

Thermal environment and maternal effects shape egg size in a freshwater fish

ZACHARY S. FEINER,^{1,†} HUI-YU WANG,² DONALD W. EINHOUSE,³
 JAMES. R. JACKSON,⁴ EDWARD S. RUTHERFORD,⁵ CHRIS SCHELB,⁶ CHRISTOPHER S. VANDERGoot,⁷
 TROY G. ZORN,⁸ AND TOMAS O. HÖÖK^{1,9}

¹Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana 47907 USA

²Institute of Oceanography, National Taiwan University, Taipei 106 Taiwan

³New York State Department of Environmental Conservation, Lake Erie Fisheries Research Unit, Dunkirk, New York 14048 USA

⁴Department of Natural Resources, Cornell University Biological Field Station, Bridgeport, New York 13030 USA

⁵NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan 48108 USA

⁶Michigan Department of Natural Resources, Southern Lake Huron Management Unit, Bay City, Michigan 48706 USA

⁷Ohio Department of Natural Resources, Sandusky Fish Research Unit, Sandusky, Ohio 44870 USA

⁸Michigan Department of Natural Resources, Marquette Fisheries Research Station, Marquette, Michigan 49885 USA

⁹Illinois-Indiana Sea Grant, Purdue University, West Lafayette, Indiana 47907 USA

Citation: Feiner, Z. S., H.-Y. Wang, D. W. Einhouse, J. R. Jackson, E. S. Rutherford, C. Schelb, C. S. Vandergoot, T. G. Zorn, and T. O. Höök. 2016. Thermal environment and maternal effects shape egg size in a freshwater fish. *Ecosphere* 7(5):e01304. 10.1002/ecs2.1304

Abstract. Offspring size determines offspring survival rates; thus, understanding factors influencing offspring size variability could elucidate variation in population dynamics. Offspring size variation is influenced through multigenerational adaptation to local environments and within-lifetime plastic responses to environmental variability and maternal effects among individuals. Moreover, offspring size variation may represent trade-offs in energy allocation within individuals that influence lifetime reproductive success. However, the mechanisms whereby environmental conditions influence offspring size, e.g., via inducing adaptive and plastic variation in population-scale maternal effects, remain poorly understood. We evaluated intra-specific variation in maternal effects, egg size, and intra-individual egg size variation in six populations of walleye (*Sander vitreus*) and related among- and within-population patterns to thermal conditions. Egg size was conserved within populations and negatively related to long-term thermal conditions among populations, while maternal effect strengths were positively related to thermal conditions, suggesting that populations inhabiting warmer environments adapted to produce smaller eggs but stronger maternal effects. Within a population, egg size was positively related to colder winters, suggesting cold winters may alter egg size through effects on maternal condition or as an adaptive maternal effect to improve offspring survival. Intra-individual egg size variation varied little among populations or with female size, but declined with increasing summer and decreasing winter temperatures. Our result suggests that environmental conditions could impact not only short-term offspring production but also spur adaptive changes in offspring phenotypes. Thus, it is necessary to account for adaptive responses to predict population dynamics under environmental changes.

Key words: Laurentian Great Lakes; life history; offspring size; phenotypic plasticity; random effects; reaction norm analysis; *Sander vitreus*.

Received 3 November 2015; accepted 19 November 2015. Corresponding Editor: E. García-Berthou.

Copyright: © 2016 Feiner et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** zfeiner@purdue.edu

INTRODUCTION

Both theoretical models (Smith and Fretwell 1974) and empirical data (Einum and Fleming 2000) indicate that the size of offspring produced by an individual female reflects a trade-off between offspring size and number that interacts with environmental effects on ensuing maternal and offspring fitness. These trade-offs may lead to adaptive differences in offspring size among populations experiencing different environments (Parichy and Kaplan 1992, Wang et al. 2012). However, all females exposed to the same environment do not produce offspring of similar phenotypes. Maternal effects (i.e., correlations between maternal and offspring phenotypes) have been observed in a wide range of taxa (e.g., Parichy and Kaplan 1992, Johnston and Leggett 2002, Badyaev et al. 2006, Allen et al. 2008), where larger females often produce larger or better provisioned offspring that exhibit improved fitness (Berkeley et al. 2004, Badyaev et al. 2006, Bestion et al. 2014). These effects may represent adaptive, transgenerational phenotypic plasticity, where the environment experienced by the mother causes her to produce offspring with phenotypes better suited to that environment (Allen et al. 2008), or reflect adaptive changes in offspring size as increases in maternal size or age shift the balance between offspring size and number (Einum and Fleming 2000). Hence, the strength and direction of maternal effects within and among populations are likely shaped by an interaction of environmental and evolutionary dynamics, meaning investigations attempting to quantify levels of adaptive or plastic variation in maternal effects are warranted.

While a large amount of literature exists on the strength, direction, and potential significance of variation in offspring size among and within populations (e.g., Johnston and Leggett 2002), much less research has evaluated offspring size variation within individuals (i.e., mothers producing eggs of varying sizes within the same clutch), which can have important implications for offspring survival and fitness (Koops et al. 2003, Einum and Fleming 2004, Allen et al. 2008). Such variation may be due to imprecise ability of females, especially those in poor condition or with high fecundity, to equally allocate energy across hundreds or thousands

of eggs (Einum and Fleming 2004). Alternatively, intra-individual offspring size variation may be a bet-hedging strategy for females facing highly unpredictable environments, where the production of a large range of offspring sizes increases the probability that at least some will have high fitness in the future environment, thus increasing the female's overall fitness (Dziminski et al. 2009). However, little research has been conducted to elucidate which of these mechanisms is a more likely explanation for much of the variation observed in empirical studies.

Offspring size variation must also be placed in the context of interannual environmental variation. For example, growth and energy allocation in fish are largely determined by the thermal environment and availability of resources throughout the year, and therefore, changes in energy allocation to gonads due to variable environmental conditions may influence the size and number of eggs and larvae produced by females (Moodie et al. 1989, Moles et al. 2008). Because larval size is one of the most important determinants of offspring survival in many fish species, variation in egg size due to local adaptation and maternal and environmental effects could have significant ramifications for recruitment and population dynamics (Berkeley et al. 2004, O'Farrell and Botsford 2006). Thus, intra-specific egg size variation could be partitioned into components including adaptive among-population differences influenced by long-term selection regimes imparted by local environments (Wang et al. 2012), within-population variation among individuals through age- or size-related maternal effects (Einum and Fleming 2000) and variable interannual environmental conditions (Atkinson et al. 2001), and within-individual variation potentially linked to bet-hedging strategies in unpredictable environments (Einum and Fleming 2004).

In this study, we attempt to disentangle the relative importance of local adaptation, maternal effects, and environmental variation by examining spatial and temporal variability in both mean egg size and intra-individual egg size variation in six populations of an iteroparous freshwater teleost, walleye (*Sander vitreus*), from the Laurentian Great Lakes region of the United States. Walleye is an economically and ecologically important piscivore (Ivan et al. 2011, Feiner and Höök 2015) that follow a determinate,

capital spawning strategy, allocating energy to gonad and egg development for several months prior to spawning in late March or early April (Malison et al. 1994). Importantly, walleye reproductive success appears to be regulated by maternal temperature and resource abundance, in addition to abiotic influences on egg and larval survival (Hokanson 1977, Madenjian et al. 1996, Hansen et al. 2015). Egg size in walleye varies significantly among distinct populations and with maternal size within populations (Moodie et al. 1989, Johnston and Leggett 2002, Wang et al. 2012). Larger walleye eggs also contain more lipids and hatch larger larvae that exhibit higher survival and growth rates when compared with smaller eggs (Moodie et al. 1989). The specific objectives of this study were to (1) ascertain the relative extent of among-population and within-population differences in egg size, intra-individual egg size variation, and the magnitude of maternal effects, and (2) evaluate the importance of both long-term and interannual thermal conditions to patterns in egg traits and maternal effects among six walleye populations

in the Great Lakes region sampled over up to 7 years of study.

METHODS

Walleye populations

From 2007 to 2013, walleye eggs were collected from six walleye populations from the Great Lakes region: Little Bay de Noc, Green Bay, Lake Michigan; Tittabawassee River, Saginaw Bay, Lake Huron; Muskegon River, Lake Michigan; the Maumee River and Sandusky River, western basin of Lake Erie; Oneida Lake, New York; and Van Buren Bay, eastern basin of Lake Erie (Fig. 1). The systems these populations inhabit vary considerably in latitude, productivity, and temperature (Fig. 1, Appendix S1: Table S1). Moreover, all six populations are spatially distinct, and natural dispersal among populations is limited (Strange and Stepien 2007, Stepien et al. 2009). Walleye from the Maumee and Sandusky rivers both inhabit western Lake Erie, and their egg traits did not significantly differ in this and another study (Wang et al.

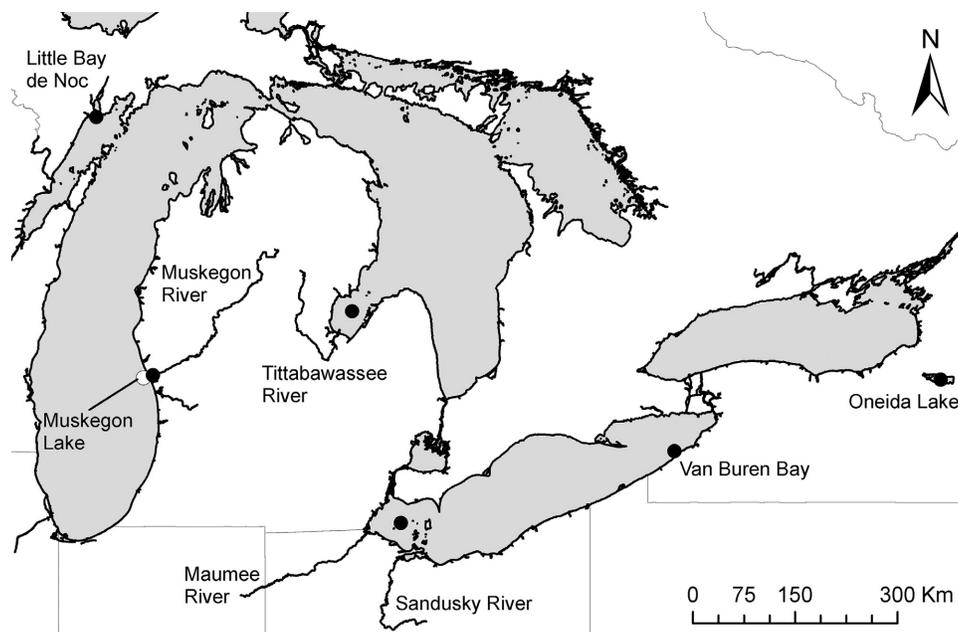


Fig. 1. Locations of sites sampled for walleye (*Sander vitreus*) eggs in springs of 2007–2013. Black points denote locations where estimated or observed epilimnetic water temperatures were used to calculate growing and cooling degree days with a base of 5°C. White point west of Muskegon Lake denotes location where Lake Michigan daily water temperature data were used to predict Muskegon Lake daily water temperatures (Appendix S2).

2012), so these populations were combined for further analyses.

Egg collection and measurement

In each population, we stripped eggs from ripe, running females collected over 1–2 days during their respective spawning runs in late March to early April (for more details on fish collections, see Wang et al. 2012 and Appendix S1). Because eggs were stripped directly from gravid females and immediately preserved in 10% formalin, we assumed that all eggs were collected at the same developmental stage (Malison et al. 1994). Each female was measured for total length (mm TL) following egg collection. All applicable institutional and national guidelines for the care and use of animals were followed. A subsample of 10 random eggs was measured to estimate mean egg diameter for each fish. In addition, for each female, we calculated the coefficient of variation of egg diameter (CV; standard deviation of the 10 egg diameters/mean egg diameter \times 100) as a measure of intra-female egg size variation to control for the positive relationship between mean and standard deviation. Egg diameter CV was natural-log transformed to more closely approximate a normal distribution.

Analysis of among-population variation

Our first objective was to disentangle the relative importance of among-population vs. within-population variation in egg size and egg size CV attributable to maternal length. Evidence of among-population variation in egg size, egg size CV, or their relative maternal effects could be suggestive of adaptation of these traits due to differences in local environmental conditions. We used a random effects model including a group-centering design (Van De Pol and Wright 2009, Dingemanse et al. 2010) to examine the influence of adaptive variation in mean egg size and egg size CV among and within walleye populations. In this case, we were interested not only in how different walleye populations varied in their average egg size or egg size CV (i.e. their intercept) but also how the strength and direction of their respective maternal influences varied (i.e., their slope with maternal length). Examining populations exposed to different environments that

may differ in both their intercept (i.e., among-population variation) and slope (i.e., within-population variation) could then allow us to evaluate potential mechanisms driving those observed differences.

Our analyses used a generalized mixed effects model in a Bayesian framework. Because we were interested in analyzing average levels of trait expression of each population, we pooled data over all years where fish were collected in each population. The mean egg diameter or egg diameter CV of each individual fish was then modeled with a random intercept for each population, random slopes for within-population effects of maternal length, and a fixed slope representing the among-population effect of mean maternal length:

$$y_{ij} = (\beta_0 + u_{0j}) + (\beta_W + u_{Wj})(x_{ij} - \bar{x}_j) + \beta_B \bar{x}_j + e_{0ij} \quad (1)$$

where y_{ij} represents mean egg diameter or egg diameter CV for each fish i from population j , β_0 the intercept, u_{0j} the random intercept effect for each population j , β_W and u_{Wj} the within-population slope and respective random effects, x_{ij} the total length of each female i from population j , \bar{x}_j the mean length of females from population j (thus $x_{ij} - \bar{x}_j$ represents total lengths centered within each population), β_B the between-populations effect of maternal length, and e_{0ij} the residual errors. The random intercepts, slopes, and errors were modeled as normal distributions with variances $\sigma_{u_{0j}}^2$, $\sigma_{u_{Wj}}^2$, and $\sigma_{e_{0ij}}^2$, respectively. Using this model, variation in the random intercepts (u_{0j}) could represent differences in mean egg size or egg size CV among populations, while variation in the random slopes (u_{Wj}) represent differences in the relative strength of their maternal effects. In addition, evidence for a between-population effect of mean maternal length (β_B) would suggest that at least some variation in trait expression among populations could be accounted for by differences in mean maternal size among populations. We also calculated the difference $\Delta\beta_{B-W} = \beta_B - \beta_W$ to quantify whether the average within-population maternal effect differed from the between-population maternal effect (Van De Pol and Wright 2009), where this difference could demonstrate whether increases in the average size of females play a different role in egg size

determination than differences in size among females of the same population.

Models were estimated using JAGS in R through the package “rjags” (Plummer 2013, R Core Team 2014), with uninformative priors for all parameters and random initial values. A 10 000 step burn-in was used to eliminate any influence of initial values, and estimates of the posterior distribution were retained from every 10th sample of the subsequent 1 000 000 steps. We confirmed convergence of the models using visual inspection of history plots and estimation of the Brooks-Gelman-Rubin statistics (Brooks and Gelman 1998). We determined the importance of effects via the estimation of 95% credible intervals (CI) as the 2.5th and 97.5th percentiles of the retained posterior estimates and as the one-tailed probability that the effect was not different from zero, i.e., $1 - P(\beta > 0)$ for positive coefficients and $1 - P(\beta < 0)$ for negative coefficients, where lower probabilities indicate more likely evidence of an effect (e.g., $P = 0.05$ for a positive β indicates only 5% of posterior draws were less than zero, suggesting a highly probable positive coefficient). The proportions of variance explained by population (β_{0j}) and maternal effects (β_{Wj}) were determined as the value of the respective variance component divided by the sum of all variance components ($\sigma_{u_{0j}}^2$, $\sigma_{u_{Wj}}^2$, and $\sigma_{e_{0ij}}^2$).

Analysis of interannual within-population variation

Our second objective was to determine the level of interannual variation in egg size, egg size CV, and maternal effects within a single population. For this analysis, we focused on the Tittabawassee River population, which was sampled for a sufficiently long timespan (7 years from 2007 to 2013) to allow for good model convergence and sufficient certainty in parameter estimation. Year and total length were included as random variables in Eq. 1, where j represented year instead of population, and total length was centered within each year j for the estimation of within-group random effects. Importance of effects was evaluated using the methods above. In this case, variation in the u_{0j} or u_{Wj} terms could indicate relative levels of plasticity in these traits, as this particular population is resident in the Saginaw Bay, Lake Huron system, and walleye spawn annually and exhibit sufficient spawning-site

fidelity to maintain genetic distinctness among spawning groups (Strange and Stepien 2007), meaning individuals collected during spawning are likely representatives of a single genetic population.

Climate data

To further investigate whether among-population variation in the long-term thermal environment or interannual variation in temperature within a population explained additional variation in mean egg size, egg size CV, or their within-population maternal effects, we first collected daily epilimnetic water temperatures from the National Oceanic and Atmospheric Administration (NOAA) Great Lakes Coastal Forecasting System (GLCFS) or in-lake temperature loggers at sites representing habitats walleye inhabit during the year prior to spawning (Fig. 1; Appendix S2). To index long-term thermal environments among our sampled populations, we calculated cumulative growing degree days above 5°C (GDD_{annual} ; Venturelli et al. 2010) for the 12 months prior to spawning (May to April) from 2007 to 2012 in each population (Appendix S2: Table S2). The average GDD_{annual} over these 6 years was calculated for each site as an index of the thermal environment fish experienced. To better capture interannual and seasonal thermal effects on egg size variation at the Tittabawassee site, we divided the year leading up to spawning into two periods based on patterns of gonadal development previously observed in walleye (Malison et al. 1994). First, cumulative growing degree days above 5°C were calculated during a growing season and energy acquisition period defined as May through September (GDD_{summer}). Second, overwinter temperatures and winter duration may influence reproductive success in percids (Hokanson 1977, Farmer et al. 2015), so we indexed the winter thermal environment as the cumulative cooling degree days below 5°C during a period of gonad development from October to April (CDD_{winter}), where more CDD_{winter} is indicative of colder, longer winters (Appendix S2: Table S3). GDD_{summer} and CDD_{winter} were only weakly correlated among years ($r = 0.21$), meaning warm summers were not necessarily preceded or followed by warm or cold winters. Our use of GDD_{summer} and CDD_{winter} allowed us to

potentially capture the importance of both summer energy acquisition and thermal suitability of winters for gonad development and egg size.

Effect of temperature on egg size variation

To examine the importance of among- and within-population variation in the thermal environment to egg size and egg size variation, we used a modified version of reaction norm analysis often used with best linear unbiased predictors (BLUPs) (Hadfield et al. 2010), regressing estimates of each random intercept or random slope from the random effects models above (i.e., Eq. 1) against respective estimates of cumulative growing or cooling degree days. Because we used Bayesian inference, we were able to sample the posterior distributions of each random intercept or slope in a given random effects model, thereby incorporating the uncertainty in each estimate and avoiding potential biases in BLUPs that often arise from frequentist point estimates of these parameters (Hadfield et al. 2010).

When evaluating among-population patterns in the thermal environment, 10 000 posterior estimates of each random slope or intercept for each population were obtained from the among-population random effects model and regressed against the 6-year average GDD_{annual} for each population, and we examined the effects of each regression coefficient using credible intervals and one-tailed probabilities as above. To evaluate whether the interannual and seasonal variation in the thermal environment explained further variation in the plasticity of egg size, egg size CV, or the strength of the maternal effect among years in the Tittabawassee population, we regressed our estimates of u_{0j} or u_{wj} against estimates of both GDD_{summer} and CDD_{winter} using the methods above. This information allowed us to make inferences about how egg size and egg size CV vary across different levels of organization, as well as determine whether differences in these traits varied with environmental conditions, which could indicate plastic responses to maternal environments.

RESULTS

Among-population variation in egg size

Mean egg diameter varied not only among Great Lakes walleye populations but also with differences in maternal length within and among

populations. The population effect explained on average 50% of variance in egg diameter, with the Maumee-Sandusky population producing smaller eggs than any other population (Fig. 2a, Table 1). Mean egg size among populations ranged roughly 0.2 mm, which corresponds to changes in egg volume of roughly 40% (and the difference between the largest and smallest mean egg sizes for individuals was nearly 0.5 mm or an increase of 300% in volume). Within-population maternal effects on egg diameter explained another 8% of the variation and were consistently positive with a high probability, but also varied significantly in

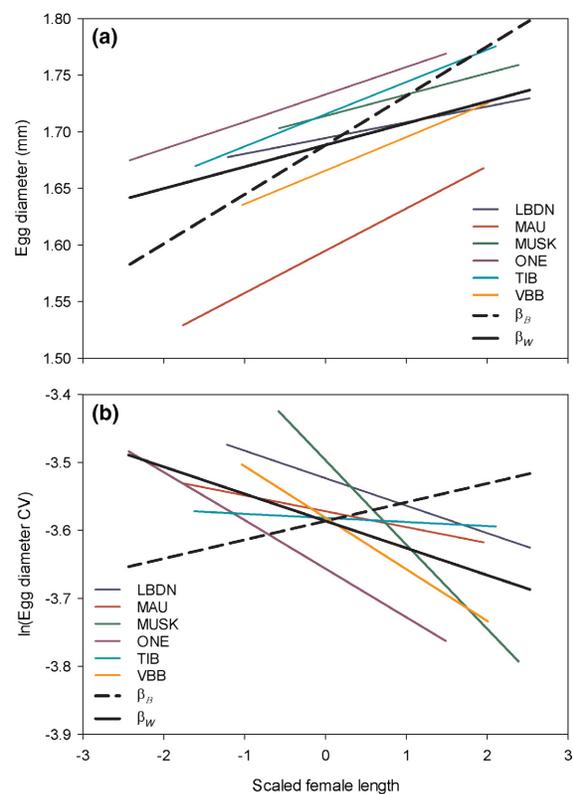


Fig. 2. Between (β_B ; dashed black line) and within (β_W ; solid black line) population variation in egg diameter (a) or egg diameter CV (b; note natural-log scale on y-axis) as related to maternal length. Colored lines represent relationships for each individual population (LBDN = Little Bay de Noc, MAU = Maumee-Sandusky rivers, MUSK = Muskegon Lake, ONE = Oneida Lake, TIB = Tittabawassee River, VBB = Van Buren Bay) from data pooled across years, where the slopes of these lines correspond to estimated β_{Wj} .

Table 1. Estimates of the mean, 2.5th and 97.5th percentiles, and one-tailed probability of not being different from zero (P) for random intercepts (β_0), random slopes (β_W), between-group slope (β_B) and variance components (σ_{ij}^2) of random effects models for among-lakes variation in egg diameter and egg size CV in walleye (*Sander vitreus*). Lake-specific mean effects are denoted as LBDN (Little Bay de Noc), MAU (Maumee-Sandusky rivers), MUSK (Muskegon River), ONE (Oneida Lake), TIB (Tittabawassee River), and VBB (Van Buren Bay).

Parameter	Among-lakes egg diameter				Among-lakes egg size CV			
	Mean	2.5%	97.5%	P	Mean	2.5%	97.5%	P
$\beta_{0,LBDN}$	1.708	1.629	1.785	0.000	-3.561	-3.617	-3.483	0.000
$\beta_{0,MAU}$	1.593	1.584	1.602	0.000	-3.570	-3.605	-3.529	0.000
$\beta_{0,MUSK}$	1.731	1.655	1.807	0.000	-3.610	-3.688	-3.552	0.000
$\beta_{0,ONE}$	1.709	1.625	1.793	0.000	-3.584	-3.649	-3.517	0.000
$\beta_{0,TIB}$	1.715	1.710	1.720	0.000	-3.581	-3.608	-3.555	0.000
$\beta_{0,VBB}$	1.676	1.645	1.707	0.000	-3.608	-3.678	-3.558	0.000
β_B	0.044	-0.039	0.126	0.104	0.028	-0.038	0.095	0.134
$\beta_{W,LBDN}$	0.011	0.002	0.020	0.011	-0.033	-0.081	0.013	0.078
$\beta_{W,MAU}$	0.034	0.025	0.042	0.000	-0.021	-0.062	0.023	0.151
$\beta_{W,MUSK}$	0.011	0.000	0.023	0.029	-0.076	-0.153	-0.013	0.006
$\beta_{W,ONE}$	0.015	0.006	0.024	0.001	-0.045	-0.095	-0.001	0.022
$\beta_{W,TIB}$	0.021	0.014	0.027	0.000	-0.004	-0.042	0.036	0.410
$\beta_{W,VBB}$	0.023	0.012	0.036	0.000	-0.059	-0.135	0.000	0.028
β_W	0.019	0.006	0.032	0.008	-0.040	-0.100	0.012	0.048
$\Delta\beta_{B-W}$	0.024	-0.059	0.109	0.215	0.067	-0.017	0.158	0.046
β_0	1.688	1.614	1.764	0.000	-3.586	-3.639	-3.538	0.000
σ_{Wij}^2	0.013	0.005	0.032	0.000	0.049	0.004	0.141	0.000
σ_{ij}^2	0.080	0.036	0.195	0.000	0.044	0.003	0.144	0.000
$\sigma_{\epsilon_{ij}}^2$	0.068	0.066	0.070	0.000	0.386	0.374	0.397	0.000

strength among populations—for example, the maternal effect coefficient for the Maumee-Sandusky population (0.034) was strongly different from zero ($P < 0.005$) and three times the magnitude of the coefficient for the Muskegon population (0.011, $P = 0.03$). These within-population effects were only marginally weaker than the between-population effect of maternal length ($P = 0.22$). The 6-year average thermal conditions experienced by each population also appeared to play a role in determining egg size. Specifically, there was a negative association between mean GDD_{annual} and mean egg size (as indicated by the population-specific random intercepts; Fig. 3a; Appendix S3: Table S1), and a positive association between mean GDD_{annual} and the strength of the maternal effect (as indicated by the population-specific random slopes; Fig. 3c; Appendix S3: Table S1).

Among-population variation in intra-female egg size CV

Among-population variation in intra-individual egg size CV exhibited a contrasting pattern to

egg diameter. The population effect explained much less variation in egg size CV, roughly equaling the explanatory power of within-population maternal effects (~9% and 10%, respectively; Table 1). Interestingly, between- and within-population effects of maternal length operated in opposite directions (Fig. 2b). Populations with larger mean maternal sizes tended to produce more variable clutches than those with smaller females. However, within populations, larger individuals produced less variable clutches. Similar to egg diameter, there was significant variation in the strength of the maternal effect among populations, ranging from virtually zero effect in the Tittabawassee River to strong negative effects in Oneida Lake and the Muskegon River. There were no apparent effects of mean GDD_{annual} on egg size CV or its respective maternal effect (Fig. 3b,d; Appendix S3: Table S1).

Within-population variation in mean egg size

Egg diameter varied both among years and with maternal length among females in the

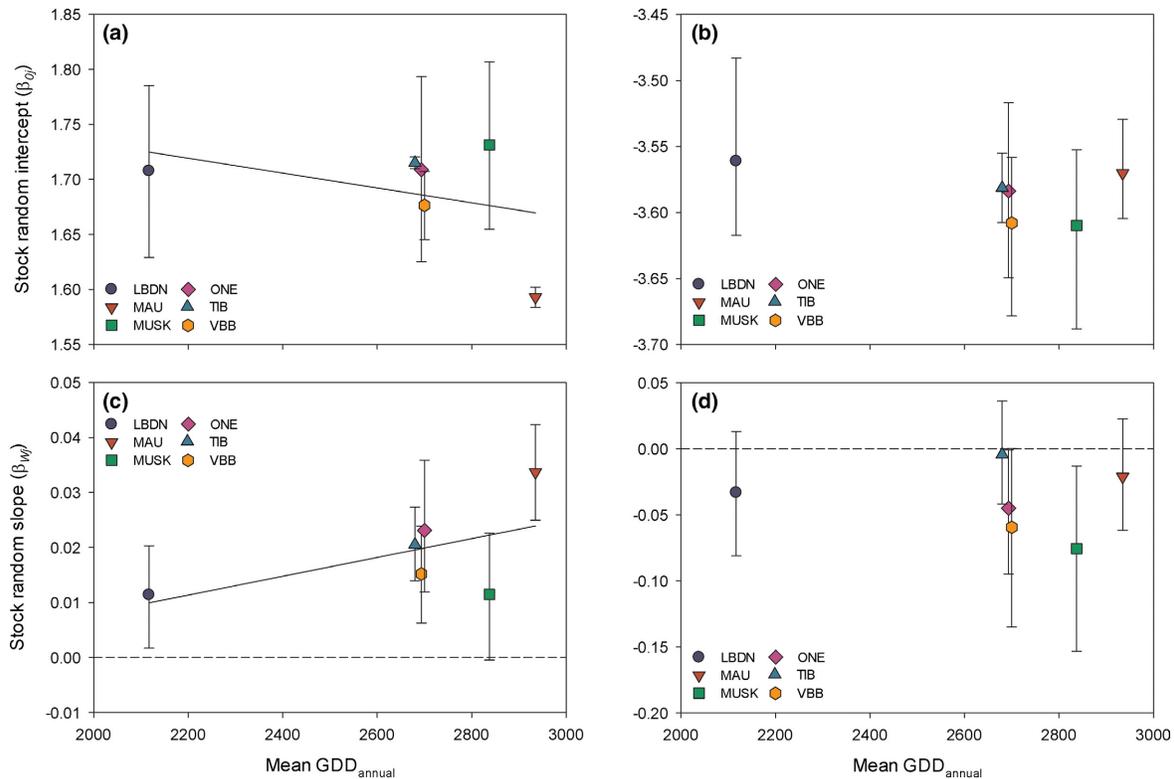


Fig. 3. Top two panels demonstrate relationships of average egg diameter (a) or egg diameter CV (b) (i.e. the population-specific random intercepts) to the 6-year average annual growing degree days above 5°C (GDD_{annual}) experienced by each population (Little Bay de Noc, LBDN; Maumee-Sandusky Rivers, MAU; Muskegon River, MUSK; Oneida Lake, ONE; Tittabawassee River, TIB; Van Buren Bay, VBB) after accounting for among-population variation due to maternal length. Lower two panels demonstrate the population-specific random slopes (i.e., the strength of the maternal effect in each population) on mean egg diameter (c) and egg diameter CV (d) and their relationship to mean GDD_{annual}. Error bars are 95% credible intervals for each intercept or slope measurement, dashed line denotes 0 (i.e., no maternal effect), and solid line displays mean linear regression estimate for relationships where $P \leq 0.05$.

Tittabawassee River. However, compared with across-population effects, mean egg diameter varied little among years (by <0.1 mm between 2007 and 2013) and year effects explained relatively limited amount of variation (34%). Within-year maternal effects explained an additional 15% of variation in egg size and were always positive, but varied considerably from year to year, with much larger coefficients in 2007, 2011, and 2013 than in any other year (Table 2; Fig. 4a). As in the among-population model, the between-year effect of maternal length was marginally stronger than the within-years effects. Mean egg diameter was positively related to CDD_{winter} in the Tittabawassee River

(Fig. 5a; Appendix S3: Table S2). The relationships between the maternal effect and both CDD_{winter} and GDD_{summer} were also positive, but the credible intervals for both slopes overlapped zero (Fig. 5c; Appendix S3: Table S2).

Within-population variation in intra-individual egg size CV

Intra-individual egg size variation in the Tittabawassee River population differed strongly among years but was not related to maternal length either within or between years (Table 2, Fig. 4b). This variation was largely related to thermal environment during the growing season, as annual egg size CV was negatively

Table 2. Estimates of the mean, 2.5th and 97.5th percentiles, and one-tailed probability of not being different from zero (P) for random intercepts (β_0), random slopes (β_W), between-group slope (β_B), and variance components (σ^2) of random effects models for among-year variation in egg diameter and egg size CV in Tittabawassee River walleye. Year-specific mean effects are denoted as 2007, 2008, 2009, 2010, 2011, 2012, and 2013.

Parameter	Feiner et al.				Among-year egg size CV			
	Mean	2.5%	97.5%	P	Mean	2.5%	97.5%	P
$\beta_{0,2007}$	1.667	1.641	1.691	0.000	-3.454	-3.571	-3.334	0.000
$\beta_{0,2008}$	1.694	1.673	1.717	0.000	-3.758	-3.856	-3.666	0.000
$\beta_{0,2009}$	1.711	1.682	1.745	0.000	-3.398	-3.533	-3.257	0.000
$\beta_{0,2010}$	1.710	1.647	1.768	0.000	-3.469	-3.716	-3.211	0.000
$\beta_{0,2011}$	1.717	1.656	1.771	0.000	-3.627	-3.862	-3.384	0.000
$\beta_{0,2012}$	1.724	1.706	1.742	0.000	-3.544	-3.633	-3.456	0.000
$\beta_{0,2013}$	1.751	1.716	1.792	0.000	-3.573	-3.737	-3.415	0.000
β_B	0.076	-0.124	0.257	0.151	-0.024	-0.808	0.780	0.466
$\beta_{W,2007}$	0.021	0.005	0.036	0.003	0.020	-0.022	0.082	0.206
$\beta_{W,2008}$	0.008	0.000	0.016	0.026	0.005	-0.031	0.040	0.383
$\beta_{W,2009}$	0.005	-0.008	0.017	0.240	0.007	-0.040	0.050	0.357
$\beta_{W,2010}$	0.006	-0.008	0.019	0.192	0.016	-0.025	0.071	0.243
$\beta_{W,2011}$	0.016	0.004	0.027	0.003	0.003	-0.042	0.041	0.420
$\beta_{W,2012}$	0.006	-0.014	0.024	0.266	0.004	-0.052	0.051	0.392
$\beta_{W,2013}$	0.039	0.021	0.056	0.000	0.005	-0.045	0.047	0.384
β_W	0.014	-0.003	0.032	0.048	0.009	-0.026	0.044	0.301
$\Delta\beta_{B-W}$	0.062	-0.138	0.243	0.194	-0.033	-0.817	0.776	0.457
β_0	1.711	1.672	1.749	0.000	-3.547	-3.717	-3.376	0.000
σ^2	0.020	0.007	0.045	0.000	0.022	0.001	0.077	0.000
$\sigma^2_{\mu_{Wij}}$	0.065	0.061	0.068	0.000	0.338	0.321	0.357	0.000
$\sigma^2_{\mu_{0ij}}$	0.045	0.019	0.110	0.000	0.199	0.091	0.454	0.000

related to CDD_{winter} and GDD_{summer} —in years with warmer summers or colder winters, females produced more consistently sized clutches (Fig. 5b; Appendix S3: Table S2). Maternal effects on egg size CV were unrelated to both GDD_{summer} and CDD_{winter} in the Tittabawassee River (Fig. 5d; Appendix S3: Table S2).

DISCUSSION

Egg size appeared to be governed by a complex interplay of among-population differences, maternal influences, and annual plasticity. Moreover, maternal effects on egg size and intra-individual egg size CV differed considerably among and within populations. These results shed new light into levels of plasticity in egg size and maternal effects and suggest that egg size expression is at least partially linked to the thermal environment experienced by the respective mothers, both over long-term (adaptation) and shorter, annual (plasticity) time scales.

Among-population differences in egg size

A negative relationship between offspring size and environmental quality has been observed in many taxa (e.g., Parichy and Kaplan 1992, Einum and Fleming 2004, Allen et al. 2008). Walleye populations that inhabited cooler systems produced larger eggs than those located in warmer environments in this study. The walleye populations studied here are separated spatially and genetically (Strange and Stepien 2007, Stepien et al. 2009). Energetic trade-offs among growth, metabolic costs, and reproductive investment also appear to vary significantly among walleye populations (Galarowicz and Wahl 2003), further supporting adaptation of important vital rates to local conditions. These results contrast the findings of Johnston and Leggett (2002), however, who found decreasing egg size with decreasing GDD. They suggested that high latitude populations may exhibit generally lower reproductive investment, and therefore smaller egg sizes. As we sampled lower latitudes than their study, egg size in our populations may

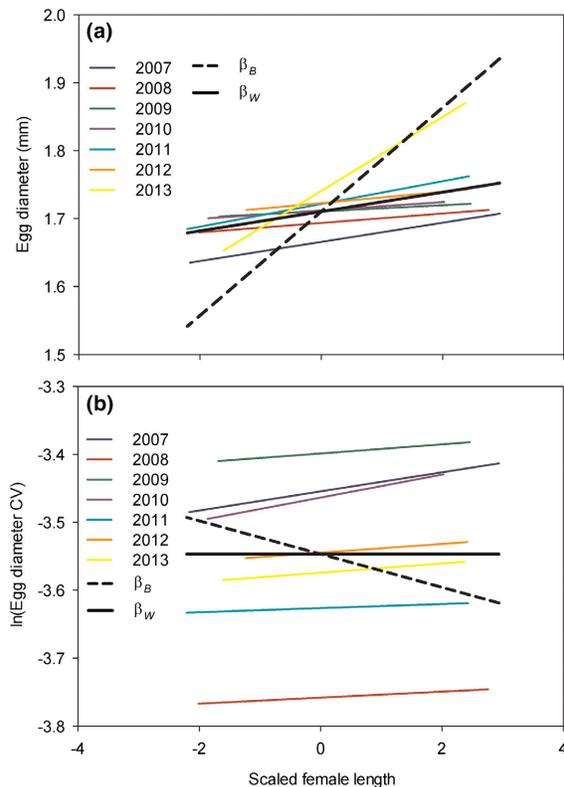


Fig. 4. Between (β_B ; dashed black line) and within (β_W ; solid black line) population variation in egg diameter (a) or egg diameter CV (b; note natural-log scale on y -axis) as related to scaled maternal length. Colored lines represent relationships for each year, where the slopes of these lines correspond to estimated β_W .

instead be driven by environmental effects on offspring survival, rather than female energetic investment. In addition, dynamics controlling larval and survival may differ between smaller inland lakes, as Johnston and Leggett (2002) sampled, and large Great Lakes systems we sampled (Pritt et al. 2014), which could influence differences in how egg size responds to the thermal environment between these types of systems. These results suggest that latitudinal clines in egg size may be nonlinear and that population-level differences in egg size we observed represent local adaptation to environmental conditions influencing variation in both female reproductive investment and offspring survival rates among walleye populations.

Differences in demography and other system characteristics that we did not explicitly consider,

such as trophic status, may have accounted for additional variation in egg size we were unable to explain. Age data were unavailable for all fish in this study, but other research suggests that the populations that produced the largest eggs, Little Bay de Noc and Muskegon Lake, are composed of fish up to 20 yr of age (Hanchin et al. 2007, Wang et al. 2012), while the other populations ranged from 2 to 15 yr old (Wang et al. 2012). Egg size has been positively related to maternal age in fish (Berkeley et al. 2004, Wang et al. 2012); thus, these differences could further influence egg size variation among populations. Variation in the trophic status and available food resources to both larvae (in the form of zooplankton) and adults (in the form of forage fish) may also influence egg size beyond what we were able to observe using only population and thermal effects. However, differences in egg size do meet previous expectations that, in general, populations inhabiting less productive, cooler systems tend to also produce the largest offspring sizes, supporting our assertion that at least some of the among-population variation we observed is due to local adaptive processes.

In all populations, the slope of the maternal length-egg size relationship was positive and different from zero, indicating that maternal effects are indeed prevalent in walleye (Johnston and Leggett 2002, Wang et al. 2012). We also observed a strong relationship between maternal effects and mean GDD_{annual} . Populations in relatively cold habitats may have adapted to produce eggs very near a physiological upper limit for the species (~2.0 mm; Moodie et al. 1989), thus reducing potential maternal effects. Species-specific physiological upper limits to egg size were observed across several marine and freshwater species (Duarte and Alcaraz 1989) and likely limit potential egg size plasticity. Again, our results contrast those of Johnston and Leggett (2002) in walleye, who reported that maternal effects were stronger at both environmental extremes of the species' range. This, however, could simply be due to the fact that they sampled more northerly populations and captured a greater amount of variation in GDD (ranging from 1000 to nearly 5000; populations in this study ranged from 1900 to 3000).

We should caution that the differences in among-population egg size and among-population maternal effects we observed may result from populations with small random

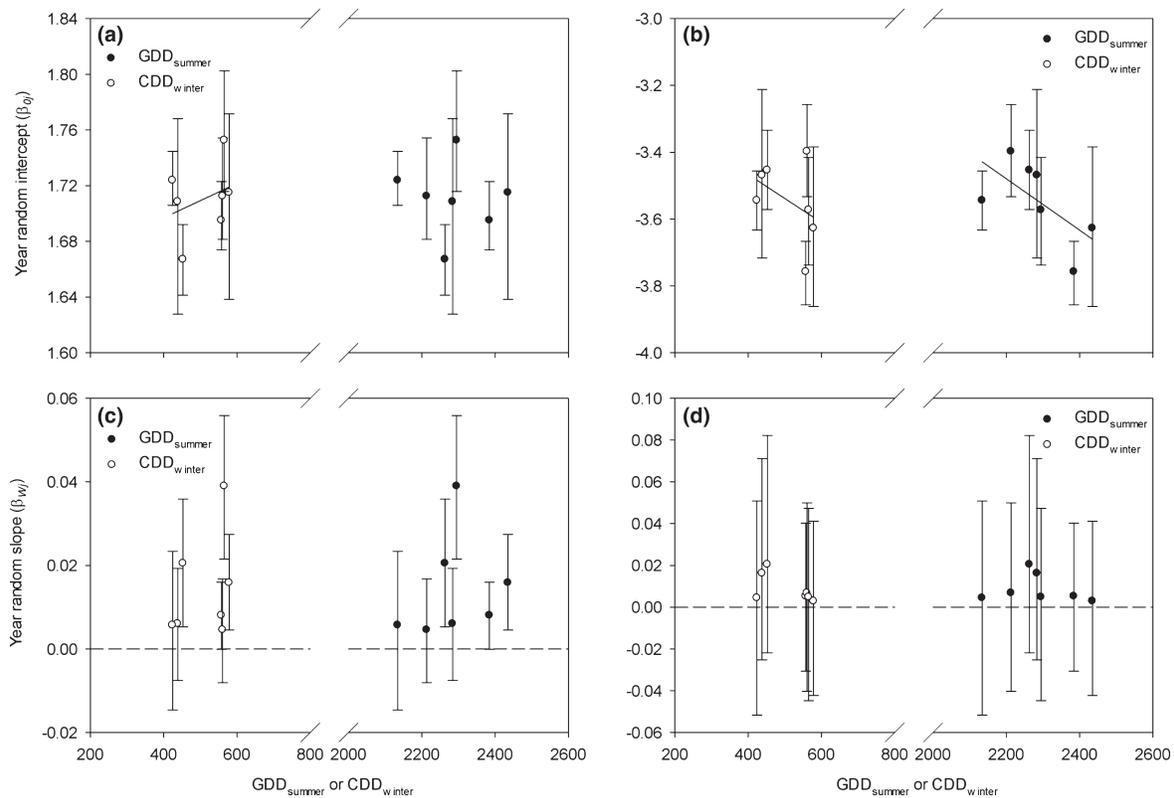


Fig. 5. Relationships of average egg diameter (a) or egg diameter CV (b) exhibited in each year (i.e., the year-specific random intercepts) to the seasonal growing degree days above 5°C (GDD_{summer} ; black points) or cooling degree days below 5°C (CDD_{winter} ; white points) in each year after accounting for among-year variation due to maternal length. Lower two panels demonstrate the year-specific random slopes (i.e., the strength of the maternal effect in each year) on mean egg diameter (c) and egg diameter CV (d) and their relationship to seasonal GDD_{summer} and CDD_{summer} . Error bars are 95% credible intervals for each intercept or slope measurement, dashed line denotes 0 (i.e., no maternal effect), and solid lines display mean linear regression estimate for relationships where $P \leq 0.05$.

intercepts (i.e., small eggs) by default exhibiting large random slopes (i.e., strong maternal effects) due to the statistical correlation between slopes and intercepts. There is good support for our observation that populations inhabiting favorable environments tend to produce smaller offspring, but further examination of maternal effects across a gradient of environmental conditions may be warranted to verify whether populations in more favorable environments do in fact produce stronger maternal effects as well. Nevertheless, we suggest that adaptive differences driven by local environmental conditions and differences in energy allocation may influence the expression of not only egg size but also the relative influence of maternal size.

Differences in intra-individual egg size CV among populations

Among-population variation in intra-individual egg size CV offered a striking contrast to the trends observed in mean egg diameter. Specifically, the patterns of among- and within-population maternal effects on egg size CV operated in opposing directions—populations with larger mean female size exhibited increased CV, but within populations, larger females tended to exhibit decreased CV. The mechanism driving these opposing patterns remains unclear. Potentially, within a single population, larger females experience reduced mass-specific metabolic costs (Cai and Summerfelt 1992), leaving more energy available to allocate toward

reproduction and a more even allocation of energy among eggs. This may also drive a correlation between egg size and intra-individual egg size variation. We observed positive maternal effects on egg size across populations, suggesting large females produced large eggs in addition to consistently sized clutches. Brook trout (*Salvelinus fontinalis*) exhibited a similar trend, where females producing large eggs also produced relatively less variable clutches than females producing small eggs in the same population (Koops et al. 2003). Energetic trade-offs between allocation toward growth or reproduction may be more significant in smaller or younger females, where their smaller, less developed ovaries may preclude complete energy absorption by oocytes (Kozłowski and Ziólko 1988) thereby increasing intra-clutch egg size variation in small individuals.

Among populations, the highest levels of intra-individual variation were observed in the generally cooler systems, which also produced larger females—potentially, the quality of larval habitats in these systems may be less predictable from year to year, which could drive relatively increased variability in egg size within individuals as a bet-hedging mechanism (Koops et al. 2003, Einum and Fleming 2004). Alternatively, shorter growing seasons in these habitats may lead to reduced female energy acquisition and increase egg size variability among all females. Lake trout (*Salvelinus namaycush*) that were raised in captivity or exploiting relatively poorer-quality prey fish assemblages in the Great Lakes (in the form of alewife *Alosa pseudoharengus*, resulting in thiamine-deficient female trout) expressed increased intra-female egg size variation compared with other inland populations, potentially because higher stress levels interrupted compensatory oocyte development in smaller eggs before spawning (Jastrebski and Morbey 2009). As these systems also tended to produce the largest eggs, increased egg size variation within the ovary may also represent an egg-packing strategy to maximize potential fecundity (e.g., particle packing; Yu and Standish 1993, Kurita and Kjesbu 2009). Unfortunately, relatively few studies have examined intra-individual egg size variation in fish. Our ability to partition among- and within-population variation allowed us to observe these trends and speculate on potential

causes, and could be used to further address hypotheses directed at the mechanisms driving these patterns. Studies limited to variation either in single populations (Dziminski et al. 2009) or among populations using few observations per population (Johnston and Leggett 2002) may miss important higher level processes that play a role in determining trait expression.

Within-population plasticity in egg size

There was relatively little interannual variation in egg size (mean egg diameter ranged < 0.1 mm) in the Tittabawassee River population. This, in conjunction with the strong differences in egg size observed among populations, would seem to offer further evidence that egg size is an adapted trait in this species. However, we did detect a positive relationship between egg size and CDD_{winter} . Walleye and other percid species exposed to long or cold winters exhibit increased rates of maturation, egg provisioning, and spawning success, suggesting that egg size and quality improves with colder winters and supporting our findings (Hokanson 1977, Hansen et al. 2015). In addition, increased egg size in response to cold temperatures is a common response to variation in the thermal environment across several ectothermic taxa (Atkinson et al. 2001). In this population, larger eggs contained more lipids (Z.S. Feiner, *unpublished data*), and in walleye and other species, larger larvae are better able to withstand starvation and escape predators (Rice et al. 1987, Moodie et al. 1989) thereby potentially mitigating the deleterious effects of poor spring habitats.

Unexpectedly, maternal effects were highly variable among years in this population, varying in mean slope by a factor of eight from the weakest year (2009, $\beta_{W,2009} = 0.005$) to the strongest (2013, $\beta_{W,2013} = 0.039$). The variation in maternal effects was largely driven by larger females increasing egg size in some years; mean egg diameters for females in the 25th percentile of length (mean = 510 mm, range = 430–570 mm) were highly similar among years (mean = 1.70 mm, range = 0.04 mm), while mean egg diameters of females in the 75th percentile of body length (mean = 666 mm, range = 593–774 mm) ranged more than three times as much (mean = 1.73 mm, range = 0.14 mm). A similar phenomenon has been observed in pike (*Esox lucius*), where

increasing maternal effects on egg size were linked to increased resource availability to large females following a decline in population density (Kotakorpi et al. 2013). Variation in food availability for females may also influence recruitment in walleye (Madenjian et al. 1996), suggesting some impact of maternal condition on egg size. Migrations of walleye from Saginaw Bay may also vary among years from little dispersal to emigration rates up to 55% (Hayden et al. 2014). Annual variation in emigration rates could expose Tittabawassee River walleye to very different conditions between Saginaw Bay and the main basin of Lake Huron (Pothoven et al. 2012) and potentially influence egg provisioning and size.

Evidence of environmental mediation of maternal effects within a single population is abundant in the literature; however, most studies tend to focus on individual responses. For example, several experiments in different taxa have documented changes in egg size or offspring dispersal of individual females in response to maternal exposure to predator cues, environmental quality, or other stresses (Dziminski et al. 2009, Bestion et al. 2014). However, interannual shifts in the population-scale relationship between offspring size and maternal phenotype as found herein are less studied even though they have now been observed in at least two fish species. It is apparent that individual studies of maternal effects are not sufficient to estimate population-scale processes and that the influence of maternal effects on offspring size likely varies interannually in many species.

Plasticity of intra-individual egg size CV within a population

Energy allocation to eggs in fish has been suggested to be limited at the scale of the individual egg independent of fecundity or maternal size (Sakai and Harada 2001a,b). Differences in the rate of energy allocation among individual eggs in the ovary, due either to ova positioning, initial composition, or vascularization of the ovary during development, could therefore produce variation in egg size. In this study, mean levels of intra-individual variation differed among years and were negatively related to both GDD_{summer} and CDD_{winter} —in years with warmer summers or colder winters, both thought to indicate

improved growth and reproductive conditions in walleye (Hokanson 1977), individuals produced more consistently sized clutches of eggs. Declines in maternal condition or energy allocation to gonads due to suboptimal summer or winter temperatures could exacerbate variation in the energy allocation process regardless of the size of the mother, leading to the patterns observed here.

Examinations of relationships between maternal traits and within-clutch variation in offspring size are rare in the literature. Similar to this study, variance in offspring length was negatively correlated with maternal age and clutch number in *Daphnia magna* (Ebert 1993). Other examinations of intra-individual offspring size variation in fish (Einum and Fleming 2004) have found generally low amounts of variation and little evidence for environmental correlates, instead suggesting that observed variance within clutches may be simply due to a lack of precise control of egg size by individual females (Jastrebski and Morbey 2009). However, the relationship of egg size CV to maternal length among populations and seasonal thermal conditions within populations suggests that such variation is not simply random variance and merits further examination, as variation in offspring size has important potential implications for offspring fitness, especially in unpredictable environments or where intra-specific competition is prevalent (Parichy and Kaplan 1992, Koops et al. 2003, Allen et al. 2008).

CONCLUSIONS

Variation in egg size has the potential to dramatically influence the future fitness of offspring and individual reproductive success. Therefore, predictions of population-level dynamics such as recruitment (e.g., O'Farrell and Botsford 2006) may be improved through elucidation of important drivers of egg size variation among and within populations and individuals. We have shown that egg size determination in walleye, a capital spawning, iteroparous fish, is composed of plastic variation in maternal effects and intra-individual variation superimposed on broader scale adaptive patterns among populations. The prevalence of positive maternal effects on egg size in this species, in concert with similar relationships between egg size and maternal size

in other species such as yellow perch (*Perca flavescens*; Andree et al. 2015), lake trout (Jastrebski and Morbey 2009), and Atlantic cod (*Gadus morhua*; Marteinsdottir and Steinarsson 1998), suggests that management practices protecting large, old females could indeed improve stock stability and productivity (Hixon et al. 2013). Our method of parsing among- and within-group variation in egg size and egg CV also allowed us to examine heretofore poorly understood influences of the thermal environment on egg characteristics at all levels of organization (among populations, within populations, and within individuals), further indicating the potential sensitivity of egg size to future changes in climate conditions. For instance, warming temperatures may induce changes to egg size and the importance of maternal effects, altering not only spawning phenology but the distribution of larval phenotypes. On broader timescales, long-term perturbations could result in evolutionary shifts in egg size and variation among populations. Therefore, changes to either offspring size or the importance of maternal phenotype could be difficult to predict and result in dramatic shifts in reproductive success of species in which recruitment is determined via similar mechanisms in early life.

ACKNOWLEDGMENTS

The authors thank Lars Rudstam and Anthony VanDeValk of Cornell University, David Fielder and Richard O'Neal of the Michigan Department of Natural Resources, the many personnel of the respective collaborating institutions, and the New York State Department of Environmental Conservation Oneida Fish Cultural Station for assistance in collecting walleye egg samples. Discussions with Rob Swihart improved our statistical analyses. Members of the Höök lab at Purdue University provided assistance collecting and processing egg samples and reviews of an earlier version of this article. This is NOAA GLERL contribution # 1796.

LITERATURE CITED

- Allen, R. M., Y. M. Buckley, and D. J. Marshall. 2008. Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *The American Naturalist* 171:225–237.
- Andree, S. R., Z. S. Feiner, J. W. Bledsoe, A. M. Cragun, and T. O. Höök. 2015. Ontogenetic variability of maternal effects in an iteroparous fish. *Ecology of Freshwater Fish* 24:384–396.
- Atkinson, D., S. A. Morely, D. Weetman, and R. N. Hughes. 2001. Offspring size responses to maternal temperature in ectotherms. Pages 269–285 in D. Atkinson and M. Thornadyke, editors. *Environment and animal development: genes, life histories and plasticity*. BIOS Scientific Publishers, Oxford, UK.
- Badyaev, A. V., T. L. Hamstra, K. P. Oh, and D. A. A. Seaman. 2006. Sex-biased maternal effects reduce ectoparasite-induced mortality in a passerine bird. *Proceedings of the National Academy of Sciences* 103:14406–14411.
- Berkeley, S. A., C. Chapman, and S. M. Sogard. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* 85:1258–1264.
- Bestion, E., A. Teyssier, F. Aubret, J. Clobert, and J. Cote. 2014. Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. *Proceedings of the Royal Society B: Biological Sciences* 281:20140701.
- Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics* 7:434–455.
- Cai, Y., and R. C. Summerfelt. 1992. Effects of temperature and size on oxygen consumption and ammonia excretion by walleye. *Aquaculture* 104:127–138.
- Dingemanse, N. J., A. J. N. Kazem, D. Réale, and J. Wright. 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution* 25:81–89.
- Duarte, C. M., and M. Alcaraz. 1989. To produce many small or few large eggs: a size-independent reproductive tactic of fish. *Oecologia* 80:401–404.
- Dziminski, M. A., P. E. Vercoe, and J. D. Roberts. 2009. Variable offspring provisioning and fitness: a direct test in the field. *Functional Ecology* 23:164–171.
- Ebert, D. 1993. The trade-off between offspring size and number in *Daphnia magna*: the influence of genetic, environmental and maternal effects. *Archiv für Hydrobiologie Supplement* 90:453–473.
- Einum, S., and I. A. Fleming. 2000. Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature* 405:565–567.
- Einum, S., and I. A. Fleming. 2004. Environmental unpredictability and offspring size: conservative vs. diversified bet-hedging. *Evolutionary Ecology Research* 6:443–455.
- Farmer, T. M., E. A. Marschall, K. Dabrowski, and S. A. Ludsin. 2015. Short winters threaten temperate fish populations. *Nature Communications* 6:7724. doi:10.1038/ncomm8724.

- Feiner, Z. S., and T. O. Höök. 2015. Environmental biology of percid fishes. Pages 61–100 in P. Kestemont, K. Dabrowski, and R. C. Summerfelt, editors. *Biology and culture of percid fishes*. First edition. Springer, Netherlands.
- Galarowicz, T. L., and D. H. Wahl. 2003. Differences in growth, consumption, and metabolism among walleyes from different latitudes. *Transactions of the American Fisheries Society* 132:425–437.
- Hadfield, J. D., A. J. Wilson, D. Garant, B. C. Sheldon, and L. E. B. Kruuk. 2010. The misuse of BLUP in ecology and evolution. *The American Naturalist* 175:116–125.
- Hanchin, P., R. P. O'Neal, R. D. Jr Clark, and R. N. Lockwood. 2007. The walleye population and fishery of the Muskegon Lake System, Muskegon and Newaygo counties, Michigan in 2002. Fisheries Special Report, Michigan Department of Natural Resources, Fisheries Division, Ann Arbor, Michigan, USA.
- Hansen, G. J. A., S. R. Carpenter, J. W. Gaeta, J. M. Hennesy, and M. J. Vander Zanden. 2015. Predicting walleye recruitment as a tool for prioritizing management actions. *Canadian Journal of Fisheries and Aquatic Sciences* 72:661–672.
- Hayden, T. A., C. M. Holbrook, D. G. Fielder, C. S. Vandergoot, R. A. Bergstedt, J. M. Dettmers, C. C. Krueger, and S. J. Cooke. 2014. Acoustic telemetry reveals large-scale migration patterns of walleye in Lake Huron. *PLoS ONE* 9:e114833.
- Hixon, M. A., D. W. Johnson and S. M. Sogard. 2013. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science* 71:2171–2185.
- Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. *Journal of the Fisheries Research Board of Canada* 34:1524–1550.
- Ivan, L. N., T. O. Höök, M. V. Thomas, and D. G. Fielder. 2011. Long-term and interannual dynamics of walleye and yellow perch in Saginaw Bay, Lake Huron. *Transactions of the American Fisheries Society* 140:1078–1092.
- Jastrebski, C. J., and Y. E. Morbey. 2009. Egg size variation in lake trout: phenotype–habitat correlations show an effect of rearing environment. *Transactions of the American Fisheries Society* 138:1342–1351.
- Johnston, T. A., and W. C. Leggett. 2002. Maternal and environmental gradients in the egg size of an iteroparous fish. *Ecology* 83:1777–1791.
- Koops, M. A., J. A. Hutchings, and B. K. Adams. 2003. Environmental predictability and the cost of imperfect information: influences on offspring size variability. *Evolutionary Ecology Research* 5:29–42.
- Kotakorpi, M., J. Tiainen, M. Olin, H. Lehtonen, K. Nyberg, J. Ruuhijärvi, and A. Kuparinen. 2013. Intensive fishing can mediate stronger size-dependent maternal effect in pike (*Esox lucius*). *Hydrobiologia* 718:109–118.
- Kozłowski, J., and M. Ziólko. 1988. Gradual transition from vegetative to reproductive growth is optimal when the maximum rate of reproductive growth is limited. *Theoretical Population Biology* 34:118–129.
- Kurita, Y., and O. S. Kjesbu. 2009. Fecundity estimation by oocyte packing density formulae in determinate and indeterminate spawners: theoretical considerations and applications. *Journal of Sea Research* 61:188–196.
- Madenjian, C. P., J. T. Tyson, R. L. Knight, M. W. Kershner, and M. J. Hansen. 1996. First-year growth, recruitment, and maturity of walleyes in western Lake Erie. *Transactions of the American Fisheries Society* 125:821–830.
- Malison, J. A., L. S. Procarione, T. P. Barry, A. R. Kapuscinski, and T. B. Kayes. 1994. Endocrine and gonadal changes during the annual reproductive cycle of the freshwater teleost, *Stizostedion vitreum*. *Fish Physiology and Biochemistry* 13:473–484.
- Marteinsdottir, G., and A. Steinarsson. 1998. Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. *Journal of Fish Biology* 52:1241–1258.
- Moles, M. D., T. A. Johnston, B. W. Robinson, W. C. Leggett, and J. M. Casselman. 2008. Is gonadal investment in walleye (*Sander vitreus*) dependent on body lipid reserves? A multipopulation comparative analysis. *Canadian Journal of Fisheries and Aquatic Sciences* 65:600–614.
- Moodie, G. E. E., N. L. Loadman, M. D. Wiegand, and J. A. Mathais. 1989. Influence of egg characteristics on survival, growth and feeding in larval walleye (*Stizostedion vitreum*). *Canadian Journal of Fisheries and Aquatic Sciences* 46:516–521.
- O'Farrell, M. R., and L. W. Botsford. 2006. The fisheries management implications of maternal-age-dependent larval survival. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2249–2258.
- Parichy, D. M., and R. H. Kaplan. 1992. Maternal effects on offspring growth and development depend on environmental quality in the frog *Bombina orientalis*. *Oecologia* 91:579–586.
- Plummer, M. 2013. rjags: Bayesian graphical models using MCMC.
- Pothoven, S. A., T. O. Höök, T. F. Nalepa, M. V. Thomas, and J. Dyble. 2012. Changes in zooplankton community structure associated with the disappearance of invasive alewife in Saginaw Bay, Lake Huron. *Aquatic Ecology* 47:1–12.
- Pritt, J. J., E. F. Roseman and T. P. O'Brien. 2014. Mechanisms driving recruitment variability in fish: comparisons between the Laurentian Great Lakes and

- marine systems. *ICES Journal of Marine Science* fsu080. doi: 10.1093/icesjms/fsu080.
- R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rice, J. A., L. B. Crowder, and M. E. Holey. 1987. Exploration of mechanisms regulating larval survival in Lake Michigan bloater: a recruitment analysis based on characteristics of individual larvae. *Transactions of the American Fisheries Society* 116:703–718.
- Sakai, S., and Y. Harada. 2001a. Why do large mothers produce large offspring? Theory and a test. *The American Naturalist* 157:348–359.
- Sakai, S., and Y. Harada. 2001b. Sink-limitation and the size-number trade-off of organs: production of organs using a fixed amount of reserves. *Evolution* 55:467–476.
- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *The American Naturalist* 108:499–506.
- Stepien, C. A., D. J. Murphy, R. N. Lohner, O. J. Sepulveda-Villet, and A. E. Haponski. 2009. Signatures of vicariance, postglacial dispersal and spawning philopatry: population genetics of the walleye *Sander vitreus*. *Molecular Ecology* 18:3411–3428.
- Strange, R. M., and C. A. Stepien. 2007. Genetic divergence and connectivity among river and reef spawning groups of walleye (*Sander vitreus vitreus*) in Lake Erie. *Canadian Journal of Fisheries and Aquatic Sciences* 64:437–448.
- Van De Pol, M., and J. Wright. 2009. A simple method for distinguishing within-vs. between-subject effects using mixed models. *Animal behaviour* 77:753–758.
- Venturelli, P. A., N. P. Lester, T. R. Marshall, and B. J. Shuter. 2010. Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): application of the growing degree-day metric. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1057–1067.
- Wang, H.-Y., D. W. Einhouse, D. G. Fielder, L. G. Rudstam, C. S. Vandergoot, A. J. VanDeValk, T. G. Zorn, and T. O. Höök. 2012. Maternal and stock effects on egg-size variation among walleye *Sander vitreus* stocks from the Great Lakes region. *Journal of Great Lakes Research* 38:477–489.
- Yu, A. B., and N. Standish. 1993. A study of the packing of particles with a mixture size distribution. *Powder Technology* 76:113–124.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1304/supinfo>