

**MATERNAL EFFECTS AND EGG SIZE VARIATION IN FISHES:
GENERAL PATTERNS AND THE INFLUENCE OF SYSTEM SIZE**

by

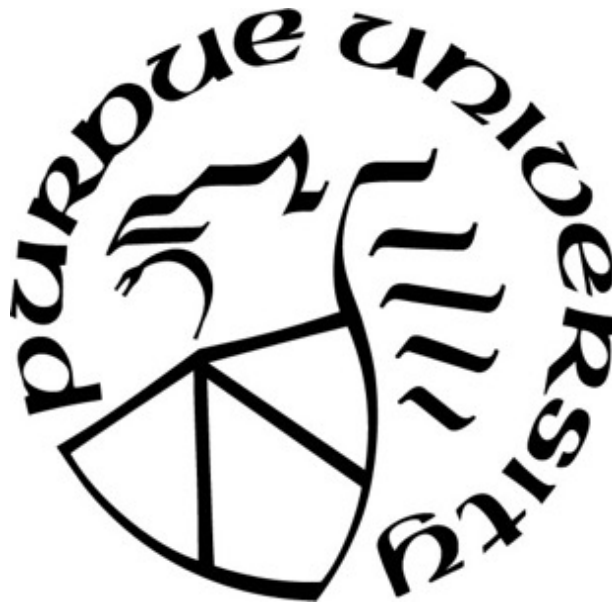
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A Thesis

Submitted to the Faculty of Purdue University

In Partial Fulfillment of the Requirements for the degree of

Master of Science



Department of Forestry and Natural Resources

West Lafayette, Indiana

May 2020

THE PURDUE UNIVERSITY GRADUATE SCHOOL
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Dedicated to my parents, Tom and Karen Koenigbauer, my sister, Emily Koenigbauer, my girlfriend, Kelsey Hurt, and my grandfather, Edward Koenigbauer

ACKNOWLEDGMENTS

I would like to thank my advisor Tomas Höök for his support of my research, guidance, and mentorship. I would also like to thank my committee members Mark Christie and Zachary Feiner for project advice and thesis revisions. I thank past and present members of the Höök lab, including Alex Gatch, Taylor Senegal, Suse LaGory, Ben Leonhardt, Patricia Nease, Marissa Cubbage, Josh Tellier, Chris Malinowski, Annie Scofield, Jay Beugly, and Matt Hamilton for assisting field collections, laboratory processing, and generally supporting me through my master's studies. I would also like to thank Claire Schraidt for her help with field collections. I thank employees from Indiana DNR (Ben Dickinson), Wisconsin DNR (Stephanie Shaw, Dan Dembkowski, Tammie Paoli), Michigan DNR (Troy Zorn, Scott Hanshue), and the Little Traverse Bay Bands of Odawa Indians (Kristopher Dey) for assistance in sample collection. I thank Robert Rode for his help with upkeep and experimental set-up at the Purdue Aquaculture Research Laboratory.

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ABSTRACT

The need to protect size and age structures from selective harvest in order to maintain sustainable fish stocks has been emphasized in recent literature. The Big Old Fat Fecund Female Fish (BOFFFF) hypothesis has been influential in discussions of changing stock management strategies, and postulates that larger, older females have a disproportionate input into stock recruitment due to physiological advantages. In this study, we utilize a meta-analysis approach to test the assumption of the BOFFFF hypothesis, that larger female fish produce larger eggs and more viable offspring, at a broad scale. Following the meta-analyses, we assess whether larger females from a subset of studies use their gonadal investment more efficiently than small females. From our meta-analyses, we found positive, significant intraspecific relationships between female size and egg size. Moreover, we found positive associations between egg size and offspring viability (offspring size and survival). However, we found in a subset of studies that although proportional survival of offspring often increases with egg size, females that produced larger eggs yielded fewer surviving offspring per unit gonadal investment. This reduced efficiency in reproductive investment is a product of the trade-off between egg size and fecundity. We conclude that although larger females may appear to produce more viable individual offspring, their input to stock recruitment, according to total stock gonadal biomass, may not be disproportionate, as stated by the BOFFFF hypothesis. However, we did not account for whether the benefits of maternal effects extend beyond the larval stage.

The theory of optimal egg size implies that fish trade off between fecundity and individual gonad investment according to their environment. Past interspecific studies suggest that in general, fishes in large, marine systems produce smaller eggs than those in small, freshwater systems. This study aims to compare egg size intraspecifically among small and large systems. In particular, we focus on populations from the Laurentian Great Lakes, which exhibit similar broadscale physical processes as marine systems, and smaller inland lakes (<1,000 ha), whose ecosystems contain many of the same species. In 2018 and 2019, we collected egg samples from spawning walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) in both inland lake and Great Lake populations. From each female, we recorded total lengths, and measured average diameters of ten eggs. Using ANCOVA models, we compared mean length-adjusted egg diameters intraspecifically among populations of both species. For both walleye and yellow perch, we found that females

from inland lakes produced larger mean length-adjusted egg diameters than those of the Great Lakes. This pattern was particularly evident for yellow perch, whereas for walleye the pattern was relatively weak, potentially due to stocking eroding population-specific selection for egg size. These intraspecific patterns are consistent with cross-system interspecific variation in fish egg size.

CHAPTER 1. INTRODUCTION

1.1 Body

As fisheries stocks decline both worldwide, and locally in the Laurentian Great Lakes region, research that elucidates factors influencing fish population dynamics is necessary to inform sustainable management strategies. Recruitment, the addition of adult fish to a population through natural reproduction, has long been considered a key process determining stock biomass (Russell 1931). However, population-level reproductive success and subsequent recruitment of individuals to fisheries stocks are often highly variable, because they are highly sensitive to various biotic and abiotic processes (Chambers and Trippel 2012; Cushing 1990; Aburto-Oropeza 2007). Such high recruitment variability can have strong influence on overall population dynamics and confound fisheries management, and therefore, prediction and elucidation of recruitment dynamics have been long-standing foci of fisheries investigations (Hilborn and Walters 2013; Szuwalski et al. 2015).

Recently, a prevailing concept in fisheries research has been that demographic factors may play a role in stock recruitment potential. Historically, relatively simple recruitment models were based upon estimates of spawning stock biomass, which is often expressed as the sum biomass of all females' gonads within a fish stock. The big old fat fecund female fish (BOFFFF) hypothesis postulates that larger, older female fish have reproductive potential that is disproportionate to their share of the total spawning stock biomass, due to physiological and behavioral advantages over smaller, younger conspecifics (Berkeley et al. 2004; Hixon et al. 2013; Barneche et al. 2018). The relationship of these larger females' phenotypes and their offspring's viability can be referred to as maternal effects, which are defined as non-genetic influences of mothers on offspring success (Green 2008). The BOFFFF hypothesis highlights three particular maternal effects: 1) that larger females produce larger eggs 2) that those larger eggs yield larger individual offspring through increased size at hatching and improved growth, and 3) that larger eggs increase their corresponding individual offspring's survival (Hixon et al. 2013). In the present study, we tested the broad-scale applicability of these three maternal effects with a meta-analysis approach.

While larger eggs may yield individual offspring with improved growth and survival, increasing average egg size may not benefit a female's potential fitness. A trade-off between egg

size and fecundity exists, where females' finite gonadal energy and space can be distributed among many small eggs or fewer larger eggs (Smith & Fretwell 1974). Therefore, according to the BOFFFF hypothesis, in order for females to have reproductive potential that is disproportionate to spawning stock biomass, the benefits of increasing egg size must outweigh the resulting loss in potential fecundity. Further, in many cases these benefits of maternal effects must also extend past offspring's larval stage in order to play a role in overall stock recruitment. Many studies report on the maternal effects that are highlighted by the BOFFFF hypothesis, but few consider the egg size vs. fecundity trade-off in their experimental designs. Using individual observations from a subset of studies, we demonstrated the relationship between egg size and potential offspring survival per unit gonadal volume, which incorporates the trade-off with fecundity, along with the duration of maternal effects.

The egg size trait may vary according to factors other than maternal size. Past studies have shown that on average, females of freshwater species produce larger eggs than those of marine species (Fuiman and Werner 2009). This may be a result of differential pressures during the early life of larvae between the two system types (Houde 1994). Freshwater species' larvae often emerge at a larger size, have shorter stage durations, and lower mortality rates than those of marine fishes. Marine species' larvae experience relatively high mortality, and their survival is often determined by whether they experience favorable conditions in a highly variable environment. Egg size also has been observed to vary intraspecifically, among populations that are located in similar systems. For example, accounting for demographic differences in females, walleye (*Sander vitreus*) egg size has been found to vary across populations in multiple studies (Johnston and Leggett 2002; Wang et al. 2012; Feiner et al. 2016).

Differences in egg size among populations may indicate some level of local adaptation. Based on the trade-off between egg size and fecundity, the theory of optimal egg size proposes that selection leads females to produce eggs of an appropriate size for their environment, in order to maximize their fitness (Smith and Fretwell 1974; Einum and Fleming 2002). As previously mentioned, variation of average egg size among Great Lakes walleye stocks is well documented, and these stocks have been characterized as genetically-distinct (Stepien et al. 1998). Therefore, local adaptation could partially explain phenotypic variation in the egg size trait of walleye.

While optimal egg size theory implies that the mean population egg size is adaptive, egg size variation is also responsive to variable environmental factors and is not genetically canalized

within populations. Egg size varies intraspecifically across populations and is associated with factors such as: temperature (Johnston and Leggett 2002; Jonsson and Jonsson 2016; Barneche et al. 2018), latitude (Fleming and Gross 1990; Beacham and Murray 1993; Kokita 2003), and productivity (Johnston and Leggett 2002; Wang et al. 2012). Moreover, annual variation in environmental conditions can influence mean population egg size (Tanasichuk & Ware 1987; Feiner et al. 2016), and controlled studies demonstrate that exposure to different temperature (Feiner et al. 2018), food availability (Hutchings 1991), and competitive interactions can affect realized egg sizes. Therefore, although genetic variation is a major component in interpopulation egg size variation, environmental and demographical features simultaneously influence egg size.

Comparisons of egg size between freshwater and marine systems, however, have only been interspecific, due to differing species occupying these different systems. Therefore, these comparisons are unable to account for the effect of different species in their analyses. The Laurentian Great Lakes display broad-scale physical processes that are similar to those of marine systems (e.g. upwellings, cross-system circulation), but are also a freshwater ecosystems (Pritt et al. 2014). Consequently, the Great Lakes' fish communities share numerous species with the smaller inland lakes found in the same region. Thereby, we were able to make intraspecific comparisons of egg size across system sizes, including the Great Lakes and smaller inland lakes. In 2018 and 2019, we performed field collections of two species: walleye and yellow perch (*Perca flavescens*), in order to acquire egg samples from spawning females. Accounting for differences in female demographics, we were able to compare average egg size across system size intraspecifically in two Great Lakes species.

Through our meta-analyses and field collections, we identified new considerations for our understanding of fisheries stock recruitment. First, our meta-analysis not only yielded significant, positive effects of increasing female size on egg size, but also significant, positive effects of larger eggs on offspring growth and survival, as highlighted by the BOFFFF hypothesis (Hixon et al. 2013). However, we also demonstrated the cost of increasing egg size on potential fecundity, and how the loss of potential fecundity may reduce the hypothesized benefit of larger females on stock recruitment. Our field observations supported past studies' findings of interpopulation egg size variation in walleye, and revealed a similar trend in yellow perch, which to our knowledge had not been previously reported. Finally, we made comparisons of average egg size between small and large systems, and observed that in general, females from smaller inland systems produced larger

eggs. These findings may inform future management practices in order to benefit fish recruitment, and therefore, sustainable fisheries stocks.

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CHAPTER 2. EXAMINING REPRODUCTIVE EFFICIENCY OF BOFFFFFS WITH A META-ANALYSIS APPROACH

2.1 Introduction

Population-level reproductive success and subsequent recruitment of individuals to adult fish populations are generally characterized by high spatio-temporal variability in response to various biotic and abiotic processes (Chambers & Trippel 2012; Cushing 1990; Aburto-Oropeza 2007). Such high recruitment variability can have strong influence on overall population dynamics and confound fisheries management, and therefore, prediction and elucidation of recruitment dynamics have been long-standing foci of fisheries investigations (Hilborn and Walters 2013; Szuwalski et al. 2015). While fish recruitment is often linked to spawner abundance and spawning stock biomass (SSB; Shepherd 1982), Berkeley et al. (2004) caution that models relating recruitment to SSB may be too simplistic, because recruitment may also depend on population demographics. Populations with broader size and age structures may temper recruitment variability in unpredictable environments by increasing diversity of spawning locations and time (Wright and Trippel 2009; Hsieh et al. 2010). Barneche et al. (2018) postulated that larger marine fishes contribute disproportionately to stock recruitment due to hyperallometric scaling of reproductive investment. Recent literature has emphasized the importance of BOFFFFFs (Big Old Fat Fecund Female Fish) for population recruitment because of their high reproductive potential. BOFFFFFs are hypothesized to limit stock variability and enhance stock productivity due to relatively high fecundity, ability to outlive unfavorable periods for reproduction, facilitation of spatio-temporally diverse spawners, and maternal effects leading to increased offspring survival (Hixon et al. 2013). Maternal effects are the non-genetic influence of a female fish's physical characteristics on her offspring's viability and growth (Green 2008). One example of a maternal effect is the positive relationship between a female fish's size (e.g. length, mass) and the size of her eggs (Chambers and Leggett 1996). Energetic investment per individual egg, and consequently growth and survival of larval fish, generally increase with egg size (Bagenal 1969; Eium and Fleming 1999). Therefore, larger female fish may have the capability to not only produce more offspring, but these offspring may also experience greater survival.

Size-selective pressures of fishing, which truncate size and age structures, may exacerbate recruitment variation and limit overall recruitment potential. That is, size selective fishing gear and regulations often promote the harvest of larger, older fish, thereby limiting the potential benefits of BOFFFFs. Various authors have suggested that changes in gear and regulations (e.g., slot limits instead of minimum size limits) may facilitate survival of larger, older fish and thereby temper recruitment variation and facilitate increased population-level recruitment potential (e.g., Berkeley et al. 2004; Birkeland and Dayton 2005; Hixon et al. 2013).

Although larger eggs may have higher individual probability of survival, fish must trade off between egg size and fecundity due to limited ovary capacity and available energy (Smith and Fretwell 1974). As a result, increased investment in individual egg quality may come at a cost of decreased maximum fecundity. The ecological theory of optimal egg size suggests that fish can maximize their quantity of successful offspring by investing a certain amount of energy and space into each egg (Einum and Fleming 2002). Fish that produce large eggs will limit efficiency due to lower fecundity, and fish that produce small eggs will limit efficiency through decreased egg viability. Therefore, fish that produce eggs of an appropriate size for their environment are the most efficient at reproduction. Further, if the maternal effect of increasing egg size with female size is adaptive, this might suggest that the appropriate egg size for an environment is dependent on female size.

While several recent studies have advocated for protection of BOFFFFs due in part to their relatively high fecundity and large egg sizes, it is not manifest that protecting large, old spawning fish will increase recruitment potential. First, there is evidence that fecundity can decrease once female fish reach a certain age (Koslow et al. 1995; Benoît et al. 2018). Second, it is not given that positive maternal size effects on egg size will lead to larger offspring with greater survival. In fact, some studies demonstrate that offspring produced by larger, older females may experience lower early life survival rates (e.g., Eslinger et al. 2010; Andree et al. 2013). This is consistent with the notion of senescence, which is not well understood for fish (Salguero-Gomez et al. 2019). Further, Andersen et al. (2019) demonstrates that by failing to account for demographic and density-dependent effects, authors such as Barneche et al. (2018) overestimate the contribution of older, larger adults to population-level reproductive output. Finally and importantly, an increase in egg size represents a loss in potential fecundity. Therefore, in order for increasing egg size alone to improve a female's production of surviving offspring, the gain in offspring survival must be high

enough to offset the loss in potential fecundity. If not, smaller, younger fish that produce relatively small eggs may yield a greater number of surviving offspring per unit mass or volume of gonad.

The two main goals of this study were 1) to evaluate the broad-scale patterns of maternal effects in fishes and 2) to demonstrate the trade-off between increasing egg size and fecundity, and its implications for the BOFFFF hypothesis. To this end, we employed a meta-analysis approach to summarize published relationships among female size, egg size, and offspring survival. We evaluated whether egg size increases with female size, and if increasing egg size is related to increased offspring size and survival. We compared the strength of maternal effects among groups such as taxonomic orders, system types, and experimental durations. Following the meta-analyses, we demonstrated the consequences of increasing egg size on the number of surviving offspring a female produces per unit gonad size. For this demonstration, we used data collected from our meta-analysis to estimate weighted average maternal effects relationships. Our prediction was that egg size, and therefore, provisioning for individual offspring, would increase with female size. We further predicted that individual offspring survival would increase with egg size. However, because of the trade-off between egg size and fecundity, we predicted that females that produced larger eggs would not produce more surviving offspring per unit gonad size.

2.2 Methods

2.2.1 Meta-analyses

In order to evaluate maternal effects across a breadth of species and environments, we employed a meta-analysis approach. As opposed to narrative reviews, meta-analyses are intended to assess consistency of effects across many studies using a structured quantitative approach to limit potential biases. By using a meta-analysis approach, we were able to include multiple past studies that evaluated similar relationships with different units of measurement (e.g. dry mass, wet mass, total length). By incorporating standardized effect sizes, we accounted for the strength of each study's observed patterns, e.g., by considering variance and sample size of individual studies (Borenstein et al. 2011). We performed two meta-analysis searches with defined terms using ISI Web of Knowledge for extraction of effect sizes from published literature (Table 2.1). The three key relationships we tested with our meta-analysis searches included: 1) female size vs. egg size, 2) egg size vs. offspring size, and 3) egg size vs. offspring survival. We reviewed all papers that

resulted from each search for information that was relevant to the specific targeted relationship. From the first search, we included studies that featured univariate tests of the relationship between female size (e.g., total length, wet mass) and egg size (e.g., diameter, mass, volume) and allowed us to calculate an effect size based on relational statistics (e.g., correlation and regression coefficients) and sample size. From the second search, we included studies that featured either a univariate test of the relationship between egg size and offspring size or the relationship between egg size and offspring survival. Following our initial survey of studies resulting from our meta-analysis searches, we performed a backward search on all studies from which we extracted effects, and thus, we included any additional relevant references from those studies.

Table 2.1. Searches used for meta-analyses. Queries were entered in ISI Web of Knowledge, and a backward search was performed on all studies from the original searches that were included in our meta-analyses.

Search	Relationship	Search Query	Date	# Results
1	Female Size ~ Egg Size	"Fish" AND "Egg" AND "Maternal" AND "Size"	2/9/18	370
2	Egg Size ~ Offspring Viability	"Fish" AND "Egg" AND "Egg Diameter OR Egg Size OR Egg Mass OR Egg Weight" AND "Growth OR Survival OR Mortality"	4/5/19	827

Examining effect size allowed us to incorporate a variety of maternal, egg, and larval measurements (e.g. egg diameter, egg mass, larval length, larval mass, female length, female mass) into our analyses. The effect that we collected from each study was Pearson's correlation (r). We incorporated multiple effects from the same study if they reported multiple separate experiments on different species or populations. When possible, we collected correlation coefficients, either as published, or by using ImageJ software to estimate values from figures (Schneider et al. 2012). To analyze effect sizes, we transformed r values to Fisher's Z values, which are normally distributed (Borenstein et al. 2011). Each study's Fisher's Z value can be weighted (W) by study variance, which is determined by the number of observations in each study (n).

$$\text{Fisher's } Z = \frac{1}{2} [\ln(1 + r) - \ln(1 - r)] \quad (2.1)$$

$$V_Z = \frac{1}{n-3} \quad (2.2)$$

$$W = \frac{1}{V_Z} \quad (2.3)$$

Mean Fisher's Z values (\bar{Z}) can be calculated for multiple maternal effect relationships by combining weighted effects from all studies (k).

$$\bar{Z} = \frac{\sum_{i=1}^k W_i Z_i}{\sum_{i=1}^k W_i} \quad (2.4)$$

Because Fisher's Z values are normally distributed, we can calculate normal confidence intervals. 95% confidence intervals were calculated using the variance of the mean Fisher's Z ($V_{\bar{Z}}$). Standard error ($SE_{\bar{Z}}$) was estimated using the mean Fisher's Z variance,

$$V_{\bar{Z}} = \frac{1}{\sum_{i=1}^k W_i} \quad (2.5)$$

$$SE_{\bar{Z}} = \sqrt{V_{\bar{Z}}} \quad (2.6)$$

then multiplied by the corresponding t-critical value for 95% confidence.

$$CI = \bar{Z} \pm SE_{\bar{Z}} \times 1.96 \quad (2.7)$$

Mean values and confidence intervals can be divided into groups, such as taxonomic order or duration of experiment. Confidence intervals that overlap with 0 imply that there is no evidence of a significant maternal effect at an alpha level of 0.05.

A common concern with meta-analyses relates to publication bias, whereby all studies are not equally likely to be published (Rothstein et al. 2005). In particular, non-significant relationships are often less likely to be published than significant relationships. We tested for potential publication biases using Egger's tests (Egger et al. 1997). Specifically, we tested the null hypothesis of symmetry of effect sizes around a mean. Egger's tests were performed for each of the three relationships: female size vs. egg size, egg size vs. offspring size, and egg size vs. offspring survival.

2.2.2 Demonstrative analyses

While analyzing effect sizes from studies that measure different variables allows us to increase statistical power, meta-analyses restrict some ability to illustrate relationships because they do not incorporate individual observations. For example, effect sizes can indicate the presence,

absence, and direction of particular relationships, but do not incorporate the coefficients of those relationships. For this reason, we selected a subset of papers from each meta-analysis search that all measured the same variables in order to demonstrate maternal effects and consequences of the egg size-fecundity trade-off.

First, we demonstrated the relationship between female size and egg size. In order to do this, we selected the subset of studies from our first meta-analysis search that included measurements of female total length and egg diameter (i.e., the most common measures of maternal and egg size, respectively; Table 2.2). From each of these studies, we recorded the range of female total lengths, experimental sample size, and linear regression coefficients for total length – egg diameter relationships. When studies did not include linear regression coefficients, we calculated them using either reported observations, or by estimating the studies' observations from figures using ImageJ software. Each studies' linear regression coefficients were then weighted by study precision ($\frac{1}{V_r}$).

$$V_{ri} = \frac{(1-r_i^2)^2}{n_i-1} \quad (2.8)$$

We combined these weighted coefficients in order to obtain a mean, weighted regression trendline for the total length – egg diameter relationship.

$$\overline{slope} = \sum \left[slope_i \left(\frac{1}{V_{ri}} \div \sum \frac{1}{V_{ri}} \right) \right] \quad (2.9)$$

We also demonstrated the trade-off of egg size and the number of surviving offspring per unit gonadal investment. To do this, we selected a subset of all possible studies from our second meta-analysis search that included measurements of egg diameter and proportional survival of offspring. For each of these studies, we recorded individual observations of egg diameters and corresponding proportional survival from each study, along with the duration of each study. Each study reported experiments of different durations, which can lead to difficulty in making comparisons. In order to account for this, we transformed each proportional survival (S) to daily instantaneous mortality (Z) based on days post hatch (hereafter dph).

$$Z = -\ln S / dph \quad (2.10)$$

We then used Z to estimate proportional survival to different durations.

$$S_{dph} = e^{-Z \times dph} \quad (2.11)$$

Table 2.2. Studies from meta-analysis search 2 that were included in the demonstration of increasing egg diameter's relationships with offspring proportional survival and number of surviving offspring produced per 1 mL gonad volume.

Study	Species	Study duration (dph)	n
Fowler 1972	<i>Oncorhynchus tshawytscha</i>	28	20
Gisbert et al. 2000	<i>Acipenser baerii</i>	10	20
Hutchings 1991	<i>Salvelinus fontinalis</i>	20	27
Iguchi & Yamaguchi 1994	<i>Plecoglossus altivelis</i>	1	55
LeBlanc et al. 2016	<i>Salvelinus alpinus</i>	138	13
Mann & Mills 1985	<i>Leuciscus leuciscus</i>	31	12
Nissling et al. 1998	<i>Gadus morhua</i>	10	126
Pitcher & Neff 2007	<i>Oncorhynchus tshawytscha</i>	80	11
Skaala et al. 2012	<i>Salmo salar</i>	1095	51
Tamada & Iwata 2005	<i>Rhinogobius sp.</i>	3	14

The relationship of egg diameter and proportional survival changes according to the duration at which we estimate survival. We demonstrated the change in these relationships across different durations by calculating proportional survival at 1, 10, 20, 30, 40, 50 and 60 dph. We also included the durations of each study's actual experiment. To calculate the number of surviving offspring per unit gonadal investment, which we represent as gonadal volume (1 mL), we first transformed individual egg diameter (D; mm) observations to egg volume (V; mm³).

$$V = \frac{4}{3}\pi\left(\frac{D}{2}\right)^3 \quad (2.12)$$

Egg volume was then converted to the number of eggs per 1 mL gonad.

$$\# \text{ eggs}^{-\text{mL}} = 1000/V \quad (2.13)$$

Finally, to estimate the number of surviving offspring per 1 mL gonad, we multiplied the number of eggs per mL by proportional survival at a given duration.

$$\# \text{ survivors}^{-\text{mL}}_{\text{dph}} = \# \text{ eggs}^{-\text{mL}} \times S_{\text{dph}} \quad (2.14)$$

This process was carried out for all aforementioned durations in each study.

2.3 Results

2.3.1 Meta-analyses

From our first meta-analysis search, we collected 195 effect sizes for the relationship between female size and egg size from 95 studies (A.1). Individual effect size values ranged from -0.959 to 2.221, with a mean of 0.510. Overall, there was a significant, positive effect of female size on egg size ($p < 0.05$; Figure 2.1). Effects for this relationship were grouped by taxonomic order, including all orders for which we calculated at least 5 effects. When grouped by taxonomic order, mean effects of female size on egg size were all significantly positive ($p < 0.05$; Figure 2.1.a). The taxonomic orders Cypriniformes and Salmoniformes had significantly stronger effects than all others ($p < 0.05$; Figure 2.1.a). We also grouped species into marine, freshwater, and anadromous. All three habitat type groups displayed significant, positive mean effects of female size on egg size ($p < 0.05$; Figure 2.1.b). Freshwater fishes displayed significantly stronger effects than marine fishes ($p < 0.05$; Figure 2.1.b), and anadromous fishes had intermediate effects, which were significantly stronger than marine fishes, but weaker than freshwater fishes ($p < 0.05$; Figure 2.1.b).

From our second meta-analysis search, we collected 74 effect sizes for the relationship between egg size and offspring size from 60 studies (not including offspring size immediately after hatch; A.2). Individual effect size values ranged from -2.599 to 2.759, with a mean of 0.730. We detected an overall significant, positive effect of egg size on larval size ($p < 0.05$; Figure 2.2). In addition, from 44 studies, we collected 56 effect sizes for the relationship between egg size and size-at-hatch. We found a significant, positive effect of egg size on hatchling size ($p < 0.05$; Figure 2.2). We grouped studies relatively equally by duration of experiment, including size-at-hatch, 1-10dph, 11-60 dph, and >60 dph. For all of these groups, we detected a significant, positive effect of egg size on larval size ($p < 0.05$; Figure 2.2). The effect of egg size on larval size was significantly weaker at experimental durations >60dph than all other duration groups ($p < 0.05$; Figure 2.2).

From our second meta-analysis search, we also collected 45 effect sizes for the relationship between egg size and offspring survival from 30 studies (A.3). Individual effect size values ranged from -1.256 to 1.799, with a mean of 0.326. We found an overall significant, positive effect of egg size on offspring survival ($p < 0.05$; Figure 2.3). The overall effect of egg size on offspring survival did not include hatching success. We grouped the studies relatively equally by duration of

experiment, including 1-10 dph, 11-60 dph, and >60 dph. The effect of egg size on offspring survival was significantly positive for all three duration groups ($p < 0.05$), and we did not detect significant differences among the groups ($p > 0.05$; Figure 2.3).

We conducted Egger's tests of symmetry for each of the three meta-analysis relationships. While we found positive mean effects for each relationship, the distribution of individual study effects were not skewed toward positive effects, i.e., they were not significantly asymmetrical ($p > 0.05$, Figure 2.4), indicating a lack of strong publication bias.

2.3.2 Demonstrative analyses

From our first meta-analysis search, we collected coefficients from 53 regression trendlines (from 46 studies) describing female total length vs. egg diameter relationships (Figure 5a). We calculated an average trendline from the 46 studies' regression coefficients by weighting each experiment by precision ($1/V_r$). The overall weighted relationship was positive and indicated that with every 10 mm increase in female total length there was a 0.026 mm increase in egg diameter:

$$\text{Egg Diameter} = 0.0026TL + 1.424 \quad (2.15)$$

When converted to egg volume, this relationship implies a decrease in the number of eggs produced per unit gonadal volume. For example, a 10 mm increase in female total length from 500 to 510 mm would lead to a 3.0% increase in average egg volume and a corresponding 2.9% decrease in number of eggs per mL of ovarian tissue (Figure 2.5b).

From our second meta-analysis search, we collected 10 regression trendlines from 10 studies describing the relationship between egg diameter and proportional survival to the studies' duration (Figure 2.6). In addition, we transformed individual proportional survival observations were transformed to seven durations: 1, 10, 20, 30, 40, 50 and 60 dph. We also included each study's actual experimental duration. Six of these studies yielded positive relationships between egg diameter and offspring proportional survival at all dph values. One study yielded a positive relationship between egg size and offspring proportional survival at shorter durations, and a negative relationship at longer durations.

Using the 10 proportional survival studies, we transformed these relationships to number of surviving offspring per 1 mL gonadal volume (Figure 2.7). We converted egg diameter observations to number of eggs per 1 mL, and were then multiplied by proportional survival to the

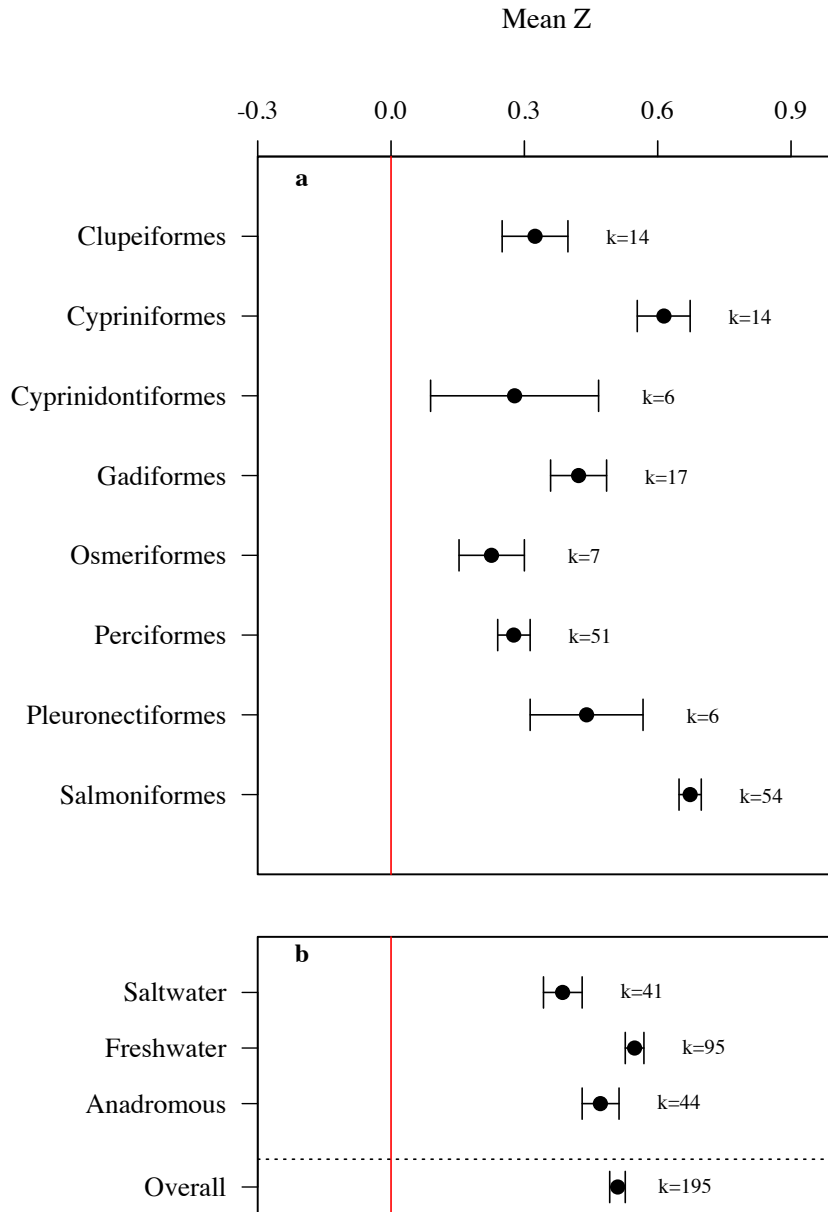


Figure 2.1. Mean effect size (Fisher's Z) of female size vs. egg size relationships, grouped by taxonomic order. Orders that contained at least five studies were included. (b) Mean effects were also grouped by habitat type. Lines represent 95% confidence intervals of mean effects. Lines that do not include zero indicate a significant mean effect at $\alpha = 0.05$.

same dph values: 1, 10, 20, 30, 40, 50, 60 dph, along with each study's actual experiment duration. Six studies yielded negative relationships between egg diameter and number of

surviving offspring per 1 mL at all dph values. The other four studies yielded negative relationships at low dph values, and positive relationships at greater dph values.

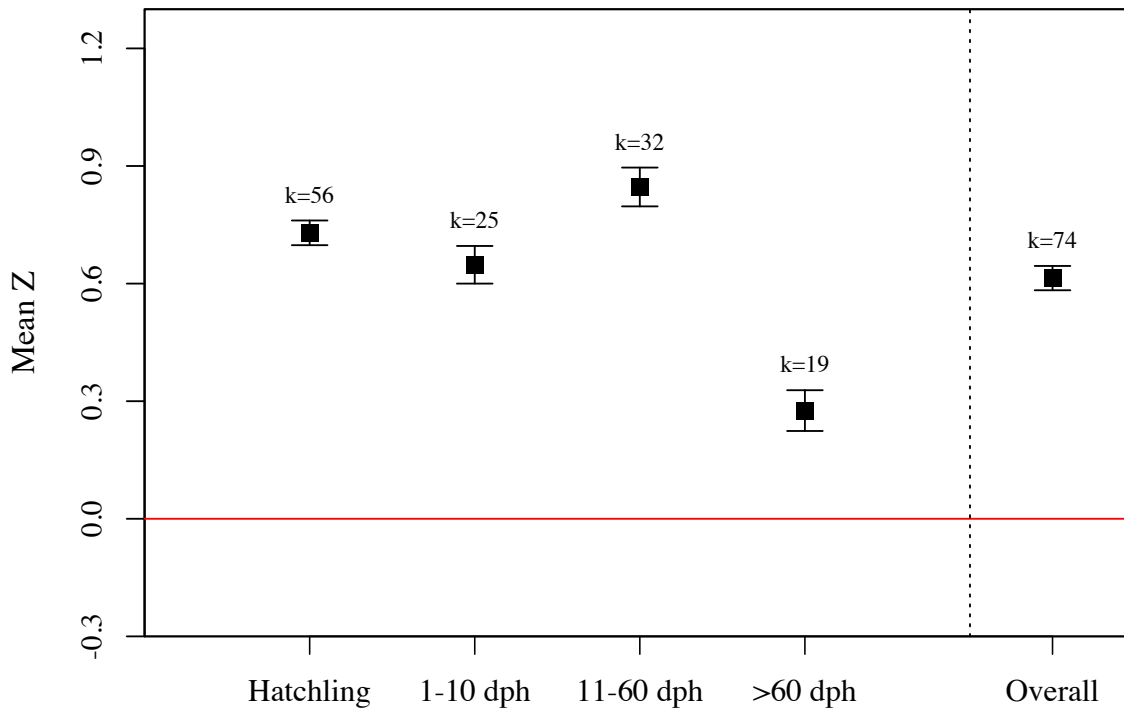


Figure 2.2. Mean effect size (Fisher's Z) of egg size vs. offspring size relationships, grouped by experiment duration (days post hatch). Lines represent 95% confidence intervals of mean effects. Lines that do not include zero indicate a significant mean effect at $\alpha = 0.05$.

2.4 Discussion

In general, our meta-analyses supported two components of the BOFFFF hypothesis: that larger females produce larger eggs, and that those larger eggs produce more viable offspring. Like past studies, we found 1) a significant, positive relationship between female size and corresponding egg size in numerous species (e.g., Hixon et al. 2014; Barneche et al. 2018), 2) an overall positive relationship between egg size and offspring size in many species (e.g., Chambers and Leggett 1996), and 3), an overall significant, positive relationship between egg size and offspring survival (e.g., Einum and Fleming 2000; Kamler 2005). We also found that maternal effects varied significantly across taxonomic orders and system types. Unlike most of these past studies, we examined maternal effects in freshwater species, and observed that they may be significantly

stronger than those in marine species. We also demonstrated that increasing egg size with increasing maternal size should lead to a decrease in number of eggs produced per unit size of ovaries. In order, for there to be a net benefit of producing larger eggs in terms of total number of surviving offspring, the increase in survival of larger offspring must overcome the loss of offspring production. Our demonstrations suggest that this is generally not the case, and therefore, the other proposed benefits of BOFFFFs could play a larger role in natural systems.

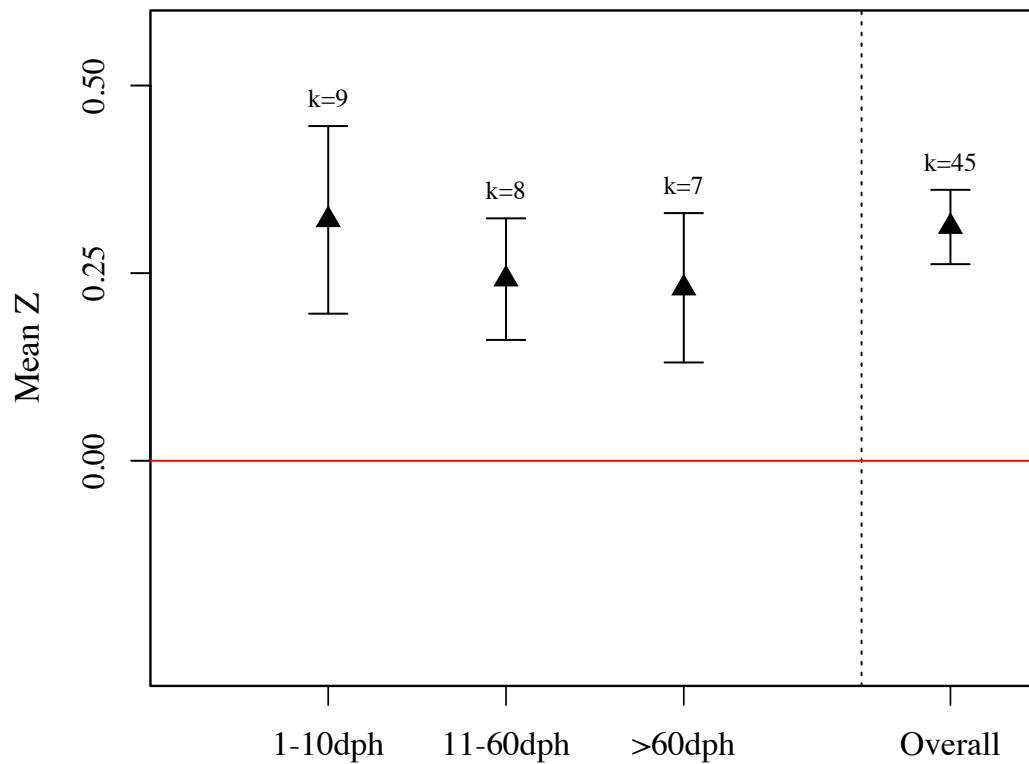


Figure 2.3. Mean effect size (Fisher's Z) of egg size vs. offspring survival relationships, grouped by experiment duration (days post hatch). Lines represent 95% confidence intervals of mean effects. Lines that do not include zero indicate a significant mean effect at $\alpha = 0.05$.

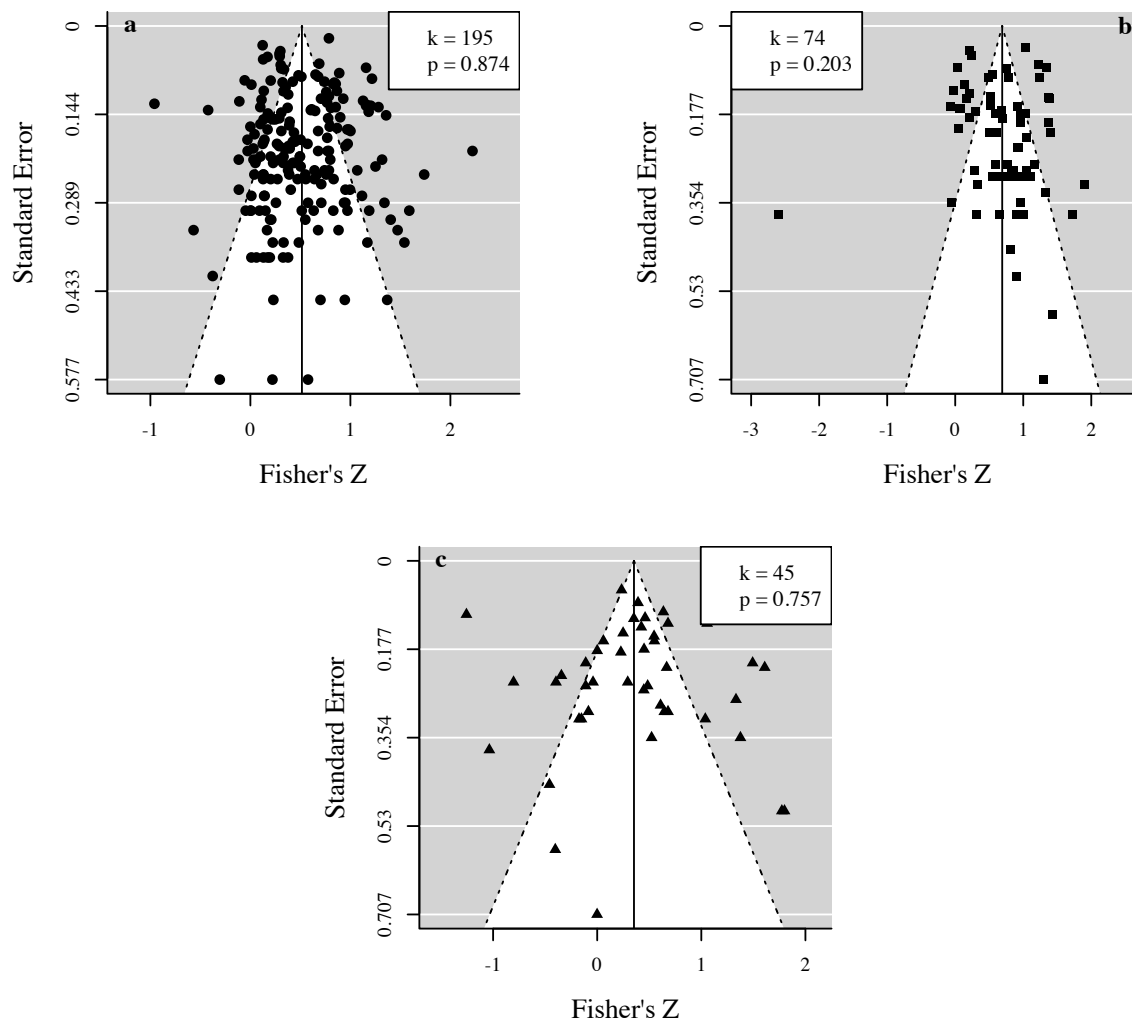


Figure 2.4. Funnel plots of mean effects (Fisher's Z) and standard error. Egger's tests of symmetry were performed for each of three meta-analysis relationships: (a) female size vs. egg size, (b) egg size vs. offspring size, and (c) egg size vs. offspring survival.

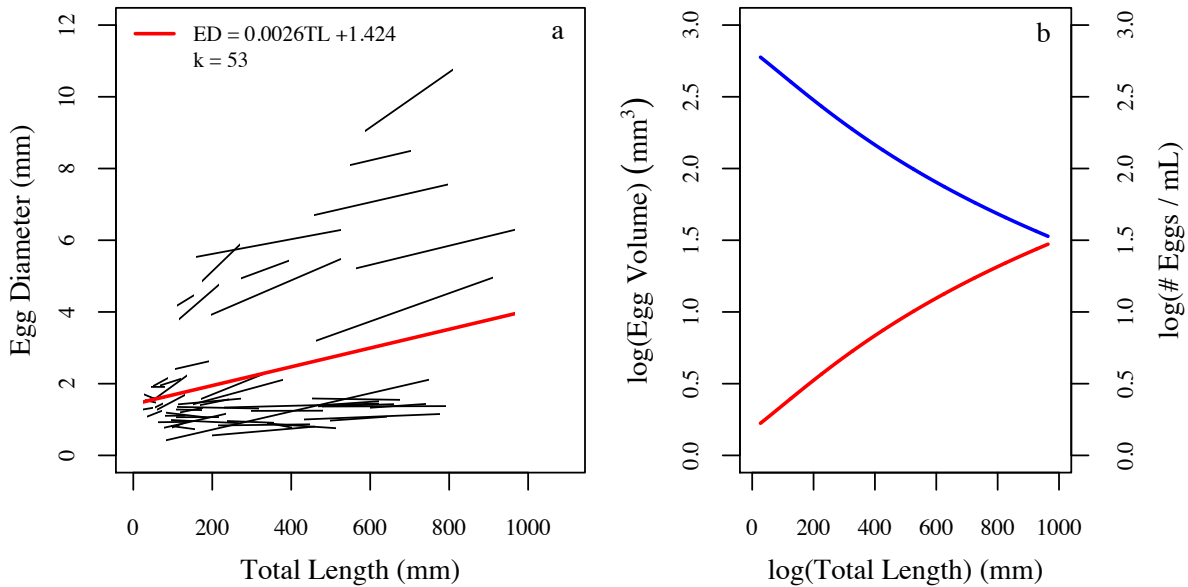


Figure 2.5. Regression trendlines for 53 total length vs. egg diameter relationships from 46 studies (a). An average trendline was calculated by weighting each trendline by precision ($1/V_r$). The average trendline from (a) was transformed to a total length vs. egg volume relationship in red (b). Egg volume was then converted to average number of eggs per mL, and a relationship between total length vs. number of eggs per mL was estimated in blue (b).

While larger females may provision individual offspring better for growth and survival, it is less clear whether larger females utilize their gonadal investment more efficiently. That is, a female utilizes gonadal investment more efficiently if she produces a greater number of surviving offspring per unit ovary space (volume) or energy. The basis of spawning stock biomass (SSB) models is that recruitment is proportional to the total gonadal biomass of a population, regardless of how that biomass is distributed in females. The BOFFFF hypothesis postulates that SSB models are too simplistic, however, because population demographics affect recruitment. Therefore, the BOFFFF hypothesis implies that larger females utilize their share of the total population's gonad biomass more efficiently, or make up a disproportionate share of the total spawning stock biomass due to allometric relationships between gonadal investment and body size.

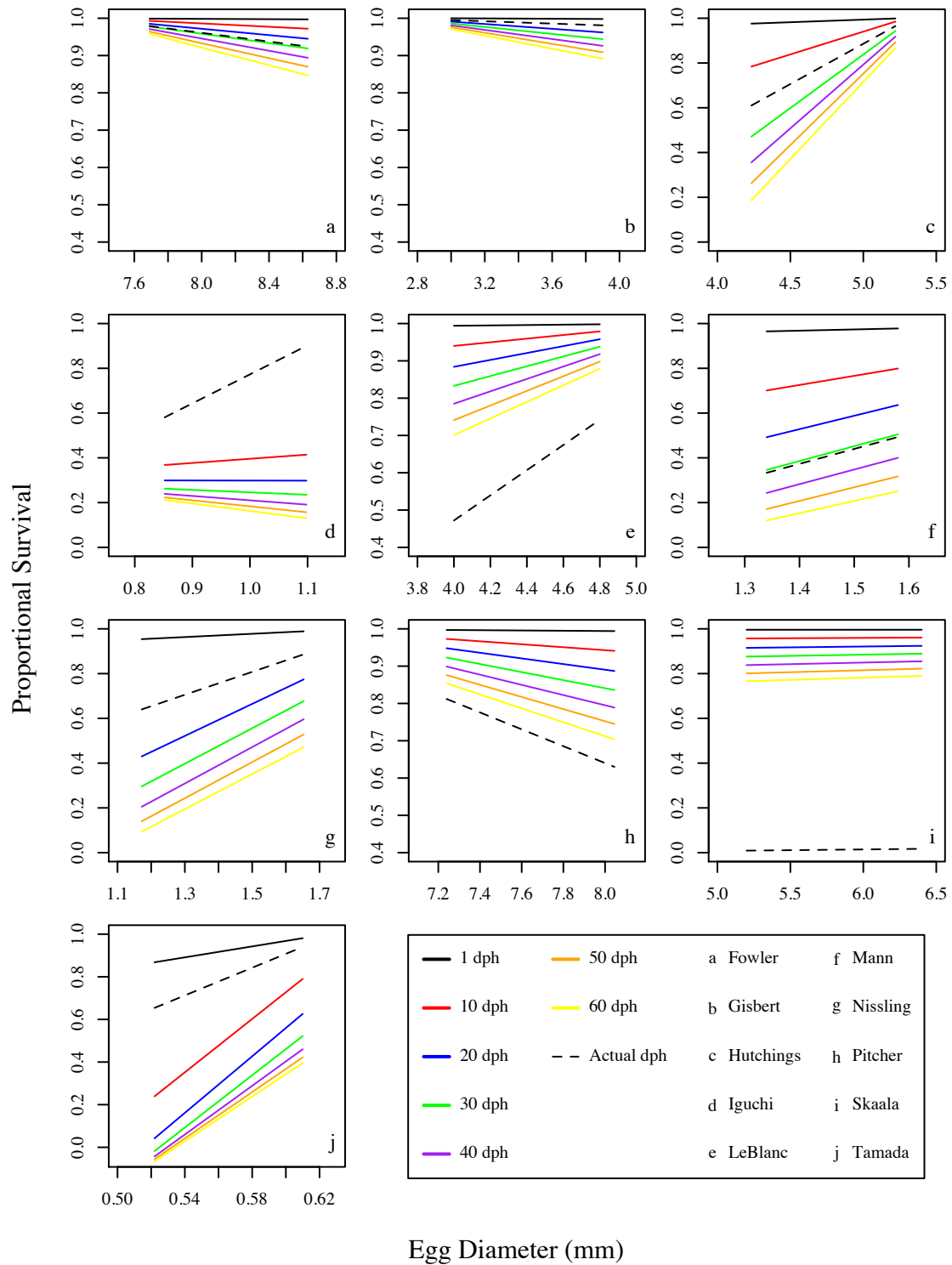


Figure 2.6. Egg diameter vs. proportional survival relationships of ten studies from our second meta-analysis search. Regression trendlines were calculated from each studies' individual observations. Proportional survival (S) at seven durations (1, 10, 20, 30, 40, 50, 60 dph) was estimated for each individual observation by transforming through instantaneous mortality (Z), and were plotted along with each study's actual experimental duration.

Our study did not support that larger females utilized gonadal investment more efficiently. We selected ten representative studies from our meta-analysis, and used those individual studies' observations to determine whether gonadal volume was more efficiently utilized by larger females. In all ten of the studies included in our analysis the egg size vs. fecundity trade-off, we found a negative relationship between egg diameter and the total number of survivors per unit gonadal volume at shorter durations. Only four studies showed a positive relationship between egg diameter and number of survivors per unit gonadal volume at any duration. Further, only two studies showed a positive relationship between egg diameter and numbers of survivors per unit gonad volume to the actual duration of the studies, and these studies lasted 138 and 1,095 dph and displayed fairly weak relationships. Thus, although our estimations of the relationship between egg size and gonadal volume efficiency were negative at short durations, they could become positive, should the benefits of egg size on offspring survival extend for a long duration, in some cases well beyond the larval stage. Nonetheless, while proportional survival typically increased with egg diameter, in the studies considered it typically did not increase enough to outweigh the potential fecundity cost of the increase in egg volume. It should be noted that laboratory studies may not fully capture the survival benefits of larger eggs that could be observed in a natural system. Further, our demonstration does not implicate that larger females have reduced fitness, because they typically have higher overall fecundity, and often exhibit greater proportional investment in their gonads than smaller females.

The effect of egg size on offspring survival may be stronger in species with longer larval duration periods. Larvae of species with relatively-short planktonic stages rely less on maternal provisioning for survival before they settle. Therefore, their survival is potentially more dependent upon habitat, environmental conditions, and density-dependent factors (Houde 1994). Contrarily, species with prolonged larval planktonic stages depend more on maternal provisioning to avoid starvation and survive until settlement. In our second demonstration, the four species that appeared to benefit from greater maternal provisioning, and therefore larger eggs, at longer durations were *Gadus morhua* (Nissling et al. 1998), *Leuciscus leuciscus* (Mann and Mills 1985), *Rhinogobius* species (Tamada and Iwata 2005), and *Salvelinus fontinalis* (Hutchings 1991). There was no apparent pattern between these species and their relative larval durations. Results of our first meta-analysis, which tested the relationship between female size and egg size, did support Houde's

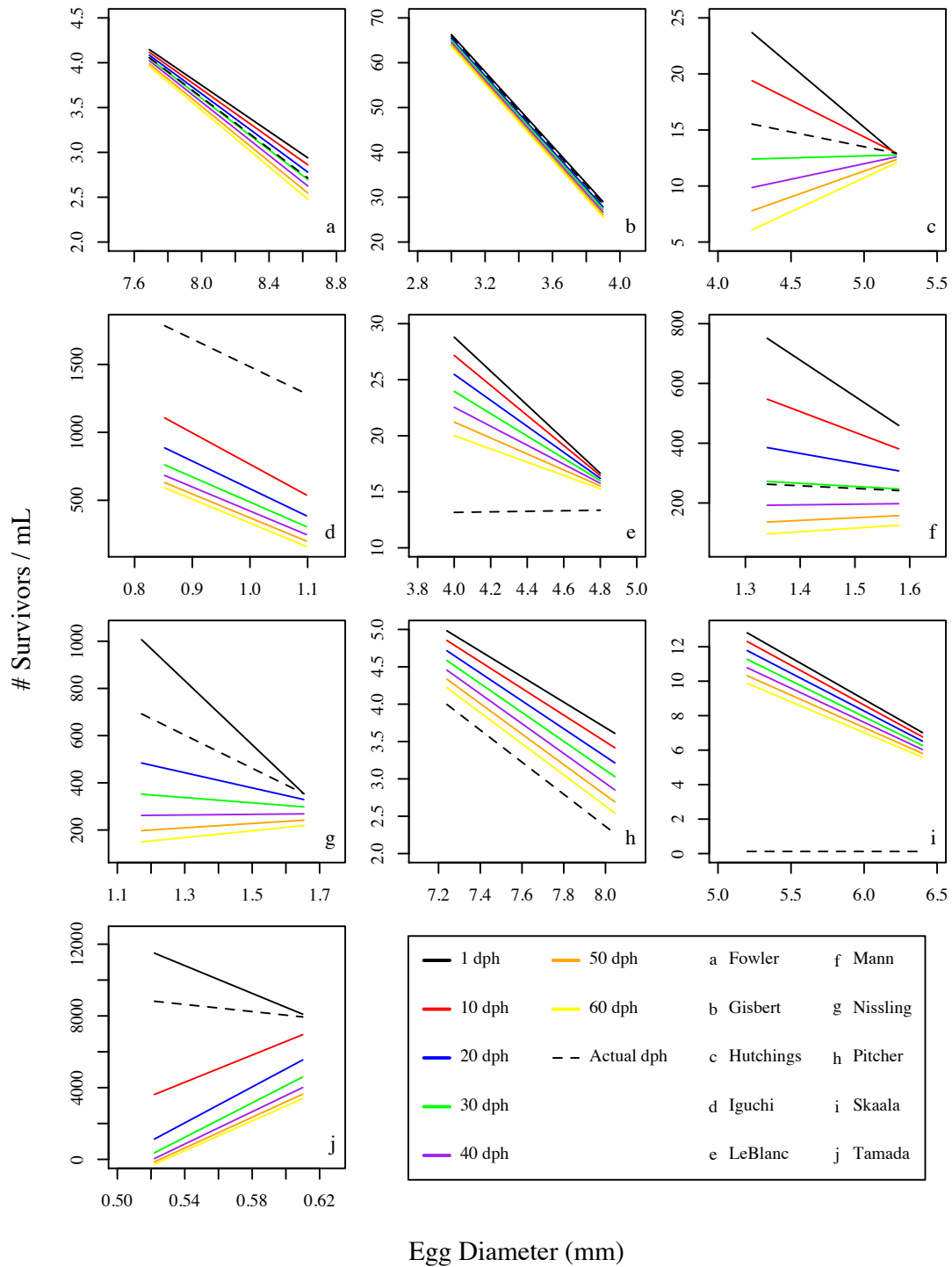


Figure 2.7. Number of surviving offspring per 1 mL gonad vs. egg diameter relationships for ten studies from our second meta-analysis search. Regression trendlines were calculated from each study's individual observations. Proportional survival (S) at seven durations (1, 10, 20, 30, 40, 50, 60 dph) was estimated by transformed through instantaneous mortality (Z), and were plotted along with each study's actual experimental duration. Egg diameter was transformed to number of eggs per mL, then multiplied by proportional survival.

(1994) observation, however, as we observed stronger maternal effects relationships in freshwater species than marine species.

Egg size variation among females may be less influential on offspring survival past the larval stage. In our study, we found that egg size had a significantly weaker effect on offspring size at experimental durations longer than 60 dph, and a slightly lower effect of egg size on offspring survival past 60 dph than from 1-10 dph. Once offspring conclude their larval stage, they may be less susceptible to starvation due to increased foraging capability. The average egg size of particular species likely are influenced by biological factors such as spawn timing, the length of spawning season, and trophic interactions of offspring (Ware 1975). Smith and Fretwell (1974) hypothesized that populations adapt an optimal egg size according to ecological pressures on recruitment. Eium and Fleming (2000) further supported the optimal egg size hypothesis with an experimental demonstration in Atlantic salmon (*Salmo salar*), and concluded that Atlantic salmon maternal effects were evolved to maximize offspring survival in the juvenile stage. Environmental predictability can not only affect the average egg size of a population, but also the variation of egg size within individual females (Eium and Fleming 2004).

The benefits of maternal effects may also vary by system type. Houde (1994) found that there are general differences in reproductive strategies and ontogenies between marine and freshwater fish species. For example, marine fishes often display longer planktonic larval durations nearly twice as long as freshwater fishes, and have higher starvation risk (Houde 1994). Therefore, survival through marine fishes' typical larval stage may depend more on slight differences in maternal provisioning than in freshwater fishes. Various studies contributing to the BOFFFF hypothesis have only included marine species in their reviews (e.g. Berkeley et al. 2004; Barneche et al. 2018). However, benefits of many smaller females, as opposed to fewer large, old females, has been estimated to benefit recruitment in freshwater species (e.g. Eslinger et al. 2010). We included both freshwater and marine species in our analyses, and found that the mean effect of maternal size on egg size was significantly stronger in marine species than freshwater species. Further, we found that anadromous fishes, which spend parts of their life histories in both system types, displayed effects that were stronger than marine fishes, but weaker than freshwater fishes. Thus, it may be worthwhile to consider system types when determining the broad-scale applicability of the BOFFFF hypothesis.

While this study contradicts the notion that larger females utilize gonadal investment more efficiently, our focus was strictly on maternal investment in individual eggs. Hixon et al. (2014) listed other components of the BOFFFF hypothesis that we did not evaluate. First, they suggest that larger females have higher fecundity. If fecundity is proportional to gonad mass or volume, it would be directly related to our demonstrations. However, gonadal investment in females is often allometrically related to their size, which was not included in our demonstrative analyses. Second, the “storage effect,” where older females of species with episodic recruitment can outlive unfavorable spawning conditions, contributes to the BOFFFF hypothesis (Longhurst 2002; Berkeley et al. 2004). Last, there may be a spatial and temporal effect of BOFFFF’s spawning strategy on recruitment. The timing and location of spawning may vary based upon maternal age, and populations with more diverse spawner age distributions may experience tempered recruitment variation due to spatio-temporal diversification of spawning and hence early life experience (e.g., Hsieh et al. 2010).

As worldwide fisheries decline, it is critical for managers to develop strategies to better protect stock biomass, and recruitment is a critical consideration for any proposed strategy. The BOFFFF hypothesis has been a popular call to action for managers to protect size and age structures in fisheries. Avoiding the truncation of these structures through selective harvest can benefit populations in many ways. However, rigorous testing of hypotheses is important to ensure their broad-scale applicability. Some studies, like those in this current analysis, may contradict certain tenants of the BOFFFF hypothesis. For example, Christie et al. (2018) found in a 16-year pedigree of a population of iteroparous *Oncorhynchus mykiss* that older, larger females had reduced lifetime fitness. While many components of the BOFFFF hypothesis may be supported in past research, we believe further studies of whether larger females utilize gonadal investment more efficiently would be beneficial.

2.5 Acknowledgements

This research was funded by the Purdue Forestry and Natural Resources Department. Carolyn Foley provided guidance in data extraction and organization for this project.

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CHAPTER 3. INTRASPECIFIC EGG SIZE COMPARISONS AMONG INLAND AND GREAT LAKES IN TWO PERCID FISHES

3.1 Introduction

Egg size, and its implications for offspring survival and population recruitment, has been long studied in fishes. Females that produce larger eggs provision their offspring for larger size-at-hatch, which may result in faster growth, increased foraging ability, and improved predator avoidance (Duarte and Alcaraz 1989; Einum and Fleming 2000). Offspring hatched from larger eggs could ultimately have increased survival to recruitment due to their expedited advancement through critical ontogenetic stages (Berkeley et al. 2004a). Although offspring may experience early life benefits from larger egg size, females may compromise between egg size and fecundity (Einum and Fleming 2000). That is, females are limited in ovary volume and reproductive energy available for gonadal investment, which implies that producing larger eggs will result in reduced fecundity (Kamler 2005). Based on this trade-off, the theory of optimal egg size proposes that selection leads females to produce eggs of an appropriate size for their environment (Smith and Fretwell 1974; Einum and Fleming 2002).

The optimal egg size for fishes may differ across systems of different size. Comparisons of egg size have been made between fish from large, marine systems to those in small, freshwater systems, but these comparisons have generally been interspecific (Duarte and Alcaraz 1989; Einum and Fleming 2002). Houde (1994) suggested that freshwater and marine fishes experience different selective environments leading these groups to generally produce different sized offspring. Freshwater species' larvae often emerge at a larger size, have shorter stage durations, and lower mortality rates than those of marine fish. Therefore, recruitment is more likely to be determined during the juvenile stage of freshwater fish, due to density-dependent factors such as competition for resources. In contrast, marine species' larvae often emerge at relatively smaller sizes, and recruitment is more likely determined in the early larval stage, based upon whether individual larvae experience favorable or unfavorable conditions in highly variable environments. While Houde's (1994) theory is based on larval size-at-hatch, it has implications for egg size, too, because egg size is directly related to hatching size (Pepin et al. 1997; Nissling et al. 1998; Rideout et al. 2005). Thus, females may benefit from producing fewer relatively large eggs to provide their

offspring with increased early life provisions in small systems, and many small eggs in large systems.

While optimal egg size theory implies that the mean population egg size is adaptive, egg size variation is also responsive to variable environmental factors and is not genetically canalized within populations. Egg size varies intraspecifically across populations and is associated with factors such as: temperature (Johnston and Leggett 2002; Jonsson and Jonsson 2016; Barneche et al. 2018), latitude (Fleming and Gross 1990; Beacham and Murray 1993; Kokita 2003), and productivity (Johnston and Leggett 2002; Wang et al. 2012). Intraspecific egg size variation among populations has been observed in marine (Chambers 1997; Llanos-Riviera and Castro 2004), anadromous (Beacham and Murray 1993, Fleming and Gross 1990), riverine (Marsh 1984; Morrongiello et al. 2012) and lacustrine species (Johnston and Leggett 2002). Egg size also varies in the Laurentian Great Lakes (hereafter Great Lakes), among populations of lake whitefish (*Coregonus clupeaformis*; Ihssen et al. 1981; Muir et al. 2014) and walleye (*Sander vitreus*; Wang et al. 2012; Feiner et al. 2016). Moreover, annual variation in environmental conditions can influence mean population egg size (Tanasichuk and Ware 1987; Feiner et al. 2016), and controlled studies demonstrate that exposure to different temperature (Feiner et al. 2018), food availability (Hutchings 1991), and competitive interactions can affect realized egg sizes. In addition, across individuals, egg size varies with demographic traits of females, such as size and age (Chambers and Leggett 1996). Therefore, although genetic variation is a major component in interpopulation egg size variation, environmental and demographical features simultaneously influence egg size.

Within a population, the average size of eggs produced by individual females can vary. Maternal effects, or the non-genetic relationship between the phenotype of mothers and their offspring, have been widely reported in fishes (Green 2008). These maternal effects likely play a role in the individual fitness of females, and may be a contributing factor to recruitment dynamics (Smith and Fretwell 1974; Scott et al. 1999; Hixon et al. 2013). One commonly observed maternal effect is the positive relationship between female size and egg size (Duarte and Alcaraz 1989; Green 2008). Annual recruitment of populations that demonstrate strong maternal effect relationships has been suggested to benefit from the presence of larger, older females (Hixon et al. 2013). Therefore, some authors have called for management of fisheries to focus on protection of particular age- and size-class distributions (Berkeley et al. 2004b; Gwinn et al. 2013).

In many ways, the Great Lakes are analogous to large marine systems (Pritt et al. 2014). Similar to marine systems, the Great Lakes are relatively oligotrophic, with patchy species densities and greater diversity nearshore. In the Great Lakes, broad physical processes (e.g. upwellings, cross-system circulation) affect species' distributions. Local physical forces and broad-scale currents can advect Great Lakes fish larvae, causing them to settle and develop in different locations than where spawning occurs (Höök et al. 2006; Beletsky et al. 2007; Oyadomari and Auer 2008). Inter-annual variability in physical processes have been found to affect year-class strengths (e.g., Zhao et al. 2009). Consequently, early life stage fishes in the Great Lakes may be exposed to environmental variability, similar to marine systems. In turn this may select for similar trade-offs between egg size and fecundity, and lead to production of relatively small eggs in the Great Lakes. However, unlike marine systems, the freshwater Great Lakes contain species that are present in smaller lakes as well. This facilitates intraspecific comparisons of egg size across different system sizes in the Great Lakes region, and evaluation of the expectation of optimal egg size theory (Smith and Fretwell 1974) and offspring size divergence proposed by Houde (1994).

In this study, we compared average egg size in walleye (*Sander vitreus*) and yellow perch (*Perca flavescens*) among populations in the Great Lakes and smaller inland lakes. Past studies demonstrate that walleye egg size may vary across populations (Johnston and Leggett 2002; Wang et al. 2012), years (Feiner et al. 2016), and be influenced by maternal effects (Johnston and Leggett 2002; Wang et al. 2012; Feiner et al. 2016). Yellow perch also display maternal effects on egg size (Andree et al. 2015), and yellow perch egg size appears to vary within populations based upon female identity (Feiner et al. 2018) and annual conditions (Farmer et al. 2015; Feiner et al. 2018). Nonetheless, to our knowledge, this is the first study to make intraspecific comparisons of egg size between inland lakes and the Great Lakes. We expected the inland lake female walleye and yellow perch exhibit egg sizes similar to freshwater fish described by Houde (1994), and that inland lake populations would produce large eggs, relative to Great Lakes populations.

3.2 Methods

3.2.1 Study species

In this study, we focused on two Great Lakes percid species: walleye and yellow perch. Both species are native to all five Great Lakes, and are fairly ubiquitous in inland systems

throughout the basin. Walleye and yellow perch are both iteroparous, employing a capital spawning strategy (Malison et al. 1994; Henderson et al. 2000; Feiner and Höök 2015). Gonad development occurs throughout the year, and for both species spawning occurs in the spring. Oocyte size is typically determined by January in yellow perch, but can continue to increase until just before spawning in walleye (Feiner and Höök 2015). Both species can be classified as demersal spawners, however, they utilize a variety of spawning habitats. Yellow perch produce a gelatinous skein that houses their eggs, which they drape across vegetation and woody debris (Feiner and Höök 2015). Walleye broadcast demersal eggs over rocky substrate in shallow water (<5 m), and will either spawn in rivers, streams, or lakes (Feiner and Höök 2015).

3.2.2 Sampling sites

In spring (April – May, 2019), we captured spawning walleye from three Great Lake and four inland lake populations (Figure 3.1). Of the Great Lake populations, two were located in Lake Michigan (Little Bay de Noc and Muskegon), and the other was located in Lake Huron (Cheboygan). While individual walleye from these populations inhabit the Great Lakes as adults, they were collected after migrating upstream to spawn in rivers. Out of the four inland lake locations, three were small, isolated systems (37.2 – 169.2 hectares). The other, Bond Falls Flowage, was a larger water body (860.8 hectares) created by the confluence of multiple rivers and damming (Table 3.1).

In spring (April – June, 2018 and 2019), we captured spawning yellow perch from four Great Lake and five inland lake populations (Figure 3.1). All Great Lake populations were from Lake Michigan; two in the southern main basin (Michigan City and St. Joseph), and the other two in northern bays (Green Bay and Traverse Bay). Note, that while we refer to these as different populations there is likely some genetic exchange among yellow perch from these different locations in Lake Michigan; in particular, yellow perch collected near Michigan City and St. Joseph are likely not distinct populations. However, St. Joseph was not included in population-level comparisons. Of the five inland lake populations, four were located in northern Wisconsin, while the other was located in northeastern Indiana. All five inland lakes were relatively small (37.2 – 427.8 hectares; Table 3.1).

3.2.3 Field collection

We collected spawning females with the help of several agencies, including: Indiana Department of Natural Resources, Little Traverse Bay Bands of Odawa Indians, Michigan Department of Natural Resources, and Wisconsin Department of Natural Resources. To capture yellow perch, we used fyke nets and benthic multifilament gill nets. To capture walleye, we used benthic multifilament gill nets, fyke nets, and boat electroshocking. Upon capture, we measured total lengths of females to the nearest 0.1 mm, and immediately placed samples of unfertilized eggs from each female in separate 20mL scintillation vials with 10% formalin solution. Unfertilized eggs were collected from flowing walleye females. Yellow perch egg samples were collected from both flowing and ripe females, but no difference in egg size between developmental stage is expected as oocyte size is determined by January, and eggs reach their maximum size a month before spawning occurs (Henderson et al. 2000; Feiner and Höök 2015). For both species, eggs were collected by applying pressure to the abdomen to stimulate release. We stored preserved egg samples for at least 2 months to standardize shrinking (Feiner et al. 2016). After a 2-month period, we photographed numerous eggs from each female together with a standardized length scale under a dissecting microscope. Using ImageJ software, we measured vertical and horizontal diameters of 10 eggs per female to the nearest 0.001 mm (Figure 3.2; Schneider et al. 2012). We estimated an egg's overall diameter as the mean of vertical and horizontal diameters and calculated average egg diameter for each female from these estimates.

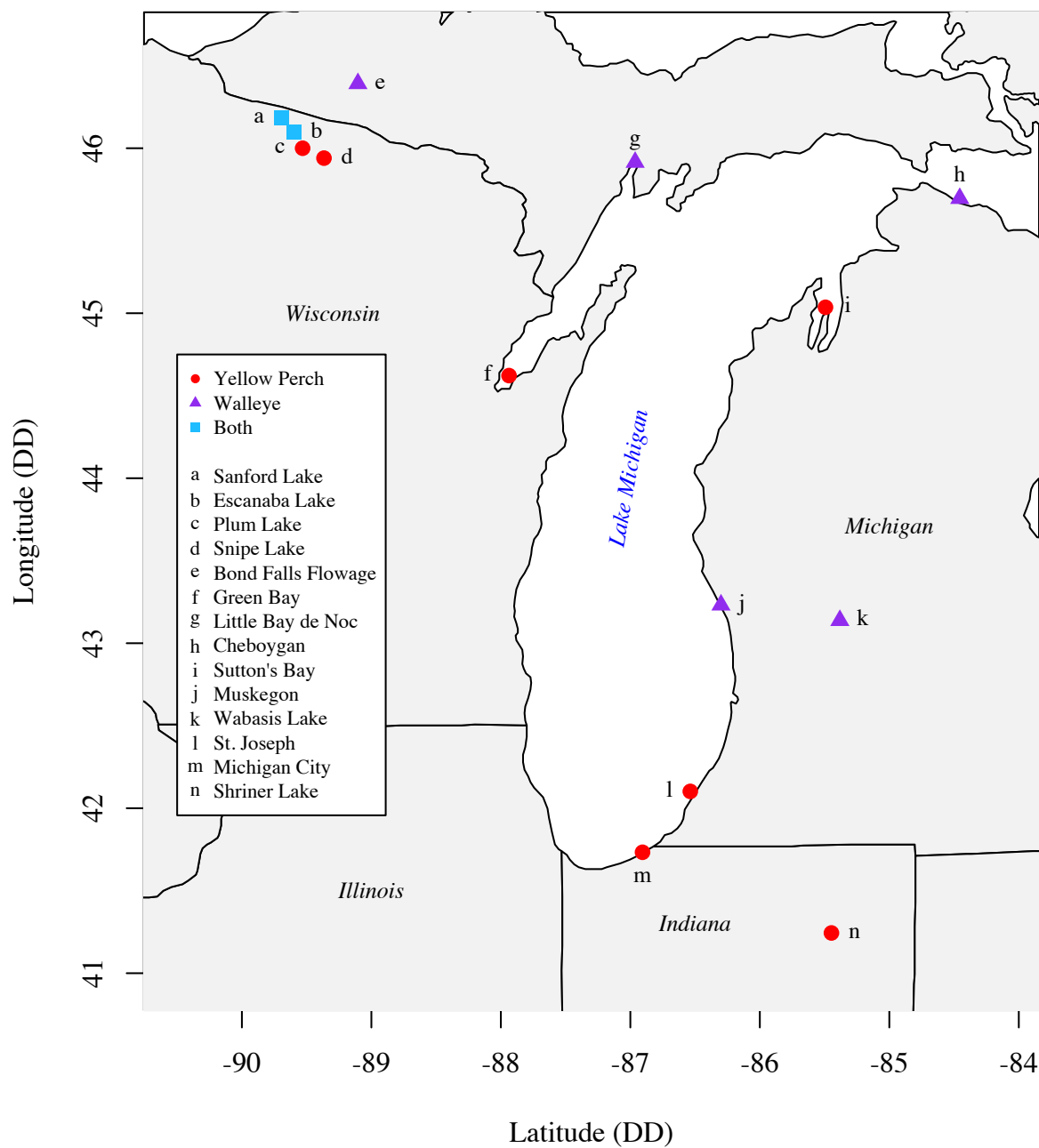


Figure 3.1. Map of populations from which we collected egg samples of spawning walleye and yellow perch in spring 2018 – 2019. Triangles and circles represent locations from which we collected walleye and yellow perch, respectively, and squares represent locations where we collected both species.

Table 3.1. Walleye and yellow perch sampling population information and summary statistics of female characteristics, including total length (TL), egg diameter (ED) and coefficient of variation of average egg diameters among females (CV).

Walleye

Location	Area (ha)	Year	n	TL (mm) mean (range)	ED (mm) mean (range)	ED CV
Great Lakes						
Cheboygan	—	2019	24	566.8 (460.0, 644.0)	1.647 (1.469, 1.929)	0.071
Little Bay de Noc	—	2019	49	643.1 (485.1, 779.8)	1.603 (1.422, 1.743)	0.040
Muskegon	—	2019	46	647.5 (535.0, 800.1)	1.598 (1.515, 1.713)	0.030
Inland Lakes						
Bond Falls Flowage	860.8	2019	97	647.5 (342.9, 985.5)	1.536 (1.419, 1.635)	0.031
Escanaba Lake	118.6	2019	88	429.8 (381.0, 579.1)	1.679 (1.408, 1.933)	0.058
Sanford Lake	37.2	2019	17	514.9 (452.1, 607.1)	1.663 (1.502, 1.807)	0.055
Wabasis Lake	169.2	2019	5	547.8 (525.0, 582.0)	1.64 (1.596, 1.728)	0.032

Yellow Perch

Location	Area (ha)	Year(s)	n	TL (mm) Mean (range)	ED (mm) mean (range)	ED CV
Great Lakes						
Green Bay	—	2019	14	220.6 (146.0, 311.0)	1.200 (1.043, 1.306)	0.061
Michigan City	—	2018, 2019	52	256.3 (133.0, 358.0)	0.979 (0.690, 1.178)	0.118
St. Joseph	—	2018	4	219.8 (210.0, 225.0)	0.868 (0.850, 0.897)	0.023
Suttons Bay	—	2018	6	204.5 (190.0, 221.0)	0.951 (0.874, 1.054)	0.063
Inland Lakes						
Escanaba Lake	118.6	2019	38	235.6 (142.2, 320.0)	1.278 (1.130, 1.458)	0.049
Plum Lake	427.8	2019	111	187.4 (142.0, 309.0)	1.169 (1.020, 1.455)	0.075
Sanford Lake	37.2	2019	4	180.3 (149.9, 231.1)	1.347 (1.237, 1.534)	0.078
Shriner Lake	48.6	2018, 2019	42	281.5 (170.0, 344.0)	1.25 (1.010, 1.250)	0.062
Snipe Lake	96.7	2019	10	170.7 (163.0, 186.0)	1.235 (1.161, 1.334)	0.048

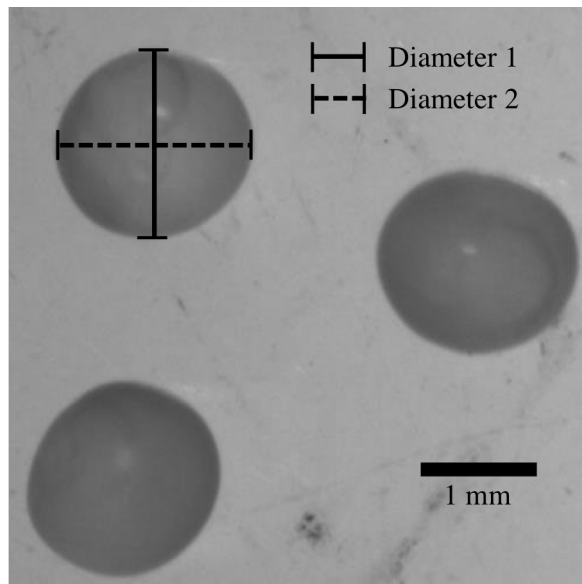


Figure 3.2. Diagram of walleye egg diameter measurement. Individual egg diameter was estimated by calculating the mean of diameters 1 and 2. Mean egg diameter was estimated by calculating the mean of 10 individual mean egg diameters.

3.2.4 Statistical analyses

The average size of a female's eggs can be related to her length (Green 2008). Therefore, in order to compare egg diameter intraspecifically among populations with different ranges of total lengths (Table 3.1), we employed analyses of covariance (ANCOVA), with total length as a covariate, and population as a factor, including populations with at least 10 individual samples. Since annual effects can influence mean population-level egg sizes across years (Feiner et al. 2018), we differentially analyzed populations by year (e.g. Michigan City 2018 and Michigan City 2019 were treated as separate populations). In order to use ANCOVA models, we first tested for homogeneity of total length - egg diameter slopes. To compare slopes, we included an interaction term (total length * population) in an ANCOVA model. If a significant difference in slopes was found among populations, we made post hoc pair-wise comparisons among populations using a Tukey's HSD test to identify which populations' slopes differed from the rest. Afterward, we conducted an ANCOVA with a subset of populations, omitting the populations with significantly different slopes, along with the interaction term. All statistical analyses were conducted using R

statistical software (R Core Team 2018) with the HH Statistical Analysis and Data Display package (Heiberger 2019) and the goeveg Functions for Community Data and Ordinations package (Goral and Schellenberg 2017).

3.3 Results

3.3.1 Walleye

In the spring of 2019, we collected egg samples from 326 mature walleye females from four inland lake populations and three Great Lake populations (Table 3.1). Female total length ranged from 342.9 mm to 985.5 mm, and egg diameter ranged from 1.408 mm to 1.933 mm (Table 3.1; Figure 3.3a). Inland lake walleye females were generally smaller than Great Lake females, with little overlap in size distributions. There was a significant difference in total length ~ egg diameter slopes among populations (ANCOVA; $p < 0.001$; Figure 3.4a). In order to compare egg diameter among populations, we removed the populations with significantly different slopes (Cheboygan and Escanaba Lake). Using the reduced dataset, we found a significant difference in average length-adjusted egg diameter among populations (ANCOVA; $p < 0.001$). One inland lake population, Sanford Lake, had a significantly larger average egg diameter than the other three populations (Figure 3.4b).

3.3.2 Yellow perch

Between 2018 and 2019 spring sampling, we collected egg samples from 301 mature female yellow perch from five inland lake populations and four Great Lake populations (Table 3.1; Figure 3.3b). Female total length ranged from 133 mm to 358 mm, and egg diameter ranged from 0.69 mm to 1.46 mm (Table 3.1). There was a significant difference in total length - egg diameter slopes among populations (ANCOVA; $p = 0.004$; Figure 3.4c). In order to compare egg diameter among populations, we removed the population with a significantly different slope (Plum Lake). Using the reduced dataset, we found a significant difference in egg diameter among populations (ANCOVA; $p < 0.001$). Data from three inland lake populations had a significantly larger egg diameter than the Great Lake populations (Green Bay and Michigan City 2018 and 2019; Figure 3.4d). Egg samples collected in Shriner Lake during 2018 were not significantly different in size

from Green Bay eggs, but were significantly larger than eggs collected in Lake Michigan near Michigan City in 2018 and 2019 (Figure 3.4d).

3.4 Discussion

For both walleye and yellow perch, mean egg diameter varied among populations, as did maternal effects, the relationship between female total length and diameter. The difference in egg diameter (adjusted for maternal size) between inland lakes and Great Lake populations was, in particular, distinct in yellow perch, while this difference was less pronounced in walleye. Three of four inland lake populations of yellow perch produced significantly larger eggs than the Great Lake populations. There was no significant difference in length-adjusted egg diameter among three walleye populations, but we found that females in Sanford Lake produced larger eggs on average than the rest of the populations (Figure 3.4b). Our hypothesis that intraspecific differences in egg size between inland lake and Great Lake populations would match the interspecific pattern of larval size between freshwater and marine fishes, postulated by Houde (1994), was strongly supported for yellow perch and marginally supported for walleye.

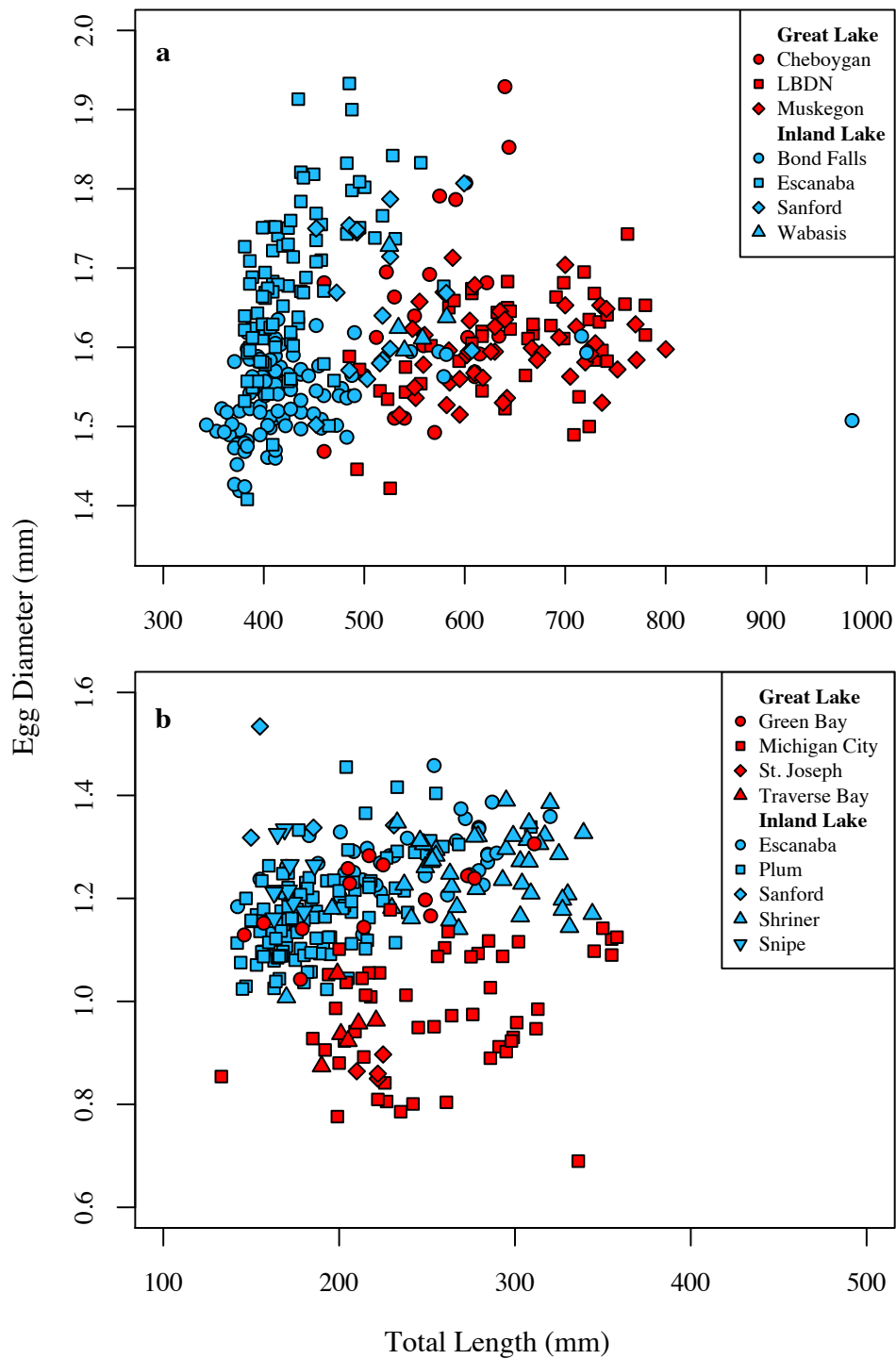


Figure 3.3 Scatterplot of egg diameter vs. female total length in Great Lake and inland lake populations for all walleye collected in 2019 (a) and yellow perch collected in both 2018 and 2019 (b). Lake types are denoted by color, and within lakes, populations are represented by different point shapes.

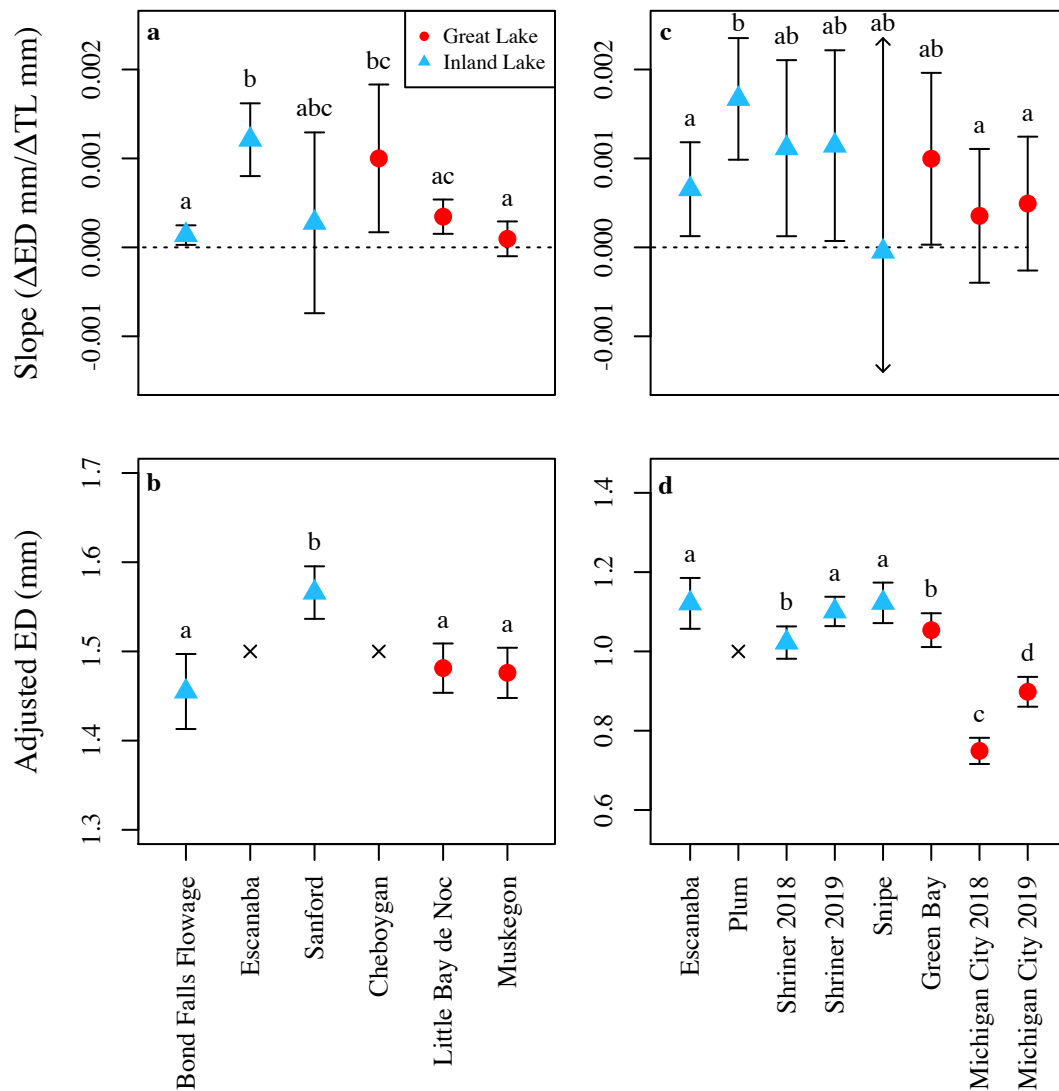


Figure 3.4. (Top) Egg diameter (ED) vs. total length slopes with 95% confidence intervals for each population initially included in ANCOVA models. (Bottom) Mean length (535.1 mm for walleye and 249.2 mm for yellow perch) – adjusted ED with 95% confidence intervals from ANCOVA using the subset of populations with homogenous slopes, populations removed from analyses marked by “X.” Walleye displayed on left (a and b); yellow perch displayed on right (c and d).

Our finding of interpopulation egg size variation, along with observations of maternal effects in both walleye and yellow perch, reflect similar studies, but also expand our understanding of percids. Like other studies, we detected a relationship between female size and egg size in walleye (Venturelli et al. 2010; Wang et al. 2012; Feiner et al. 2016) and yellow perch (Lauer et al. 2005; Andree et al. 2015), indicating some level of maternal effects in both species. Multiple

examples exist of interpopulation variation of egg size in walleye (Johnston and Leggett 2002; Wang et al. 2012; Feiner et al. 2016). Heibo et al. (2005) found variation among populations in reproductive investment of congeneric Eurasian perch (*Perca fluviatilis*), however, to our knowledge this may be the first evidence of interpopulation variation of egg size in yellow perch. By including observations from both Great Lake and inland lake populations, our intraspecific comparisons length-adjusted egg size demonstrated that population-level differences are partially aligned with system size.

The distributions of walleye total lengths did not overlap entirely between inland lake and Great Lake individuals. As a result, it is somewhat difficult to compare egg diameter between the two lake types visually. Of the four populations included in our comparison, three were similar in length-adjusted egg diameter, with only one, Sanford Lake, being significantly larger than the rest. Escanaba Lake females, which were removed from the population-level comparison, produced the largest eggs on average (Table 3.1), and would have resulted in a similar relatively large length-adjusted value as Sanford Lake. The maternal effect relationships of walleye populations in our study were notably weak, outside of the Cheboygan and Escanaba Lake populations (Figure 3.4a).

Differential spawning behavior may have complicated our comparisons among walleye populations. While, in fact, we compared inland lake walleye to those from Great Lakes populations, the Great Lake walleye for this study were sampled in tributaries, rather than their respective proper lakes. Although Great Lake walleye can spawn over reef structures, state agencies that facilitated collections for this study collected river-spawning fish. Individuals sampled from the inland lakes in this study were captured within their respective lakes, rather than in tributaries. Females of potamodromous species, like the Great Lakes walleye from this study, may benefit from producing larger eggs to provision their offspring for the period in which they drift downstream, when they may be susceptible to starvation. Maruyama et al. (2003) found that fluvial-lacustrine females produced larger eggs on average than those of lacustrine populations in a *Rhinogobius* species. Similarly, Closs et al. (2013) compared closely-related amphidromous and lacustrine species and found that lacustrine species generally produce larger eggs. Moreover, Kinnison et al. (2001) found that increasing the energetic cost of migration leads chinook salmon (*Oncorhynchus tshawytscha*) females to produce smaller eggs. Future studies that make within-

population comparisons of egg diameter between spawning strategies may further advance our understanding of walleye reproductive strategies.

Supplemental stocking may also have affected the average egg size of some populations included in our study. We found no records of yellow perch stocking in any of the populations in this study. However, the walleye populations have all been stocked, with varying levels of recency and frequency. Populations that are managed by the state of Michigan, including Bond Falls Flowage, Cheboygan, Little Bay de Noc, Muskegon, and Wabasis Lake, have all been stocked within the past decade. All three Great Lake populations have been stocked with fingerlings that were reared from adults of their own respective populations. Interestingly, Bond Falls Flowage has been stocked with fingerlings of the Bay de Noc strain, and we detected no difference in length-adjusted egg diameter between our Bond Falls Flowage and Little Bay de Noc samples. Historically, the two Wisconsin lakes, Escanaba and Sanford, were stocked, but have not received additional stocking since the 1950s (WDNR; Stephanie Shaw, personal communication). Evidence of hybridization between wild and stocked walleye was found in the Ohio River (White et al. 2005). Therefore, it is reasonable to suspect an effect of stocking on the genotypes of walleye populations in this study. Egg size variation has a partial genetic basis, and the addition of outside alleles through frequent stocking may alter the local genotype for the trait.

The observed differences in yellow perch egg size among system sizes and populations could partially be due to local genotypes. Mean length-adjusted egg diameter of yellow perch females from the Michigan City population was far smaller than from any other population. This difference may be due to unfavorable spawning habitat. Unlike the other populations sampled for this study, Michigan City has a flat, sandy bottom that does not offer beds of vegetation or woody debris upon which yellow perch can drape their skeins. This may result in high variability of yellow perch eggs and larvae experiencing unfavorable conditions for development in Michigan City. Physical characteristics of spawning habitat have been observed to play a role in the egg size of other species (Quinn et al. 1995). Poor spawning habitat, such as what is found in Michigan City, may favor females with increased fecundity and smaller eggs on average, to maximize chances of offspring survival. Green Bay, another population of Lake Michigan, had a significantly larger mean length-adjusted egg diameter, and the two populations have been found to be genetically distinct (Miller 2003). Green Bay is a more productive and perhaps stable environment than the main basin of

Lake Michigan, which could also contribute to the observed differences in mean population egg size.

Egg size patterns likely partially reflect genetic differences and selection, but are likely also responsive to temporal and spatial environmental variation. In this study, we found a significant difference in yellow perch mean length-adjusted egg diameter across years within two populations: Michigan City and Shriners Lake (Figure 4b). Although we did not sample walleye across years, Feiner et al. (2016) observed interannual differences in egg size within walleye populations. Similarly, in a multi-year study of yellow perch in a research pond, Feiner et al. (2018) demonstrated an annual effect on egg size. Farmer et al. (2015) reported that yellow perch from the same population in Lake Erie will produce different sized eggs according to the length of winter. Feiner et al. (2018) also found that individual identity strongly influenced yellow perch egg size, and together with Andree et al. (2015), demonstrated maternal effects on yellow perch egg size. Individual identity and maternal effects suggests that demographic changes across years, in addition to environmental conditions, could partially contribute to interannual variation in mean egg size.

Varying reproductive traits, such as egg size, have implications for population recruitment. Past studies have shown a positive relationship between egg size and offspring survival in percid species (Moodie et al. 1989; Venturelli et al 2010; Andree et al. 2015). Heyer et al. (2001) found that survival of larvae to the adult stage, and thus, recruitment, varied with maternal effects of yellow perch. Therefore, our findings of larger average egg size in females from inland lakes than in females from Great Lakes align with Houde's (1994) suggestion of differential recruitment pressures across system sizes. These observations may support the theory of optimal egg size, where particular environments favor females that produce relatively small or large eggs, leading to differences among populations (Smith and Fretwell 1974). While the egg size trait likely depends upon a combination of genetic, environmental, and individual factors, its intraspecific variation among system sizes and populations is an indication that location-specific reproductive strategies may play a role in recruitment.

3.5 Acknowledgements

Field collection was aided by Alexander Gatch, Jayson Beugly, Claire Schraidt, Taylor Senegal, Susanna LaGory, Ben Leonhardt, and Patricia Nease from Purdue University. Employees

from Indiana DNR (Ben Dickinson), Wisconsin DNR (Shephanie Shaw, Dan Dembkowski, Tammie Paoli), Michigan DNR (Troy Zorn, Scott Hanshue), and the Little Traverse Bay Bands of Odawa Indians (Kristopher Dey) assisted in collecting yellow perch and walleye samples.

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APPENDIX

A.1 Meta-analysis female size vs. egg size

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