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Differences in egg quantity and quality among hatchery- and wild-origin Chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: Each year, millions of hatchery-raised juvenile salmon are released into the wild to help bolster salmon populations all over North America. These fish often differ from their wild-origin conspecifics in terms of survival and reproductive success after release, but our understanding of their reproductive investment is limited. We examined differences in egg number (gonad mass and fecundity) and quality (mass, lipids, fatty acids) between spawning hatchery- and wild-origin Chinook salmon (*Oncorhynchus tshawytscha*) from Lake Ontario. Hatchery-origin females were found to not differ significantly in body size, age, egg total lipids, and fatty acid content of eggs relative to wild-origin females, but hatchery-origin females allocated significantly less body mass and neutral lipids into egg and gonadal development compared with wild-origin females. We also examined diets of both groups of females using stable isotopes and found that carbon and nitrogen stable isotopes suggested limited differences in the diet between hatchery- and wild-origin adult females. The results from the present study provide evidence that the differing environmental conditions and associated selection pressures of captive environments during early life in hatchery settings can alter certain life-history traits later in adult development, namely gonad mass and egg size, and could contribute to differences in their performance in the wild.

Résumé : Chaque année, des millions de saumons juvéniles élevés en alevinières sont relâchés à l'état sauvage pour aider à accroître les populations de saumons partout en Amérique du Nord. Si, dans bien des cas, ces poissons diffèrent de leurs congénères élevés à l'état sauvage en ce qui concerne leur survie et leur succès de reproduction après le lâcher, la compréhension de leur investissement dans la reproduction est limitée. Nous avons examiné les différences en ce qui a trait au nombre (masse des gonades et fécondité) et à la qualité (masse, lipides, acides gras) des œufs entre des saumons quinnats (*Oncorhynchus tshawytscha*) en frai du lac Ontario, élevés en alevinière et à l'état sauvage. Si les femelles issues d'alevinières ne différaient pas de manière significative des femelles élevées à l'état sauvage sur le plan de la taille du corps, de l'âge et des lipides totaux et du contenu en acides gras dans les œufs, elles affectaient significativement moins de masse corporelle et de lipides neutres au développement des œufs et des gonades que leurs congénères élevées à l'état sauvage. Nous avons également examiné le régime alimentaire des deux groupes de femelles à l'aide des isotopes stables et constaté que les isotopes stables du carbone et de l'azote semblaient indiquer des différences limitées du régime alimentaire entre les femelles adultes issues d'alevinières et de milieux naturels. Les résultats de l'étude indiquent que des différences sur le plan des conditions ambiantes et des pressions de sélection associées du milieu captif au début de la vie dans les milieux d'alevinière peuvent modifier certains caractères du cycle biologique plus tard durant le développement des adultes, notamment la masse des gonades et la taille des œufs, et pourraient en partie expliquer des différences en ce qui concerne leur performance à l'état sauvage. [Traduit par la Rédaction]

Introduction

"Hatchery-origin" can be used to describe individuals that are artificially fertilized and subsequently raised in a controlled hatchery setting until eventually released back into the wild as juveniles. Such practices differ substantially from natural recruitment, as hatcheries impose a soft selection pressure to the developing offspring, where temperature and diet are favourable and no predators or other natural selection pressures are present (Fleming et al. 1994; Einum and Fleming 1999; Heath et al. 2003). Such benign environments can result in unintentional selection on critical early life-history traits and lead to the divergence of hatchery fish from their wild counterparts (Swain and Riddell 1990; Fleming et al. 1994; McDermid et al. 2010). As a result, hatchery-reared fish are more likely to develop traits that may be adaptive in captivity but maladaptive in nature and tend to do less well when in the wild (Fleming et al. 1994; Reisenbichler and Rubin 1999; Miller et al. 2004). Maladaptive changes in egg quality can be especially detrimental, as the quality of the egg determines the survival of the embryo and profoundly influences fitness in both mother and offspring (Roff 1992; Brooks et al. 1997).

Egg quality, reflected in attributes such as size and composition (especially lipids and their constituent fatty acids (FAs)), can have a major impact on the early life history and survival of both wild and captive fish populations (Brooks et al. 1997). Normally in the wild, juveniles emerging from larger eggs are larger in size, with greater survival rates and fitness compared with smaller individuals (Einum and Fleming 1999, 2000). In contrast, hatchery environments relax natural selection on egg size (Einum and Fleming

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1999; Heath et al. 2003), and as a result smaller offspring from smaller eggs are more likely to survive and reproduce under hatchery conditions than in the wild (Einum and Fleming 1999). A previous study by Einum and Fleming (1999) found that in the brown trout (*Salmo trutta*), for example, offspring emerging from small eggs in a hatchery setting had similar growth and survival rates as those from large eggs, but had high mortalities and reduced fitness when in natural environments. The reduction of mortality in hatchery environments alone may influence the evolution of maladaptive egg traits and potentially reduce offspring survival when in the wild (Einum and Fleming 1999; Heath et al. 2003).

In contrast with the numerous studies focusing exclusively on egg size in hatchery- versus wild-origin individuals (Jonsson et al. 1996; Einum and Fleming 1999; Heath et al. 2003), very few studies have compared other egg quality traits such as the composition of the egg itself. Presumably, larger eggs are advantageous to the offspring in part because of their larger yolk reserves (Brooks et al. 1997), which provides the embryo with nutrients and energy during early life (reviewed in Wiegand 1996; Johnson 2009). In teleost fish, the egg yolk is composed mostly of protein and lipid reserves and provides structural materials, energy, and micronutrients to the embryo prior to exogenous feeding (Wiegand 1996; Pickova et al. 1997; Johnson 2009). Among the FAs, essential fatty acids (EFA) of the *n*-3 and *n*-6 configuration are especially important, as these cannot be synthesized de novo and have important implications in offspring growth and survival (Wiegand 1996). For example, the *n*-3 polyunsaturated fatty acid (PUFA) docosahexaenoic acid (22:6(*n*-3), DHA) is vital in normal brain and retinal development (Bell and Dick 1991; Bell et al. 1995; Wiegand 1996). Similarly, deficiencies in the EFA eicosapentanoic acid (20:5(*n*-3), EPA), DHA, and arachidonic acid (20:4(*n*-6), AA) are linked to abnormalities in development, decreased hatching success, and low offspring survival in numerous teleost fishes (Sargent et al. 1995; Wiegand 1996; Bessonart et al. 1999).

In Lake Ontario, the Chinook salmon (*Oncorhynchus tshawytscha*) population has been stocked annually with hatchery-raised progeny since their introduction in the mid-1960s. Initially, Chinook salmon were introduced into Lake Ontario to establish a top predator as a biological control of nuisance fish species (e.g., alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*)) and to support recreational fisheries (Crawford 2001). Currently, Chinook salmon comprise ~40% of all salmonid catch in Lake Ontario (Stewart and Schaner 2002) and represent an important component of the Lake Ontario ecosystem and food web structure. Evidence of naturally reproducing Chinook salmon was first observed in Lake Ontario tributaries in the 1980s (reviewed in Crawford 2001), and currently it is estimated that 50% of spawning adults in Lake Ontario tributaries are of wild origin (Bowlby et al. 2004). However, it remains unclear whether this species can maintain its current population size without ongoing stocking programs, and thus hatchery-raised Chinook salmon juveniles continue to be released annually into Lake Ontario tributaries.

The life cycle of hatchery- and wild-origin Chinook salmon differs substantially during spawning and early offspring development. Both hatchery- and wild-origin salmon migrate to Lake Ontario tributaries to spawn in late September through to October at the age of 2–4 years old (Kocik and Jones 1999). In the wild, fertilized eggs incubate in gravel redds under natural selection pressures and surviving alevins emerge in the spring and feed off their yolk sac for several weeks until exogenous feeding begins. Mortality is typically high during the early feeding period, as offspring are subjected to several selection pressures, including exposure to predators, competition for food sources, and adverse environmental conditions. In contrast, hatchery-origin fish are derived from gametes obtained from the wild that are artificially fertilized and subsequently reared in a controlled hatchery setting. Offspring are reared under soft selection pressures, where food abundance is high, predation is negligible, and other natural selection pressures are presumably limited. Hatchery-raised fry are released into natural streams in the spring (OMNRF 2011), at which point they probably experience lower survival and growth rates compared with wild-origin individuals (reviewed in Olla et al. 1998). Previous studies on hatchery- and wild-origin fishes suggest that differences in breeding schemes and selection pressures during early development have the potential to reduce the reproductive success of hatchery fish in the wild (Heath et al. 2003; Neff et al. 2011; reviewed in Fraser 2008; Whitcomb et al. 2014).

Currently, it is unknown if differences in environmental conditions experienced by hatchery- and wild-origin Lake Ontario Chinook salmon during early development lead to differences in their life-history traits later as adults. Maladaptive changes in egg quality induced by captive rearing could reduce offspring survival in the wild, thus impeding supplementation efforts and negatively affecting salmon populations. While previous studies suggest differences in body size between spawning hatchery- and wild-origin Lake Ontario Chinook salmon (Bowlby et al. 2004), it is unknown if they have also diverged in reproductive traits. As such, the objective of the present study was to examine differences in reproductive traits, particularly egg quality, between hatchery- and wild-origin Lake Ontario Chinook salmon. The results from this study will provide important insights into how hatchery rearing may affect egg quality in salmonids and as such will be relevant to rehabilitation and supplementation efforts for imperiled populations of salmon all over North America.

Methods

Field sampling

Gravid female Chinook salmon were collected from the Credit River (43°34′N, 79°42′W), a spawning tributary of Lake Ontario, from 1 to 9 October 2012, using standard electrofishing techniques (see Pitcher and Neff 2007). Upon collection, females were humanely euthanized and the origin of the female identified by the presence (wild-origin) or absence (hatchery-origin) of the adipose fin. All hatchery-reared Chinook salmon stocked into the Credit River and throughout Lake Ontario in 2008 and 2009 were marked by removing the adipose fin (Connerton et al. 2011; OMNRF 2011). This is the standard practice implemented by both the Ontario Ministry of Natural Resources and Forestry (OMNRF) and the New York State Department of Environmental Conservation for all hatchery-reared individuals (Connerton et al. 2011). As such, all sampled fish without an adipose fin were classified as hatchery origin, and all fish with an adipose fin were classified as wild origin.

For each female, fork length (FL, ±1 mm) was recorded, and body mass (±0.5 g) was measured both before (total body mass) and after (somatic mass) all eggs were removed. Gonad mass was calculated as the difference between total body mass and somatic mass, while fecundity was estimated as gonad wet mass divided by mean wet mass per egg. Female condition was estimated as the residual of the $\log_e$ soma mass versus $\log_e$ FL regression for the pooled sample of the two groups (Kaufman et al. 2007). A subsample of skinless, axial muscle was removed, placed in a small plastic bag, and frozen at –20 °C for stable isotope analysis. Otoliths were removed from a subset of females and age was estimated by counting annuli on sectioned otoliths (OMNRF 2011). Subsamples of eggs from each female were placed in plastic bags, transported fresh to the laboratory, then frozen at –20 °C. Other subsamples of eggs were stored in 50 mL falcon tubes, frozen in liquid nitrogen vapour, and stored at –80 °C for lipid and FA analyses.

Egg size

Mean wet mass per egg (used for estimating fecundity, above) was estimated by weighing five replicates of ten fresh egg tissue to

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the nearest 0.001 g. Egg samples frozen at –20 °C were weighed, freeze-dried, and reweighed to determine dry matter content (freeze-dried mass/frozen mass). Mean dry mass per egg was estimated by weighing three replicates of ten freeze-dried eggs to the nearest 0.001 g. Mean dry mass per egg was used as our index of egg size in all subsequent analyses. Freeze-dried eggs were then ground to a powder in a ball mill, stored at –20 °C, and used for lipid determinations (see below).

Egg lipid content

Total lipid content was determined using a chloroform–methanol extraction procedure modified from the methods of Folch et al. (1957). Briefly, approximately 0.2 g of ground freeze-dried egg tissue was weighed into a clean, glass centrifuge tube with 5 mL of 2:1 chloroform–methanol solvent and allowed to soak overnight. Following soaking, the mixture was vortexed for 10 s and centrifuged for 10 min at 1000*g*. The supernatant was removed and transferred into a second clean glass centrifuge tube (hereinafter referred to as the supernatant tube). The remaining residue was then further extracted in 3 mL of solvent. Pooled supernatants were washed with 2.5 mL 0.8% potassium chloride solution by agitating on a wrist action shaker (Burell Scientific) for 15 min. The supernatant tube was then centrifuged for 10 min at 1000*g*, the upper aqueous layer discarded, and the lower chloroform layer containing the lipid extract was transferred into a preweighed glass vial. Each vial was allowed to dry overnight in a fume hood, placed in a desiccator for 1 h, and reweighed to determine total lipid content. Crude lipid extracts were further separated into neutral and polar fractions using prepacked silica gel cartridges (Sep-Pak, Waters corporation, Milford, Massachusetts) using methods described by Juaneda and Rocquelin (1985).

Egg FA profile

FA profiles of the neutral and polar fractions of the salmon egg lipids were determined by flame ionization gas chromatography as previously described by Wiegand et al. (2004), with the exception that preliminary separation of the neutral and polar lipids was done using Sep-Pak 6 cm^3 (500 mg) silica cartridges rather than hand-made silica gel columns. Purity of the separated neutral and polar lipid fractions and the FAME preparations was confirmed by thin layer chromatography using hexane – diethyl ether – acetic acid (80:20:1) as the developing solvent (Wiegand and Idler 1982).

Stable isotope analysis

To determine if observed differences in hatchery- and wild-origin females may be related to dietary history, we examined their stable isotope compositions. Muscle samples from each of 13 hatchery-origin and 15 wild-origin females were freeze-dried for 48 h, homogenized with a mortar and pestle, and lipid-extracted using methods outlined in McMeans et al. 2010. Lipid-extracted samples were weighed (400–600 μg) into tinfoil capsules and analyzed for nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) stable isotopes using an isotope ratio mass spectrometer (Thermo Finnigan, San Jose, California, USA) coupled with an elemental analyzer (Costech, Valencia, California, USA) at the Chemical Tracers Laboratory at the Great Lakes Institute for Environmental Research, University of Windsor.

Stable isotope ratios were expressed in standard delta notation (δ) as the differences from international standards in parts per thousand based on the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N, and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard ratio was based on PeeDee Belemnite for ^{13}C and atmospheric nitrogen for ^{15}N (Dennis et al. 2010; Peterson and Fry 1987). Precision was assessed by the standard deviation of replicate analyses of two standards (NIST 8414 and internal lab standard (tilapia muscle), both $n = 21$), measured to be 0.1‰ and 0.2‰ for $\delta^{15}N$, respectively, and 0.1‰ for $\delta^{13}C$ for both standards. The accuracy based on the analysis of certified NIST standards for $\delta^{15}N$ was 0.08 (NIST 8547) and –0.2 (NIST 8547) and for $\delta^{13}C$ was –0.2 (NIST8542) and 0.01 (NIST8573). Accuracy was determined by the mean difference in stable isotope values from the certified value, where $n = 39$ for each standard.

Statistical analyses

All statistical analyses were performed using SPSS statistical software (IBM, version 21.0). Dependent variables representing egg quantity and quality traits included fecundity (egg number), gonad mass (g wet), egg size (dry mass, mg), egg lipid content (% of dry mass), egg polar lipid content (% of total lipids), egg neutral lipid content (% of total lipids), and FA profile (FAs as proportion of total FAs). Percentages of identified FAs were normalized to a total of 100% to render them proportional to each other (see Wiegand et al. 2004). Independent variables representing maternal traits included age (years), somatic mass (g wet), FL (mm), and relative condition (residual $\log_e$ mass).

Differences in maternal and egg traits were individually compared between the hatchery- and wild-origin females by two-sample *t* tests, analysis of covariance (ANCOVA), and analysis of variance (ANOVA). We used female FL as the primary covariate in most ANCOVA models, but used other covariates (e.g., egg size, egg lipid content) if they appeared to reduce residual variation better than female length. As the allocation of egg lipids may be limited by the size of the egg, we included egg size as a covariate for percent total lipid, neutral lipid, and polar lipid content. Similarly, we also included female condition as a covariate influencing egg lipid content (Kaufman et al. 2007). FA profiles were first analyzed on an individual FA basis by ANCOVA. In this approach, we examined FAs that were of particular interest because of their known physiological roles, their high relative abundance, or their contributions to variation uncovered in principal components analysis (i.e., 16:0, 18:0, 16:1(*n*-7), 18:1 *n*-9 (oleic acid, OA), AA, EPA, 22:5(*n*-3), DHA). We then conducted a more comprehensive comparison of FA profiles between groups by calculating principal components (PCs) from the relative abundances of the 25 most abundant FAs and analyzing the first two PCs (eigenvalue > 1) as dependent variables in ANCOVA models. All dependent variables expressed as proportions (total, polar and neutral lipids, FA relative abundance) were arcsine-square-root-transformed prior to analysis.

Results

Maternal traits

We collected samples from a total of 50 female Chinook salmon spawning in the Credit River, of which 27 were hatchery origin and 23 were wild origin. All females were 3 or 4 years of age (Table 1). There were no significant differences in FL (*t* test, $t = 0.08$, df = 48, $p = 0.94$) or somatic mass (*t* test, $t = 1.01$, df = 48, $p = 0.32$) between the hatchery- and wild-origin females. Sampled females of hatchery origin demonstrated a wider range in their body size than sampled females of wild origin (Table 1). There were three hatchery-reared females of distinctly smaller body size (FL < 800 mm), and although these individuals were not omitted as outliers, their effects on all subsequent analyses were examined. Additionally, there was no significant difference in female body condition between the two groups of salmon, as there was no difference in the residuals of the overall $\log_e$ mass – $\log_e$ length regression (*t* test, $t = 1.08$, df = 48, $p = 0.29$).

Gonad mass and fecundity

There was no significant interaction between the effects of female FL and origin (hatchery or wild) on gonad mass (ANCOVA, heterogeneity of slopes, $F_{[1,46]} = 1.69$, $p = 0.20$, $\eta^2 = 0.03$, 95% CI

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Table 1. Summary statistics of maternal, reproductive, and egg traits analyzed for hatchery- and wild-origin spawning Chinook salmon (*Oncorhynchus tshawytscha*) from the Credit River, Lake Ontario.

	Hatchery-origin (n = 27)			Wild-origin (n = 23)		
	Mean ± SD	Range (min.–max.)	CV (%)	Mean ± SD	Range (min.–max.)	CV (%)
Maternal and reproductive traits						
Age (years)	3.09±0.30	3–4	10	3.27±0.47	3–4	13
Fork length (mm)	880.85±63.41	748–971	7.2	879.65±47.65	811–985	5.4
Somatic mass (g)	6880.37±1485.78	3175–8981	22	6545.65±799.51	5148–7734	12
Gonad mass (g)	1370.30±537.62	290.0–1370.30	39	1772.96±724.38	567–3207	41
Fecundity	4602.40±1822.14	932.13–9041.06	40	5374.36 ± 1982.64	1568.03–9768.93	37
Egg traits						
Egg size (dry mass, mg)	106.19±14.10	82.85–127.62	13	114.70±14.80	82.21–137.50	13
% Total lipids	28.59±1.36	25.12–31.21	4.8	29.03±1.23	26.41–31.62	4.2
% Neutral lipids	60.21±2.09	55.47–63.61	3.5	61.33±1.76	58.96–65.60	2.9

(–113.35, 24.40)), and following removal of the interaction term, the covariate female FL did not significantly influence gonad mass (ANCOVA, covariate effect, $F_{[1,47]} = 0.45$, $p = 0.51$). Gonad mass was larger in wild-origin females, and this differences was statistically significant (ANOVA, $F_{[1,48]} = 5.07$, $p = 0.03$; Fig. 1A). These results did not change when using somatic mass as the covariate (ANCOVA, main effect, $F_{[1,47]} = 4.91$, $p = 0.03$, $\eta^2 = 0.094$, 95% CI (–771.19, –37.16)).

Fecundity ranged from 932 to 9041 among the hatchery-origin females and from 1568 to 9769 among the wild-origin females (Table 1). There was no interaction between the effects of female FL and origin on fecundity (ANCOVA, heterogeneity of slopes, $F_{[1,46]} = 1.20$, $p = 0.28$, $\eta^2 = 0.025$, 95% CI (–322.55, 95.30)), and following removal of the interaction term, FL did not significantly influence female fecundity (ANCOVA, covariate effect, $F_{[1,47]} = 0.25$, $p = 0.62$, $\eta^2 = 0.0049$, 95% CI (–121.98, 73.78)). Fecundity did not differ significantly between hatchery- and wild-origin Lake Ontario Chinook salmon (ANOVA, $F_{[1,48]} = 2.06$, $p = 0.16$, $\eta^2 = 0.041$, 95% CI (–1860.85, 322.71)).

Egg size

There was no significant interaction between female FL and origin on egg size (ANCOVA, heterogeneity of slopes, $F_{[1,46]} = 1.16$, $p = 0.29$, $\eta^2 = 0.018$, 95% CI (–2.11, 0.64)). Following removal of the interaction term, egg size increased significantly with female FL (ANCOVA, covariate effect, $F_{[1,47]} = 16.3$, $p < 0.001$) and differed significantly between hatchery- and wild-origin Chinook salmon (ANCOVA, $F_{[1,47]} = 5.90$, $p = 0.019$; Fig. 1B). Mean egg sizes adjusted to a female size of 880 mm FL were 96 and 104 mg for hatchery- and wild-origin females, respectively. There appeared to be a stronger trade-off between egg size and fecundity in hatchery- than wild-origin females (Fig. 2). However, the slope of this relationship did not differ significantly between the two groups (ANCOVA, heterogeneity of slopes, $F_{[1,46]} = 3.38$, $p = 0.07$, $\eta^2 = 0.066$, 95% CI (–0.008, 0.00)).

Egg lipid content

We found no significant interaction between the effects of female FL and origin on egg total lipid content (ANCOVA, heterogeneity of slopes, $F_{[1,46]} = 0.027$, $p = 0.87$, $\eta^2 = 5.91 \times 10^{-4}$, 95% CI (–0.13, 0.16)), and following removal of the interaction term, female FL did not significantly influence the percentage of egg total lipids (ANCOVA, covariate effect, $F_{[1,47]} = 0.33$, $p = 0.57$, $\eta^2 = 6.20 \times 10^{-3}$, 95% CI (–0.49, 0.085)). Mean egg lipid concentrations were 28.6% and 29.0% for the hatchery- and wild-origin females, respectively, and this difference was not statistically significant (ANOVA, $F_{[1,48]} = 1.42$, $p = 0.24$, $\eta^2 = 2.87 \times 10^{-2}$, 95% CI (–1.18, 0.30); Fig. 3A). Repeating this analysis using female condition or egg size as the covariate did not change the outcome (all $p > 0.15$).

There was no significant interaction between female FL and origin on egg neutral lipid content (ANCOVA, heterogeneity of slopes, $F_{[1,46]} = 0.13$, $p = 0.72$, $\eta^2 = 2.87 \times 10^{-3}$, 95% CI (–0.002, 0.003)), and following removal of the interaction term, there was no significant relationship between egg neutral lipid content and female FL (ANCOVA, covariate effect, $F_{[1,47]} = 1.45$, $p = 0.23$, $\eta^2 = 0.045$, 95% CI (0.000, 0.002)), but wild-origin females produced eggs with a higher proportion of lipids in the neutral fraction (ANOVA, $F_{[1,48]} = 4.15$, $p = 0.048$; Fig. 3B). Repeating this analysis using female condition or egg size as the covariate did not change the outcome (origin effect $p < 0.05$).

Fig. 1. Relationship between female fork length (mm) and (A) gonad mass (g) and (B) egg size (dry mass, mg) in hatchery- (shaded circles) and wild-origin (open circles) Chinook salmon (*Oncorhynchus tshawytscha*) spawning in the Credit River, Lake Ontario.

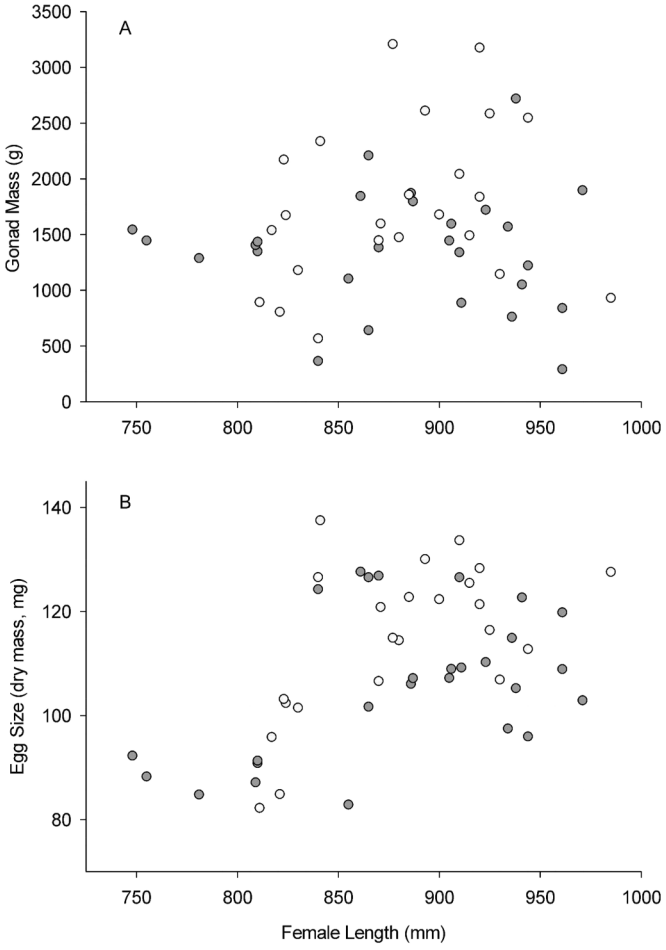

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Fig. 2. Relationship between fecundity (egg number) and egg size (dry mass, mg) in hatchery- (shaded circles) and wild-origin (open circles) Chinook salmon (*Oncorhynchus tshawytscha*) spawning in the Credit River, Lake Ontario.

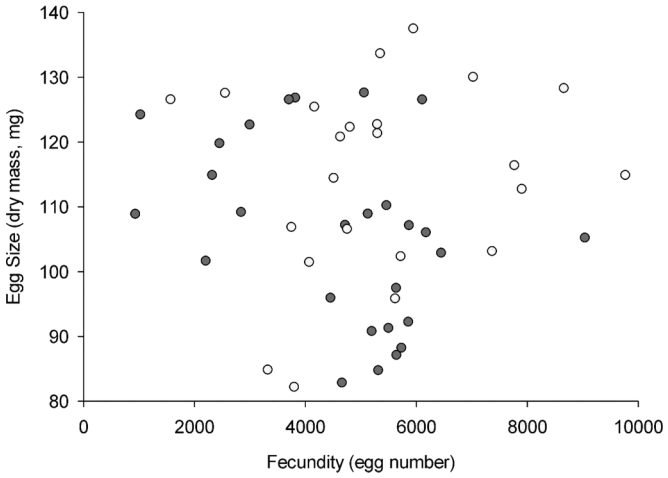
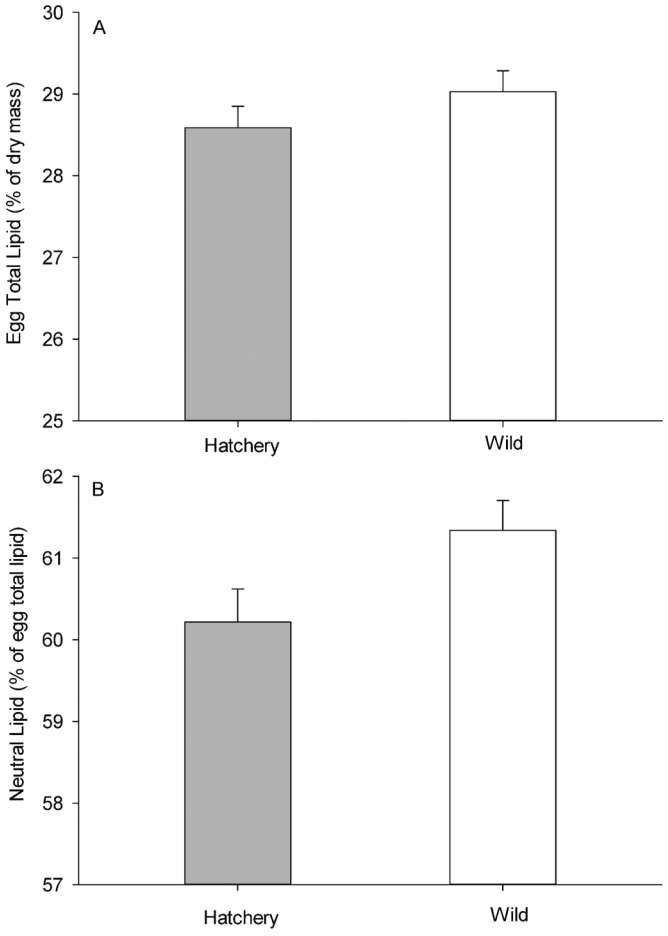


Fig. 3. Mean (+ standard error) (A) egg total lipid (% of egg dry mass) and (B) neutral lipid (% of egg total lipid) in hatchery- and wild-origin Lake Ontario Chinook salmon (*Oncorhynchus tshawytscha*).



Egg FA composition: individual FAs

Owing to contamination during FA methyl ester extraction, only nine hatchery-origin females were included in all polar lipid FA analysis. Overall FA profiles differed little between the two groups of salmon in both the neutral and polar lipid fractions (Table 2). The neutral lipids were rich in monounsaturated fatty acids, especially 16:1(*n*-7) and OA, compared with the polar lipids, and the reverse was true for saturated fatty acids. Of particular note was the high percentage of 18:0 in the polar lipids. Although totals of both (*n*-3) and (*n*-6) PUFA were similar in the neutral and polar lipids, the neutral lipids were richer in both (*n*-3) and (*n*-6) C18 FAs, while the polar lipids were richer in DHA and AA. EPA percentages were about 1% higher in the polar lipids than in the neutral lipids. The ratios of both total (*n*-3)/(*n*-6) and of DHA/EPA and the sums of AA + EPA were higher in the polar lipids (Table 2).

Relationships between relative abundances of individual FAs and maternal and egg traits were generally weak and not statistically significant, as were differences in individual FAs between hatchery- and wild-origin fish. However, there were a few exceptions in the neutral fraction. Hatchery-origin females allocated slightly more AA to their egg neutral lipids than wild females (ANCOVA, $F_{[1,17]} = 4.891$, $p = 0.041$). Relative abundances of OA in the neutral lipids increased with egg size in both groups of fish but did not differ between them. In contrast, relative abundances of 22:5(*n*-3) in neutral lipids did not vary with egg size but did differ between groups (ANCOVA, $F_{[1,17]} = 6.893$, $p = 0.018$). Wild

Table 2. Mean percentages (± standard deviation) of individual fatty acids, fatty acid families, and ratios in neutral and polar egg lipids of hatchery- and wild-origin Lake Ontario Chinook salmon (*Oncorhynchus tshawytscha*).

	Neutral lipid		Polar lipid	
Fatty acid	Wild (*n* = 10)	Hatchery (*n* = 10)	Wild (*n* = 10)	Hatchery (*n* = 9)
Saturated				
14:0	2.9±0.4	2.9±0.2	0.9±0.2	0.9±0.2
15:0	0.4±0.1	0.4±0.03	0.4±0.1	0.4±0073
16:0	8.5±0.6	8.9±0.5	13.5±1.3	14.1±1.4
18:0	2.8±0.3	2.5±0.4	10.4±1.0	9.5±1.1
Monounsaturated				
16:1(*n*-9)	1.3±0.2	1.2±0.08	0.6±0.09	0.6±0.08
16:1(*n*-7)	5.9±0.5	5.7±0.4	1.3±0.4	1.4±0.4
17:1	0.8±0.1	0.7±0.1	0.6±0.06	0.6±0.05
18:1(*n*-9)	15.5±2.3	15.4±1.7	9.8±0.9	10.0±0.8
18:1(*n*-7)	3.3±0.2	3.3±0.2	3.0±0.3	3.1±0.2
20:1(*n*-9)	0.7±0.1	0.7±0.1	1.1±0.1	1.0±0.1
20:1(*n*-7)	0.2±0.06	0.2±0.03	0.1±0.04	0.1±0.04
Polyunsaturated *n*-3				
18:3(*n*-3)	5.6±0.6	6.0±0.4	1.3±0.4	1.5±0.4
18:4(*n*-3)	2.0±0.3	1.9±0.3	0.5±0.1	0.4±0.1
20:3(*n*-3)	1.4±0.2	1.4±0.09	1.0±0.1	1.1±0.09
20:4(*n*-3)	4.8±0.5	4.8±0.4	1.8±0.3	2.0±0.2
20:5(*n*-3), EPA	9.3±0.8	9.3±0.3	10.7±0.6	10.5±0.4
22:5(*n*-3)	6.1±0.7	5.5±0.4	6.2±0.4	5.9±0.5
22:6(*n*-3), DHA	12.6±1.2	13.3±1.1	22.8±1.5	22.4±1.4
Polyunsaturated *n*-6				
18:2(*n*-6)	5.5±0.4	5.6±0.3	1.5±0.4	1.6±0.4
18:3(*n*-6)	0.6±0.4	0.4±0.05	0.2±0.03	0.2±0.02
20:2(*n*-6)	0.7±0.1	0.7±0.06	0.8±0.1	0.8±0.1
20:3(*n*-6)	0.8±0.1	0.7±0.08	0.5±0.1	0.5±0.03
20:4(*n*-6), AA	6.3±0.3	6.6±0.4	9.1±0.5	9.3±0.3
22:4(*n*-6)	0.6±0.1	0.6±0.04	0.4±0.07	0.5±0.2
22:5(*n*-6)	1.2±0.3	1.2±0.1	1.4±0.2	1.3±0.2
Sum SFA	14.6±0.7	14.7±0.7	25.2±1.5	24.9±1.4
Sum MUFA	27.8±2.2	27.0±1.7	16.5±1.4	16.9±1.2
Sum (*n*-3) PUFA	41.9±1.6	42.2±1.5	44.2±0.9	43.8±1.1
Sum (*n*-6) PUFA	15.7±0.7	16.1±0.9	14.0±0.9	14.3±0.7
AA + EPA	15.6±2.1	15.9±1.9	19.8±1.1	19.7±0.04
Sum (*n*-3)/sum (*n*-6)	2.7	2.6	3.2	3.1
EPA/AA	1.5	1.4	1.2	1.1
DHA/EPA	1.4	1.4	2.1	2.1

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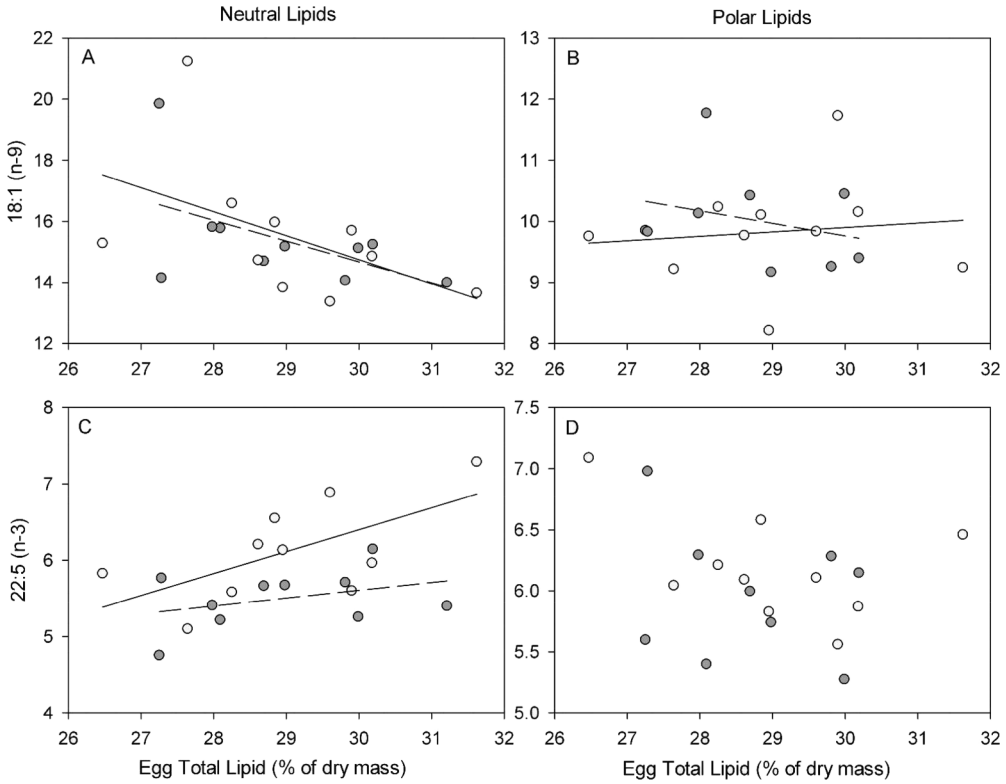
Fig. 4. Relationship between egg total lipid (% of dry mass) and proportion of fatty acids 18:1(*n*-9) (A and B) and 22:5(*n*-3) (C and D) in polar and neutral egg lipid fractions of hatchery- (shaded circles, dashed line) and wild-origin (open circles, solid line) Lake Ontario Chinook salmon (*Oncorhynchus tshawytscha*). Only significant ($p = 0.05$) relationships are shown with a dashed or solid regression lines.



females allocated a slightly higher percentage of 22:5(*n*-3) to their egg neutral lipids than hatchery-reared females (Table 2). Relative abundances of OA decreased (covariate effect, $F_{[1,17]} = 5.918$, $p = 0.0026$; Fig. 4A), and relative abundances of 22:5(*n*-3) increased (covariate effect, $F_{[1,17]} = 6.322$, $p = 0.022$; Fig. 4C) in the neutral fraction with increasing egg total lipid content, but significant differences between groups were only evident for the latter FA ($F_{[1,17]} = 8.209$, $p = 0.011$; Fig. 4C). Percentages of 22:5(*n*-3) were slightly higher in neutral lipids of eggs from the wild-origin females than in those from the hatchery-reared females (Fig. 4C).

Egg FA composition: principal components analysis

For FAs of the neutral fraction of egg lipids, most of the variation among females was due to variation in relative abundances of OA, 22:5(*n*-3), DHA, and AA. The first two PCs accounted for 58% and 22% of the total observed variance (Table 3), respectively, and separation of hatchery- and wild-origin females was negligible along both axes (Fig. 5A). Among the maternal and egg traits examined as potential covariates, only egg total lipid content accounted for significant variation in either PC1 or PC2, and it was used as the primary covariate in subsequent analyses.

In the analysis of neutral lipid FA PC1, we observed no significant interaction between egg total lipid content and female origin (ANCOVA, heterogeneity of slopes, $F_{[1,16]} = 0.05$, $p = 0.82$, $\eta^2 = 2.53 \times 10^{-3}$, 95% CI (–0.762, 0.612)). Following removal of the interaction term, we found that PC1 was positively related to egg total lipid content (ANCOVA, covariate effect, $F_{[1,17]} = 5.44$, $p = 0.032$) but did not differ between our two groups of females (ANCOVA, $F_{[1,16]} = 0.01$, $p = 0.92$, $\eta^2 = 4.71 \times 10^{-4}$, 95% CI (–0.826, 0.911)). For PC2, no interaction was observed between egg total lipid content and female origin (ANCOVA, heterogeneity of slopes, $F_{[1,16]} = 0.28$, $p = 0.61$, $\eta^2 = 0.014$, 95% CI (–0.862, 0.519)), and following removal of the interaction term, there was no significant effect of either egg total lipid (ANCOVA, covariate effect, $F_{[1,17]} = 2.37$, $p = 0.14$, $\eta^2 = 0.11$, 95% CI (–0.580, 0.091)) or female origin (ANCOVA, $F_{[1,17]} = 2.67$, $p = 0.12$, $\eta^2 = 0.12$, 95% CI (–1.559, 0.198)) on PC2. Similarly, we found no effect of female origin on either PC1 or PC2 when other covariates were used in the ANCOVA model.

For FAs in the polar fraction of egg lipids, most of the variation among females was due to variation in relative abundances of DHA, 18:0, 16:0, and OA. The first two PCs accounted for 52% and 27% of the total observed variance (Table 3), respectively, and there was no clear separation of hatchery- and wild-origin females on either axis (Fig. 5B). We analyzed the polar lipid PCs following a similar ANCOVA model as for neutral lipid, starting with egg total lipid content as the covariate.

In the analysis of polar lipid FA PC1, we observed no significant interaction between egg total lipid content and female origin (ANCOVA, heterogeneity of slopes, $F_{[1,15]} = 1.12$, $p = 0.31$, $\eta^2 = 0.063$, 95% CI (–1.291, 0.435)). Following removal of the interaction term, we found that PC1 was not related to egg total lipid content (ANCOVA, covariate effect, $F_{[1,16]} = 0.09$, $p = 0.76$, $\eta^2 = 5.97 \times 10^{-3}$, 95% CI (–0.474, 0.351)) and did not differ between hatchery- and wild-origin females (ANCOVA, $F_{[1,16]} = 0.45$, $p = 0.51$, $\eta^2 = 0.027$, 95% CI (–0.698, 1.345)). For PC2, no interaction was observed between egg total lipid content and female origin (ANCOVA, heterogeneity of slopes, $F_{[1,15]} = 0.010$, $p = 0.94$, $\eta^2 = 5.16 \times 10^{-4}$, 95% CI (–0.789, 0.857)), and following removal of the interaction term, there was no significant effect of either egg total lipid (ANCOVA, covariate effect, $F_{[1,16]} = 1.05$, $p = 0.32$, $\eta^2 = 0.049$, 95% CI (–0.557, 0.203)) or female origin (ANCOVA, $F_{[1,16]} = 3.02$, $p = 0.10$, $\eta^2 = 0.15$, 95% CI (–1.708, 0.174)). Similarly, we found no effect of female origin on either PC1 or PC2 when other covariates were used in the ANCOVA model.

Stable isotopes

C:N ratios in lipid-extracted muscle tissue were 3.2 ± 0.1 for all samples ($n = 28$), indicating low lipid levels. Levels of $\delta^{13}C$ did not

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Table 3. Factor loadings of the first two principal components of 25 major fatty acids in the neutral ($n = 10$) and polar ($n = 9$) lipid fractions.

	Neutral lipid		Polar lipid	
Fatty acid	PC1	PC2	PC1	PC2
Saturated				
14:0	0.208	0.123	0.175	–0.023
15:0	0.027	0.006	0.041	–0.021
16:0	–0.378*	–0.180	**–0.565***	**–1.148***
18:0	0.041	0.083	**–0.791***	**0.571***
Monounsaturated				
16:1(*n*-9)	0.019	0.078	0.051	0.009
16:1(*n*-7)	–0.025	0.287	0.360*	–0.037
17:1	0.052	0.075	–0.009	0.018
18:1(*n*-9), OA	**–1.945***	**0.088**	**0.702***	**–0.264**
18:1(*n*-7)	0.078	0.067	0.088	0.056
20:1(*n*-9)	0.069	0.024	0.003	0.083
20:1(*n*-7)	0.000	0.010	0.010	0.023
Polyunsaturated *n*-3				
18:3(*n*-3)	0.324*	0.080	0.403*	–0.048
18:4(*n*-3)	0.197	0.143	0.103	0.030
20:3(*n*-3)	0.104	0.029	0.057	0.017
20:4(*n*-3)	0.331	0.195	0.084	0.166
20:5(*n*-3), EPA	–0.221	–0.099	0.255	–0.030
22:5(*n*-3)	**0.394***	**0.148**	–0.108	0.351*
22:6(*n*-3), DHA	**0.092**	**–1.139***	**–1.310***	**–0.041**
Polyunsaturated *n*-6				
18:2(*n*-6)	0.217	0.139	0.337*	–0.036
18:3(*n*-6)	–0.023	0.121	0.021	0.011
20:2(*n*-6)	0.072	0.025	0.030	0.054
20:3(*n*-6)	0.044	0.052	0.026	0.037
20:4(*n*-6), AA	**0.172**	**–0.318***	0.018	0.080
22:4(*n*-6)	0.172	0.000	0.028	0.056
22:5(*n*-6)	0.089	–0.057	–0.011	0.086
Eigenvalues	4.558	1.698	3.703	1.906
Percentage of the variance	58.490	21.790	51.801	26.662
Cumulative variance	58.490	80.279	51.801	78.463

Note: Values with factor loadings greater than 0.3 are indicated with an asterisk, and those fatty acids that explain the majority of the variance between groups are in bold.

differ based on female origin (means ± SE: wild-origin: –22.0 ± –0.1; hatchery-origin: –21.9 ± 0.1; $t = -0.83$, df = 27, $p = 0.42$). However, levels of $\delta^{15}N$ were significantly higher in hatchery-origin females (15.7 ± 0.05) compared with wild-origin females (15.5 ± –0.1; $t = -2.95$, df = 27, $p = 0.007$).

Discussion

The present study is the first, to our knowledge, to analyze variation in early life-history traits in the Lake Ontario Chinook salmon population and provides a comprehensive analysis of differences in egg quality among hatchery- and wild-origin salmon. We found that certain components of the female's reproductive biology did differ between hatchery- and wild-origin females, while other important aspects of egg quality did not. More specifically, hatchery-origin females were found to allocate significantly less energy into egg and gonadal development, but produced eggs of similar total lipid concentration and FA composition as their wild counterparts. The results from the present study suggests that the differing environmental conditions and associated selection pressures of captive rearing during early life can alter certain life-history traits later in development, namely gonad mass and egg size.

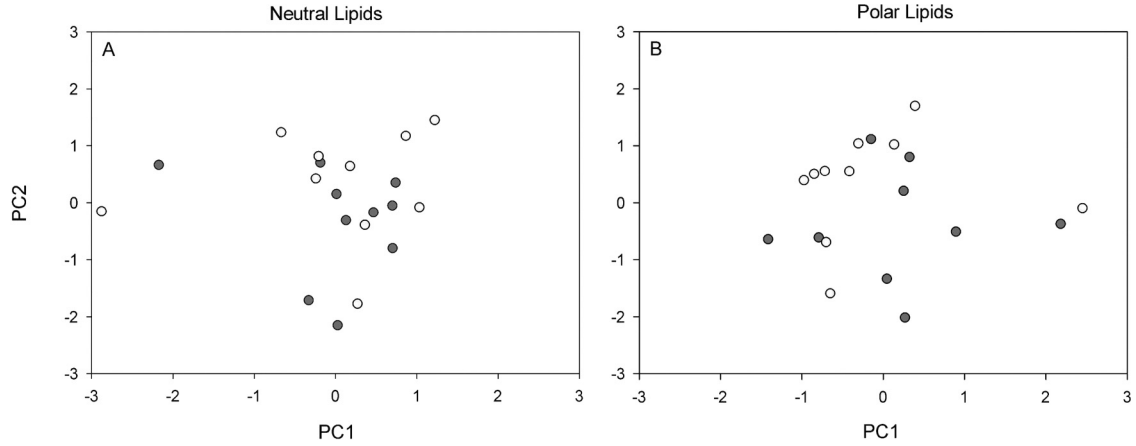
Bowlby et al. (2004) previously recorded that wild-origin Lake Ontario Chinook salmon are significantly longer (~49 mm longer FL) than hatchery-origin individuals. Contrary to this finding, however, we found no significant differences in either FL or somatic mass between hatchery- and wild-origin females, although hatchery-origin females were more variable in both of these traits. This greater variability in body size could be due to a number of factors, which ultimately reflects the female's ability to adjust to her new environmental conditions. Previous studies suggest that hatchery-reared fish released into natural environments consume less food and fewer prey types and experience depressed growth and survival rates compared with wild-origin fish (Reisenbichler and Rubin 1977; reviewed by Olla et al. 1998; Ireland et al. 2002). In brown trout, for example, hatchery-reared fish were initially observed to consume fewer and different prey types compared with wild fish, but these differences disappeared after a few weeks in the wild (Johnsen and Ugedal 1986, 1989, 1990). Although the female's foraging ability may improve with experience, the female's ability to adjust to her new environment and acquire novel prey items may result in the more variable growth rates observed here among hatchery-origin females.

Differences in prey types and foraging ability may not only result in variation in growth rates between our two groups of salmon, but may also play a role in their gonadal development. We found that hatchery-origin Lake Ontario Chinook salmon produced gonads that were significantly smaller compared with their wild counterparts. Gonad mass has previously been found to increase with adult body size in other salmonids (Hendry and Berg 1999; Kinnison et al. 2001; Campbell et al. 2006) and is also highly dependent on feeding rates and quality of food sources (Sasayama and Takahashi 1972; Cerdá et al. 1994; reviewed in Izquierdo et al. 2001). Gonad mass was not strongly related to female size in Lake Ontario Chinook salmon.

The occurrence of small egg sizes among hatchery-reared females has been previously studied in numerous teleost fishes (Jonsson et al. 1996; Einum and Fleming 1999; Heath et al. 2003). Although egg size has been found to be under genetic control in fishes, including salmonids (e.g., Heath et al. 2003; Gall and Neira 2004), captive environments can alter this trait, thereby negatively impacting offspring viability when stocked into the wild. A previous study on a population of farmed Chinook salmon, for example, suggested that the soft selection pressure of captive environments enables fecundity selection to drive the evolution of significantly smaller eggs (Heath et al. 2003). Here, hatchery-reared females appeared to make greater trade-offs between egg size and egg number compared with their wild counterparts; however, this relationship was not statistically significant. Previous studies also suggest that maternal investment into egg size is limited not only by the amount of maternal reserves but also by her condition, phenotype, and environment (Mousseau and Fox 1998; Sakai and Harada 2001; Filin 2015). As such, low-condition females are often unable to allocate their resources as efficiently during reproduction, resulting in the production of many smaller-sized eggs (e.g., Sakai and Harada 2001; Filin 2015). A similar trend may drive the relationship observed here, resulting in significantly smaller eggs among hatchery fish and a greater trade-off between egg size and egg number. Alternatively, previous studies suggest that mothers may prepare their offspring for similar environmental conditions to those they experienced as juveniles (Jonsson et al. 1996; Taborsky 2006). In the Atlantic salmon (*Salmo salar*), for example, hatchery females that experienced rapid growth rates and low mortalities as juveniles were found to produce smaller eggs than wild conspecifics of corresponding size (Jonsson et al. 1996). A similar mechanism may influence the differences in egg sizes observed here among hatchery- and wild-origin Lake Ontario Chinook salmon.

While there were important differences between wild- and hatchery-reared females in terms of gonad size, egg size, and egg neutral lipid content, the FA profiles of the eggs were relatively similar between the two groups. The FA profiles of the polar lipids were very similar to those of two populations of Pacific Chinook salmon (Ashton et al. 1993), especially for 16:0, 18:0, and 22:6(*n*-3).

Fig. 5. Scatterplots of the first two principal components (PC1 and PC2, see text for details) from fatty acid profiles of (A) neutral egg lipids and (B) polar egg lipids in hatchery- (shaded circles) and wild-origin (open circles) Lake Ontario Chinook salmon (*Oncorhynchus tshawytscha*).



The major difference, as expected, was the higher relative abundance of (*n*-6) PUFA in the Lake Ontario fish, reflecting their freshwater diet. There is evidence of strong selection pressure to maintain egg polar lipid DHA percentages within narrow ranges among individuals within species (Wiegand 1996), and our results are consistent with this hypothesis. Egg neutral lipids are more highly influenced by maternal diet than are polar lipids (Wiegand 1996). Accordingly, the few differences we observed in FA composition among females, and between groups, were in the neutral fraction. The similarity in the neutral lipid profiles of the two groups suggests that the diets were quite similar, at least in terms of FA composition. Unlike some other freshwater species (Wiegand et al. 2014), there were few maternal somatic influences on egg FA profiles or influences of egg parameters such as size or lipid content. This suggests that there were few, if any, dietary differences among females of different size in this study.

Carbon and nitrogen stable isotopes also suggested limited differences in the diet between hatchery- and wild-origin adult females. Based on recent summer collections of stomach contents, Lake Ontario Chinook salmon fed almost 100% on alewife (Tim Johnson and Brian Weidel, personal communication), consistent with longer-term trends in their diet (Brandt 1986; Rand and Stewart 1998; Lantry 2001). The Chinook salmon $\delta^{13}C$ and $\delta^{15}N$ values found here are consistent with a high alewife diet based on the stable isotope values reported for Lake Ontario forage fish (Rush et al. 2012). Slightly lower $\delta^{15}N$ values in the wild-origin females may reflect feeding on smaller alewife and (or) on lower trophic-level prey during the winter. Hatchery-origin juvenile (<90 cm) Chinook salmon in Lake Ontario tributaries have been reported to consume more invertebrates than wild juveniles (Johnson 2008); whether this continues for the larger individuals is unknown. As well, the lack of winter-specific data on the diet of these salmon also limits our ability to explain the $\delta^{15}N$ differences. Regardless, the difference in $\delta^{15}N$ is very small, less than 1/20 of a trophic level if we assume a standard diet tissue discrimination factor of 3.4‰ for freshwater ecosystems (Post 2002). This suggests only very minor differences in diets between hatchery- and wild-origin adult Chinook salmon females.

Despite their implications in supplementing socioeconomically and ecologically important fish populations, captive-reared progeny experience substantial differences in growth and survival in the hatchery setting compared with their wild counterparts that may negatively impact their reproductive success later in life. A number of studies suggest that maternal investment into egg quality traits is largely environmentally driven (Einum and Fleming 1999; Johnston and Leggett 2002) and highly dependent on the condition the mother experiences as a juvenile (Jonsson et al. 1996). For example, previous studies suggest that females that grow rapidly as juveniles are more likely to produce smaller eggs as adults (Jonsson et al. 1996; Taborsky 2006; Burton et al. 2013), and exposure to predators in juvenile stages can induce the production of larger eggs as an adult in some fish species (Segers and Taborsky 2012). The absence of natural selection pressures and rapid growth experienced by hatchery-reared fish likely serve as the main factors driving the differences between hatchery- and wild-origin salmon. Although the purpose of a hatchery setting is to create a suitable environment that yields high offspring survival and rapid growth rates, it is likely that hatchery and wild fish might not ever achieve a similar maternal investment later in life, unless fry are stocked out earlier in development or other selection pressures are introduced to the hatchery environment.

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References

Ashton, H.J., Farkvam, D.O., and March, B.E. 1993. Fatty acid composition of lipids in the eggs and alevins from wild and cultured chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish Aquat. Sci. **50**(3): 648–655. doi:10.1139/f93-074.

Bell, M.V., and Dick, J.R. 1991. Molecular species composition of the major diacyl glycerophospholipids from muscle, liver, retina, and brain and cod (*Gadus morhua*). Lipids, **26**: 565–573. doi:10.1007/BF02536419.

Bell, M.V., Batty, R.S., Dick, J.R., Fretwell, K., Navarro, J.C., and Sargent, J.R. 1995. Dietary deficiency of docosahexaenoic acid impairs vision at low light intensities in juvenile herring (*Clupea harengus*) L. Lipids, **30**: 443–449. doi:10.1007/BF02536303. PMID:7637565.

Bessonart, M., Izquierdo, M.S., Salhi, M., Hernandez-Cruz, C.M., Gonzalez, M.M., and Fernandez-Palacios, H. 1999. Effect of dietary arachidonic acid levels on growth and survival of gilthead sea bream (*Sparus aurata*) L. larvae. Aquaculture, **179**: 265–275. doi:10.1016/S0044-8486(99)00164-7.

Bowlby, J.N., Gross, M.R., and Patterson, W.P. 2004. The biology and interactions of hatchery and wild Chinook salmon in Lake Ontario. *In* Annual report of

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the Lake Ontario Management Unit. Great Lakes Fishery Commission, Niagara Falls, Ont.

Brandt, S.B. 1986. Food of trout and salmon in Lake Ontario. J. Gt. Lakes Res. **12**: 200–205. doi:10.1016/S0380-1330(86)71719-X.

Brooks, S., Tyler, C.R., and Sumpter, J.P. 1997. Egg quality: what makes a good egg. Rev. Fish. Biol. Fish. **7**: 387–416. doi:10.1023/A:1018400130692.

Burton, T., McKelvey, S., Stewart, D.C., Armstrong, J.D., and Metcalfe, N.B. 2013. Offspring investment in wild Atlantic salmon (*Salmo salar*): relationships with smolt age and spawning condition. Ecol. Freshw. Fish. **22**: 317–321. doi:10.1111/eff.12019.

Campbell, B., Beckman, B.R., Fairgrieve, W.T., Dickey, J.T., and Swanson, P. 2006. Reproductive investment and growth history in female coho salmon. Trans. Am. Fish. Soc. **135**: 164–173. doi:10.1577/T05-115.1.

Cerdá, J., Camillo, M., Zanuy, S., and Ramos, J. 1994. Effect of food ration on estrogen and vitellogenin plasma levels, fecundity and larval survival in captive sea bass, *Dicentrarchus labrax*: preliminary observations. Aquat. Living. Resour. **7**: 255–266. doi:10.1051/alr:1994028.

Connerton, M.J., Balk, C.J., Prindle, S.E., Lantry, J.R., Daniels, M.E., Bowlby, J.N., Bronte, C.R., and Holey, M.E. 2011. Mass marking of Chinook salmon in Lake Ontario. In Bureau of Fisheries Lake Ontario Annual Report. New York State Department of Environmental Conservation, Albany, New York.

Crawford, S.S. 2001. Salmonine introductions to the Laurentian Great Lakes: an historical review and evaluation of ecological effects. Can. Spec. Publ. Fish. Aquat. Sci. No. 132.

Dennis, C.A., MacNeil, M.A., Rosati, J.Y., Pitcher, T.E., and Fisk, A.T. 2010. Diet discrimination factors are inversely related to $\delta^{15}N$ and $\delta^{13}C$ values for food for fish under controlled conditions. Rap. Commun. Mass Spectrom. **24**: 3515–3520. doi:10.1002/rcm.4807.

Einum, S., and Fleming, I.A. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. Proc. R. Soc. B Biol. Sci. **266**: 2095–2100. doi:10.1098/rspb.1999.0893.

Einum, S., and Fleming, I.A. 2000. Highly fecund mothers sacrifice offspring survival to maximize fitness. Nature, **405**: 565–567. doi:10.1038/35014600. PMID:10850714.

Filin, I. 2015. The relationship between maternal phenotype and offspring size, explained by overhead material costs of reproduction. J. Theor. Biol. **364**: 168–178. doi:10.1016/j.jtbi.2014.09.007. PMID:25219621.

Fleming, I.A., Jonsson, B., and Gross, M.R. 1994. Phenotypic divergence of sea-ranched, farmed, and wild salmon. Can. J. Fish. Aquat. Sci. **51**(12): 2808–2824. doi:10.1139/f94-280.

Folch, J., Lees, M., and Stanley, G.H. 1957. A simple method for the isolation and purification of total lipids from animal tissue. J. Biol. Chem. **226**: 497–509. PMID:13428781.

Fraser, D.J. 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. Evol. Appl. **1**: 535–586. PMID:25567798.

Gall, G.A.E., and Neira, R. 2004. Genetic analysis of female reproduction traits of farmed coho salmon (*Oncorhynchus kisutch*). Aquaculture, **234**: 143–154. doi:10.1016/j.aquaculture.2004.01.029.

Heath, D.D., Heath, J.W., Bryden, C.A., Johnson, R.M., and Fox, C.W. 2003. Rapid evolution of egg size in captive salmon. Science, **299**: 1738–1740. doi:10.1126/science.1079707. PMID:12637746.

Hendry, A.P., and Berg, O.K. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. Can. J. Zool. **77**(11): 1663–1675. doi:10.1139/z99-158.

Ireland, S.C., Siple, J.T., Beamesderfer, R.C.P., Paragamian, V.L., and Wakkinen, V.D. 2002. Success of hatchery-reared juvenile white sturgeon following release in the Kootenai River, Idaho. J. Appl. Ichthyol. **18**: 642–650. doi:10.1046/j.1439-0426.2002.00364.x.

Izquierdo, M.S., Fernández-Palacios, H., and Tacon, A.G.J. 2001. Effect of broodstock nutrition on reproductive performance in fish. Aquaculture, **197**: 25–42. doi:10.1016/S0044-8486(01)00581-6.

Johnsen, B.O., and Ugedal, O. 1986. Feeding by hatchery- reared and wild brown trout *Salmo trutta* L. in a Norweigian stream. Aquacult. Fish. Manage. **17**: 281–287. doi:10.1111/j.1365-2109.1986.tb00115.x.

Johnsen, B.O., and Ugedal, O. 1989. Feeding by hatchery-reared brown trout, *Salmo trutta* L. released in lakes. Aquacult. Fish. Manage. **20**: 97–104. doi:10.1111/j.1365-2109.1989.tb00445.x.

Johnsen, B.O., and Ugedal, O. 1990. Feeding by hatchery- and pond-reared brown trout *Salmo trutta* L. fingerlings released in a lake and in a small stream. Aquacult. Fish. Manage. **21**: 253–258. doi:10.1111/j.1365-2109.1990.tb00462.x.

Johnson, J.H. 2008. Diet composition and feeding periodicity of wild and hatchery subyearling Chinook salmon in Lake Ontario. J. Gt. Lakes. Res. **34**: 590–598. doi:10.1016/S0380-1330(08)71604-6.

Johnson, R.B. 2009. Lipid deposition in oocytes of teleost fish during secondary oocyte growth. Rev. Fish. Sci. **17**: 78–89. doi:10.1080/10641260802590004.

Johnston, T.A., and Leggett, W.C. 2002. Maternal and environmental gradients in the egg size of an iteroparous fish. Ecology, **83**(7): 1777–1791. doi:10.2307/3071764.

Jonsson, N., Jonsson, B., and Fleming, I.A. 1996. Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon? Funct. Ecol. **10**: 89–96. doi:10.2307/2390266.

Juaneda, P., and Rocquelin, G. 1985. Rapid and convenient separation of phospholipids and nonphosphorus lipids from rat heart. Lipids, **20**: 40–41. doi:10.1007/BF02534360. PMID:2982073.

Kaufman, S.D., Johnston, T.A., Leggett, W.C., Moles, M.D., Casselman, J.M., and Schulte-Hostedde, A.I. 2007. Relationships between body condition indices and proximate composition in adult walleyes. Trans. Am. Fish. Soc. **136**: 1566–1576. doi:10.1577/T06-262.1.

Kinnison, M.T., Unwin, M.J., Hendry, A.P., and Quinn, T.P. 2001. Migratory costs and evolution of egg size and number in introduced and indigenous salmon populations. Evolution, **55**: 1656–1667. doi:10.1111/j.0014-3820.2001.tb00685.x. PMID:11580025.

Kocik, J.F., and Jones, M.L. 1999. Pacific salmonines in the Great Lakes basin. *In* The Great Lakes Fisheries Policy and Management: a binational perspective. Michigan State University Press, East Lansing, Mich.

Lantry, J.R. 2001. Spatial and temporal dynamics of predation by Lake Ontario trout and salmon. Master's thesis. College of Environmental and Forestry, State University of New York, Syracuse.

McDermid, J.L., Sloan, W.N., Wilson, C.C., and Shuter, B.J. 2010. Early life history variation among hatchery- and wild-origin lake trout reared in a hatchery environment. Trans. Am. Fish. Soc. **139**: 21–28. doi:10.1577/T08-130.1.

McMeans, B.C., Svavarsson, J., Dennard, S., and Fisk, A.T. 2010. Diet and resource use among Greenland sharks (*Somniosus microcephalus*) and teleosts sampled in Icelandic waters, using $\delta^{13}C$, $\delta^{15}N$, and mercury. Can. J. Fish. Aquat. Sci. **67**(9): 1428–1438. doi:10.1139/F10-072.

Miller, L.M., Close, T., and Kapuscinski, A.R. 2004. Lower fitness of hatchery and hybrid rainbow trout compared to naturalized populations in Lake Superior tributaries. Mol. Ecol. **13**: 3379–3388. doi:10.1111/j.1365-294X.2004.02347.x. PMID:15487997.

Mousseau, T.A., and Fox, C.W. 1998. The adaptive significance of maternal effects. Trends. Ecol. Evol. **13**(10): 403–407. doi:10.1016/S0169-5347(98)01472-4.

Neff, B.D., Garner, S.R., and Pitcher, T.E. 2011. Conservation and enhancement of wild fish populations: preserving genetic quality versus genetic diversity. Can. J. Fish. Aquat. Sci. **68**(6): 1139–1154. doi:10.1139/f2011-029.

Olla, B., Davis, M.W., and Ryer, C.H. 1998. Understanding how the hatchery environment represses or promotes the development of behavioral survival skills. Bull. Mar. Sci. **62**: 531–550.

OMNRF. 2011. Lake Ontario Fish Communities and Fisheries: 2010 annual report of the Lake Ontario Management Unit. Ontario Ministry of Natural Resources and Forestry, Picton, Ont.

Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. **18**: 293–320. doi:10.1146/annurev.es.18.110187.001453.

Pickova, J., Dutta, P.C., Larson, P.-O., and Kiessling, A. 1997. Early embryonic cleavage pattern, hatching success, and egg-lipid fatty acid composition: comparison between two cod (*Gadus morhua*) stocks. Can. J. Fish. Aquat. Sci. **54**(10): 2410–2416. doi:10.1139/f97-148.

Pitcher, T.E., and Neff, B.D. 2007. Genetic quality and offspring performance in Chinook salmon: implications for supportive breeding. Conserv. Genet. **8**: 607–616. doi:10.1007/s10592-006-9204-z.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology, **83**: 703–718. doi:10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2.

Rand, P.S., and Stewart, D.J. 1998. Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario. Can. J. Fish. Aquat. Sci. **55**(2): 318–327. doi:10.1139/f97-254.

Reisenbichler, R.R., and Rubin, S. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. J. Fish. Res. Board. Can. **34**: 123–128. doi:10.1139/f77-015.

Reisenbichler, R.R., and Rubin, S.P. 1999. Genetic changes from artificial propagation of Pacific salmon affect the productivity and viability of supplemented populations. ICES J. Mar. Sci. **56**: 459–466. doi:10.1006/jmsc.1999.0455.

Roff, D.A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York.

Rush, S.A., Paterson, G., Johnson, T.B., Drouillard, K.G., Haffner, G.D., Hebert, C.E., Arts, M.T., McGoldrick, D.J., Backus, S.M., Lantry, B.F., Lantry, J.R., Schaner, T., and Fisk, A.T. 2012. Long-term impacts of invasive species on a native top predator in a large lake system. Freshw. Biol. **57**: 2342–2355. doi:10.1111/fwb.12014.

Sakai, S., and Harada, Y. 2001. Why do large mothers produce large offspring? Theory and a test. Am. Nat. **157**: 348–359. PMID:18707295.

Sargent, J.R., Bell, J.G., Bell, M.V., Henderson, R.J., and Tocher, D.R. 1995. Requirement criteria for essential fatty acids. J. Appl. Ichthyol. **11**: 183–198. doi:10.1111/j.1439-0426.1995.tb00018.x.

Sasayama, Y., and Takahashi, H. 1972. Effect of starvation and unilateral astrastion in male goldfish *Carassius auratus*, and a design of bioassay for fish gonadaotropin using straved goldfish. Bull. Fac. Fish. Hokkaido Univ. **22**: 267–283.

Segers, F.H.I.D., and Taborsky, B. 2012. Juvenile exposure to predator cues induces a larger egg size in fish. Proc. R. Soc. B Biol. Sci. **279**: 1241–1248. doi:10.1098/rspb.2011.1290.

Stewart, T., and Schaner, T. 2002. Lake Ontario salmonid introductions, 1970–1999: stocking, fishery and fish community influences. Chapter 12. *In* Annual Report of the Lake Ontario Management Unit, Picton, Ont.

Swain, D.P., and Riddell, B.E. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of Coho

salmon, *Oncorhynchus kisutch*. Can. J. Fish. Aquat. Sci. **47**(3): 566–571. doi:10.1139/f90-065.

Taborsky, B. 2006. Mothers determine offspring size in response to own juvenile growth conditions. Biol. Lett. **2**: 225–228. doi:10.1098/rsbl.2005.0422. PMID: 17148368.

Whitcomb, A.C., Banks, M.A., and O'Mailey, K.G. 2014. Influence of immune-relevant genes on mate choice and reproductive success in wild-spawning hatchery-reared and wild-born coho salmon *Oncorhynchus kisutch*. Can. J. Fish. Aquat. Sci. **71**(7): 1000–1009. doi:10.1139/cjfas-2013-0501.

Wiegand, M.D. 1996. Composition, accumulation and utilization of yolk lipids in teleost fish. Rev. Fish. Biol. Fish. **6**: 259–286. doi:10.1007/BF00122583.

Wiegand, M.D., and Idler, D.R. 1982. Synthesis of lipids by the rainbow trout (*Salmo gairdneri*) ovary *in vitro*. Can. J. Zool. **60**(11): 2683–2693. doi:10.1139/z82-344.

Wiegand, M.D., Johnston, T.A., Martin, J., and Leggett, W.C. 2004. Variation in neutral and polar lipid compositions of ova in ten reproductively isolated populations of walleye (*Sander vitreus*). Can. J. Fish. Aquat. Sci. **61**(1): 110–121. doi:10.1139/f03-146.

Wiegand, M.D., Johnston, T.A., Porteous, L.R., Ballenova, A.J., Casselman, J.M., and Leggett, W.C. 2014. Comparison of ovum lipid provisioning among lake whitefish, walleye and northern pike co-habiting in Bay of Quinte (Lake Ontario, Canada). J. Gt. Lakes Res. **40**: 721–729. doi:10.1016/j.jglr.2014.07.004.

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