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ARTICLE

Transgenerational effects of egg nutrients on the early development of Chinook salmon (*Oncorhynchus tshawytscha*) across a thermal gradient

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Abstract: The transgenerational effect of maternal diet, expressed as variation in the composition and quantity of egg nutrients available to offspring during endogenous development (i.e., prior to free-feeding), has the potential to greatly influence the response of offspring phenotypes to varying environmental conditions. For this study, we examined how natural variation in the fatty acid and proximate composition of eggs from three Chinook salmon (*Oncorhynchus tshawytscha*) populations influenced early development across a thermal gradient using a common garden hatchery experiment. We found that the relative quantity of fat, lean mass, and water in the eggs was similar among populations. However, the fatty acid composition of the eggs differed among all populations. After controlling for egg mass, egg fatty acid and proximate composition influenced hatch length, swim-up length, and hatch to swim-up growth. Importantly, the magnitude and direction of these egg quality effects depended on the population of origin and temperature. Overall, our results demonstrate that natural variation in egg nutrient composition, likely driven by maternal diet, has transgenerational effects on offspring development under varying thermal conditions.

Résumé : L'effet transgénérationnel du régime alimentaire maternel, exprimé par la variation de la composition et de la quantité des nutriments de l'œuf disponibles pour la progéniture durant le développement endogène (c.-à-d., avant l'alimentation libre) a le potentiel d'influencer considérablement la réaction des phénotypes de progéniture à des conditions ambiantes variables. Nous avons examiné l'influence de la variation naturelle de la composition d'acides gras et de macronutriments des œufs de trois populations de saumons chinooks (*Oncorhynchus tshawytscha*) sur le développement précoce le long d'un gradient thermique en utilisant une expérience de jardin commun en écloserie. Nous avons constaté que les quantités relatives de gras, de masse maigre et d'eau dans les œufs étaient semblables d'une population à l'autre. Toutefois, la composition d'acides gras des œufs différait d'une population à l'autre. Une fois prise en compte la masse des œufs, la composition d'acides gras et de macronutriments des œufs influençaient la longueur à l'éclosion, la longueur des alevins nageants et la croissance entre ces deux stades. Fait important, l'ampleur et la direction de ces effets de la qualité des œufs dépendaient de la population d'origine et de la température. Collectivement, nos résultats démontrent que la variation naturelle de la composition des nutriments des œufs, qui découle probablement du régime alimentaire maternel, a des effets transgénérationnels sur le développement de la progéniture dans des conditions thermiques variables. [Traduit par la Rédaction]

Introduction

Transgenerational effects arise when the parental phenotype or environment shapes the development and phenotypic traits of offspring (i.e., parental effects; Badyaev and Uller 2009). These transgenerational effects can be transferred to the offspring generation through epigenetic variation, milk or yolk resources, hormones, immune factors, or behaviours (Bonduriansky et al. 2012). Such transgenerational effects can have profound fitness consequences for offspring and have been found to occur in a wide variety of taxa (Galloway and Etterson 2007; Storm and Lima 2010; Coslovsky and Richner 2011; Hafer et al. 2011; Salinas and Munch 2012; Helle et al. 2012; Triggs and Knell 2012; Franzke and Reinhold 2013; Shama et al. 2014, 2016; Zizzari et al. 2016). Although there is evidence of paternal effects (Etterson and Galloway 2002; Triggs and Knell 2012), most transgenerational effects are mediated by maternal effects because mothers tend to control the allocation of resources to offspring (Bernardo 1996; Mousseau and Fox 1998; Räsänen and Kruuk 2007). In most fish species, mothers provide little parental care, and the manipulation of egg quality is an important mechanism through which environmental cues are transmitted to offspring (Segers and Taborsky 2012; Jonsson and Jonsson 2016).

The quality of an egg is typically characterized in terms of egg size and the quality of nutrient stores (Kjorsvik et al. 1990; Brooks et al. 1997). Much of the research on egg quality has focused on egg size because of its close association with offspring size and fitness (Heath and Blouw 1998; Einum and Fleming 1999, 2000). Because there is a consistent, positive relationship between egg size and offspring size, the effects of egg size variation on offspring phenotypes is well understood (Heath and Blouw 1998). In contrast, the influence of egg nutrient composition on offspring traits is not as clear.

Yolk nutrients are deposited in the egg during vitellogenesis in the months or weeks prior to spawning (Tyler and Sumpter 1996; Wiegand 1996; Johnson 2009; Lubzens et al. 2010). Yolk nutrients are broadly composed of lipids, protein, carbohydrate, and micronutrients (Brooks et al. 1997). Of these components, lipids are the

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primary energy resource used by fish during the endogenous feeding stage (Wiegand 1996). Lipids also serve as precursors for hormones and have important structural and functional roles in cell membranes (Wiegand 1996; Sargent et al. 1999). The diverse functions of lipids during development are supported by the various fatty acids (FAs) that form the lipid reserve. Essential polyunsaturated fatty acids (PUFAs) from the n-3 and n-6 series are particularly important because they cannot be synthesized de novo and are required for the proper development and survival of offspring (Sargent et al. 1999). Docosahexaenoic acid (DHA, 22:6n-3) is found in high concentrations in the retina, brain, and spinal cord of fishes (Bell and Dick 1991; Mourente 2003), and deficiencies in DHA have been associated with impaired visual systems, brain development, and larval behaviour (Bell et al. 1995; Ishizaki et al. 2001). DHA and eicosapentaenoic acid (EPA, 20:5n-3) are major polyunsaturated FAs found in the cell membranes of fishes and support cell membrane function and integrity (Sargent et al. 1995, 1999). The DHA/EPA ratio has been shown to affect offspring development because of the competitive interactions between these FAs in metabolism (Watanabe 1993; Rodriguez et al. 1997; Gapasin and Duray 2001). Furthermore, EPA and arachidonic acid (ARA, 20:4n-6) both serve as precursors to eicosanoid hormones that are essential for the regulation of various physiological processes (Sargent et al. 1995; Tocher 2003). Overall, offspring that have lipid stores low in DHA, EPA, and ARA experience reduced growth, neural development, and survival (Sargent et al. 1995; Wiegand 1996; Copeman et al. 2002).

The thermal environment that offspring experience can influence how the FA composition and quantity of lipid affect development and survival. Because fish are poikilothermic, most physiological processes are affected by water temperature. The membrane function of a cell is affected by temperature (e.g., membrane fluidity), and the maintenance of membrane function at different temperatures requires membrane lipids with qualities that match the environment (March 1993; Robertson and Hazel 1997). For example, there is a general shift in the lipid composition of cell membranes from unsaturated FAs, mostly PUFA, at low temperatures to more saturated FAs at warm temperatures (Hazel 1984, 1995; Robertson and Hazel 1997). This shift in FAs with temperature is apparent at the individual level, with larval fishes having a greater ratio of polyunsaturated to saturated fatty acids (PUFA:SFA) when raised at low temperatures relative those raised at higher temperatures (Laurel et al. 2012). Furthermore, the ability of fish to digest SFAs decreases with a decrease in temperature, whereas the digestibility of PUFAs is not appreciably influenced by temperature (Ng et al. 2004). Finally, an increase in temperature can lead to a higher metabolic rate (Clarke and Johnston 1999) and cost of development (Mueller et al. 2015) as well as a reduced yolk sac conversion efficiency (Heming 1982; Rombough 1994), which means that a developing embryo or larva can have a higher energy demand in warm water and require greater lipid stores for growth.

Most of our knowledge about the effects of FA composition on offspring development is derived from aquaculture studies using simplified or enriched diets that do not accurately reflect the complex natural diets of fishes. In the wild, lipids deposited in the egg are derived either directly from the maternal diet or from stored lipids in somatic and visceral tissues (i.e., indirectly from diet; Wiegand 1996; Johnson 2009). FAs that are ≥14 carbons long are often stored with little to no modification into the tissues of vertebrates (Iverson 2009). As a result, the composition of the FAs in the tissues of fishes largely reflects their diet, albeit integrated over different time scales depending on the tissue (Budge et al. 2006; Iverson 2009). This quality of FAs has been used to infer dietary differences among populations or ecotypes (i.e., trophic biomarker; Ashton et al. 1993; Wiegand et al. 2004, 2007; Scharnweber et al. 2016; Torniainen et al. 2017) and to determine food web structure (Strandberg et al. 2015; Happel et al. 2016; Mohan et al. 2016). Previous studies have shown that the FA composition of eggs can vary among populations when exposed to different diets (Ashton et al. 1993; Wiegand et al. 2004) and that this variation can influence offspring phenotypes by shaping the quantity of essential FAs and energy available for development (Czesny et al. 2009). However, there is a lack of research on how natural variation in FA composition can influence offspring growth and survival across an environmental gradient.

Here, we use Laurentian Great Lakes Chinook salmon (*Oncorhynchus tshawytscha*) populations to test the hypothesis that variation in egg FA and proximate composition will affect the expression of offspring phenotypes during the endogenous feeding stage at different temperatures. We predict that offspring growth and survival will be positively related to the relative quantity of PUFAs in eggs at low temperature and that this relationship will decrease in strength with an increase in temperature. We also predict that offspring growth and survival will be positively related to the relative quantity of lipids in eggs and that this relationship will increase with an increase in temperature. We also tested the hypothesis that the FA composition of eggs can serve as a trophic biomarker and will be different among Chinook salmon populations. Chinook salmon forage in the Great Lakes proper until they reach sexual maturity. While foraging, Chinook salmon originating from different regions within a lake are heterogeneously distributed both spatially and temporally (Marklevitz et al. 2016). Chinook salmon also show philopatry to their natal spawning tributaries, and populations will stage at the mouth of their natal tributaries until there are favourable environmental conditions for upstream migration (Adlerstein et al. 2007). These spatially variable foraging patterns may expose Chinook salmon populations to different prey communities throughout oogenesis, resulting in population differences in the FA composition of eggs.

Materials and methods

Gamete collection

Eggs and sperm were collected from sexually mature, prespawning Chinook salmon captured in the Credit (43°34′39.58″N, 79°42′8.57″W), Pine (44°13′10.12″N, 79°57′24.84″W), and Sydenham (44°33′34.36″N, 80°56′39.49″W) rivers. Chinook salmon were captured in the Credit River on 1 October 2012 using electrofishing, in the Pine River from 19 to 27 September 2012 using a combination of dip nets and seine nets, and in the Sydenham River from 22 September to 6 October 2012 using a fish trap built into the Mill Street Dam. Water temperatures at the time of capture were 14 °C, 10–12 °C, and 12.5–14.5 °C for the Credit, Pine, and Sydenham rivers, respectively. All captured individuals were first assessed for sexual maturity by massaging the abdomen to determine if eggs–sperm were readily released. Those found to be sexually mature (i.e., released gametes) were anesthetized by immersing them in a clove oil solution (20 mg·L^{-1}), measured for fork length, and sampled for eggs (~500) or milt (few millilitres). Visually unhealthy salmon (e.g., emaciated, skin lesions, or tumors) were not used for this experiment, and we released all Chinook salmon after sampling was complete. The collected eggs and milt were stored in a cooler at ~4 °C and transported directly back to the hatchery at Western University. Once at the hatchery, half the eggs from each female were used for hatchery rearing, 30 were placed in cryotubes and put in a freezer at −80 °C for FA analysis, and the remainder were put in a freezer at −20 °C for proximate composition analysis.

Egg mass and proximate composition

A total of 18 Credit River, 26 Pine River, and 21 Sydenham River females were used for egg mass and composition analysis. Twenty-five eggs per female were weighed to determine egg wet mass. The proximate composition of the eggs from each female was determined by measuring the fat, lean mass, and water content. Several

eggs from each female (~10) were dried at 60 °C for ~ 48 h until a stable dry mass was obtained. The dried samples were then crushed into a fine powder using a mortar and pestle. The fat was extracted from the samples using a Soxhlet apparatus and petroleum ether (30–60 °C boiling range) for 8 h. Petroleum ether was used to extract fat from the dried egg samples because it extracts neutral lipids, which are used as energy reserves, and not structural lipids (Dobush et al. 1985). The lean mass left over after fat extraction is composed of protein, ash, and carbohydrate. Previous studies on salmon have shown that the lean mass of salmon tissues is primarily composed of protein (~97%), while ash (~2%) and carbohydrate (<0.5%) are found in small quantities (Jonsson and Jonsson 1997; Jonsson et al. 1997; Hendry and Berg 1999). The proximate composition of eggs was calculated as the percent fat, lean mass, and water of egg wet mass and as the percent fat and lean mass of egg dry mass.

Egg FA profiles

Egg FA composition was determined by first extracting the total lipids from a sample of 6–10 eggs per female using the method of Folch et al. (1957). Each sample of eggs was homogenized, and ~50 mg was transferred to a centrifuge tube containing 2 mL of chloroform:methanol (2:1 *v*/*v*) with 0.01% butylated hydroxytoluene (BHT). Heptadecanoic acid (17:0, 3 mg·mL^{-1}) was then added to the solution as an internal standard, and the solution was centrifuged at 3750*g* for 15 min. After centrifugation, 1 mL of 0.25% potassium chloride was added to the solution, and the centrifuge tube was placed in a warm water bath at 70 °C for 10 min. The aqueous layer was then discarded and the remaining organic layer was transferred to a preweighed 4 mL vial. The sample was dried using a gentle stream of nitrogen, reweighed to determine total lipid, and then resuspended using a solution of chloroform:methanol (2:1 *v*/*v*) with 0.01% BHT to a concentration of 1–5 mg sample·mL^{-1} solution.

We then transferred 150 μg of the total lipid sample to a 2 mL vial and dried under nitrogen. 0.5 mol·L^{-1} methanolic-HCl (200 μg) was then added to the dried sample and placed in a drying oven at 90 °C for 30 min to covert the FAs to methyl esters. Then 800 μL of ultrapure water was added after cooling, and three successive extractions were done on the sample using 500 μL of hexane. The hexane extractions were combined, dried under nitrogen, and resuspended using 100 μL hexane. The fatty acid methyl esters were separated using an Agilent 6890N gas chromatograph (Agilent Technologies, Santa Clara, California, USA). We used a DB-23 high-resolution column (Agilent Technologies), a flame ionization detector, and He as a carrier gas (1.9 mL·min^{-1}). The temperature program was 2 min at 80 °C, increase to 180 °C at a rate of 5 °C·min^{-1}, hold for 3 min, increase to 200 °C at a rate of 1.5 °C·min^{-1}, hold for 0 min, increase the temperature to 240 °C at a rate of 10 °C·min^{-1}, and hold for 3 min at 240 °C. The FAs were identified by comparing the relative retention times (retention time/retention time of internal standard) to those derived from known standards (Supelco 37 FAME Mix, Supelco C8-C24 FAME Mix and Supelco PUFA No. 3 from menhaden oil, Sigma-Aldrich). For our analyses, we did not include FAs with a composition <0.1% of the total lipid content. This resulted in the removal of 20:0, 22:0, 24:0, 22:1(n-9), 24:1(n-9), 16:3(n-4), 22:2(n-6), and 22:5(n-6) from the data set.

Hatchery rearing

Eggs from each female were partitioned into six egg containers (40 eggs per container; 6 cm diameter × 5 cm height) and then fertilized with milt from males of the same population using a paternal half-sibling breeding design (one male × two females; Lynch and Walsh 1998). A paternal half-sib breeding design was used because it allowed us to fertilize the greatest number of unique females while also controlling for genetic effects, relative to other breeding designs, such as maternal half-sib or family block designs. The fertilizations resulted in 18 Credit River, 26 Pine River, and 21 Sydenham River families. Two egg containers per family (80 eggs) were then transferred to upwelling incubation trays at a mean (±SD) temperature of 6.5 ± 0.8 °C, 9.4 ± 0.3 °C, and 15.2 ± 0.02 °C. These temperature regimes reflect the natural range of temperatures the populations would experience in the wild during incubation (range: 18–0 °C; Thorn and Morbey 2018). Dead or unfertilized eggs (i.e., white in colour) were removed from egg containers daily. All removed eggs were preserved in Stockard's solution and later assessed for evidence of embryonic development (Boyd et al. 2010). This allowed us to correct our calculation of hatch success (i.e., the number of live alevins) by excluding unfertilized embryos. The developing embryos remained in the egg containers until the study was terminated at swim-up stage, which is when the fish have fully absorbed the yolk sac. Swim-up was chosen as the end point of the experiment because swim-up is the last point in which the offspring are still dependent on maternally derived energy stores. All animal procedures were approved by the Western University Animal Care Subcommittee (2007-043-05).

Early life history traits

We measured hatch length, swim-up length, hatch to swim-up growth rate, hatch success, and hatch to swim-up survival during the experiment. All length measurements were taken from the anterior tip of the snout to the posterior tip of the hypural plate (i.e., standard length). The hatch length of individuals from each family was measured by taking a photograph of a family in a Petri dish of water at 50% hatch and using the computer software ImageJ (https://imagej.nih.gov/ij/) to measure the individuals in the photograph. The position of the Petri dish was constant among photographs, and a ruler was placed in each picture for scale. Swim-up length was measured using a set of handheld calipers to the nearest 0.1 mm. ImageJ was used to measure hatch length instead of calipers to reduce handling stress and any associated mortalities. We validated the use of ImageJ by measuring a subset of individuals using both calipers and ImageJ and found that the two techniques produced highly consistent measurements (linear regression: $\beta \pm SE = 0.99 \pm 0.04$, $P < 0.001$, $R^2 = 0.98$, $N = 15$). Hatch to swim-up growth rate was calculated as

$$G = \frac{L_S - L_H}{\Delta D}$$

where L_S is swim-up length (mm), L_H is hatch length (mm), and ΔD is the number of degree-days between hatch and swim-up length measurements (Jensen et al. 2008). Degree-days were calculated as the sum of mean daily water temperatures over the period of time between hatch and swim-up (Jensen et al. 2008). Hatch success was measured as the number of fertilized embryos that successfully hatched. Finally, hatch to swim-up survival was the number of live alevins that survived until the termination of the experiment at the swim-up stage. All sample sizes and summary data for the early life history traits by population and temperature can be found in the online Supplementary materials (Tables S1 and S2[1]).

Statistical analysis

Statistical analyses were conducted using family means for length and growth traits and individual data for survival traits in the R statistical computing environment (R Core Team 2016). Egg wet mass and proximate composition were compared among the populations using an analysis of variance (ANOVA) and post hoc

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0013.

Table 1. Female length, egg wet mass, and egg proximate composition of Chinook salmon (*Oncorhynchus tshawytscha*) collected in the Credit (n = 18), Pine (n = 26) and Sydenham (n = 21) rivers.

	Credit River	Pine River	Sydenham River
Female trait			
Fork length (cm)	88.93±1.62	74.51±1.26	75.78±1.43
Egg trait			
Wet mass (g)	0.284±0.011	0.177±0.007	0.207±0.008
Wet mass composition			
Lipid (g·g wet mass^{-1})	0.076±0.003	0.074±0.002	0.071±0.002
Lean mass (g·g wet mass^{-1})	0.469±0.005	0.479±0.006	0.490±0.005
Water (g·g wet mass^{-1})	0.455±0.006	0.447±0.006	0.439±0.006
Dry mass composition			
Lipid (g·g dry mass^{-1})	0.139±0.004	0.132±0.003	0.127±0.003
Lean mass (g·g dry mass^{-1})	0.861±0.004	0.868±0.003	0.873±0.003

Note: Values are presented as mean ± standard error and calculated from family-level data.

Tukey tests. Given that egg mass is often correlated with female length, we also compared egg mass among the populations using an analysis of covariance (ANCOVA) with female length as a covariate. The egg FA composition was compared among the populations using principal components analysis (PCA; Tabachnick and Fidell 2007). The FA composition data was first arcsine-square-root-transformed to normalize the data. Principal component (PC) scores with eigenvalues >1 were compared among populations using an ANOVA to determine if there were any significant differences in egg FA composition among populations (Tabachnick and Fidell 2007).

Linear and generalized linear mixed models were used to assess the effects of egg FA composition on growth–size and survival traits, respectively. We first fit a "full" model using the general form

$$Z = \mu + P + T + E + \mathrm{PC}_n + L + P \times T + P \times E + T \times E + P \times \mathrm{PC}_n + T \times \mathrm{PC}_n + P \times L + T \times L + \mathrm{Sire} + e$$

where P is the population of origin, T is the temperature treatment, E is the mean egg mass of each family, PC_n is the nth principal component from the PCA, L is the proportion of egg dry mass that was lipid, Sire is the random effect of sire, and e is the unexplained residual variation. The generalized linear models contained the additional random effect of female identity nested in sire. All possible two-way interactions with temperature and population were included in the model. Linear and generalized linear mixed models were fit using the lme4 package (Bates et al. 2015). We then performed backwards stepwise model selection by iteratively removing nonsignificant terms from the model until the log-likelihood of the nested model was significantly reduced (α = 0.05; Table S3[1]; Zuur et al. 2009). We first removed nonsignificant two-way interactions and then removed nonsignificant to the main effects. The variables retained in the reduced models were individually assessed by removing each variable from the model and comparing the nested model with the full model using a likelihood ratio test. The variance explained by the fixed effects (marginal R^2) and the full model (conditional R^2) was calculated for the final models following Nakagawa and Schielzeth (2013). We visualized interactions between temperature–population and the egg composition metrics using partial dependence plots. Relationships were plotted with 95% confidence intervals estimated using parametric bootstrapping run for 500 iterations.

Table 2. Mean percentage (± standard error) of individual fatty acids, fatty acid families, and fatty acid ratios in Chinook salmon (*Oncorhynchus tshawytscha*) eggs collected from the Credit (n = 18), Pine (n = 26), and Sydenham (n = 21) rivers.

Fatty acid	Credit River	Pine River	Sydenham River
Saturated			
14:0	2.1±0.3	1.3±0.2	2.0±0.1
16:0	14.1±0.4	15.5±0.4	16.1±0.4
18:0	5.8±0.3	7.7±0.3	7.3±0.2
Monounsaturated			
16:1(n-9)	1.2±0.1	1.0±0.1	1.1±0.1
16:1(n-7)	5.6±0.2	7.9±0.4	7.6±0.3
18:1(n-9)	22.1±0.5	27.3±0.5	23.9±0.7
18:1(n-7)	5.2±0.2	8.0±0.3	7.2±0.3
20:1(n-9)	0.8±0.1	0.7±0.1	0.9±0.1
Polyunsaturated n-3			
18:3(n-3)	4.7±0.2	1.8±0.1	1.8±0.1
18:4(n-3)	1.2±0.1	0.6±0.1	0.6±0.1
20: 3(n-3)	1.1±0.1	0.5±0.1	0.7±0.2
20:4(n-3)	3.2±0.1	1.5±0.1	1.9±0.1
20:5(n-3)	8.0±0.3	5.5±0.2	6.3±0.2
22:5(n-3)	3.3±0.2	2.8±0.1	3.2±0.2
22:6(n-3)	8.9±0.6	7.6±0.4	8.9±0.5
Polyunsaturated n-4			
16:2(n-4)	0.4±0.1	0.4±0.1	0.3±0.1
Polyunsaturated n-6			
18:2(n-6)	5.1±0.1	4.1±0.2	3.8±0.1
20:2(n-6)	0.7±0.1	0.5±0.1	0.6±0.1
20:3(n-6)	0.4±0.1	0.4±0.1	0.4±0.1
20:4(n-6)	6.0±0.2	5.1±0.2	5.3±0.1
∑ SFA	21.9±0.7	24.5±0.5	25.4±0.6
∑ MUFA	34.8±0.8	44.8±0.7	40.6±1.0
∑ PUFA	43.1±1.4	30.6±0.7	33.8±1.2
∑ PUFA n-3	30.5±1.2	20.2±0.6	23.4±1.0
∑ PUFA n-6	12.3±0.3	10.1±0.2	10.2±0.2
n-3:n-6	2.5±0.1	2.0±0.1	2.3±0.1
DHA:EPA	1.1±0.1	1.4±0.1	1.4±0.1

Results

Egg wet mass and proximate composition

Egg wet mass was different among the three populations, with the Credit River having the heaviest eggs and the Pine River having the lightest eggs ($F_{[2,62]}$ = 41.2, P < 0.001; Table 1). After controlling for female length, egg wet mass was similar between the Credit and Sydenham rivers, while the Pine River had significantly lighter eggs than the other two populations ($F_{[2,60]}$ = 10.6, P < 0.001). Proximate composition of the eggs was quite similar among the populations (Table 1). There were no differences among the populations in the proportion of fat ($F_{[2,62]}$ = 1.3, P = 0.29), lean mass ($F_{[2,62]}$ = 3.1, P = 0.05), or water ($F_{[2,62]}$ = 1.6, P = 0.22). Similarly, fat content on a dry mass basis did not differ among the populations ($F_{[2,62]}$ = 2.8, P = 0.07) nor did the lean mass ($F_{[2,62]}$ = 2.8, P = 0.07).

Egg FA composition

We identified 20 FAs in the Chinook salmon eggs (Table 2). Of these FAs, 16:0, 18:1(n-9), 18:1(n-7), 20:5(n-3), and 22:6(n-3) were particularly abundant in the eggs of all three populations. PCA revealed that the populations differed in egg FA composition (Fig. 1). The first five PCs had eigenvalues >1 and explained 79% of the variation (Table 3). For PC1, there was high positive loadings for the PUFAs and negative loadings for SFAs and monounsaturated fatty acids (MUFAs). PC2 had a strong positive loading for

Fig. 1. Scatterplots of (*a*) principal components 1 and 3 and (*b*) principal components 1 and 4 from a principal component analysis of Chinook salmon (*Oncorhynchus tshawytscha*) egg fatty acid composition among the Credit, Pine, and Sydenham rivers. The ellipses are the 95% confidence ellipses for the populations. [Colour online.]

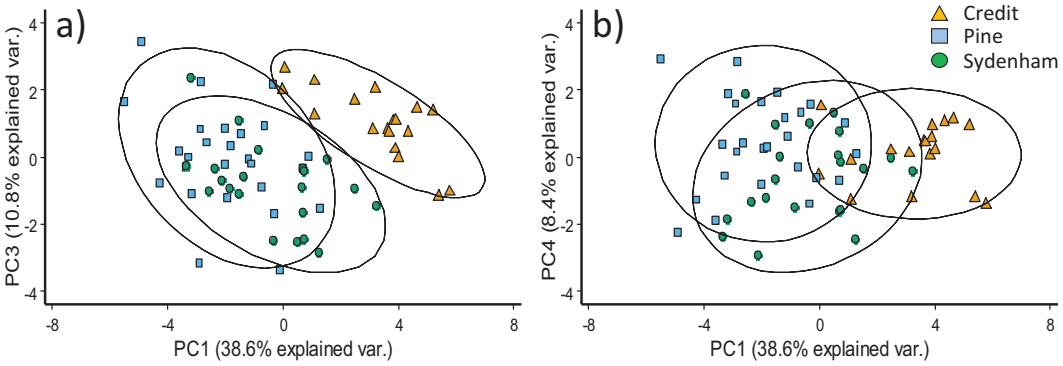


Table 3. Factor loadings for the first five principal components from a principal components analysis on the fatty acid composition of eggs from the Credit, Pine and Sydenham rivers.

	PC1	PC2	PC3	PC4	PC5
Saturated					
14:0	0.04	−0.49	−0.02	−0.14	0.17
16:0	−0.20	−0.04	0.16	−0.45	0.05
18:0	−0.27	0.20	0.035	−0.12	−0.13
Monounsaturated					
16:1(n-9)	0.08	−0.37	0.02	0.16	0.15
16:1(n-7)	−0.24	−0.30	−0.10	−0.01	0.24
18:1(n-9)	−0.26	−0.04	0.09	0.24	−0.27
18:1(n-7)	−0.29	0.11	−0.18	0.19	−0.15
20:1(n-9)	0.12	−0.32	−0.26	−0.16	−0.46
Polyunsaturated n-3					
18:3(n-3)	0.28	0.09	0.36	−0.03	0.09
18:4(n-3)	0.26	−0.28	0.12	0.14	0.05
20:3(n-3)	0.23	−0.07	0.14	−0.09	−0.31
20:4(n-3)	0.30	0.13	0.24	−0.08	−0.13
20:5(n-3)	0.31	0.01	−0.10	−0.05	0.26
22:5(n-3)	0.23	0.31	−0.29	0.01	−0.05
22:6(n-3)	0.23	0.19	−0.42	−0.07	0.09
Polyunsaturated n-4					
16:2(n-4)	0.02	−0.17	0.050	0.59	0.11
Polyunsaturated n-6					
18:2(n-6)	0.18	0.15	0.50	0.09	−0.07
20:2(n-6)	0.22	−0.28	−0.11	−0.20	−0.40
20:3(n-6)	0.13	0.05	−0.16	0.43	−0.31
20:4(n-6)	0.25	0.09	−0.28	0.01	0.30
Eigenvalue	7.71	2.84	2.16	1.68	1.37
Variance explained (%)	38.6	14.2	10.8	8.4	6.8

22:5(n-3) and high negative loadings for 14:0, 16:1(n-7), 16:1(n-9), and 20:1(n-9). PC3 had high positive loadings for 18:2(n-6) and 18:3(n-3) and a strong negative loading for 22:6(n-3). PC4 had strong positive loadings for 20:3(n-6) and 16:2(n-4) and a strong negative loading for 16:0. Finally, PC5 had a strong positive loading for 20:4(n-6) and strong negative loadings for 20:1(n-9), 20:2(n-6), 20:3(n-3), and 20:3(n−6).

Of the retained PCs, there were differences among populations for PC1 ($F_{[2,62]} = 46.9$, $P < 0.001$), PC3 ($F_{[2,62]} = 9.2$, $P < 0.001$), and PC4 ($F_{[2,62]} = 3.7$, $P = 0.03$), whereas there were no differences among populations for PC2 ($F_{[2,62]} = 1.3$, $P = 0.28$) or PC5 ($F_{[2,62]} = 1.0$, $P = 0.39$). The most striking difference was along PC1, where eggs from the Credit River had a higher proportion of n-3 PUFAs and eggs from the Pine River had a higher proportion of SFAs and MUFAs (Fig. 1). The FA profiles of Sydenham River eggs fell between the extremes of the Credit and Pine rivers.

Table 4. Parameters, marginal R^2, and conditional R^2 of the hatch length (HL), swim-up length (SL), and growth rate (GR) models.

Trait	Parameters	R^2_M	R^2_C
HL	$\mu + P + T + E + \text{PC1} + L + P \times E + P \times \text{PC1} + T \times \text{PC1} + P \times L$	0.91	0.92
SL	$\mu + P + T + E + \text{PC1} + P \times E + T \times E + P \times T + P \times \text{PC1}$	0.90	0.97
GR	$\mu + P + T + E + L + P \times E + P \times T + T \times L + P \times L$	0.59	0.68

Note: Parameters included in the models were population (*P*), temperature (*T*), egg mass (*E*), PC1 score, and lipid content (*L*). Two-way interactions between the variables are denoted with a times symbol (×). The random effect of sire was included in all models. The marginal R^2 and conditional R^2 represent the variance explained by the fixed effects and the full model, respectively.

Only PC1 was considered in models of growth–size and survival for two reasons. First, PC1 explained 38.6% of the variation in FA composition, which was much higher than the other PC axes (Table 3). Second, the inclusion of additional PC axes in the analysis would result in a full model that was over-parameterized. Prior to using PC1 as predictor variable, we tested for any correlations between PC1 and egg mass within the populations and found that they were only weakly correlated (Credit: $r = 0.29$, $P = 0.03$; Pine: $r = 0.38$, $P < 0.001$; Sydenham: $r = 0.29$, $P = 0.02$).

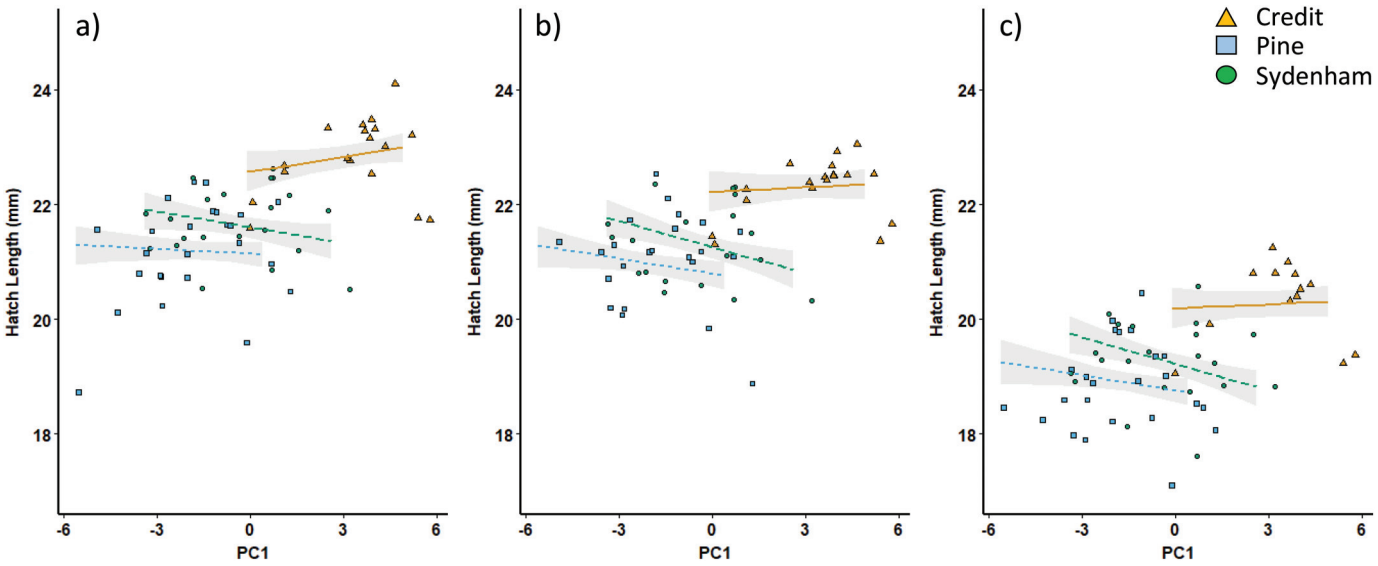
Hatch length

Hatch length was influenced by all the egg quality covariates; however, the covariates were involved in several two-way interactions with temperature and population (Table 4; Table S4[1]). Temperature had a large effect on hatch length, and there was a marked decreased in length at 15.2 °C (Fig. 2). Hatch length was affected by a temperature × PC1 interaction ($\chi^2_2 = 7.34$, $P = 0.03$), whereby the relationship between PC1 and hatch length was positive at 6.5 °C, but close to zero at 9.4 and 15.2 °C (Fig. 2). The relationship between hatch length and PC1 varied across populations, with the Credit River having a positive slope and the Pine and Sydenham rivers having a negative slope (population × PC1: $\chi^2_2 = 8.54$, $P = 0.01$; Fig. 2). The quantity of lipid also influenced hatch length, with the Pine River having a positive slope and the Credit and Sydenham rivers having a negative slope (population × lipid: $\chi^2_2 = 13.76$, $P = 0.001$; Table S4[1]). Finally, hatch length was positively related to egg mass in all populations, but the strength of the relationship varied among populations (population × egg mass: $\chi^2_2 = 15.65$, $P < 0.001$; Table S4[1]).

Swim-up length

Swim-up length was influenced by egg mass and PC1, but the relationships depended on population and temperature (Table 4; Table S5[1]). Egg mass was positively related to swim-up length, and the slope of the relationship depended on population (population ×

Fig. 2. Relationship between hatch length and PC1 at (*a*) 6.5 °C, (*b*) 9.4 °C, and (*c*) 15.2 °C from a linear mixed model. Egg mass and lipid content were set at their respective population-level mean values. Shaded regions around each regression line represent the 95% confidence interval estimated using parametric bootstrapping. [Colour online.]



egg mass: χ^2_2 = 38.49, P < 0.001) and temperature (temperature × egg mass: χ^2_2 = 20.21, P < 0.001; Table S5[1]). PC1 influenced swim-up length differently among the populations, with the Credit River having a positive slope and the Pine and Sydenham rivers having a negative slope (population × PC1: χ^2_2 = 32.14, P < 0.001; Fig. 3). Swim-up length also varied by population and temperature (χ^2_4 = 73.22, P < 0.001; Table S5[1]).

Growth rate

Growth rate was affected by interactions involving egg mass and lipid content (Table 4; Table S6[1]). The relationship between growth rate and lipid content varied by population (population × lipid: χ^2_2 = 8.40, P < 0.02) and temperature (temperature × lipid: χ^2_2 = 13.95, P < 0.001; Fig. 4). The positive relationship between growth rate and lipid content was stronger for the Credit River than both the Pine and Sydenham rivers. Furthermore, the slope of the growth rate – lipid relationship increased with temperature treatment, whereby the steepest relationship was present at 15.2 °C (Fig. 4). Egg mass was also positively related to growth rate, and the slope of the relationship varied across populations, with the Pine River having the greatest slope and the Sydenham River having the weakest slope (population × egg mass: χ^2_2 = 6.63, P = 0.04; Table S6[1]). Growth rate also varied by population and temperature (χ^2_4 = 61.45, P < 0.001; Table S6[1]).

Survival traits

The median survival ranged from 93.4% to 100% and 96.0% to 100% for hatch success and hatch to swim-up survival, respectively (Table S2[1]). The high survival is most notable for hatch to swim-up survival, where many families experienced 100% survival. We did not perform model selection or interpret the results from the survival models for two reasons. First, there was very little variation in survival to explain with the models. Second, the full model for hatch success had poor predictive performance, with a conditional R^2 of 0.23 (highest R^2 achieved). Taken together, the hatch success and hatch to swim-up survival models did not provide biologically meaningful results.

Discussion

In this study, we show that there are transgenerational effects of maternal diet, expressed as variation in egg nutrient content, on the development of Chinook salmon progeny reared under three different temperatures. The egg nutrient component involved in the transgenerational effect varied among traits, where hatch length was affected by both the FA composition (PC1 axis) and lipid content, swim-up length was affected by FA composi-

Fig. 3. Relationship between swim-up length and PC1 from a linear mixed model. Egg mass was set at their respective population means, while temperature was set at 6.5 °C. Shaded regions around each regression line represent the 95% confidence interval estimated using parametric bootstrapping. [Colour online.]

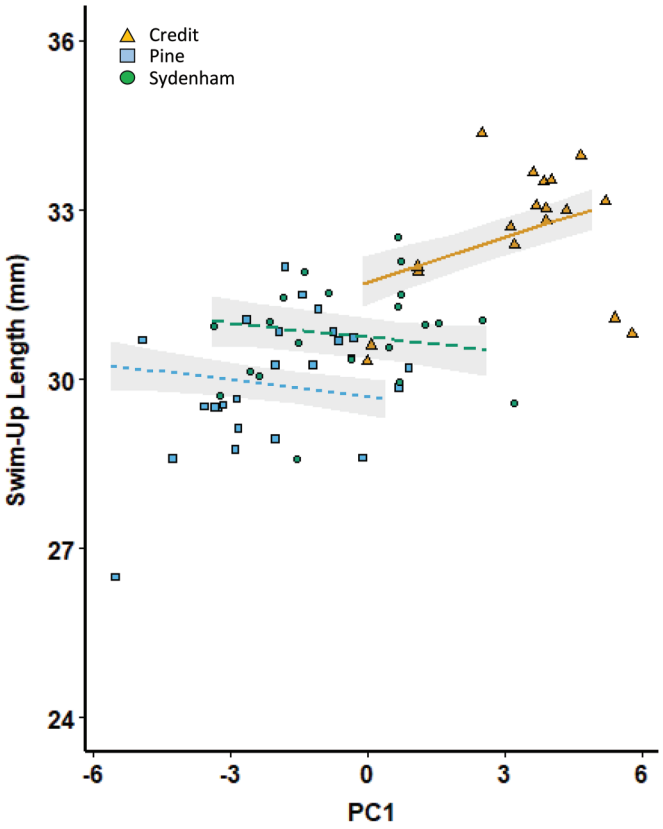
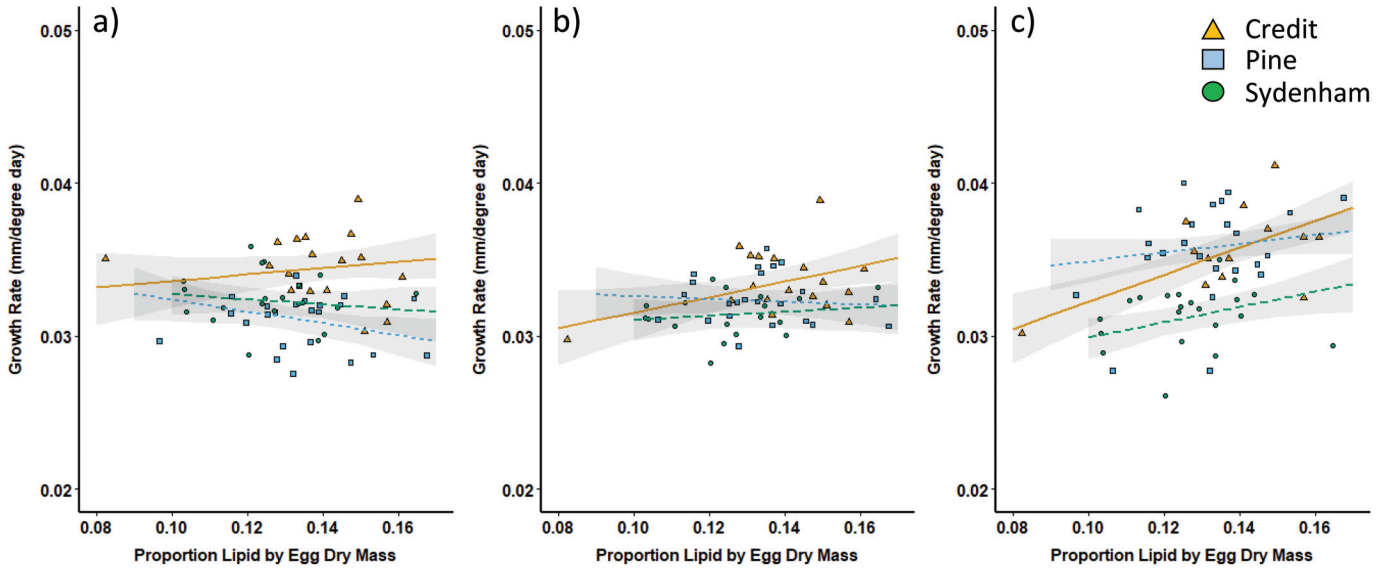


Fig. 4. Relationship between growth rate and egg lipid content at (*a*) 6.5 °C, (*b*) 9.4 °C, and (*c*) 15.2 °C from a linear mixed model. Egg mass and PC1 scores were set at their respective population-level mean values. Shaded regions around each regression line represent the 95% confidence interval estimated using parametric bootstrapping. [Colour online.]



tion, and growth rate was affected by lipid content. Importantly, the relationship between the traits and egg nutrient content was dependent on population and (or) temperature. Egg wet mass and temperature were more important predictors than the egg nutrient content for all the traits, regardless of developmental stage (*t* values: Tables S4–S6[1]).

Hatch and swim-up length were influenced by an interaction between FA composition and population, where eggs with a high PUFA content achieved the largest length in the Credit River and eggs with a high SFA and MUFA content achieved the largest length in the Lake Huron populations (Pine and Sydenham rivers). The presence of a population × FA composition interaction suggests that the metabolism of each population is adapted to the forage base available to mothers during egg development. If the developing offspring used FAs in the same way regardless of population (i.e., no divergence), then we would expect to see all three populations achieve the largest length with a similar egg FA composition. Instead, we see the largest offspring lengths achieved with egg FA compositions that reflect those available in their population of origin (i.e., maternal forage base). Such divergence in metabolism could be due to variation in the selective use of FAs for energy, where the Credit River population relies heavily on PUFAs (e.g., DHA and EPA) and the Lake Huron populations rely heavily on SFAs (e.g., 16:0) and MUFAs (e.g., 18:1(n-9); Tocher 2003). If true, this divergence in metabolism has occurred in ~10 generations since the populations were first introduced to the Great Lakes from a common genetic source (Thorn and Morbey 2018). Similar metabolic divergence has been found within an aquaculture setting where a domesticated strain of coho salmon (*Oncorhynchus kisutch*) had a significantly greater feed conversion efficiency relative to its source population after 16 generations (Neely et al. 2008). The connection between offspring metabolism and maternal diet, via egg FA content, could be the result of selection acting directly on offspring metabolism or a correlated response to selection acting on adult metabolism. However, further research is required to determine the metabolic and evolutionary mechanisms behind the among-population variation in FA use during development.

Hatch length was also affected by an interaction between temperature and FA composition. Consistent with our prediction, there was a positive relationship between hatch length and the relative quantity of PUFAs at 6.5 °C and a very weak relationship at 9.4 and 15.2 °C. The positive relationship between hatch length and the relative quantity of PUFAs in the cold temperature treatment is likely related to the temperature sensitivity of membrane function and metabolism to FA composition (Hazel 1984, 1995; Robertson and Hazel 1997). At cold temperatures, PUFAs are selectively incorporated into cell membranes to maintain membrane function (Craig et al. 1995; Snyder et al. 2012; Ma et al. 2015). Furthermore, the digestibility of PUFAs is maintained at low temperature, whereas it is reduced for SFAs, making PUFAs a preferred source of energy for growth at low temperature (Olsen and Ringo 1998). Offspring hatching from eggs with a higher quantity of PUFAs would be capable of attaining a larger size before depleting their reserve of PUFAs (Hazel 1995). The developmental advantage of having lipid reserves rich in PUFAs would be reduced with increasing temperature as other FAs are more efficiently utilized, which is consistent with the lack of a hatch length – PUFA relationship at higher temperatures.

Growth rate increased with the proportion of lipid in an egg, and as predicted, the relationship depended on the rearing temperature. The positive percent lipid – growth rate relationship was only present at 15.2 °C and not in the colder treatments. The appearance of a percent lipid – growth rate relationship at high temperature is related to the temperature dependence of metabolism in ectotherms. As temperature increases, metabolic rate increases (Schulte 2015) and conversion efficiency is reduced (Heming 1982; Rombough 1994; Kullgren et al. 2013). The combined effects of higher metabolic rate and reduced conversion efficiency at high temperature put a greater energetic demand on the endogenous energy resources of developing larvae. This increased energy demand at high temperature can deplete lipid stores prior to swim-up or compromise the development of larvae with small stores leading to reduced survival for these individuals (Fisher et al. 2007). Furthermore, offspring provided with less lipid stores appear to have reduced growth rates relative to offspring with large lipid stores at high temperature, which can lead to reduced offspring size at emergence. It is possible that females able to invest more lipids into their eggs will have a better fitness in warmer temperatures.

Variation in the FA composition of the eggs most likely reflects dietary differences among the Great Lakes Chinook salmon populations. The Credit River eggs tended to have a higher proportion n-3 PUFAs, whereas the Lake Huron populations had more SFAs

and MUFAs. The difference between the Lake Ontario (Credit River) eggs and the Lake Huron (Pine and Sydenham rivers) eggs is not surprising given that they are from lake systems with a different prey fish composition (Bunnell et al. 2014). Chinook salmon in the Great Lakes preferentially prey upon alewife (*Alosa pseudoharengus*) (Diana 1990; Warner et al. 2008; Jacobs et al. 2013; Happel et al. 2017), and the abundance of alewife in 2012, when our fish were collected, differed between Lakes Huron and Ontario (OMNRF 2013; Warner et al. 2013). In Lake Huron, the alewife abundance was unusually low and unlikely to make any substantial contribution to the diet of Chinook salmon (Warner et al. 2013), whereas the alewife abundance in Lake Ontario was much greater (OMNRF 2013). Furthermore, alewife tend to have higher concentrations of n-3 and n-6 PUFAs relative to other prey fish in the Great Lakes (Honeyfield et al. 2012). Taken together, differences in the contribution of alewife to the diet of Chinook salmon likely accounts for much of the difference in the FA composition we found between the lake systems.

Within Lake Huron, we also found differences in the FA composition of eggs from the Sydenham River and Pine River females. Recent work by Marklevitz et al. (2016) suggests that there is regional structuring of Chinook salmon in Lake Huron. The Pine and Sydenham rivers are both located in southern Georgian Bay, and our results suggest that there is a possibility of fine-scale, population-level structuring of Chinook salmon in Lake Huron. Vitellogenesis occurs over a period of months (Tyler et al. 1990; Tyler and Sumpter 1996), and the FA composition of eggs will integrate dietary signals over this period (Pickova et al. 1999). Therefore, the differences we found between the Pine and Sydenham rivers only partially reflect dietary differences due to spatial variation during prespawning staging and will also reflect spatial variation while actively feeding within the main basin of the lake.

The transgenerational effects of maternal egg nutrient allocation on offspring development has several potential management implications. The forage base available to mothers during the period of vitellogenesis will have a direct influence on the composition of lipids deposited as yolk (Wiegand 1996; Pickova et al. 1999; Johnson 2009). Thus, the lipid composition of Chinook salmon eggs will track shifts in the prey fish community among regions and (or) years and, depending on the environmental context, could be an important unaccounted source of spatial–temporal variation in juvenile recruitment. In addition, anthropogenic climate change is poised to increase water temperatures in lakes and rivers around the globe (Punzet et al. 2012; Isaak et al. 2012; O'Reilly et al. 2015), including the Great Lakes watershed (Trumpickas et al. 2009). Higher water temperatures during endogenous feeding will increase the amount of energy per offspring required for development. This shift in the cost of early life history development could reduce the productivity of Chinook salmon, along with other salmonids, in the Great Lakes unless females compensate by allocating more energy, on a relative basis, to each offspring. Finally, the FA composition eggs can serve as a trophic biomarker and can be used to better understand the foraging habitats of a specific population (Happel et al. 2016). Before we can fully understand any management implications, however, more research needs to be done on the connection between transgenerational effects of maternal diet, success during juvenile life history stages, and population dynamics.

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