

Maternal influences on population dynamics: evidence from an exploited freshwater fish

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Abstract. We used a field experiment, population modeling, and an analysis of 30 years of data from walleye (*Sander vitreus*; a freshwater fish) in Lake Erie to show that maternal influences on offspring survival can affect population dynamics. We first demonstrate experimentally that the survival of juvenile walleye increases with egg size (and, to a lesser degree, female energy reserves). Because egg size in this species tends to increase with maternal age, we then model these maternal influences on offspring survival as a function of maternal age to show that adult age structure can affect the maximum rate at which a population can produce new adults. Consistent with this hypothesis, we present empirical evidence that the maximum reproductive rate of an exploited population of walleye was approximately twice as high when older females were abundant as compared to when they were relatively scarce. Taken together, these results indicate that age- or size-based maternal influences on offspring survival can be an important mechanism driving population dynamics and that exploited populations could benefit from management strategies that protect, rather than target, reproductively valuable individuals.

Key words: age structure; demographics; egg size; Lake Erie; maternal effects; maternal influences; offspring survival; population dynamics; recruitment; relative fecundity; *Sander vitreus*; walleye.

INTRODUCTION

In most populations, adult females vary in their ability to produce viable offspring. This variation stems, in part, from maternal influences (MI; the combined effect of maternal phenotype and maternal genotype) on offspring survival (see reviews by Roach and Wulff 1987, Mousseau and Dingle 1991, Bernardo 1996, Rossiter 1996, Mousseau and Fox 1998). Because population growth rate depends on the production of new individuals (i.e., recruitment), population dynamics should depend on the extent to which MI affect the survival of offspring. For example, MI are hypothesized to delay or accelerate life history responses to the environment, which can stabilize or destabilize a population or cause it to cycle (Rossiter 1996, Ginzburg

1998, Kazantseva and Alekseev 2007). Similarly, if older, larger females produce offspring that have a higher survival rate than offspring from younger, smaller females, then population dynamics should depend on population demographics such as adult age or size structure (Forbes and Peterman 1994, Murawski et al. 2001, O'Farrell and Botsford 2006, Lucero 2008, Venturelli et al. 2009). If true, then age- or size-related MI on offspring survival represent a mechanism of population dynamics that, like other demographic characteristics (e.g., density, sex ratio), can be influenced by exploitation (Solemdal 1997).

Despite theoretical support for the effects of this type of MI at the population level, empirical evidence for this phenomenon is very limited. In laboratory populations of soil mites, egg size and maternal age affected population dynamics over many generations (Benton et al. 2005, 2008). Among wild populations of mammals, birds, and insects, survival-based MI on population dynamics have been inferred either from MI on the life history and long-term survival of offspring (Albon et al. 1987, Reid et al. 2003) or the degree of consistency between observed time series and population models that included MI on survival (e.g., Ginzburg and Taneyhill 1994, Kendall et al. 2005). In wild fishes such

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as haddock (*Melanogrammus aeglefinus*; Marshall and Frank 1999) and Atlantic cod (*Gadus morhua*; Martensdottir and Thorarinsson 1998, Marshall et al. 1999), population dynamics are consistent with MI on offspring survival, but this mechanism has only been demonstrated in one population of Atlantic cod (Cardinale and Arrhenius 2000, Vallin and Nissling 2000). Similarly, although a recent meta-analysis suggests that MI on survival can affect the maximum reproductive rate of populations of long-lived, marine species (Venturelli et al. 2009), differences in relative fecundity (i.e., MI on egg production) could also have contributed to this pattern.

This paper builds on the results of Venturelli et al. (2009) by presenting three concordant lines of evidence that MI on offspring survival can affect a population's maximum reproductive rate. Our study organism was walleye (*Sander vitreus*), a large, freshwater predator that exhibits a periodic life history (i.e., slow-growing, late-maturing, long-lived, iteroparous, and highly fecund; Winemiller and Rose 1992) and is heavily exploited throughout North America (see Plate 1). Maternal influences on survival in walleye are evidenced by positive effects of both maternal age or size (Johnston 1997, Johnston et al. 2007) and egg quality (e.g., egg size, lipid content; Moodie et al. 1989, Czesny and Dabrowski 1998, Johnston et al. 2005, 2007) on the survival of laboratory-reared eggs and larvae. Egg size also tends to have a positive effect on larval size (Moodie et al. 1989, Johnston 1997, Johnston et al. 2007), which, in turn, influences survival through negative effects on cannibalism, deformities, and starvation (Moodie et al. 1989, Johnston and Mathias 1993, 1996). Because these studies suggest that MI on survival occur later in the life of offspring than has previously been examined, we first report on a large-scale experiment that was designed to quantify MI on the survival of juvenile walleye after two months in naturalized ponds. We then develop a population model to determine whether MI of the magnitude and duration that we observed in the pond experiment can influence population dynamics. Specifically, we model different age-selective harvest strategies to demonstrate that, when juvenile survival increases with maternal age, a population of relatively old adult females will produce new individuals at a consistently higher rate than an equivalent population of young adult females. Finally, we use a 30-year time series of empirical data on the long-term dynamics of the heavily exploited Lake Erie walleye population to show that the presence of older females was associated with a twofold increase in the maximum reproductive rate of this population.

METHODS

Pond experiment

We conducted an experiment in naturalized ponds to quantify effects of both maternal and paternal quality on the relative survival of communally reared, full-

sibling offspring. Over three nights in April 2002, adult walleye ($n = 25$ males and 25 females) were netted from the Napanee River ($44^{\circ}12'02''$ N, $76^{\circ}59'08''$ W), a tributary to the Bay of Quinte, Lake Ontario (Wiegand et al. 2007). Each female was then matched to a male that was selected randomly, without replacement (see Plate 1). This matching procedure was repeated three times to produce three experimental populations, each with 25 unique families of full-sibling offspring (Appendix A: Fig. A1).

For each parental pair, eggs (40 000 [6500] eggs; mean [95% CL]) and milt (1.2 [0.2] mL) were mixed as described in Johnston et al. (2005). Fertilized eggs were then pooled by experimental population and incubated in flow-through bell jar hatchery systems at a seasonal photoperiod (15 h light : 9 h dark) and water temperature ($8\text{--}14^{\circ}\text{C}$). At four days post-hatch (day 4), a random sample of 300 larvae was taken from each population, euthanized by an overdose of anesthetic, measured for total body length (to the nearest 0.2 mm), and then preserved in 95% ethanol. On day 5, a subsample of $\sim 100\,000$ larvae (estimated volumetrically) from each population was stocked into a separate, fishless culture pond (Appendix A: Fig. A1). Each pond was ~ 0.5 ha in surface area, with a maximum depth of ~ 2 m. To stimulate the production of invertebrate prey, ponds received treatments of organic fertilization (fermented soybean meal) once every two weeks. On day 66, another random sample of 300 offspring was taken from each pond, euthanized, measured for fork length (FL; to the nearest 1 mm), and then preserved in 95% ethanol. Parentage assignment of day 4 and day 66 offspring was by microsatellite DNA analysis of seven loci by means of polymerase chain reaction (PCR) amplification and PAPA 2.0 software (see Appendix A).

The relative survival rate of offspring of specific sires and dams was estimated by comparing, between the beginning and the end of the experiment, the proportional distribution of offspring among sires or dams within a population, and then averaging by sire or dam across the three populations (Appendix A). For each parent, we obtained the following measures of parental quality (1) age, body length, condition, residual growth rate (percentage deviation around mean size-at-age), and the total lipid content of somatic and liver tissues; (2) the size (dry mass), total lipid content, and fatty acid profiles of eggs from females; and (3) the density of sperm in the milt, sperm tail length, and mean sperm swimming velocity from males (Appendix A).

Population modeling

Venturelli et al. (2009) used an analytical model to show that MI on survival can affect the maximum reproductive rate of a population through changes in the mean age of breeding adults. To determine how MI of the magnitude that we observed in our pond experiment might interact with age structure to affect the reproductive rate of a typical population of walleye, we developed

a deterministic, density-dependent, stage-within-age matrix projection model (Rose et al. 2003, Murphy 2006; Appendix B: Fig. B1) in which offspring survival was assumed to increase with maternal age.

Simulations began with the production of offspring by different age classes of mature females and ran until the population equilibrated. The annual contribution of each age class to egg production was calculated by assuming a 1:1 sex ratio and then multiplying the total mass of females in an age class by a constant relative fecundity (egg number per unit body mass). Offspring in their first year of life were modeled daily through four stages of development: separately by female age class as eggs (30 d), free-swimming larvae (60 d), and early juveniles (90 d), and then as a single group of late (overwintering) juveniles (180 d). Thereafter, age-1 offspring were modeled on an annual (360 d) time step through to maturity (age-4) and senescence (age-20; Appendix B: Fig. B1). Additional parameters for length-, mass-, and fecundity-at-age (Appendix B: Table B1) were assumed to be fixed (i.e., not density dependent) so that effects of MI on population dynamics could be evaluated in isolation.

Instantaneous rates of natural mortality for each stage were either obtained or derived from the literature (Appendix B). We incorporated MI into rates of larval and early juvenile mortality by (1) assigning an egg size to each adult female age class, (2) using these egg sizes to predict daily rates of relative offspring survival (Table 1), and then (3) subtracting the relative offspring survival rate that was specific to each egg size from the natural mortality rate of larvae and early juveniles (Appendix B). Thus, offspring mortality during the larval and early juvenile stages declined with maternal age in accordance with the positive relation between egg size and maternal age that is typical of most populations of walleye (Appendix B: Fig. B2) and other highly fecund, demersal-spawning fish (Einum and Fleming 2002). We considered our model to be conservative with respect to likely effects of MI because: (1) we modeled a relation between larval survival and maternal age that reflected a conservative interpretation of the larval survival–egg size relation that was observed in the pond experiment and (2) we did not model MI beyond the late juvenile stage, despite evidence that winter mortality decreases with body size in juvenile walleye (e.g., Rose et al. 1999). Finally, natural mortality in the early juvenile stage was further modified via a linear relation between early juvenile mortality and abundance that produced a Ricker-type relation (Hilborn and Walters 1992) between egg production and age-1 abundance (Appendix B).

To alter the mean age of spawning adults in this population, we added harvest mortality to the natural mortality rate of specific age classes according to three harvest strategies: harvest young (harvest restricted to age classes 2, 3, and 4 in what is typically known as a harvestable or fishable slot), harvest all (all age classes

harvested), and harvest old (harvest eliminated each age class in turn, beginning with the oldest). We modeled these three strategies because each is an extreme, but not uncommon, form of harvest that affects mean age in a unique way. For each harvest strategy, we generated a relation between the abundance of one-year-olds and egg production by evaluating the model at equilibrium over a series of incremental increases in fishing mortality. We then estimated the slope at the origin (α_0) of each relation by dividing age-1 abundance by egg production at the point along the relation at which egg production was equal to $\sim 0.5\%$ of unexploited levels. This slope represents a population's maximum reproductive rate and is related directly to its maximum sustainable exploitation rate (Myers et al. 1999).

Population dynamics in Lake Erie

To evaluate empirical evidence for MI on the maximum reproductive rate of a wild population, we analyzed published data (Appendix C) on the Lake Erie walleye population over a period when variation in exploitation rate had produced large changes in the mean age of adult females. The total annual egg production and subsequent recruitment of walleye in Lake Erie from 1947 to 1976 ($\pm 95\%$ CL) were estimated using published mark–recapture data, estimates of total harvest and age-specific catch per unit effort, young-of-the-year trawl surveys, age-specific maturity schedules, length- and mass-at-age data, and a relation between relative fecundity (RF, egg number per unit body mass) and body length from 1966 (Appendix C). Because age-at-maturity, length-at-age, and mass-at-age data were specific to individual years or groups of years, estimates of egg production and recruitment for the period 1947–1976 largely accounted for density-dependent changes in life history.

We analyzed these data as follows. First, to account for environmental effects on recruitment, we incorporated two widely accepted indicators of environmental quality, spring warming rate (ΔT , in degrees Celsius per gram; Shuter et al. 1979) and water level (W , in meters; Koonce et al. 1996), into a likelihood-based model selection framework that also included total annual egg production and the mean age of adult females as predictor variables. Because reproduction is a prerequisite for recruitment, we only considered the eight linear regression models in which egg production was a variable. According to a small-sample, bias-corrected form of Akaike's information criterion (AIC_c ; Anderson 2008), evidence was strongest for two multiple linear regression models: $\log(\text{eggs})$, ΔT , and W (adjusted $R^2 = 0.59$, $n = 30$, AIC_c rank = 1, $w_1 = 0.42$, where w_i is the probability that this model i is the best model given the data and the model set), and the full model ($\log(\text{eggs})$, ΔT , W , and mean age; adjusted $R^2 = 0.63$, $n = 30$, AIC_c rank = 2, $w_2 = 0.24$, $\Delta_2 = 1.1$, where Δ_i is the difference in AIC_c values between model 1 and model 2). All coefficients for both models were significant at $P \leq$

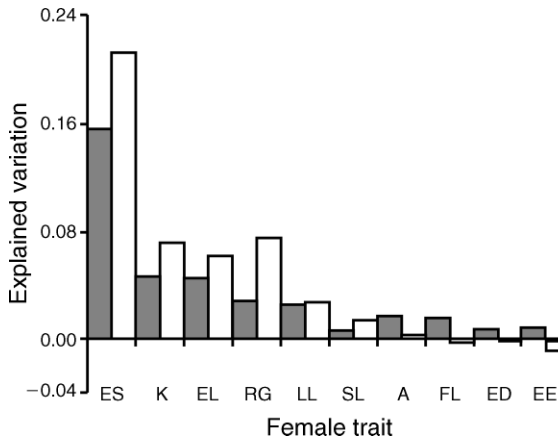


FIG. 1. Independent (solid bars) and joint (open bars) contributions to the proportion of variance in relative offspring survival rate of walleye (*Sander vitreus*) that was explained by each female trait, as determined by hierarchical partitioning. Independent and joint contributions refer to effects that were specific to that trait and effects that were shared with other traits, respectively. The total (independent + joint) variation explained by each trait is given in parentheses following the abbreviations: ES (0.37), egg size (mg dry mass); K (0.12), condition ($\text{g}\cdot\text{mm}^{-3}\cdot 10^5$); EL (0.11), egg lipid (proportion of dry mass); RG (0.10), residual growth (%); LL (0.05), arcsine square root liver lipid (proportion of dry mass); SL (0.02), arcsine square root somatic lipid (proportion of dry mass); A (0.02), age (years); FL (0.01), fork length (mm); ED (0.01), arcsine square root egg docosahexaenoic acid (proportion of EL); EE (<0.01), egg residual eicosapentaenoic:arachidonic acid ratio.

0.03. Using the full model, we then fixed ΔT and W at mean observed values ($0.21 \pm 0.02^\circ\text{C}/\text{g}$ and 174.21 ± 0.13 m, respectively) and predicted four relations between $\log(\text{recruitment})$ and $\log(\text{egg production})$: one for each mean age equal to (1) the minimum observed value (3.03 years), (2) the maximum observed value (4.44 years), (3) the mean of the 15 smallest observed values (3.29 ± 0.11 years), and (4) the mean of the 15 largest observed values (4.01 ± 0.14 years). The first two of these mean age scenarios establish the range of stock-recruitment relations that are possible given the data, and the last two scenarios identify the mean position of

these relations when mean age is below and above the median (3.66 years). Finally, we estimated the α_0 of each of these relations by taking the inverse logarithm of their respective intercepts. Lake Erie walleye and environment data for the period 1947–1976 are provided in Appendix C.

RESULTS AND DISCUSSION

Pond experiment

Does the early survival of walleye depend on parental quality? Parental walleye in the pond experiment spanned a range of ages (4–20 years) and lengths (455–742 mm) that were representative of the source population (T. A. Johnston, *unpublished data*). Among these adults, measures of gamete quality for both sexes (egg size and lipid content; sperm swimming speed and sperm concentration in the milt) varied approximately twofold (Appendix A: Tables A4 and A5). Offspring survival rates over 62 days also varied among adults such that offspring were more evenly distributed among parents at the beginning of the experiment than at the end (see Appendix A: Tables A2 and A3).

Hierarchical partitioning (Mac Nally 2000, Mac Nally and Walsh 2004) based on maternal traits showed that the relative survival of juvenile walleye over 62 days was influenced most strongly by egg size (Fig. 1). Female condition, residual growth, and egg lipid content were also important. According to AIC_c , empirical support for multiple linear regression models based on egg size, female condition, residual growth, and egg lipid content was strongest for the model that included only egg size ($w_i = 0.32$, adjusted $R^2 = 0.34$); support was similar for the model that included both egg size and maternal condition ($w_i = 0.15$, adjusted $R^2 = 0.39$; Table 1). We found little evidence for an effect of paternal quality on offspring survival (Table 1; see Appendix A for details), and no evidence that either parental size or relative offspring survival rate increased or decreased with spawning day. Regression diagnostics for both univariate and multiple regression models followed Quinn and Keough (2002).

TABLE 1. Multiple linear regression models for which there was strong evidence ($\Delta_i < 2$) that parental traits influenced relative offspring survival rate of walleye (*Sander vitreus*) in the pond experiment.

Parent	Model	$\log(\hat{\sigma}^2)$	AIC_c	AIC_c rank	Δ_i	w_i	Adj. R^2
Dam	$0.048 \times \text{ES} - 0.028$	-4.26	-99.32	1	0.000	0.319	0.34
	$0.045 \times \text{ES} + 0.038 \times \text{K} - 0.064$	-4.31	-97.75	2	1.561	0.146	0.39
Sire	$-0.037 \times \text{SD} + 0.072$	-4.03	-93.73	1	0.000	0.178	0.02
	$1.31 \times 10^{-4} \times 5V + 0.013$	-4.03	-93.59	2	0.134	0.167	0.00
	$4.32 \times 10^{-4} \times \text{A} + 0.025$	-4.02	-93.29	3	0.436	0.144	-0.02
	$-0.063 \times \text{LL} + 0.054$	-4.02	-93.29	4	0.437	0.143	-0.02

Notes: Sample sizes were $n = 25$ dams and 25 sires. Model selection was based on the corrected Akaike's information criterion (AIC_c ; Anderson 2008). Abbreviations are: ES, egg size (mg dry mass); K, condition ($\text{g}\cdot\text{mm}^{-3}\cdot 10^5$); EL, egg lipid (proportion of dry mass); SD, $\log(\text{sperm density})$ (millions of sperm/ μL of milt); 5V, average sperm path velocity (VAP, in $\mu\text{m}/\text{s}$) at 5 s after activation; A, age (years); LL, arcsine square-root liver lipid (proportion of dry mass); $\hat{\sigma}^2$, residual variance; Δ_i , AIC_c differences; w_i , Akaike weight; Adj. R^2 = adjusted coefficient of multiple determination. Adult walleye were netted from the Napanee River, a tributary to the Bay of Quinte, Lake Ontario, for use in the pond experiment.

These results suggest that female walleye exhibit strong MI on juvenile survival under seminatural field conditions. This finding is consistent with laboratory experiments showing effects of walleye egg size on both hatching success (Johnston 1997) and larval survival up to 13 d post-hatch (Moodie et al. 1989, Johnston et al. 2005). These authors also reported a positive effect of egg size on both larval size (Moodie et al. 1989, Johnston 1997) and feeding success (Moodie et al. 1989). In our experiment, offspring size after two months was related positively to egg size ($\ln(\text{fork length}) = 4.096 + 0.155 \times \ln(\text{egg size})$, $r^2 = 0.22$, $n = 25$, $P = 0.017$). Because offspring survival in fish depends on the competitive advantage that body size confers on larger larvae in food-limited environments (Sogard 1997), it is likely that offspring survival in this study was mediated through positive effects of egg size on both offspring size and feeding success. The presence of strong MI on survival into the juvenile stage also corroborates results from rainbow trout and steelhead trout (*Oncorhynchus mykiss*) after one year in a hatchery (Herbinger et al. 1995) and six months in a stream (Seamons et al. 2004) that show that MI do not necessarily weaken as offspring develop (Bernardo 1996, Chambers and Leggett 1996, Heath and Blouw 1998).

Although egg size and offspring survival were not related to maternal age or size in our sample of 25 females from the Bay of Quinte, the larger sample ($n = 62$) of females that was collected from this population over the period 2002–2004 (Wiegand et al. 2007) showed positive associations between maternal size and both egg size (ANCOVA, $R^2 = 0.34$, $P = 0.002$) and lipid content. These observations are consistent with evidence from other walleye populations that (1) egg size increases with maternal age or size (Appendix B: Fig. B2; Johnston and Leggett 2002) and (2) larval survival increases with either maternal age or size (Johnston 1997, Johnston et al. 2007) or with aspects of egg quality that themselves increase with maternal age or size (Moodie et al. 1989, Johnston 1997, Czesny and Dabrowski 1998). The frequent appearance of associations between maternal age, egg size, and offspring survival in both field and laboratory studies of walleye justifies an assessment of the potential influence of such relations on walleye population dynamics.

Population modeling

Associations between maternal age, egg size, and offspring survival are a common feature of walleye studies. But can MI on offspring survival affect the dynamics of an exploited walleye population? To test this hypothesis, we combined the relation between offspring survival and egg size that was observed in our pond experiment (Table 1) with a relation between egg size and maternal age that is typical of walleye populations (Appendix B). We then incorporated the resultant relation between offspring survival and maternal age into a matrix population model in which

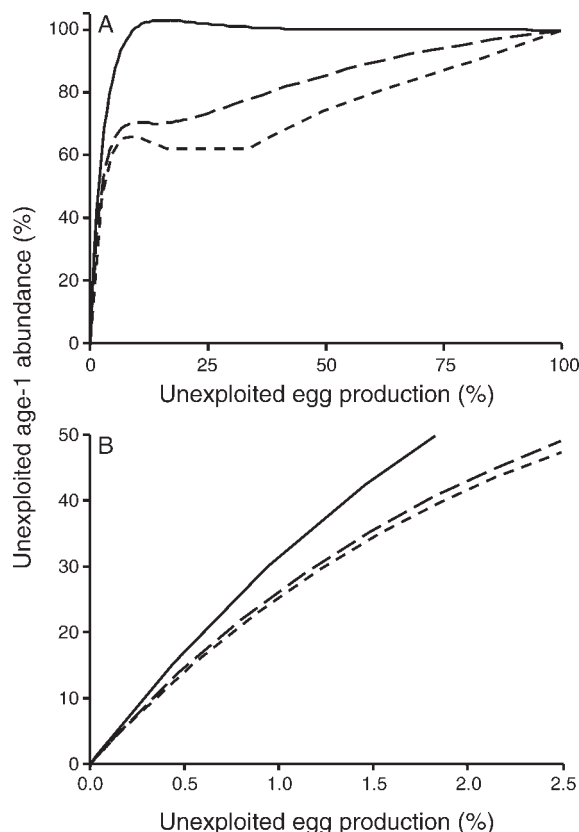


FIG. 2. Simulated stock–recruitment relations of walleye (*Sander vitreus*) showing maternal influences on recruitment. Egg production and resulting abundance of age-1 recruits (both expressed as a percentage of unexploited levels) are at two scales: (A) over the full range of values and (B) near the origin (where egg production was low because of high harvest mortality). Each line is from one of three harvest strategies: harvest young (solid line; ages 2, 3, and 4 harvested), harvest all (long dashes; all age harvested), and harvest old (short dashes; age classes eliminated in sequence from oldest to youngest). Any point along a line represents the egg production and corresponding recruitment at equilibrium for a given harvest mortality. For a given level of egg production, differences in recruitment among harvest strategies are due to the positive relation between larval survival and maternal age and the effect of a particular harvest strategy on the mean age of spawners.

maternal age classes were subjected to one of three strategies of harvest: harvest young, harvest all, or harvest old.

Model simulations produced a distinct stock–recruitment relation for each of the three harvest strategies (Fig. 2A). These results show that the MI on survival that were observed in our single-season pond experiment are strong enough to affect the dynamics of an exploited population of walleye when these MI scale with maternal age and are applied across all individuals over many seasons. Furthermore, because (1) recruitment over the entire range of egg production was highest when older age classes were protected from harvest and (2) the protection of older age classes translated into a

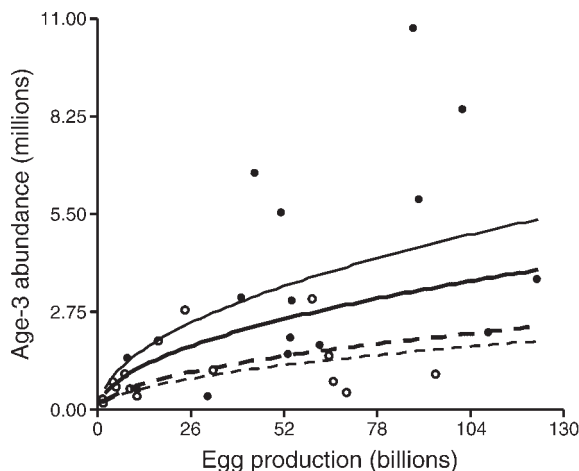


FIG. 3. The stock–recruitment relation of walleye (*Sander vitreus*) in Lake Erie from 1947 to 1976 showing maternal influences on recruitment. Each data point is an estimate of total annual egg production and corresponding age-3 abundance when the mean age of adult females was either above (solid circles) or below (open circles) the median value of 3.66 years. Egg production estimates incorporated density-dependent life history changes, and recruitment estimates are presented here with the effects of spring warming rate (ΔT) and water level (W) removed. Curves were predicted using a multiple linear regression model: $\log(\text{recruitment}) = 0.50 \times \log(\text{egg production}) + 0.31 \times \text{mean age} + 6.28 \times \Delta T + 0.65 \times W - 121.36$. ΔT and W were fixed at mean observed values of 0.21°C/g and 174.21 m, respectively, and mean age was equal to the minimum observed (3.03 years; thin, dashed line), maximum observed (4.44 years, thin, solid line), mean of values below the median (3.29 ± 0.11 years; thick, dashed line), or mean of values above the median (4.01 ± 0.14 years; thick, solid line). All model coefficients were significant at $P \leq 0.03$. The slope at the origin (α_0) of the stock–recruitment relation (10^{-5} age-3 recruits/egg) associated with each of these four mean ages was 0.55, 1.52, 0.66, and 1.12, respectively.

1.2-fold increase in α_0 over strategies that either ignore age structure or target older age classes (Fig. 2B), we conclude that, when MI increase with maternal age, a population's maximum reproductive rate will increase with the mean age of adult females.

The relative response of α_0 to different harvest strategies was independent of both the strength of density dependence (see Appendix B) and our estimate of mortality in the first year of life. However, this relative response was sensitive to the slope of the relation between egg size and maternal age (or FL), which can vary in both time and space in walleye (Appendix B: Fig. B2; Johnston and Leggett 2002, Wiegand et al. 2007). As the slope of the egg size–maternal age relation increased from 0 (egg sizes equal across all ages) to 0.1 mg dry mass/yr (egg sizes increase with maternal age to a maximum that is typical of walleye in the middle of their range; Johnston and Leggett 2002), harvest-induced changes in α_0 increased linearly from zero to twofold. Qualitatively, this result is entirely predictable because the strength of MI on survival in this model depended on the strength of the

egg size–age relation; if egg size did not vary with age, then MI were effectively absent from the model. Quantitatively, this result illustrates how the impact of age-based MI on the dynamics of wild populations can vary from year to year as a result of known variation in the strength of the egg size–maternal age relation (Johnston and Leggett 2002).

Population dynamics in Lake Erie

Because harvesting tends to remove from a population older, larger individuals (i.e., those individuals that might contribute the most to recruitment), our model predicts that, if MI increase with maternal age or size, then maximum reproductive rate will be lowest when the mean age of adults is low and highest when the mean age of adults is high (see also Venturelli et al. 2009). However, the extent to which MI on survival affect the dynamics of an actual population will depend on both the strength and consistency of this relation and the relative influence of many other physical and biological factors (Hilborn and Walters 1992). What evidence is there for MI on maximum reproductive rate in the wild?

Consistent with experimental evidence for strong MI on survival (Table 1, Fig. 1), as well as model predictions based on the assumption that these MI scale with age (Fig. 2), our analysis of published data from an exploited population of walleye in Lake Erie found that (1) recruitment (i.e., offspring survival) tended to be higher when the mean age of adult females was high relative to when it was low (Fig. 3) and (2) the slope at the origin (α_0) of the stock–recruitment relation increased 1.68-fold when the mean age of adult females increased from 3.29 to 4.01 years (comparison of group means) and 2.75-fold when the mean age of adult females increased from 3.03 to 4.44 years (maximum vs. minimum values; Fig. 3). This positive effect of mean age on recruitment in Lake Erie suggests that MI on survival are related to the mean age of spawners and occur over multiple breeding seasons and at a magnitude that is sufficient to affect the dynamics of natural populations of walleye. Relative to other exploited fishes, a 1.68- to 2.75-fold difference in α_0 is consistent with the results presented in Venturelli et al. (2009), which suggest that MI contributed to a doubling of α_0 among long-lived, marine fishes. It is also qualitatively consistent with evidence that recruitment in Baltic cod increases with the relative abundance of older females, which tend to produce eggs that are neutrally buoyant at depths at which temperature, salinity, and oxygen conditions are favorable for survival (Cardinale and Arrhenius 2000, Vallin and Nissling 2000).

With respect to other mechanisms of population dynamics, adult walleye in Lake Erie are not cannibalistic (one case of cannibalisms in 14 893 adults examined between 1979 and 1994; Madenjian et al. 1996), and our analysis controlled for effects of temperature and water quality. Results are also largely independent of density-dependent processes (e.g., life history changes, Allee

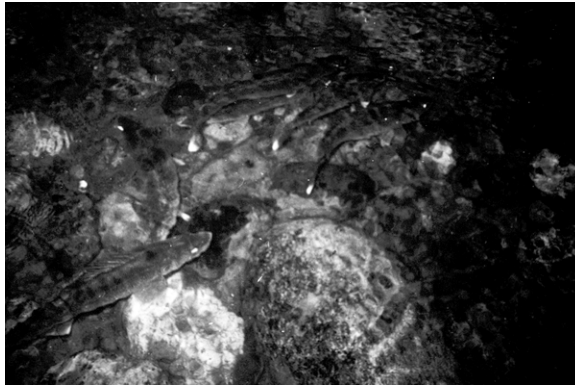


PLATE 1. (Left) A nighttime spawning aggregation of walleye (*Sander vitreus*) in the Nipigon River, Ontario, Canada, 1956. (Right) Two project members strip milt from a male walleye, Napanee River, Ontario, Canada. Photo credits: left, Dick Ryder; right, R. Montgomerie.

effects) because (1) both curves in Fig. 3 cover a similar range of egg production (i.e., population density); and (2) we incorporated observed changes in age-at-maturity, length-at-age, and mass-at-age into our estimates of total annual egg production. Interannual variation in relative fecundity (RF) is one exception. Although relations between RF and total length (TL) can vary annually in fishes (Venturelli et al. 2009), the absence of RF data from years other than 1966 in the period 1947–1976 forced us to assume a constant RF–TL relation in all years (Appendix C). To determine the sensitivity of our results to this assumption, we used data from 1966 to generate four alternative RF scenarios: (1) a neutral RF relation in which the mean observed RF value (82 eggs/g) was applied to all length classes in all years; (2) a steep, positive RF relation in which the highest (125 eggs/g) and lowest (45 eggs/g) observed RF values were associated with the largest and smallest females, respectively, in all years; (3) a steep, negative RF relation in which the highest and lowest observed RF values were associated with the smallest and largest females; and (4) a density-dependent RF in which the observed slope (0.075) declined linearly to 0 as the estimate of spawning female abundance increased from 0.3 million to 2.7 million individuals. This last scenario was based on evidence in other fishes (e.g., Atlantic cod; Yoneda and Wright 2004) that RF–age relations weaken with increasing density. For each of these scenarios, we repeated our analysis. We found that α_0 increased 1.64 to 1.72 times when the mean age of spawners increased from 3.29 to 4.01 years and 2.62 to 3.05 times when the mean age of spawners increased from 3.03 to 4.44 years. Because these results are similar to our original estimates of 1.68 and 2.75, we conclude that evidence for MI on maximum reproductive rate in this population was robust to assumptions about the nature of the RF–TL relation.

In discussing MI on population dynamics, it is also instructive to highlight several differences between our model and an actual population of walleye. First, our

MI–age relation was a necessary simplification of a complex process. In walleye, there is evidence that MI on survival stem from positive effects of maternal quality on spawning time or duration (Zhao et al. 2009), hatching success, and egg, yolk, and larval size (e.g., Moodie et al. 1989, Johnston 1997, Johnston et al. 2005, 2007). These MI tend to increase with maternal age and (or) size because naïve spawners are often inferior spawners (e.g., Carr and Kaufman 2009) and because optimal egg size often increases with clutch size as a result of density-dependent effects on egg and larval survival (Einum and Fleming 2002, Hendry and Day 2003, Kamler 2005). And although senescence dictates that MI are unlikely to persist as wild fish approach maximum age, survival to maximum age in a harvested population is also unlikely (Kamler 2005). The strength of MI on survival is also sure to vary over time and among populations. Therefore, although this study establishes that MI on survival can affect population dynamics, a detailed understanding of the importance of this mechanism to specific populations will require further study. Second, whereas our model assumed fixed, knife-edge maturity at four years of age, maturity in Lake Erie walleye was density-dependent, with 4–98% of females in a given year maturing as early as age-3. Because three- and four-year-olds together accounted for an average 54% (range 4–100%) of the total annual abundance of adult females, the observed differences in mean age between the maximum and minimum observed values (1.41 years) and the “high” and “low” groups (0.72 years) mask relatively large differences in the distribution of abundance among ages. For example, if we describe the high and low groups in terms of the percentage of adult females that were “old” (i.e., ≥ 5 years of age), it shows that 21% of adult females were old when mean age was high, but only 7% when mean age was low. Finally, we recognize that other factors (e.g., spring warming rate, water level) contribute to the dynamics of wild populations. However, the relative importance of MI on offspring survival stems, not only

from its relative effect on recruitment, but also from the fact that it can be managed through exploitation. In other words, managers have little influence over the environment, but they can choose to protect those individuals that are likely to produce the most recruits under both favorable and unfavorable environmental conditions.

Conclusions

Our results support the view that juvenile survival in walleye varies with maternal quality through associations between egg size, egg quality, and other factors that are related to the age or size of a female. They also demonstrate, for the first time in a species of freshwater fish, that MI on offspring survival can produce relatively large changes in a population's maximum reproductive rate. Together with similar evidence in long-lived marine fishes (Cardinale and Arrhenius 2000, Vallin and Nissling 2000, Venturelli et al. 2009), a soil mite (Benton et al. 2005, 2008), and a pest moth (Kendall et al. 2005), our study shows that the effects of maternal quality on offspring survival can be an important mechanism that should be considered when interpreting (e.g., Kendall et al. 2005, Anderson et al. 2008) and forecasting population dynamics. For example, although total egg production in fish can be a more accurate measure of reproductive potential than adult biomass when RF varies among years or individuals (Marshall et al. 1998), this approach ignores potential effects of MI on the viability of eggs unless it is complemented by information on population structure with respect to those maternal characteristics (e.g., age, size) that correlate with offspring survival (e.g., Marteinsdottir and Thorarinsson 1998).

More generally, our results provide further support for a change in the way that populations are managed: if certain individuals in a population contribute more to recruitment than others, then these individuals should be a priority of management (e.g., Forbes and Peterman 1994, Marteinsdottir and Thorarinsson 1998, Murawski et al. 2001, Berkeley et al. 2004, Law 2007, Secor 2007, Venturelli et al. 2009). We do not recommend strategies that ignore overall mortality; rather, we recommend additional controls on the distribution of mortality among individuals of varying reproductive value. While it seems obvious to suggest that exploited populations that exhibit MI on survival would benefit from strategies that protect rather than target reproductively valuable individuals, many populations are managed as though their dynamics depend solely on population size and extrinsic factors such as climate. Fishing regulations that either ignore age structure or promote the harvest of older individuals through minimum limits on harvestable size (Myers and Mertz 1998) are one example. The selective removal of reproductively valuable individuals through trophy hunting or fishing (Allendorf and Hard 2009) is another. Such strategies should be reevaluated given increasing evidence that they can erode the

reproductive rate of a population through harvest-induced demographic change (Venturelli et al. 2009) and evolution (Law 2007, Allendorf and Hard 2009) and thereby contribute to a reduction in a population's resilience to both environmental variability and exploitation (Berkeley et al. 2004, Law 2007, Secor 2007, Anderson et al. 2008).

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APPENDIX A

Additional information related to the pond experiment (*Ecological Archives* E091-137-A1).

APPENDIX B

Additional information related to the population model (*Ecological Archives* E091-137-A2).

APPENDIX C

Information related to the analysis of Lake Erie walleye (*Ecological Archives* E091-137-A3).