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**Interacting effects of identity, size, and winter severity
determine temporal consistency of offspring phenotype**

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Abstract: Offspring size can strongly influence offspring fitness; however, the importance of female identity to offspring size determination is poorly understood, despite the potential for identity effects to drive offspring size adaptation and population dynamics. We tracked reproductive investment (skein mass) and mean egg diameter, mass, and density produced by individual female yellow perch (*Perca flavescens*) over four spawning years to determine the influences of maternal identity, size, and winter severity to reproductive trait variation. Individual identity significantly influenced egg diameter and mass, but did not affect egg density or skein mass. All egg traits were negatively influenced by winter severity prior to spawning, and egg mass and diameter were also negatively related to maternal size. Our results suggest that individual effects can comprise a large amount of the intrapopulation variation in reproductive traits in populations, which may be unaccounted for in studies examining only environmental or phenotypic effects. Accounting for potential identity effects would likely improve our understanding of constraints on offspring size plasticity and potential responses of offspring size in populations experiencing environmental change.

Keywords: Reproduction, plasticity, identity, linear mixed model, fish eggs

Introduction

Offspring size has important implications for offspring fitness and population-level reproductive success across many taxa (Rollinson and Hutchings 2013). Therefore, there is considerable interest in understanding factors important to determining offspring size. For instance, environmental factors may directly (Atkinson et al. 2001) and indirectly (Taborsky 2006) impact maternal condition, leading to interannual variation in egg size within and among populations. Many species also exhibit maternal size effects, often with larger females producing fitter offspring (Bernardo 1996a). There can also be a significant genetic component to offspring size determination, evidenced by adaptation of egg size to local climatic regimes (Feiner et al. 2016b) and rapid shifts in offspring size distributions in domesticated populations responding to novel selection pressures (Heath et al. 2003).

A significant genetic component to offspring size should manifest in the wild as a high level of repeatability of offspring size within individuals. Such patterns have been documented in birds, with high levels of individual consistency observed for several egg size dimensions within several taxa (Christians 2002). However, the consistency of offspring size among individuals in other oviparous taxa which follow a type III reproductive strategy with smaller eggs and higher fecundity compared to the type II strategy of birds remains unclear and poorly studied (but see Kjesbu et al. 1996; Ford and Seigel 2006). Organisms producing many small eggs might be expected to have reduced control over egg size or experience increased environmental inputs into egg size determination due to the difficulty of equally allocating energy across thousands of eggs. Therefore, type III strategists may exhibit higher plasticity in egg size traits, which could influence their resilience to ecosystem change (Mousseau and Fox

1998; Ernande et al. 2004; Donelson et al. 2012) . These types of studies would offer crucial evidence for the contributions of identity (and potential genetic effects) to offspring phenotype relative to the importance of environment or maternal phenotype (i.e., plastic responses). Understanding these patterns could elucidate individual-level variance in offspring size and disentangle the influences of selection and plasticity on reproductive success. Should individual effects play a large role in egg size determination, such results could provide further evidence for conservation programs to manage populations to maintain population and individual genetic diversity, in addition to current efforts to manage for diversity in size or age structure (Hsieh et al. 2010; Schindler et al. 2010).

We assessed the importance of maternal identity, size, and environment to egg size variation by tracking the egg traits of individually tagged female yellow perch (*Perca flavescens*) across four spawning seasons. Yellow perch exhibit effects of both maternal size (usually in the form of positive relationships between size and age and egg traits; Heyer et al. 2001; Lauer et al. 2005; Andree et al. 2015) and maternal environmental experience on egg phenotypes (Farmer et al. 2015; Feiner et al. 2016a), similar to many iteroparous species of fish (Heath and Blouw 1998; Green and McCormick 2005; Kotakorpi et al. 2013) and other taxa (Croxall et al. 1992; Parichy and Kaplan 1992; Fox et al. 1997; Potti 1999; Sheldon and West 2004). Such variation can have important effects on offspring fitness, usually with larger eggs producing larger larvae with higher survival rates (Heyer et al. 2001; Rollinson and Hutchings 2013). Furthermore, because this species allocates energy to reproduction over winter, winter conditions may influence reproductive success (Farmer et al. 2015). Thus, by following egg traits of specific females as they grew in size and experienced various natural environmental conditions over time, this experiment provides an opportunity to examine the cumulative effects of maternal identity,

maternal size, and environment on the determination of egg size and reproductive investment. In addition, understanding patterns mediating reproductive allocation in yellow perch, which exhibits patterns in reproductive investment similar to many other iteroparous species, could lead to insights applicable to a wide range of taxa with similar life history traits.

Materials and methods

Egg collection

Eggs were collected from mature, spawning females in the spring of four consecutive years from 2013 to 2016. All female yellow perch were free-swimming broodstock individuals living in a single 0.5-acre aquaculture pond maintained year-round at the Purdue University Aquaculture Research Laboratory (ARL) from a population initiated in 1992 from yellow perch captured in North Carolina, USA. This broodstock population was maintained via natural spawning in the pond with periodic supplementation through manual spawning, rearing, and release of larvae back into the ponds. During our study, females were collected just before spawning each spring via partially draining and seining the aquaculture pond with 2 to 3 seine hauls until 60 to 70 individuals were captured (or, in subsequent years, recaptured). In the initial year, all gravid females were individually tagged with a 12-mm passive integrated transponder (PIT) tag (Oregon RFID, Portland, OR, USA) injected into the dorsal muscle just anterior to and below the dorsal fin on the right side of the fish. These tagged individuals were then held in a 2407 L round tank at 13 °C until spawning, which occurred within two weeks of fish sampling. Females were checked for spawning condition twice daily, and all females that spawned independently in the tank were removed and the eggs discarded (to avoid the influence of water hardening on egg characteristics). Female yellow perch, like all *Perca* species, produce a long,

gelatinous, ribbon-like matrix, referred to as a skein, which contains and protects the eggs (Newsome and Tompkins 1985). Ripe females were manually stripped of the entire skein, which we assumed to contain all eggs (see Andree et al. 2015; Feiner et al. 2016a) for details on spawning methods). Once spent, females were weighed (0.1 g), measured (1 mm total length [TL]), and released into a recovery tank. Skeins that were stripped from these females were first weighed as an indicator of total reproductive investment (Andree et al. 2015), and a 15 to 35 g subsample was removed and preserved in 10% formalin solution for later analysis of egg traits. In subsequent study years (2014 – 2016), female yellow perch were seined from the ponds and only previously PIT-tagged individuals were retained. All tagged females that had spawned before collection were measured, weighed, and released. All gravid females were held and spawned following the same egg stripping protocol as 2013 (see sample sizes in Table 1). Only fish that were spawned in multiple years (either consecutive or non-consecutively) were included in analysis.

Egg traits were measured each year after two months of preservation to allow egg shrinkage to normalize (Feiner et al. 2016b). Eggs were removed from the skein using forceps, and two subsamples of 20 to 30 eggs were placed into pre-weighed aluminum tins and dried at 70 °C for 48 h. The dry mass (to 0.1 mg) of each egg sample was then divided by the number of eggs in the sample to determine an average egg dry mass for each subsample. These values were then averaged to determine mean egg dry mass for each female. To determine egg diameter, an additional 10 eggs were removed from the skein, photographed under a dissecting microscope, and the diameter measured (to 0.1 μm) along two perpendicular axes, as yellow perch eggs are not perfectly spherical. The mean of these two axes was calculated as the diameter of each egg, and these 10 egg diameters were averaged to determine the mean egg diameter of each female.

Egg density (mg mm^{-3}) was determined by calculating the mean volume of eggs using the calculation for the volume of a sphere and the average egg diameter, and dividing the mean egg mass by this estimated egg volume.

Winter severity data

Winter thermal conditions have been shown to be important to reproductive allocation in yellow perch (Farmer et al. 2015; Feiner et al. 2016a) and closely related species (Feiner et al. 2016b). To evaluate effects of a potentially influential environmental variable (winter severity) on interannual egg size variation after accounting for potential individual identity and maternal effects, daily maximum and minimum air temperatures were obtained from the West Lafayette, IN, USA, weather station approximately 18 km from the ARL (latitude: 40.4122, longitude: -86.9369) from the NOAA National Climatic Data Center from 2012 to 2016 (Menne et al. 2012). Daily mean air temperature was calculated as the mean of these maximum and minimum values. To develop an index of winter severity, the cumulative degree days (CDD) below 5 °C (a potential maximum temperature for proper reproductive allocation in yellow perch; Hokanson 1977) was calculated for each winter from October through April preceding each spawning event, where more CDD would suggest a more severe (colder, longer, or both) winter leading up to that spawning season (Table 1).

Statistical analysis

All statistical analyses were performed in R version 3.3.2 (R Core Team 2014). We evaluated interannual variation in egg size and skein mass among and within individuals using two methods: comparison of the coefficient of variation (CV) of measurements across different levels of organization, and linear mixed modeling. First, CVs were compared to assess

differences in the variation of egg traits or skein mass among and within years and individuals. The specific levels we sought to compare were 1) total variation across all observations (i.e., all individuals in all years), 2) among-individual variation within years, and 3) within individual variation across years (for individuals that were sampled multiple spawning years). Because we were able to measure the diameters of multiple eggs from an individual female each spawning event, we also determined 4) the CV of egg diameters within individuals within a given year (i.e., within-clutch variation). Coefficients of variation were determined as the standard deviation divided by the mean of each organizational level. For within-year and within-individual levels, CVs were first estimated within each year (or individual), then averaged across years (or individuals). The means and 95% confidence intervals of these CVs were estimated using 10,000 bootstraps re-sampled with replacement (R package ‘boot’; Davison and Hinkley 1997; Canty and Ripley 2016). Significant differences between levels were then determined by non-overlapping confidence intervals.

Second, linear mixed models were constructed to examine the effects of individual identity, maternal mass, and winter severity (represented by CDD) using R package ‘lme4’ (Bates et al. 2015). Maternal mass after spawning was used as an index of maternal size, and was centered and scaled to a mean of zero and standard deviation of one to improve model convergence and standardize the interpretability of the maternal mass effect. The full linear mixed model included 1) random intercepts for fish identity to evaluate whether there was consistent variation in egg traits among individuals over years, 2) random slopes for maternal mass within females to evaluate the consistency of maternal effects across individuals, and 3) fixed effects for CDD and maternal mass to evaluate their overall effect on egg traits. The significance of random and fixed effects was determined via χ^2 tests and bootstrapped 95%

confidence intervals that did not overlap zero. Marginal R^2 (i.e., variation explained by fixed effects) and conditional R^2 (i.e., variation explained by combined fixed and random effects) were estimated to assess the relative explanatory power of identity, size, and CDD (R package ‘piecewiseSEM’; Nakagawa and Schielzeth 2013; Lefcheck 2015). To further assess the importance of the identity effect, repeatability (R , considered a potential indicator of heritability in phenotypic traits; Lessells and Boag 1987; Dohm 2002) of each trait was determined as the proportion of total variance comprised by among-individual variance in the random effects model, and uncertainty in repeatability was estimated using bootstrapped 95% confidence intervals (R package ‘boot’, following Nakagawa and Schielzeth 2010). Because we were able to spawn relatively few (nine) fish in the final study year (Table 1), the mixed models were run including and excluding those data to determine whether the observed effects were influenced by the small sample size that year. Results were similar including and excluding those data, with the exception of a dilution of the individual identity and female mass effects on egg mass, which were marginally and non-significant, respectively, after exclusion of 2016 samples (Table S1¹). Due to the similarity of results, we only report results including all years of data here.

Results

Adults

Females significantly increased in length (ANOVA: $F_{3,158} = 4.48$, $P = 0.005$) and mass (ANOVA: $F_{3,160} = 13.33$, $P < 0.001$) during the study (Table 1), indicating sufficient conditions

¹Supplementary material are available with the article though the journal Web site
<https://mc06.manuscriptcentral.com/cjfas-pubs>

for female growth in the holding ponds. Specifically, both female length and mass significantly increased from 2013 to the remainder of years of the study.

Variation in egg traits among levels

We observed significant differences among levels of organization (e.g., across all measurements, among females each year, within females across years, and within females within years) in the coefficient of variation for egg diameter and egg mass. Specifically, CV in egg diameter was highest across all observations and lowest among eggs produced within a single clutch by a single individual, as might be expected. In addition, egg diameters were more variable across all observations than they were among individuals within years. Interestingly, there was no difference in the amount of variation in egg diameter observed either among individuals within years or within individuals across years (Fig. 1a). This pattern was even more distinct for egg mass: there was no difference in total egg mass CV or the CV of egg masses within individuals across years. However, variation in egg mass was lower among individuals within years than either total or within-individual variation (Fig. 1b). Neither egg density or skein mass showed any significant differences in CV across organizational levels (Fig. 1c, 1d), although egg density exhibited a similar pattern as egg mass.

Mixed linear modeling

Variation in egg diameter exhibited significant effects of individual identity, female mass, and winter severity as represented by CDD (Table 2). Specifically, there was significant variation in random intercepts, indicating consistent variation in egg diameter among individuals over time, but no variation in random slopes, indicating consistent relationship between female mass and egg diameter among individuals. Across individuals, there was a significantly negative

fixed effect of female mass (Fig. 2a), as well as a significantly negative effect of CDD (i.e., colder winters resulted in smaller eggs; Fig. 3a). About 29.5% of the variation in egg diameter was explained by these fixed effects; including random effects increased model explanatory power to 58.6%. Corresponding to the significant individual identity effect, repeatability of egg diameter within individuals was also significant ($R = 0.41$, 95% CI: 0.21 – 0.69).

Similar to egg diameter, there were significant effects of individual identity, female mass, and CDD on egg mass. There was significant variance in random intercepts (i.e., a significant identity effect), and significantly negative effects of female mass and CDD on egg mass (Table 2; Fig. 2b, 3b). Winter severity and female mass explained a relatively large proportion of the total variance explained by the model (marginal $R^2 = 0.532$), whereas the addition of identity effects explained relatively less variation in egg mass (conditional $R^2 = 0.657$). Repeatability of egg mass was lower than observed for egg diameter, but still significant ($R = 0.26$, 95% CI: 0.04 – 0.43).

There was only a significant negative effect of CDD on egg density (Table 2). Female mass and individual identity had apparently no effect on the determination of egg density (Fig. 2c, 3c). Therefore, there was no explanatory power of the random effects, whereas fixed effects explained 38.1% of the variation in egg density. Similarly, within-individual repeatability was negligible for this trait ($R = 0$, 95% CI unable to be estimated due to lack of among-individual variance).

Lastly, skein mass exhibited very different relationships to female traits and environmental conditions as compared to those observed in egg traits. Specifically, the random slopes term was significant, indicating different relationships between skein mass and female

mass among individuals, whereas there was no evidence for significant variance in random intercepts (i.e., no identity effect; Table 2). Among fixed effects, there was a significantly positive effect of female mass (Fig. 2d), but no effect of CDD on skein mass (Fig. 3d). Female size and winter severity explained about 17.8% of the variation in skein mass combined, and including identity effects increased explanatory power to 54.2%. There was low, non-significant repeatability for skein mass within individuals ($R = 0.05$, 95% CI: 0.00 – 0.17).

Discussion

Individual identity and winter severity explained a significant proportion of variance in egg size, demonstrating individual consistency in egg size acting in concert with plastic responses to environmental conditions. Although there have been few rigorous examinations of within-individual egg size variation in fishes, some studies have found interannual consistency in egg size, relatively high heritability ($h^2 > 0.30$) of egg traits, and rapidly evolving egg size in response to hatchery selection regimes (e.g., rainbow trout [*Oncorhynchus mykiss*]; Gall and Huang 1988; Atlantic cod [*Gadus morhua*]; Kjesbu et al. 1996; Chinook salmon [*Oncorhynchus tshawytscha*]; Heath et al. 2003). Moreover, wild populations experiencing different environmental conditions often exhibit concordant differences in offspring size (Moles et al. 2008; Feiner et al. 2016b). These results support the idea that there is an important genetic component to egg size, a major determinant of offspring survival in many taxa (Rollinson and Hutchings 2013), which regulates a consistent plastic response to environmental change (winter severity) among individuals..

All egg traits were not equally affected by individual, maternal, and environmental effects. In particular, variability in egg diameter was most directly influenced by fish identity,

254 whereas egg density and skein mass exhibited virtually no repeatability at the individual level.
255 In highly fecund animals such as fish and amphibians, egg size and egg number necessarily
256 trade-off, leaving individuals balancing the benefits of large offspring with increasing total
257 reproductive output (Einum and Fleming 2000). Similar to this study, metrics of egg size appear
258 to be relatively more repeatable and heritable than metrics of egg number (e.g., fecundity, clutch
259 size, clutch mass) in birds, reptiles, and amphibians, despite large variances in the overall
260 number and morphology of eggs produced by these taxa (Lessells et al. 1989; Kaplan 1992;
261 Christians 2002; Ford and Seigel 2006; Collin 2010). In addition, our results support the
262 previous assertion that repeatability in egg size is generally higher in birds than in fish or
263 amphibians (Christians 2002). Thus, differences in egg size repeatability among taxa following
264 a type II or type III reproductive strategy may result from differences in fecundity (e.g., few eggs
265 in birds and reptiles versus hundreds or thousands of eggs in fish and amphibians) or egg
266 morphology (large, hard-shelled eggs versus small eggs) operating within the physical
267 constraints of the organism, including oviduct and ovary size, which may more strongly limit
268 within-individual variation in egg size in birds and reptiles (Bernardo 1996b). In addition, vagile
269 taxa like birds may be more resilient to environmental variation than less mobile taxa, increasing
270 their ability to moderate egg size or potentially increasing selective gradients for optimal egg
271 sizes and resulting in relatively high heritability in egg traits (Christians 2002).

272 Despite relatively high repeatability in egg diameter and moderate repeatability in egg
273 mass, egg size and number were also significantly influenced by winter severity.
274 Environmentally-driven variation in reproductive investment, often exhibited as changes in egg
275 size, number, or composition, appears to be common in many taxa. For example, variation in
276 clutch size has been linked to variation in maternal provisioning or environmental quality in

reptiles (Ljungström et al. 2016), fish (Duponchelle et al. 2000), and birds (Haywood and Perrins 1992), whereas others have noted improved offspring quality with improved maternal condition (McCormick 2003; Perez and Fuiman 2015). Increasing energy reserves to offspring with limited ability to physically increase egg size would likely result in more highly plastic egg density or other measures of egg quality less constrained by egg size (i.e., lipid or fatty acid content; Czesny et al. 2005). Interestingly, in this study these environmental effects were as strong or stronger than individual identity effects on egg traits. Egg diameter and mass exhibited similar or lower variation among individuals spawning the same year as compared to variation among clutches from the same individual, while there was no difference in variation in egg density or skein mass within or among years. This suggests that females were responding similarly to winter severity prior to spawning within their individual capacity to do so, by altering egg size and overall reproductive investment. Variation in such measures of egg quality can significantly influence offspring fitness across oviparous species (Duncan 1987; Uller and Olsson 2010; Andree et al. 2015), and therefore could offer an avenue to plastically alter offspring quality while avoiding significant changes in offspring size. Thus, studies seeking to understand variability in multifaceted life history traits like offspring size or fitness should recognize disparities in the responses of seemingly related traits (e.g., egg diameter and egg density) to maternal and environmental effects.

The specific environmental effect we observed was a negative effect of winter severity on egg traits and reproductive investment, meaning long, cold winters caused females to produce lighter skeins and smaller, lighter, and less dense eggs. This effect was unexpected, as previous research has suggested yellow perch and similar species require cold winters for egg production (Hokanson 1977), and that colder or longer winters have generally moderate to positive effects

on egg quality (Farmer et al. 2015; Feiner et al. 2016a, 2016b). Potentially, harsh winters reduced available food resources in the aquaculture ponds, thereby depleting female lipid reserves and decreasing reproductive investment (Moles et al. 2008). Supporting this, poor quality maternal environments have been shown to reduce egg or offspring fitness in a number of taxa (Duncan 1987; Izquierdo et al. 2001; Blomberg et al. 2014), reinforcing the importance of considering the impact of both maternal and offspring environments on offspring fitness. In addition, the yellow perch used in this study originated from a warmer climate (North Carolina) and may be maladapted to more severe winters at higher latitudes, which may be supported by the tolerance of warm winter temperatures exhibited by this population (Feiner et al. 2016a) and general evidence for adaptive differences in egg traits along thermal or latitudinal clines in other species (e.g., Fleming and Gross 1990; Du et al. 2010). We acknowledge, however, that this was a temporally limited study, and that data covering a wider range of winter severity over a longer period would be needed to conclusively demonstrate a causative link between winter conditions and egg traits. However, the combination of a strong directional effect of winter CDD and similar amounts of interannual variation in egg traits among and within females suggests that both environmental plasticity and maternal identity are important to egg phenotype. Moreover, variability in the relative importance of environment and identity effects among populations or over time could explain a significant amount of the unexplained variation in offspring size often observed in studies that ignore these potential interactions (Moles et al. 2008).

Most examinations of maternal size effects on egg traits have reported positive maternal effects, where larger mothers produce larger or higher quality offspring, in contrast to our findings (Heyer et al. 2001; Berkeley et al. 2004; Olin et al. 2012; Hixon et al. 2013; Feiner et al. 2016b). However, a number of studies have found weak or negligible maternal effects in fish,

including situations where the “bigger is better” hypothesis has been explicitly contradicted (Bernardo 1996a; Jacobs and Sherrard 2010; Régnier et al. 2013), and a negative relationship between maternal size and age and early life larval survival has been observed in the same population of yellow perch studied herein (Andree et al. 2015). Mechanisms for a negative relationship between maternal size or age and egg traits are less studied, but one possibility is the oncoming senescence of old, very large individuals, leading to negative or quadratic relationships between female size or age and egg size (Johnston and Leggett 2002; Wang et al. 2012, Moorad and Nussey 2016). In this study, most of our females began the four year experiment at very large sizes for yellow perch (> 300 mm), and a previous study found fish as old as 11 years in the broodstock population, near the upper limit for yellow perch (Andree et al. 2015; Feiner et al. 2015). Thus, senescence is a plausible mechanism for the negative relationship between female size (and, necessarily, age, although it was not measured) and egg size in this study.

Managing for diversity in population size or age structure has been suggested to improve population resilience and mitigate temporal variability in population dynamics through portfolio effects on reproductive phenology, spawning phenology, and offspring size distributions (Hsieh et al. 2010). Our results suggest that management for other population-level measures of genetic or phenotypic diversity may be as important as diversifying age or size structures to increase phenotypic diversity of offspring (Johnson et al. 2015). Interannual variation in the number or identity of successfully reproducing adults driven by environmental stochasticity in the relationship between offspring phenotype and fitness may have significant repercussions on population dynamics across multiple generations (Benton et al. 2005). Should strong repeatability of egg size indicate high levels of heritability for this trait, egg size could be

evolutionarily responsive to changes in the environment that alter the selective landscape for parents or offspring, with important ramifications for species conservation and population management issues. For example, selective harvest regimes that erode phenotypic or genetic diversity while altering population demography or density may also cause the evolution of offspring traits, leading to increasingly erratic population dynamics and an increased probability of population collapse (Hsieh et al. 2010; Salinas et al. 2012; Kotakorpi et al. 2013; Allendorf et al. 2014; Johnson et al. 2015). Artificial breeding programs may unintentionally and rapidly select for offspring phenotypes unsuited for natural environments (Krist 2011; Christie et al. 2012a), thereby posing a risk to potential conservation programs through introgression with wild individuals from receiving populations (Christie et al. 2012b). Lastly, a number of taxa also exhibit significant interpopulation variability in offspring size that appears to be related to environmental conditions (Fleming and Gross 1990; Azevedo et al. 1996; Parry et al. 2001; Du et al. 2010). Climatic changes in the form of altered thermal or hydrological regimes that influence offspring fitness could lead to evolution of offspring size with uncertain effects on the ability of such populations to adapt to climate change or other anthropogenic disturbances (Wheelwright et al. 2012). Further studies aimed at partitioning the importance of phenotypic plasticity, genetic, and environmental effects on offspring traits could address the implications of genetic constraints on phenotypic plasticity in offspring traits (Reneker and Kamel 2016), or predict plastic and evolutionary change in offspring size in artificial populations (Heath et al. 2003).

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References

- Allendorf, F.W., Berry, O., and Ryman, N. 2014. So long to genetic diversity, and thanks for all the fish. *Mol. Ecol.* **23**(1): 23–25. doi:10.1111/mec.12574.
- Andree, S.R., Feiner, Z.S., Bledsoe, J.W., Cragun, A.M., and Höök, T.O. 2015. Ontogenetic variability of maternal effects in an iteroparous fish. *Ecol. Freshw. Fish* **24**(3): 384–396. doi:10.1111/eff.12153.
- Atkinson, D., Morely, S.A., Weetman, D., Hughes, R.N., Atkinson, D., and Thorndyke, M. 2001. Offspring size responses to maternal temperature in ectotherms. *In* *Environment and Animal Development: Genes, Life Histories and Plasticity*. BIOS Scientific Publishers, Oxford, UK. pp. 269–285.
- Azevedo, R.B.R., French, V., and Partridge, L. 1996. Thermal evolution of egg size in *Drosophila melanogaster*. *Evolution* **50**(6): 2338–2345. doi:10.2307/2410702.
- Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**(1): 1–48. doi:10.18637/jss.v067.i01.
- Benton, T.G., Plaistow, S.J., Beckerman, A.P., Lapsley, C.T., and Littlejohns, S. 2005. Changes in maternal investment in eggs can affect population dynamics. *Proc. Biol. Sci.* **272**(1570): 1351–1356.
- Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* **85**(5): 1258–1264. doi:10.1890/03-0706.
- Bernardo, J. 1996a. Maternal effects in animal ecology. *Am. Zool.* **36**(2): 83–105. doi:10.1093/icb/36.2.83.
- Bernardo, J. 1996b. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. *Am. Zool.* **36**(2): 216–236. doi:10.1093/icb/36.2.216.
- Blomberg, E.J., Gibson, D., Atamian, M.T., and Sedinger, J.S. 2014. Individual and environmental effects on egg allocations of female greater sage-grouse. *The Auk* **131**(4): 507–523. doi:10.1642/AUK-14-32.1.
- Canty, A., and Ripley, B. 2016. boot: Bootstrap R (S-Plus) Functions. R.
- Christians, J.K. 2002. Avian egg size: variation within species and inflexibility within individuals. *Biol. Rev.* **77**(1): 1–26. doi:10.1017/S1464793101005784.

- Christie, M.R., Marine, M.L., French, R.A., and Blouin, M.S. 2012a. Genetic adaptation to captivity can occur in a single generation. *Proc. Natl. Acad. Sci.* **109**(1): 238–242. doi:10.1073/pnas.1111073109.
- Christie, M.R., Marine, M.L., French, R.A., Waples, R.S., and Blouin, M.S. 2012b. Effective size of a wild salmonid population is greatly reduced by hatchery supplementation. *Heredity* **109**(4): 254–260. doi:10.1038/hdy.2012.39.
- Collin, R. 2010. Repeatability of egg size in two marine gastropods: brood order and female size do not contribute to intraspecific variation. *Mar. Ecol. Prog. Ser.* **410**: 89–96. doi:10.3354/meps08638.
- Croxall, J.P., Rothery, P., and Crisp, A. 1992. The effect of maternal age and experience on egg-size and hatching success in Wandering Albatrosses *Diomedea exulans*. *Ibis* **134**(3): 219–228. doi:10.1111/j.1474-919X.1992.tb03803.x.
- Czesny, S., Rinchard, J., and Dabrowski, K. 2005. Intrapopulation variation in egg lipid and fatty acid composition and embryo viability in a naturally spawning walleye population from an inland reservoir. *North Am. J. Fish. Manag.* **25**(1): 122–129. doi:10.1577/M03-202.1.
- Davison, A.C., and Hinkley, D.V. 1997. *Bootstrap methods and their applications*. Cambridge University Press, Cambridge, United Kingdom.
- Dohm, M.R. 2002. Repeatability estimates do not always set an upper limit to heritability. *Funct. Ecol.* **16**(2): 273–280. doi:10.1046/j.1365-2435.2002.00621.x.
- Donelson, J.M., Munday, P.L., McCormick, M.I., and Pitcher, C.R. 2012. Rapid transgenerational acclimation of a tropical reef fish to climate change. *Nat. Clim. Change* **2**(1): 30–32. doi:10.1038/nclimate1323.
- Du, W.-G., Ji, X., Zhang, Y.-P., Lin, Z.-H., and Xu, X.-F. 2010. Geographic variation in offspring size of a widespread lizard (*Takydromus septentrionalis*): importance of maternal investment. *Biol. J. Linn. Soc.* **101**(1): 59–67. doi:10.1111/j.1095-8312.2010.01492.x.
- Duncan, D.C. 1987. Variation and heritability in egg size of the northern pintail. *Can. J. Zool.* **65**(4): 992–996. doi:10.1139/z87-157.
- Duponchelle, F., Cecchi, P., Corbin, D., Nuñez, J., and Legendre, M. 2000. Variations in fecundity and egg size of female Nile tilapia, *Oreochromis niloticus*, from man-made lakes of Côte d'Ivoire. *Environ. Biol. Fishes* **57**(2): 155–170. doi:10.1023/A:1007575624937.
- Einum, S., and Fleming, I.A. 2000. Highly fecund mothers sacrifice offspring survival to maximize fitness. *Nature* **405**(6786): 565–567. doi:10.1038/35014600.

- 438 Ernande, B., Dieckmann, U., and Heino, M. 2004. Adaptive changes in harvested populations:
439 plasticity and evolution of age and size at maturation. *Proc. R. Soc. B Biol. Sci.*
440 **271**(1537): 415–423. doi:10.1098/rspb.2003.2519.
- 441 Farmer, T.M., Marschall, E.A., Dabrowski, K., and Ludsins, S.A. 2015. Short winters threaten
442 temperate fish populations. *Nat. Commun.* **6**. doi:10.1038/ncomms8724.
- 443 Feiner, Z.S., Chong, S.C., Knight, C.T., Lauer, T.E., Thomas, M.V., Tyson, J.T., and Höök, T.O.
444 2015. Rapidly shifting maturation schedules following reduced commercial harvest in a
445 freshwater fish. *Evol. Appl.* **8**(7): 724–737. doi:10.1111/eva.12285.
- 446 Feiner, Z.S., Coulter, D.P., Guffey, S.C., and Höök, T.O. 2016a. Does overwinter temperature
447 affect maternal body composition and egg traits in yellow perch *Perca flavescens*? *J. Fish*
448 *Biol.* doi:10.1111/jfb.12929.
- 449 Feiner, Z.S., Wang, H.-Y., Einhouse, D.W., Jackson, J.R., Rutherford, E.S., Schelb, C.,
450 Vandergoot, C.S., Zorn, T.G., and Höök, T.O. 2016b. Thermal environment and maternal
451 effects shape egg size in a freshwater fish. *Ecosphere* **7**(5). doi:10.1002/ecs2.1304.
- 452 Fleming, I.A., and Gross, M.R. 1990. Latitudinal clines: a trade-off between egg number and size
453 in Pacific salmon. *Ecology* **71**(1): 1–11. doi:10.2307/1940241.
- 454 Ford, N.B., and Seigel, R.A. 2006. Intra-individual variation in clutch and offspring size in an
455 oviparous snake. *J. Zool.* **268**(2): 171–176. doi:10.1111/j.1469-7998.2005.00006.x.
- 456 Fox, C.W., Thakar, M.S., and Mousseau, T.A. 1997. Egg size plasticity in a seed beetle: an
457 adaptive maternal effect. *Am. Nat.* **149**(1): 149–163.
- 458 Gall, G.A.E., and Huang, N. 1988. Heritability and selection schemes for rainbow trout: Female
459 reproductive performance. *Aquaculture* **73**(1): 57–66. doi:10.1016/0044-8486(88)90041-
460 5.
- 461 Green, B., and McCormick, M. 2005. Maternal and paternal effects determine size, growth and
462 performance in larvae of a tropical reef fish. *Mar. Ecol. Prog. Ser.* **289**: 263–272.
463 doi:10.3354/meps289263.
- 464 Haywood, S., and Perrins, C.M. 1992. Is clutch size in birds affected by environmental
465 conditions during growth? *Proc. Biol. Sci.* **249**(1325): 195–197.
- 466 Heath, D.D., and Blouw, D.M. 1998. Are maternal effects in fish adaptive or merely
467 physiological side effects? *In* *Maternal Effects as Adaptations. Edited by T.A. Mousseau*
468 *and C.W. Fox. Oxford University Press. pp. 189–198.*
- 469 Heath, D.D., Heath, J.W., Bryden, C.A., Johnson, R.M., and Fox, C.W. 2003. Rapid evolution of
470 egg size in captive salmon. *Science* **299**(5613): 1738–1740.
471 doi:10.1126/science.1079707.

- 472 Heyer, C.J., Miller, T.J., Binkowski, F.P., Caldarone, E.M., and Rice, J.A. 2001. Maternal effects
473 as a recruitment mechanism in Lake Michigan yellow perch (*Perca flavescens*). Can. J.
474 Fish. Aquat. Sci. **58**(7): 1477–1487. doi:10.1139/f01-090.
- 475 Hixon, M.A., Johnson, D.W., and Sogard, S.M. 2013. BOFFFFs: on the importance of
476 conserving old-growth age structure in fishery populations. ICES J. Mar. Sci. J. Cons. **71**:
477 2171–2185. doi:10.1093/icesjms/fst200.
- 478 Hokanson, K.E.F. 1977. Temperature requirements of some percids and adaptations to the
479 seasonal temperature cycle. J. Fish. Res. Board Can. **34**: 1524–1550.
- 480 Hsieh, C., Yamauchi, A., Nakazawa, T., and Wang, W.-F. 2010. Fishing effects on age and
481 spatial structures undermine population stability of fishes. Aquat. Sci. **72**(2): 165–178.
482 doi:10.1007/s00027-009-0122-2.
- 483 Izquierdo, M.S., Fernández-Palacios, H., and Tacon, A.G.J. 2001. Effect of broodstock nutrition
484 on reproductive performance of fish. Aquaculture **197**(1–4): 25–42. doi:10.1016/S0044-
485 8486(01)00581-6.
- 486 Jacobs, M.W., and Sherrard, K.M. 2010. Bigger is not always better: Offspring size does not
487 predict growth or survival for seven ascidian species. Ecology **91**(12): 3598–3608.
488 doi:10.1890/09-2072.1.
- 489 Johnson, D.W., Freiwald, J., and Bernardi, G. 2015. Genetic diversity affects the strength of
490 population regulation in a marine fish. Ecology. doi:10.1890/15-0914.1.
- 491 Johnston, T.A., and Leggett, W.C. 2002. Maternal and environmental gradients in the egg size of
492 an iteroparous fish. Ecology **83**(7): 1777–1791. doi:10.1890/0012-
493 9658(2002)083[1777:MAEGIT]2.0.CO;2.
- 494 Kaplan, R.H. 1992. Greater maternal investment can decrease offspring survival in the frog
495 *Bombina orientalis*. Ecology **73**(1): 280. doi:10.2307/1938739.
- 496 Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production
497 in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **53**(3): 610–
498 620.
- 499 Kotakorpi, M., Tiainen, J., Olin, M., Lehtonen, H., Nyberg, K., Ruuhijärvi, J., and Kuparinen, A.
500 2013. Intensive fishing can mediate stronger size-dependent maternal effect in pike (*Esox*
501 *lucius*). Hydrobiologia **718**(1): 109–118. doi:10.1007/s10750-013-1607-5.
- 502 Krist, M. 2011. Egg size and offspring quality: a meta-analysis in birds. Biol. Rev. **86**(3): 692–
503 716. doi:10.1111/j.1469-185X.2010.00166.x.
- 504 Lauer, T.E., Shroyer, S.M., Kilpatrick, J.M., McComish, T.S., and Allen, P.J. 2005. Yellow
505 perch length–fecundity and length–egg size relationships in Indiana waters of Lake
506 Michigan. North Am. J. Fish. Manag. **25**(3): 791–796. doi:10.1577/M04-087.1.

- 507 Lefcheck, J.S. 2015. piecewiseSEM: Piecewise structural equation modeling in R for ecology,
508 evolution, and systematics. *Methods Ecol. Evol.* **7**(5): 573–579. doi:10.1111/2041-
509 210X.12512.
- 510 Lessells, C.M., and Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. *The Auk*
511 **104**(1): 116–121. doi:10.2307/4087240.
- 512 Lessells, C.M., Cooke, F., and Rockwell, R.F. 1989. Is there a trade-off between egg weight and
513 clutch size in wild lesser snow geese (*Anser c. caerulescens*)? *J. Evol. Biol.* **2**(6): 457–
514 472. doi:10.1046/j.1420-9101.1989.2060457.x.
- 515 Ljungström, G., Stjernstedt, M., Wapstra, E., and Olsson, M. 2016. Selection and constraints on
516 offspring size-number trade-offs in sand lizards (*Lacerta agilis*). *J. Evol. Biol.* **29**(5):
517 979–990. doi:10.1111/jeb.12838.
- 518 McCormick, M.I. 2003. Consumption of coral propagules after mass spawning enhances larval
519 quality of damselfish through maternal effects. *Oecologia* **136**(1): 37–45.
520 doi:10.1007/s00442-003-1247-y.
- 521 Menne, M.J., Durre, I., Vose, R.S., Gleason, B.E., and Houston, T.G. 2012. An overview of the
522 global historical climatology network-daily database. *J. Atmospheric Ocean. Technol.*
523 **29**(7): 897–910. doi:10.1175/JTECH-D-11-00103.1.
- 524 Moles, M.D., Johnston, T.A., Robinson, B.W., Leggett, W.C., and Casselman, J.M. 2008. Is
525 gonadal investment in walleye (*Sander vitreus*) dependent on body lipid reserves? A
526 multipopulation comparative analysis. *Can. J. Fish. Aquat. Sci.* **65**(4): 600–614.
527 doi:10.1139/f07-186.
- 528 Moorad, J.A., and Nussey, D.H. 2016. Evolution of maternal effect senescence. *Proc. Natl.*
529 *Acad. Sci.* **113**(2): 362–367. doi:10.1073/pnas.1520494113.
- 530 Mousseau, T.A., and Fox, C.W. 1998. The adaptive significance of maternal effects. *Trends*
531 *Ecol. Evol.* **13**(10): 403–407. doi:10.1016/S0169-5347(98)01472-4.
- 532 Nakagawa, S., and Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a
533 practical guide for biologists. *Biol. Rev. Camb. Philos. Soc.* **85**(4): 935–956.
534 doi:10.1111/j.1469-185X.2010.00141.x.
- 535 Nakagawa, S., and Schielzeth, H. 2013. A general and simple method for obtaining R^2 from
536 generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**(2): 133–142.
537 doi:10.1111/j.2041-210x.2012.00261.x.
- 538 Newsome, G.E., and Tompkins, J. 1985. Yellow perch egg masses deter predators. *Can. J. Zool.*
539 **63**(12): 2882–2884. doi:10.1139/z85-430.
- 540 Olin, M., Jutila, J., Lehtonen, H., Vinni, M., Ruuhijärvi, J., Estlander, S., Rask, M., Kuparinen,
541 A., and Lappalainen, J. 2012. Importance of maternal size on the reproductive success of

- 542 perch, *Perca fluviatilis*, in small forest lakes: implications for fisheries management.
543 Fish. Manag. Ecol. **19**(5): 363–374. doi:10.1111/j.1365-2400.2012.00845.x.
- 544 Parichy, D.M., and Kaplan, R.H. 1992. Maternal effects on offspring growth and development
545 depend on environmental quality in the frog *Bombina orientalis*. Oecologia **91**(4): 579–
546 586. doi:10.1007/BF00650334.
- 547 Parry, D., Goyer, R.A., and Lenhard, G.J. 2001. Macrogeographic clines in fecundity,
548 reproductive allocation, and offspring size of the forest tent caterpillar *Malacosoma*
549 *disstria*. Ecol. Entomol. **26**(3): 281–291. doi:10.1046/j.1365-2311.2001.00319.x.
- 550 Perez, K.O., and Fuiman, L.A. 2015. Maternal diet and larval diet influence survival skills of
551 larval red drum *Sciaenops ocellatus*. J. Fish Biol. **86**(4): 1286–1304.
552 doi:10.1111/jfb.12637.
- 553 Potti, J. 1999. Maternal effects and the pervasive impact of nestling history on egg size in a
554 passerine bird. Evolution **53**(1): 279. doi:10.2307/2640940.
- 555 R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for
556 Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/>.
- 557 Régnier, T., Bolliet, V., Gaudin, P., and Labonne, J. 2013. Bigger is not always better: egg size
558 influences survival throughout incubation in brown trout (*Salmo trutta*). Ecol. Freshw.
559 Fish **22**(2): 169–177. doi:10.1111/eff.12018.
- 560 Reneker, J.L., and Kamel, S.J. 2016. The maternal legacy: female identity predicts offspring sex
561 ratio in the loggerhead sea turtle. Sci. Rep. **6**: 29237. doi:10.1038/srep29237.
- 562 Rollinson, N., and Hutchings, J.A. 2013. The relationship between offspring size and fitness:
563 integrating theory and empiricism. Ecology **94**(2): 315–324.
- 564 Salinas, S., Perez, K.O., Duffy, T.A., Sabatino, S.J., Hice, L.A., Munch, S.B., and Conover, D.O.
565 2012. The response of correlated traits following cessation of fishery-induced selection.
566 Evol. Appl. **5**(7): 657–663. doi:10.1111/j.1752-4571.2012.00243.x.
- 567 Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., and
568 Webster, M.S. 2010. Population diversity and the portfolio effect in an exploited species.
569 Nature **465**(7298): 609–612. doi:10.1038/nature09060.
- 570 Sheldon, B.C., and West, S.A. 2004. Maternal dominance, maternal condition, and offspring sex
571 ratio in ungulate mammals. Am. Nat. **163**(1): 40–54. doi:10.1086/381003.
- 572 Taborsky, B. 2006. Mothers determine offspring size in response to own juvenile growth
573 conditions. Biol. Lett. **2**(2): 225–228. doi:10.1098/rsbl.2005.0422.
- 574 Uller, T., and Olsson, M. 2010. Offspring size and timing of hatching determine survival and
575 reproductive output in a lizard. Oecologia **162**(3): 663–671. doi:10.1007/s00442-009-
576 1503-x.

577 Wang, H.-Y., Einhouse, D.W., Fielder, D.G., Rudstam, L.G., Vandergoot, C.S., VanDeValk,
578 A.J., Zorn, T.G., and Höök, T.O. 2012. Maternal and stock effects on egg-size variation
579 among walleye *Sander vitreus* stocks from the Great Lakes region. J. Gt. Lakes Res.
580 **38**(3): 477–489. doi:10.1016/j.jglr.2012.06.002.

581 Wheelwright, N.T., Graff, E.S., and Norris, D.R. 2012. Relative consistency in size, shape, and
582 coloration of savannah sparrow eggs within and between breeding seasons. The Condor
583 **114**(2): 412–420. doi:10.1525/cond.2012.110149.

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Tables

Table 1. Sample size (N) of all fish (used to determine trait coefficients of variation) and number of repeat spawners (used in regression analyses) of female yellow perch included in the study. Sample sizes in parentheses denote number of individuals used for analysis of skein mass. Mean (standard deviation) of maternal total length (mm), maternal mass (g), egg diameter (mm), egg mass (mg), egg density (mg mm⁻³), and skein mass (g) as measured from all spawning female yellow perch sampled each year are also shown. Cumulative degree days (CDD) below 5 °C from October through April were used as an index of winter severity.

Trait	2013	2014	2015	2016
N – all fish	72 (68)	39 (36)	39 (22)	9 (9)
N – repeat spawners	48 (46)	33 (30)	24 (23)	9 (9)
Maternal length	308.72 (47.88)	329.64 (30.56)	333.87 (33.72)	331.43 (31.77)
Maternal mass	331.57 (125.61)	427.18 (140.15)	473.26 (137.58)	508.97 (169.92)
Egg mass	0.23 (0.03)	0.15 (0.04)	0.17 (0.03)	0.21 (0.02)
Egg diameter	1.07 (0.05)	1.00 (0.05)	1.01 (0.05)	0.97 (0.03)
Egg density	0.19 (0.02)	0.14 (0.03)	0.16 (0.02)	0.22 (0.02)
Skein mass	127.21 (53.72)	129.91 (49.28)	129.55 (59.00)	86.09 (60.28)
CDD	747.35	1235.375	1090.05	544.85

Table 2. Linear mixed modeling results and sample sizes (N; egg mass was not recorded for two females in 2013), including mean and bootstrapped 95% confidence intervals (CI) for the standard deviations of random intercepts (female identity effects; $\sigma_{intercept}$), variance in random slopes (the effect of maternal mass within females; σ_{slope}), and the fixed effects of female mass and cooling degree days below 5°C (CDD). Results from χ^2 -tests with associated degrees of freedom (d.f.) and P -values to evaluate the significance of random and fixed effects are also shown.

Model	Parameter	Mean	CI	χ^2	χ^2 d.f.	P
Egg diameter N = 114	$\sigma_{intercept}$	0.03745	0.01679, 0.04855	10.61	1	0.0011
	σ_{slope}	0.00327	0.00035, 0.02689	0.3262	2	0.8495
	female mass	-0.02970	-0.04179, -0.01595	21.81	1	<0.0001
	CDD	-0.00007	-0.00011, -0.00004	12.80	1	0.0003
Egg mass N = 112	$\sigma_{intercept}$	0.01770	0.00458, 0.02465	4.252	1	0.0392
	σ_{slope}	0.00175	0.00026, 0.01605	0.2025	2	0.9037
	female mass	-0.01102	-0.01812, -0.00336	10.63	1	0.0011
	CDD	-0.00014	-0.00016, -0.00011	74.44	1	<0.0001
Egg density N = 112	$\sigma_{intercept}$	0.00000	--	0	1	>0.9999
	σ_{slope}	0.00000	--	0	2	>0.9999
	female mass	0.00510	-0.00563, 0.01584	0.9084	1	0.3405
	CDD	-0.00019	-0.00024, -0.00014	53.44	1	<0.0001
Skein mass N = 108	$\sigma_{intercept}$	11.300	1.7969, 25.079	0.1331	1	0.7152
	σ_{slope}	31.530	15.346, 42.580	20.701	2	<0.0001
	female mass	22.549	9.6189, 34.445	6.9303	1	0.0085
	CDD	0.01238	-0.01955, 0.04594	0.5489	1	0.4588

Figure captions

Fig. 1. Coefficient of variation (CV; standard deviation / mean) of egg traits (a: egg diameter, b: egg dry mass, c: egg density, d: skein mass) produced by yellow perch over four years at different levels of organization (from left to right within each plot): total CV across all individuals and years, CV across all individuals spawned within a single year (Among-ind. within years), and CV within individuals spawned in multiple years (Within-ind. among years). For egg diameter (panel a), CV of egg diameters measured from within a clutch produced by a single individual (Within clutch) are also shown. Points represent the mean CV observed at each level, and error bars represent bootstrapped 95% confidence intervals. Significant differences (non-overlapping intervals) denoted by different letters.

Fig. 2. Within- and among-individual relationships between scaled female mass and egg traits (a: mean egg diameter, b: mean egg mass, c: mean egg density, and d: skein mass) as repeatedly measured over four years in mature female yellow perch. Thin gray lines represent individual relationships estimated from random effects model after accounting for environmental (winter severity) effects, and thick black line represents overall relationship after accounting for winter severity.

Fig. 3. Relationships between cumulative degree days (CDD) below 5 °C and residualized egg traits (after accounting for the effects of scaled female mass and individual identity) for a) mean egg diameter, b) mean egg mass, c) mean egg density, and d) skein mass. Small points are individual measurements, large diamonds are the mean residual for that year, and the lines and shaded regions show the mean regression relationship $\pm$ 95% confidence intervals.

Fig. 1. Coefficient of variation (CV; standard deviation / mean) of egg traits (a: egg diameter, b: egg dry mass, c: egg density, d: skein mass) produced by yellow perch over four years at different levels of organization (from left to right within each plot): total CV across all individuals and years, CV across all individuals spawned within a single year (Among-ind. within years), and CV within individuals spawned in multiple years (Within-ind. among years). For egg diameter (panel a), CV of egg diameters measured from within a clutch produced by a single individual (Within clutch) are also shown. Points represent the mean CV observed at each level, and error bars represent bootstrapped 95% confidence intervals. Significant differences (non-overlapping intervals) denoted by different letters.

113x85mm (300 x 300 DPI)

Fig. 2. Within- and among-individual relationships between maternal mass and egg traits (a: mean egg diameter, b: mean egg mass, c: mean egg density, and d: skein mass) as repeatedly measured over four years in mature female yellow perch. Thin gray lines represent individual relationships estimated from random effects model after accounting for environmental (winter severity) effects, and thick black line represents overall relationship after accounting for winter severity.

152x127mm (300 x 300 DPI)

Fig. 3. Relationships between cumulative degree days (CDD) below 5 °C and residualized egg traits (after accounting for the effects of female mass and individual identity) for a) mean egg diameter, b) mean egg mass, c) mean egg density, and d) skein mass. Small points are individual measurements, large diamonds are the mean residual for that year, and the lines and shaded regions show the mean regression relationship $\pm$ 95% confidence intervals.

152x127mm (300 x 300 DPI)