid changes in age and size at maturity in Lake Erie yellow perch (*Perca flavescens*) are not explained by harvest

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Key words: Fisheries, Harvest-induced trait change, Laurentian Great Lakes, Life history, Phenotypic plasticity

Abstract: Harvest can change phenotypic traits of populations through immediate demographic consequences, evolutionary responses to harvest selection, or developmental responses by individuals. This study investigated the plastic phenotypic effects of harvest on size and age at maturity in a commercially exploited freshwater fish. We tested an individual growth and life history plasticity model using lagged correlations incorporating how harvesting of ages 2 and older fish influenced the abundance of juvenile fish, resource availability, individual growth rates, and carry-over responses in age and size at maturity. Our test used cohort data for Lake Erie yellow perch (*Perca flavescens*). Age and size at maturity fluctuated widely and rapidly across 23 cohorts between 1991 and 2013, suggesting phenotypic plasticity contributed strongly to maturation dynamics. The changes in maturity could not be explained by responses to harvest, as expected under the plasticity model. In Lake Erie, age and size at maturity in yellow perch appear to be responding to other drivers, such as harvest-induced dynamics of other fish stocks or ecosystem changes that are independent of harvest.

28 **Introduction**

29 The prominent trends in phenotypic traits observed in exploited populations suggest the
30 effects of harvest can extend beyond demographic changes in population size, age structure and
31 sex ratio (Jørgensen et al. 2007; Anderson et al. 2008; Sharpe and Hendry 2009). Non-
32 demographic phenotypic effects of harvest are concerning because any effects on age and length
33 at maturity can result in losses of biodiversity, reduced productivity and economic value (Eikeset
34 et al. 2013), and increased risk of population collapse (Hard et al. 2008; Kuparinen et al. 2011;
35 Pinsky and Palumbi 2014). Harvest can cause phenotypic change through three processes:
36 phenotypic selection within a generation resulting from gear selectivity, evolutionary responses
37 over multiple generations to phenotypic selection acting on heritable phenotypic variation, and
38 plastic growth rate responses and subsequent changes in maturation (Rochet 1998).
39 Distinguishing among these processes is important because evolutionary changes in phenotypes
40 may be more difficult to reverse than plastic changes when harvest is relaxed (Conover et al.
41 2009; Dunlop et al. 2009; Enberg et al. 2009). Unfortunately, the relative importance of these
42 processes in harvested natural populations remains uncertain because developmental plastic and
43 evolutionary changes are difficult to infer solely from phenotypic data (Heino et al. 2008; Nusslé
44 et al. 2009).

45 Changes in the growth rate of immature individuals can be a proximal cause of
46 maturation plasticity in many fishes (Alm 1959; Engelhard and Heino 2004; Enberg et al. 2012).
47 We assume that in the face of energy limits, maturation age and size trade off against immature
48 growth rate so that faster growing juveniles mature earlier and at smaller size than slower
49 growing juveniles. This juvenile trade-off links plastic responses in maturation to the influence
50 of resource availability through plastic growth responses. After maturation, individuals allocate

energy to reproduction at the expense of further somatic growth. This generates a trade-off between immature growth and lifetime growth for individuals of similar ages (Stearns 1992). The scope for smaller adult body size in fish is high because size at maturity is approximately two thirds of asymptotic size and earlier maturation at smaller size leads to smaller size at later ages when adult growth rate is reduced following maturation (Charnov and Berrigan 1990). Plasticity in maturation and adult size may be expressed in many fishes when immature growth rate responds to changes in resource availability.

Changes in individual growth rate and maturation may occur in a population when harvest changes per capita resource availability. Harvest that reduces population abundance sufficiently to increase the per capita resource availability can generate density-dependent compensatory responses in individual growth rates (Trippel 1995; Kuparinen and Merilä 2007). These responses are thought to be common in harvested fishes (Lorenzen and Enberg 2002; Engelhard and Heino 2004). Changes in growth of immature individuals are then expected to influence maturation schedules expressed as a change in duration of developmental periods (Dunlop et al. 2005). Such plastic changes in age and size at maturation are important when they influence stock productivity or yield (Law and Grey 1989; Eikeset et al. 2013) and the resilience of stocks to variation in harvest or other environmental conditions (Trippel 1995; Heino and Godø 2002).

Density-dependent population regulation can strongly affect life history dynamics in freshwater fish populations, including Great Lake stocks of yellow perch (Purchase et al. 2005a). For example, Feiner et al. (2015) observed changes in life history traits related to changes in level of harvest. Age and size at maturity increased in yellow perch stocks in Lake Huron and Lake Michigan after the level of harvesting was reduced, but remained unchanged or slightly

decreased in persistently harvested Lake Erie stocks (Feiner et al. 2015). However, the mechanisms behind these changes are unknown because mean age and size at maturity were averaged over a decade of cohorts and compared between decades. A finer temporal scale analysis is required to understand whether harvest can drive changes in maturation over shorter intervals in harvested fishes. This is especially true for species like yellow perch with a generation time of less than 5 years. Analyses of freshwater fish stocks are also of value because most analyses to date have been for marine stocks, and there is uncertainty about whether freshwater species responses are similar to what is observed in heavily exploited marine fisheries (Dunlop et al. 2015).

Yellow perch in Lake Erie, N. America (Fig. 1) provide an opportunity to study the extent to which harvest contributes to phenotypic changes in a freshwater fishery. Yellow perch are harvested commercially by gillnets and trap-nets and recreationally by hook and line, and these activities contribute considerable economic value to the Great Lakes region (Brenden et al. 2013). Yellow perch in Lake Erie have a generation time of three to four years and a long and variable history of commercial and recreational harvest (Baldwin et al. 2009). Furthermore, long term data are available from government agencies (Belore et al. 2016). Our assumption that plastic responses in maturation can be driven by variation in growth rate is reasonable because immature growth and maturation schedules vary within and among yellow perch cohorts (Purchase et al. 2005a; Feiner et al. 2015). The general level of harvesting (harvest intensity hereafter) has been high, but variable in Lake Erie. For example, one measure of fishing intensity (instantaneous fishing mortality; F) from all forms of fishing declined from 2.37 year^{-1} between 1975 – 1985 to 0.91 year^{-1} between 1985 – 1998, and then to 0.33 year^{-1} between 1998 – 2013 (Fig. 2). The annual allowable catch of yellow perch (4.180 million kg for 2017) is set by the

Lake Erie Commission (LEC) based on recommendations from the Lake Erie Standing Committee and the Yellow Perch Task Group (Brenden et al. 2013). LEC apportions the allowable catch to individual states and the province of Ontario based on proportions of lake area. The Ontario Ministry of Natural Resources and Forestry (OMRNF) manages the Canadian commercial fisheries through an individually transferable quota system begun in 1984 (Brenden et al. 2013).

We empirically evaluated a conceptual model where individual juvenile life history responds plastically to the consequences of annual variation in the harvest of adult spawners (Fig. 3). The model assumes an indirect effect of harvest on recruitment that subsequently affects juvenile survival, growth and maturity. The relationship between parental stock size and subsequent recruitment governs any effect of harvest on recruitment. We assume a Ricker stock-recruitment relationship for Lake Erie yellow perch because larger fish strongly cannibalize smaller perch (Knight et al. 1984). We further assume that, under current conditions, any change in recruitment will be positively correlated with, or independent of, any change in stock size, because stock size in the most heavily fished west basin of Lake Erie (MU1) has been low from 1999 - 2013 (Zhang et al. 2017).

The plasticity model we evaluate assumes that a large harvest of adults reduces total annual reproduction resulting in a reduced abundance of young of the year (YOY). We posit that reduced abundance of YOY reduces intraspecific competition and increases the availability of resources, and so increases individual growth rate. Rapidly growing individuals will then mature at an earlier age (Policansky 1993; de Roos et al. 2006) and smaller size (Grift et al. 2003; Dieckmann and Heino 2007; Thorpe 2007) several years after the direct effect of harvest on the abundance of parents (Fig. 3). Our model predicts an indirect, negative correlation between

annual harvest and annual estimates of age and length at 50% maturity lagged over a 2-3 year developmental period (Froese and Pauly 2016) following harvest. We also test a suite of predicted relationships that comprise the causal chain leading to the predicted correlation between harvest intensity and age and length at maturity to better understand the phenotypic effects of harvest on yellow perch, which are currently unknown. Table 1 summarizes predictions of the graphical model shown in Figure 3. Our analysis focuses on females because of their larger impact on population dynamics through fecundity and potential maternal effects relative to that of males.

Methods

For each yellow perch cohort from 1991-2013, our tests required estimates of age and length at maturity, annual intensity of harvest, abundances of young of the year (YOY, age 0+), juveniles (age 1), and ages 2 and older fish, and estimates of growth in the first and second year (Table 1). The Lake Erie yellow perch fishery consists of four main management units (MUs, Fig. 1): MU1 (western basin), MU2 (west-central basin), MU3 (east-central basin including data collected from sub-area Pennsylvania Ridge), and MU4 (eastern basin; data from subunit MU5 were sparse and were excluded). The estimates needed for our tests were calculated yearly for the entire lake and for each management unit. We extracted data for annual cohorts (corresponding to birth year) from the Lake Erie partnership index fishing survey database (a gillnet survey independent of the fishery) maintained by the Lake Erie Management Unit (Ontario Ministry of Natural Resources and Forestry 2016) and from the Yellow Perch Task Group Report (Belore et al. 2014).

Maturation is the process within an individual of allocating energy during development to germinal tissue with the endpoint being the production of ripe gametes. In fish, this process starts soon after fertilization when gonadal tissue appears in the early embryo. Age and length at maturation are a result of this process (Thorpe 2007). In this study, it was not possible to determine age or length at maturation for individuals. We instead used an individual's maturity status at the time of capture as an indicator of when they matured. Maturity at the time of capture includes fish that could have matured in a previous year at a smaller length and age. Consequently, estimates of age and length at maturity from capture samples are usually greater than the age and length at maturation. Age and length at maturity are commonly measured metrics in many fisheries studies, while age and length at maturation are much more difficult to measure. In our study of Lake Erie yellow perch, age and length at 50% maturity (A_{50} and L_{50} , respectively) and their 95% confidence intervals were estimated using logistic regression to estimate the probability of being mature (versus immature) in relation to length and age, and then using inverse prediction to estimate the length or age corresponding to a probability of maturity of 0.5 (Jørgensen 1990; O'Brien 1999). Age at maturity was increased by 1 year because maturity was assessed from fall samples whereas these yellow perch spawn in May (Purchase et al. 2005b).

The relative abundances of age 1 (juvenile) and ages 2 and older yellow perch for each management unit were estimated using annual arithmetic mean catch of yellow perch per bottom gang (CPUE) from the Lake Erie partnership index fishing survey database (Table 2). The CPUE was calculated as the mean number of yellow perch per bottom gang in variable mesh size monofilament gill nets from the fisheries independent partnership survey (gillnets are composed of 25 panels of 13 different mesh sizes; 32, 38, 44, 51, 57, 64, 70, 76, 89, 102, 114, 127, 140, 152

mm stretched measure; Ontario Ministry of Natural Resources and Forestry 2016). The index gear may not fully sample all age 1 fish (especially smallest fish), but is believed to select all lengths of ages 2 and older yellow perch (A. Cook, Ontario Ministry of Natural Resources and Forestry, Wheatley, Ontario, personal communication, 2016). The number of gangs fished annually from 1991 to 2013 varied from 58 to 144 with a mean of 125. Detailed information on the partnership index fishing sampling protocol, site selection, sex determination and aging is available from OMRNF (OMRNF and OCFA 2016). Relative abundance of ages 2 and older and juveniles were averaged across MUs to estimate mean relative abundance for the whole lake (Table 2).

Abundance of YOY fish was estimated as the arithmetic mean density (catch per hectare) based on fall trawl surveys conducted in each management unit in each year (Table S1). The density of YOY for the whole lake was estimated as the mean density of YOY for the four MUs. Data for CPUE and YOY density were $\ln$ transformed, while data for juvenile (age 1) fish were $\ln(\text{CPUE}+1)$ transformed (Table 2) to accommodate three years of sampling when no juvenile fish were caught.

Growth in the first year and second year was estimated for each cohort from the fishery-independent partnership index fishing survey data. Growth in the first year was estimated as the mean size of age 1 individuals. Growth in the second year was estimated as mean size increase from age 1 to 2 (Table 2). The estimates of growth in the first year could be biased upwards, because the smallest age 1 fish may not be captured in the index fishing gear. However, we believe our estimate provides a reasonable index of first year growth because gear size was standardized, so a larger range of sizes should be captured in years when growth rate is higher

than in years when growth rate is lower. In addition, size at age 1 was positively correlated with size at age 2 ($r = 0.62$, $p < 0.002$).

Three measures of harvest intensity were considered: the estimated biomass of fish harvested from commercial and recreational fisheries divided by the CPUE of ages 2 and older from the fishery-independent index survey (harvest ratio), the total biomass harvested divided by biomass of ages 2 and older (exploitation ratio) estimated by the Yellow Perch Task Group, and the instantaneous fishing mortality (F ; year^{-1}) estimated by the Yellow Perch Task Group. Three measures were considered because quantifying harvest intensity is challenging when multiple gear types are used to harvest a population and because different information and methods were used to calculate each measure. Harvest ratio was estimated using fishery-independent index survey data from Belore et al. (2014). Alternatively, estimates of the biomass of ages 2 and older used to calculate exploitation ratio and instantaneous fishing mortality were made using a statistical catch-at-age model (Brooks and Deroba 2015). For prediction B, interpretation of the correlation between biomass of ages 2 and older fish and harvest ratio is complicated, because harvest ratio is calculated using the biomass of ages 2 and older fish (a part-whole correlation; Sokal and Rohlf 2012). This is not the case for equivalent tests involving exploitation ratio and F . Conversely, values of exploitation ratio and F are based on models of population abundance and biomass that include their own assumptions about observational, structural, and estimation uncertainty (Brooks and Deroba 2015). No one measure is ideal because, although the three measures of harvest intensity at the whole lake scale were positively and significantly correlated with each other (r values range from 0.63 to 0.90, all p 's < 0.002 , Table S3; values for the whole lake were obtained by averaging values across the four MUs), the three measures varied in the

208 magnitude of their coefficient of variation (Table S2 and S3). Thus we analyzed our model using
209 ln transformed values of all three measures of harvest intensity.

210 The predicted relationships between independent and time-lagged dependent variables
211 summarized in Table 1 were tested assuming a generation time of 2 and 3 years (Froese and
212 Pauly 2016). We then relaxed the assumption of a 2-3 year lag time and used cross-correlation
213 analysis to explore relationships between harvesting and L_{50} and A_{50} over lag times up to 8 years
214 (2-3 generations). We did this to consider the possibility that maternal effects in yellow perch
215 (Andree et al. 2015) could extend maternal environmental influences across generations and to
216 account for any changes in maturation schedule due to fishing or other factors that could change
217 generation time in the population (Dunlop et al. 2009).

218 Prior to our analyses, the time series data were detrended and pre-whitened to minimize
219 the possibility that changes occurring at multiple temporal scales would confound our cross-
220 correlation analyses. To achieve this, we first tested for a linear relationship between each
221 variable and time (year) and, if significant, detrended the variable using a linear regression
222 against time. The residuals were then used as the detrended variable. We then inspected the
223 partial and full autocorrelation of each variable (detrended or not) (Probst et al. 2012). When
224 evidence of autocorrelation was observed for a variable, an autoregressive integrative moving
225 average (ARIMA) model was used to reduce the chance of spurious correlations arising from
226 temporally adjacent values. Variables that were detrended and subjected to ARIMA modeling
227 are identified in Table 2. All analyses were conducted in R 3.0.2 (R Core Team 2014).

228 Results

Annual cohort estimates of A_{50} and L_{50} varied widely between 1991 and 2013 for the whole lake (Fig. 4). Mean A_{50} ranged from 1.5 to 3.2 years for the whole lake (mean = 2.5 years, SD = 0.37, Table 2) and mean L_{50} ranged from 149 mm to 184 mm (mean = 167 mm, SD = 9.82, Table 2). Over this period, there was no evidence that either A_{50} or L_{50} changed in a consistent direction. L_{50} in particular declined from 1991 to 1996 (176 mm to 149 mm), increased until 2004 (183 mm), then declined until 2009 (157 mm) before increasing again (Fig. 4). Similar trends were observed for all management units (Table 2, Fig. 4, panels C to I). Annual cohort means of A_{50} and L_{50} were positively correlated at both the whole lake ($r = 0.69$, $p < 0.001$, Fig. 5) and the individual MU scales (MU1: $r = 0.75$, $p < 0.0001$; MU2: $r = 0.56$, $p < 0.01$; MU3: $r = 0.73$, $p < 0.0001$; and MU4: $r = 0.70$, $p < 0.001$) (Fig. 5).

Overall, we found no consistent evidence to support our plastic life history model. The findings were generally not consistent with our first prediction that A_{50} and L_{50} in Lake Erie yellow perch would be negatively related to the harvest intensity 2-3 years earlier, although the degree of support differed depending on the measure of harvest intensity (Prediction A; Table 1, Fig. 3). When harvest ratio was considered, L_{50} did not decrease significantly two to three years after the year of harvest, both for tests at the whole lake level and for each management unit (Prediction A1; Table 1, Fig. 6, panels A and B). All correlations between harvest ratio and L_{50} two or three years later were negative but small for the whole lake and for individual MUs (Table 3). The same outcomes were observed for exploitation ratio (Table 3). Analyses considering F differed for prediction A. Correlations between F and L_{50} were negative and statistically significant for a time lag of 3 years at the whole lake level and for MU1 and MU3 (Table 3), but not MU2 and MU4. Outcomes for analyses considering A_{50} instead of L_{50} (Prediction A2) were similar (Table 1). When considering harvest ratio, there was no evidence

for a negative correlation with A_{50} at either the whole lake level or individual management units. The same outcome was observed for exploitation ratio. For F , however, significant correlations were observed between F and A_{50} 3 years later for MU2 and MU4, but not for the whole lake or MU1 and MU3. The MUs where significant correlations were observed between F and A_{50} were not consistent with the MUs where correlations were observed between F and L_{50} (Table 3).

Our prediction that harvest reduced spawning stock size (Prediction B; Fig. 3) was supported in analyses involving harvest ratio and exploitation ratio, but equivocal for analyses involving F . The CPUE of ages 2 and older yellow perch in the year of harvest was negatively related with harvest ratio at the whole lake (Fig. 6, panel C) and consistently for each of the MUs (Table 3). CPUE of ages 2 and older in the year of harvest was also consistently and negatively correlated with exploitation ratio in all cases (Table 3), suggesting the results for harvest ratio were not a consequence of a part-whole correlation effects. Significant negative correlations between F and the abundance of age 2 and older fish were only observed for MU1 and MU4, and not for the whole lake or MU2 and MU3 (Table 3).

There was little evidence that the reductions in spawning abundance due to harvest had any carryover effects on individual juvenile growth of the next generation. Densities of YOY in the year after (or CPUE of age 1 fish two years later) were unrelated to CPUE of ages 2 and older fish in the year of harvest, at the whole lake level (Fig. 6, panel D and E) or in the individual MUs, except for MU1 where the significant negative correlation observed was counter to what was predicted (Table 4, relationship C2). Immature fish did not grow significantly faster at lower densities (Prediction D). The density of YOY fish was unrelated to growth rate in the same year (size at age 1) both for the whole lake (Fig. 6, panel F) and for the MUs (Table 4). CPUE of age 1 fish was also unrelated to growth in the 2nd year (size increase from age 1 to age

2; Fig. 6. Panel G, Table 4). With one exception involving MU1, using size at age 2 as a metric of juvenile growth did not qualitatively change these results.

Similarly there was little evidence for any relationship between individual juvenile growth and A_{50} and L_{50} (Prediction E). A_{50} and L_{50} were not significantly correlated with size at age 1 or the increase in size from age 1 to 2 at the whole lake level (Fig. 6, panel H, I) and for each MU (Table 4). Using size at age 2 as a metric of juvenile growth did not change these results with respect to L_{50} (whole lake and all MUs) or to A_{50} (whole lake and MUs 1 and 4, but was negative in MUs 2 and 3).

Finally, there was no evidence for a relationship between harvesting and A_{50} or L_{50} at time lags greater than 2-3 years. In cross-correlation analyses, A_{50} and L_{50} were unrelated to harvest ratio at across lags of up to 8 years, for the whole lake and for each MU. The same outcomes were obtained using the other two indices of harvest intensity.

Discussion

We found little evidence that annual changes in A_{50} and L_{50} for Lake Erie yellow perch could be explained by changes in the intensity of commercial and recreational harvesting. A_{50} and L_{50} of yellow perch varied considerably over the 23-year period. However, this variation was generally unrelated to harvest 2 - 3 years before (Prediction A), as expected for plastic changes in maturation to occur, although some support for harvest effects was observed when the instantaneous fishing mortality was considered. We did find evidence that the abundance of 2 year and older fish was higher when measures of harvest intensity were lower (Prediction B: for harvest and exploitation ratios but not for instantaneous fishing mortality). However the abundances of YOY 1 year later and age 1 individuals 2 years later were unrelated to the

abundance of 2 year and older fish in the spawning stock responsible for the cohort (Prediction C). In addition, we found little evidence that juvenile growth rates responded to changes in abundance (Prediction D) or that A_{50} and L_{50} responded to changes in juvenile growth rate (Prediction E). In summary, we conclude that the changes in A_{50} and L_{50} cannot be explained by plastic responses to harvest intensity during the time period considered because we were unable to obtain consistent evidence for the overall relationship predicted between A_{50} and L_{50} and measures of harvest intensity (Prediction A), and for key predicted relationships comprising the causal mechanism (Predictions C to E, Tables 1 and 4).

Three features of the variation in A_{50} and L_{50} suggest it reflects the outcome of plastic responses in maturation. First, the highly polygenic nature of life history traits are expected to express more plasticity relative to other traits (Houle 1992), and genetic and environmental effects on maturation can generate sizable variation in A_{50} and L_{50} between individuals within and among populations (Bernardo 1993). In Lake Erie yellow perch, temporally-based coefficients of variation (CV) for A_{50} and L_{50} across annual cohorts were 14.8% and 5.8%, respectively. These values are similar in magnitude, although not directly comparable, to spatially derived CV estimates of 23.8% and 16.6%, respectively, across 72 inland Ontario yellow perch populations (Purchase et al. 2005a; 2005b). Second, the direction of changes in maturity characters reversed over only a few years. This variability is contrary to the steady declines in A_{50} and L_{50} observed in many commercially harvested marine and freshwater fishes (Trippel 1995; Olsen et al. 2004; Sharpe and Hendry 2009). Third, the rates of change in A_{50} and L_{50} were also high when compared to rates observed in other commercially harvested fish. For example, A_{50} and L_{50} in Lake Erie yellow perch cohorts declined at rates of -51.8 and -33.1 kilodarwin (-36% and -18% changes), respectively, from 1991 to 1996 (1991 – 1997 for A_{50}),

but then increased at rates of 231.2 and 62.7 kilodarwin (37.0% and 17.1% changes), respectively from 2001 to 2004 (2002 – 2004 for A_{50}). These rates of change are much faster than the -19.4 and -17.2 kilodarwin declines (26.0% and 20.0% changes), respectively, reported for A_{50} and L_{50} in four marine fishes (Darimont et al. 2009) or the -10.5 and -10.3 kilodarwin mean changes in A_{50} and L_{50} observed in other commercial fish stocks (Sharpe and Hendry 2009). Alternatively, the annual changes in A_{50} and L_{50} could reflect rapid, year-to-year changes in harvest selectivity, but we know of no major changes in gear type and fishing operations beyond harvest intensity over the study period. The annual changes in A_{50} and L_{50} could also reflect annual variation in other sources of selection (e.g. natural predators) that influence distributions of age and length among cohorts (discussed further below; Zhang et al. 2015).

Our conclusion that the fluctuations in A_{50} and L_{50} of Lake Erie yellow perch cannot be explained by contemporary harvesting contrasts with the findings of an earlier study relating maturation and harvest in the Great Lakes yellow perch. Feiner et al. (2015) tested for changes in A_{50} in stocks of yellow perch from Lakes Erie, Huron, and Michigan. They found that female A_{50} had increased in stocks where harvest was reduced, but had declined in the western Lake Erie stock (MU1) where intensive commercial harvest was maintained. The difference between studies may be due to differences in temporal scale of analysis. Feiner et al. (2015) used decadal estimates of A_{50} compared across three sequential decades, whereas we analyzed annual cohort estimates to understand whether harvest influenced dynamics on a finer time-scale.

It is valuable to consider why we did not observe declines in A_{50} and L_{50} with increasing harvest. We first consider the quality of the data and our modeling method before considering other aspects of Lake Erie yellow perch. There is a possibility that we were unable to detect an effect of harvest on A_{50} and L_{50} because of the modest duration of the time series and number of

cohorts available for analysis. However, we observed consistent support for the predicted negative relationship between harvest intensity and spawning population abundance (Prediction B) when considering harvest ratio and exploitation ratio, but not F . Interpretation of the analyses involving F are complicated because its calculation is based on a statistical catch at age model that requires modeled estimates of population abundance and biomass that generate uncertainty in the harvest intensity. The consistent support for prediction B with at least two of the measures of harvest intensity suggests that statistical power alone is an incomplete explanation for the failure of the model. There is also the possibility that our data lacked sufficient variation in harvest intensity to detect correlations using comparisons among cohorts. We consider this unlikely. Coefficients of variation (CVs) for our measures of harvest intensity for Lake Erie yellow perch were comparable to CVs of 0.11 to 0.36 for measures of harvest intensity used in analyses of four harvested marine fishes where fishing-induced evolution is suspected (Heino et al. 2002; Pardoe et al. 2009; Marty et al. 2014; McAdam and Marshall 2014). Further, the 2-3 year generation time of yellow perch means that the 23 year time series is long enough that seven complete generations of fish were exposed to harvest, allowing time for any effects of harvest to manifest through all life stages multiple times.

We also explored whether Lake Erie yellow perch could have experienced different population dynamical phases between 1991-2001, when A_{50} and L_{50} were declining, and 2002-2013, when A_{50} and L_{50} were fluctuating over time. Tests of the plasticity model again provided no consistent support for changes in A_{50} and L_{50} being due to contemporary harvest (Table S4). During the period from 1991-2001, L_{50} was negatively and significantly correlated with harvest ratio, but not exploitation ratio or F (Prediction A), and there was no support for density-dependent responses in growth rate (Prediction D) or growth rate influencing L_{50} (Prediction E)

(Table S5). There was also no significant negative correlation between A_{50} and the measures of harvest intensity, and no significant correlations in support of density-dependent growth rates and growth-dependent age at maturity (Table S5). Similarly, during the period from 2002-2013, neither A_{50} nor L_{50} was negatively correlated with harvest ratio, exploitation rate, or F , and there was no support for density-dependent responses in growth rate (Prediction D) or for growth rate influencing L_{50} (Table S5).

Conversely, there could be features of the Lake Erie yellow perch fishery that reduce the likelihood of harvest affecting maturation in the way we expected. We assumed that in the face of energy limits, variation in maturation would be predominantly determined by variation in immature growth rate with faster growing juveniles maturing earlier and at smaller size than slower growing juveniles (as could result from a positively sloped maturation reaction norm). However, any plastic responses to harvest could be affected by additional factors, including the shape of the maturation reaction norm (e.g., linear or non-linear; increasing or decreasing maturation probability with age or size), variability of growth trajectories within the population, the probabilistic nature of maturation, and size selectivity of harvest (see e.g., Heino and Dieckmann 2008; Dunlop et al. 2009). Most probabilistic maturation reaction norms (PMRNs) estimated for fishes to date have negative slopes, where slower growing individuals mature at smaller sizes than faster growing individuals (Heino and Dieckmann 2008); however, PMRNs with horizontal (e.g. Vainikka et al. 2009) and positive slopes (e.g. Dunlop et al. 2005) have also been observed, complicating predictions. The lack of an effect of growth on A_{50} in our study, however, suggests that a horizontal slope of the maturation reaction norm was not a primary cause of our findings because this would reduce variation in L_{50} , which is abundantly expressed among annual cohorts here. Feiner et al. (2015) measured PMRNs for yellow perch in Lakes

Erie, Huron and Michigan, pooling data by decade for three time periods; these tended to be mostly flat to slightly negative for the three age classes of females considered. Estimates of PMRNs at an annual cohort scale for the Lake Erie yellow perch could reveal further insights into maturation dynamics and are a focus of future research.

Another possibility is that after at least a century of exploitation, the ability of Lake Erie yellow perch to respond to further harvest pressure has reached a limit. A recent model comparing Great Lakes yellow perch, Atlantic cod (*Gadus morhua*), and Great Lakes lake whitefish (*Coregonus clupeiformis*), predicted yellow perch to have the least capacity to evolve in response to harvest because of their high rates of natural mortality which likely already favoured early maturation (Dunlop et al. 2015). This early maturation could also limit the extent of maturation plasticity possible, especially given the seasonality of the Great Lakes. Over the last century, mean female length at maturity in Lake Erie yellow perch has declined from 210 mm in 1927-1937 (Jobes 1952) to 179 mm in 1960 - 1966 to 165 mm in 1990 - 1999 and 166 mm in 2000 – 2010. Although L_{50} varied from 150 mm to 185 mm across the period examined here, we do not know how much size at maturity has varied annually among cohorts in the past.

The consistent absence of relationships between juvenile density, individual growth and maturity suggests that other mechanisms may be missing from the plasticity model. Annual abundances of spawning fish over the period we analyzed may have been in a range where recruitment was independent of spawning stock size (Zhang et al. 2017), possibly accounting for why abundances of YOY and juveniles were not significantly correlated with spawning stock (Predictions C1 and C2), and limiting the opportunity for density-dependent responses in growth rate and maturation. Density-dependent responses in juvenile growth, survival and maturation occur in fishes, including other populations of yellow perch (Jansen 1996; Lorenzen and Enberg

2002; Purchase et al. 2005a), but the lack of support for reduced growth in abundant cohorts (Prediction D) suggests other factors may regulate growth in addition to or instead of competition within cohorts (Purchase et al. 2005b). One possibility is that growth rates are influenced more strongly by competition among rather than within cohorts. The 2003 cohort was one of the largest cohorts in the recent history of Lake Erie yellow perch. Individuals from the following 2004 cohort matured later and at larger sizes than those in the 2003 cohort. Alternatively, growth rates may be suppressed by annual variation in predation risk. Stock-recruitment analyses suggest that yearling walleye (*Sander vitreus*) may exert a strong top-down effect on yellow perch recruitment in Lake Erie through predation on YOY (Zhang et al. 2015).

Lastly, a very real possibility is that environmental factors other than harvest could be driving the rapid, large and reversible changes in maturity in Lake Erie yellow perch. Lake-wide effects on energy availability may supersede density-dependent growth responses in yellow perch (Purchase et al. 2005b). Lake Erie has experienced recent ecological disturbances that could influence yellow perch maturation. The arrival of invasive dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) and round goby (*Neogobius melanostomus*) have altered water quality (Munawar et al. 2005; Bunnell et al. 2014), the behaviour and energetics of predator and prey fishes (Stapanian et al. 2009), and the energy pathways within the lake (Vanderploeg et al. 2002; Hecky et al. 2004). In addition, yellow perch recruitment is also weaker following short, warm winters than following cold winters (Farmer et al. 2015), which could induce annual variation in growth rate and maturation as modeled here but independent of harvest. Eutrophication can influence the life history and production of fishes (Arend et al. 2011) and has emerged as a recent concern following large algal blooms in the lake (Michalak et al. 2013; Scavia et al. 2014). Assessing the extent to which maturation has fluctuated synchronously

435 among species would be one step toward understanding the role of lake-wide environmental
436 change in Lake Erie.

437 Age and length at maturity in Lake Erie yellow perch have fluctuated rapidly over the
438 past 23 cohorts potentially in response to annual variation in an unknown environmental factor
439 other than harvest intensity. This is in contrast to the pronounced and steady declines in age and
440 length at maturity observed in several harvested marine fish stocks (Trippel 1995; Darimont et
441 al. 2009; Sharpe and Hendry 2009). Our analysis focused on phenotypic change and did not
442 specify whether that change was the result of evolution, phenotypic plasticity, or some
443 combination of the two. The processes responsible for rapid changes in Lake Erie yellow perch
444 maturity remain undetermined, but contemporary harvest pressure can be excluded as a major
445 causal factor over the last several decades. Identifying the factors driving maturation dynamics
446 will be challenging given the multifarious ways in which the Lake Erie ecosystem is changing,
447 but this is important given the influence of maturation dynamics on the productive capacity of
448 this commercially important species.

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Tables

Table 1. Prediction matrix of the relationships in Fig. 3 for the effect of: A) Harvest ratio, measured as $\ln(\text{Total catch in millions of kg/CPUE of ages 2 and older})$, on female A_{50} or L_{50} 2 and 3 years later; B) Harvest ratio on CPUE of ages 2 and older in the year of harvesting; C1-C2) Abundance of ages 2 and older on density of YOY in the next year (1 year lag) and on the CPUE of age 1 (2 year lag); D1-D2) YOY density on 1st year growth (mean female size at age 1) and CPUE of age 1 year fish on 2nd year growth (mean female size increase from age 1 - 2); E1-E2) Early female growth in 1st year and in 2nd year on female length or age at 50% maturity (1 year lag and no lag). Test outcomes were determined using Pearson's product moment correlation coefficient (r) at $\alpha = 0.05$.

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Predictions from Fig. 3	Independent variable	Dependent variable	Direction of predicted relationship	Test Outcome
A	Harvest ratio (t0)*	♀ L ₅₀ , A ₅₀ (t2 & t3)	Negative	Not supported
B	Harvest ratio (t0)	CPUE ages 2 & older (t0)	Negative	Supported
C1	CPUE ages 2 & older (t0)	Density YOY (t1)	Positive/no relationship	Supported
C2	CPUE ages 2 & older (t0)	CPUE age 1 (t2)	Positive/no relationship	Supported
D1	Density YOY (t0)	♀ Growth in 1 st year (t0)	Negative	Not supported
D2	CPUE age 1 (t0)	♀ Growth in 2 th year (t0)	Negative	Not supported
E1	♀ Growth in 1 st year (t0)	♀ L ₅₀ , A ₅₀ (t1)	Negative	Not supported
E2	♀ Growth in 2 th year (t0)	♀ L ₅₀ , A ₅₀ (t0)	Negative	Not supported

679 * tn indicates the variable was lagged n years in the analysis, e.g. in prediction A harvest ratio in the year it was measured (t0) was
 680 related to length at maturity two (t2) and three (t3) years later.

681 **Table 2.** Summary statistics of the variables used to test the model in Figure 3, including number
682 of years of data available (N), minimum (Min), maximum (Max) and mean values (Mean), the
683 coefficient of variation (CV), and whether prior to cross correlation analysis the variable was
684 detrended (DT) and pre-whitened using an ARIMA model. L_{50} , growth in first year and second
685 year are in mm, A_{50} is in years, harvest ratio is million kg/mean catch per bottom gang ages 2
686 and older, CPUE ages 2 and older and CPUE age 1 is the mean number of yellow perch catch per
687 bottom net set, density YOY is number per hectare. The variables are summarized for data
688 aggregated across the lake and for each of four management units (MUs).

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Area	Variable	N	Min	Max	Mean	CV	DT	ARIMA
Whole	♀ A ₅₀	23	1.5	3.2	2.5	0.15	N	AM(1)
Lake	♀ L ₅₀	23	149	184	167	0.06	N	AR(1)
	ln(Harvest ratio)	23	2.4	4.6	3.1	0.20	Y	AR(1)
	ln(CPUE ages 2 & older)	23	3.2	5.9	5.0	0.15	Y	AR(1)
	ln(Density YOY)	23	1.6	6.0	4.1	0.27	N	AR(1)
	ln(CPUE age 1 +1)	23	0.7	6.2	4.1	0.33	N	AR(1)
	♀ Growth in 1st year	23	132	156	143	0.04	N	
	♀ Growth in 2th year	23	29	64	48	0.16	N	
MU1	♀ A ₅₀	23	0.2	3.1	2.5	0.25	N	
	♀ L ₅₀	23	138	187	167	0.07	N	AR(1)
	ln(Harvest ratio)	23	0.4	2.6	1.6	0.32	N	
	ln(CPUE ages 2 & older)	23	3.9	6.3	5.1	0.11	N	AR(1)
	ln(Density YOY)	23	2.2	7.0	4.6	0.27	N	
	ln(CPUE age 1 +1)	23	0	6.89	4.4	0.37	N	
	♀ Growth in 1st year	22	131	158	143	0.05	N	

	♀ Growth in 2th year	22	15	55	43	0.21	N	
MU2	♀ A ₅₀	23	1.4	3.1	3.0	0.17	N	AR(1)
	♀ L ₅₀	23	149	178	164	0.05	N	MA(1)
	ln(Harvest ratio)	23	1.4	4.4	2.4	0.28	Y	AR(1)
	ln(CPUE ages 2 and older)	23	2.6	6.2	4.9	0.17	Y	AR(1)
	ln(Density YOY)	23	0.5	5.0	3.1	0.43	N	AR(1)
	ln(CPUE age 1 +1)	23	1.2	5.9	4.0	0.38	N	AR(1)
	♀ Growth in 1st year	23	134	176	147	0.07	N	
	♀ Growth in 2th year	23	28	69	49	0.23	Y	AR(1)
MU3	♀ A ₅₀	23	1.6	3.4	2.6	0.19	N	
	♀ L ₅₀	23	145	184	167	0.06	N	AR(1)
	ln(Harvest ratio)	20	-0.3	3.1	0.9	0.92	Y	AR(1)
	ln(CPUE ages 2 & older)	20	3.4	7.1	5.9	0.19	Y	AR(1)
	ln(Density YOY)	23	-0.7	5.2	2.8	0.61	N	AR(1)
	ln(CPUE age 1 +1)	20	0	6.2	3.0	0.66	N	
	♀ Growth in 1st year	22	127	152	139	0.05	N	MA(1)

	♀ Growth in 2th year	21	23	64	42	0.26	Y	AR(1)
MU4	♀ A ₅₀	20	1.9	3.5	2.7	0.15	N	
	♀ L ₅₀	21	119	207	171	0.14	N	MA(1)
	ln(Harvest ratio)	21	-1.5	3.6	0.6	1.87	N	AR(2)
	ln(CPUE ages 2 & older)	21	-0.2	5.6	3.7	0.39	Y	MA(1)
	ln(Density YOY)	23	-0.8	5.9	3.5	0.5	N	AR(1)
	ln(CPUE age 1 +1)	21	0	4.9	3.7	0.58	Y	
	♀ Growth in 1st year	18	126	172	141	0.07	N	
	♀ Growth in 2th year	17	30	75	55	0.18	N	MA(1)

689

690 **Table 3.** Pearson correlation coefficients (*r*) obtained for tests of model predictions A1, A2 and B (Table 1, Figure 3) for three
691 measures of harvest intensity: harvest ratio, exploitation ratio, and instantaneous fishing mortality per year (*F*). A1) Harvest ratio and
692 female *L*₅₀; A2) Harvest ratio and female *A*₅₀; B) harvest ratio and CPUE of ages 2 and older. Lag times *t*₀, *t*₂, and *t*₃ refer to the time
693 in years between the dependent and independent variables. Correlation coefficients were estimated for the whole lake and for each of
694 four management units (MU). Values in bold are statistically significant at *p* < 0.05.
695

Area	Pre-diction	Independent variable	Dependent variable		Harvest intensity indices		
					Harvest ratio	Exploitation ratio	<i>F</i> Year ⁻¹
Whole Lake	A1	Harvest (<i>t</i> ₀)*	♀ <i>L</i> ₅₀ (<i>t</i> ₂)	<i>r</i>	0.1	0.05	0.09
				<i>p</i>	0.67	0.58	0.65
				<i>df</i>	19	19	19
		Harvest (<i>t</i> ₀)	♀ <i>L</i> ₅₀ (<i>t</i> ₃)	<i>r</i>	-0.02	-0.03	-0.6
				<i>p</i>	0.47	0.45	0.002
				<i>df</i>	18	18	18
	A2	Harvest (<i>t</i> ₀)	♀ <i>A</i> ₅₀ (<i>t</i> ₂)	<i>r</i>	0.31	0.16	0.22
				<i>p</i>	0.92	0.75	0.83
				<i>df</i>	19	19	19

MU1	B	Harvest (t0)	♀ A ₅₀ (t3)	r	-0.04	-0.12	-0.18
				<i>p</i>	0.44	0.31	0.23
				df	18	18	18
		Harvest (t0)	CPUE ages 2 & older (t0)	r	-0.96	-0.64	-0.26
				<i>p</i>	<0.0001	0.0005	0.12
				df	21	21	21
	A1	Harvest (t0)	♀ L ₅₀ (t2)	r	-0.1	-0.09	-0.03
				<i>p</i>	0.34	0.34	0.45
				df	19	19	19
		Harvest (t0)	♀ L ₅₀ (t3)	r	-0.2	-0.21	-0.56
				<i>p</i>	0.2	0.2	0.005
				df	18	2118	18
	A2	Harvest (t0)	♀ A ₅₀ (t2)	r	0.01	0.17	0.31
				<i>p</i>	0.52	0.77	0.92
				df	19	19	19
		Harvest (t0)	♀ A ₅₀ (t3)	r	-0.13	-0.12	-0.15
				<i>p</i>	0.30	0.3	0.26
				df	18	18	18

MU2	B	Harvest (t0)	CPUE ages 2 & older (t0)	r	-0.92	-0.8	-0.57
				<i>p</i>	<0.00001	<0.0001	0.002
				df	21	21	21
	A1	Harvest (t0)	♀ L ₅₀ (t2)	r	0.04	0.39	0.19
				<i>p</i>	0.56	0.96	0.79
				df	19	19	19
		Harvest (t0)	♀ L ₅₀ (t3)	r	-0.07	0.28	-0.23
				<i>p</i>	0.39	0.89	0.17
				df	18	18	18
	A2	Harvest (t0)	♀ A ₅₀ (t2)	r	0.27	0.8	-0.31
				<i>p</i>	0.88	0.89	0.08
				df	19	19	19
		Harvest (t0)	♀ A ₅₀ (t3)	r	-0.16	-0.23	-0.48
				<i>p</i>	0.25	0.16	0.02
				df	18	18	18
	B	Harvest (t0)	CPUE ages 2 & older (t0)	r	-0.97	-0.37	-0.1
				<i>p</i>	<0.00001	0.04	0.32
				df	21	21	21

MU3	A1	Harvest (t0)	♀ L ₅₀ (t2)	r	0.12	0.12	-0.02
				<i>p</i>	0.7	0.69	0.47
				df	17	19	19
		Harvest (t0)	♀ L ₅₀ (t3)	r	-0.19	-0.18	-0.55
				<i>p</i>	0.23	0.23	0.006
				df	16	18	18
	A2	Harvest (t0)	♀ A ₅₀ (t2)	r	0.38	0.43	0.2
				<i>p</i>	0.94	0.97	0.81
				df	17	19	19
		Harvest (t0)	♀ A ₅₀ (t3)	r	-0.12	-0.18	-0.16
				<i>p</i>	0.32	0.22	0.25
				df	16	18	18
	B	Harvest (t0)	CPUE ages 2 & older (t0)	r	-0.88	-0.55	0.06
				<i>p</i>	<0.00001	0.006	0.6
				df	18	18	18
MU4	A1	Harvest (t0)	♀ L ₅₀ (t2)	r	-0.26	0.14	-0.19
				<i>p</i>	0.15	0.72	0.22
				df	16	18	18

A2	Harvest (t0)	♀ L ₅₀ (t3)	r	-0.07	0.05	-0.19
			p	0.4	0.59	0.21
			df	15	17	17
	Harvest (t0)	♀ A ₅₀ (t2)	r	-0.14	0.09	-0.09
			p	0.30	0.64	0.35
			df	15	17	18
B	Harvest (t0)	♀ A ₅₀ (t3)	r	-0.51	-0.32	-0.46
			p	0.02	0.1	0.03
			df	14	16	16
	Harvest (t0)	CPUE ages 2 & older (t0)	r	-0.81	-0.55	-0.21
			p	<0.0001	0.005	0.18
			df	19	19	19

696 * tn indicates the variable was lagged n years in the analysis, e.g. in prediction A, harvest ratio in the year it was measured (t0) was
697 related to length at maturity two (t2) and three (t3) years later.

698 **Table 4.** Pearson correlation coefficients (r) for the model predictions C to E (Fig. 3 and Table
699 1). C1) CPUE of ages 2 and older and density of YOY; C2) CPUE of ages 2 and older and
700 CPUE of age 1; D1) density of YOY and female growth in first year (mean female size at age 1);
701 D2) CPUE of age 1 and female growth in second year (size increase from age 1 to age 2); E1)
702 growth in first year and female L_{50} , and E2) growth in second year and female L_{50} . Correlation
703 coefficients were estimated for the whole lake and for each of four management units (MU).
704 Values in bold are statistically significant at $p < 0.05$.

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Pre-diction	Independent variable	Dependent variable		Management units				Whole
				MU1	MU2	MU3	MU4	Lake
C1	CPUE ages 2 & older (t0)	Density YOY (t1)	r	-0.16	-0.12	-0.04	-0.09	-0.22
			p	0.23	0.3	0.44	0.35	0.16
			df	20	20	18	18	20
C2	CPUE ages 2 & older (t0)	CPUE age 1 (t2)	r	-0.39	-0.17	0.13	-0.31	-0.14
			p	0.03	0.24	0.68	0.11	0.27
			df	19	19	14	15	19
D1	Density YOY (t0)	♀ Growth 1st year (size at age 1) (t0)	r	-0.29	0.15	-0.3	0.25	0.003
			p	0.1	0.76	0.09	0.83	0.51
			df	20	21	20	16	21
D2	CPUE age 1 (t0)	♀ Growth 2nd year (size change 1 - 2) (t0)	r	-0.18	-0.07	0.3	0.2	-0.12
			p	0.2	0.37	0.88	0.77	0.29
			df	20	21	16	15	21
E1	♀ Growth 1st year (size at age 1) (t0)	♀ L ₅₀ (t1)	r	0.16	-0.16	-0.25	0.19	-0.19
			p	0.76	0.23	0.14	0.75	0.2

			df	19	20	19	13	20
E2	♀ Growth 2nd year	♀ L ₅₀ (t ₀)	r	0.21	-0.08	-0.15	-0.21	-0.2
	(size change 1 - 2) (t ₀)		p	0.82	0.64	0.26	0.2	0.18
			df	20	21	19	15	21

705 * tn indicates the variable was lagged n years in the analysis, e.g. in prediction A harvest ratio in the year it was measured (t₀) was
 706 related to length at maturity two (t₂) and three (t₃) years later.

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707 **Figure captions**

708 **Fig. 1.** Map of Lake Erie showing the four management units (MUs) for yellow perch numbered
709 from west to east (MU5 is within MU4 and is not shown). The black square in the lower right
710 insert shows the location of Lake Erie within North America (modified from Belore et al. 2016).

711

712 **Fig. 2.** Estimates from 1975 – 2013 of Lake Erie yellow perch population size in millions
713 (shading), harvest ratio (solid black line), instantaneous fishing mortality ($F \text{ year}^{-1}$; solid gray
714 line), exploitation ratio (black dash line). On the horizontal axis the black arrow indicates the
715 starting year of this study.

716

717 **Fig. 3.** Conceptual model of plasticity in individual life history describing the direct relationships
718 between harvest, ages 2 and older abundance, YOY and age 1 abundance, growth and female age
719 or size at 50% maturity as solid arrows. The overall cumulative indirect effect of harvest on
720 maturity is shown as a dashed arrow. Time refers to the lag time in years between harvest and
721 each response (e.g. the effect of harvesting is expected to affect growth one and two years later).
722 The letter at each causal arrow indicates the predicted relationship shown in brackets under the
723 arrow and described in Tables 1 and 3: A) Increased harvest reduces female body age and length
724 at 50% maturity; B) increased harvest lowers the abundance of ages 2 and older; C) fewer age 2
725 and older spawners reduces the abundance of younger age classes; D) lower abundance of
726 younger individuals increases individual juvenile growth rate; E) increased individual juvenile
727 growth rate decreases female age and length at 50% maturity.

Fig. 4. Time series of female length and age at 50% maturity (L_{50} and A_{50} , respectively) for yellow perch from Lake Erie. Times series are provided for the entire lake and separately for each management unit. Whole lake (panels A, B), MU1 (panels C, D), MU2 (panels E, F), MU3 (panels G, H), and MU4 (I, J). Vertical bars express 95% confidence intervals. Estimates of L_{50} and A_{50} indicated by an open circle (o) are unreliable (A_{50} 95% CI $> \pm 10.2$ years and L_{50} 95% CI $> \pm 200.0$ mm). Note the changed vertical scale among MUs.

Fig. 5. Relationships between length at 50% maturity (L_{50}) and age at 50% maturity (A_{50}) for female yellow perch in Lake Erie between 1991 and 2013 ($n = 23$ annual cohorts). Regression equations and statistical details for the whole lake and MU's: Whole lake; $L_{50} = 121.2 + 18.2 * A_{50}$, $R^2 = 0.45$, $p < 0.001$; MU1, $L_{50} = 104.9 + 24.1 * A_{50}$, $R^2 = 0.54$, $p < 0.0001$; MU2, $L_{50} = 136.9 + 11.4 * A_{50}$, $R^2 = 0.28$, $p < 0.01$; MU3, $L_{50} = 125.0 + 16.1 * A_{50}$, $R^2 = 0.40$, $p < 0.0001$; MU4, $L_{50} = 78.8 + 35.3 * A_{50}$, $R^2 = 0.46$, $p < 0.001$.

Fig. 6. Panels summarizing relationships predicted by the plastic life history model (Fig. 3, Table 1) for the whole lake: A) Harvest ratio and female L_{50} two years later; B) harvest ratio and female L_{50} three years later; C) harvest ratio and CPUE of ages 2 and older (regression line: $\ln(\text{CPUE ages 2 and older}) = -0.01 - 0.99 * \ln(\text{harvest ratio})$, $R^2 = 0.92$, $p < 0.0001$); D) CPUE of ages 2 and older and density of YOY year later; E) CPUE of ages 2 and older and CPUE of age 1 two years later; F) density of YOY and female growth in first year; G) CPUE of age 1 and female growth in second year; H) female growth in first year and female L_{50} year later; I) female growth in second year and female L_{50} . The sign appearing in parentheses in the upper right

750 corner of each panel indicates the predicted relationship between variables. With the exception of
751 C, all correlation coefficients were non-significant ($p > 0.05$).

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