Environ Biol Fish (2023) 106:1061–1078
https://doi.org/10.1007/s10641-022-01377-8

Egg size–related traits during the first year of growth and smolting in hatchery and wild juveniles of steelhead trout *Oncorhynchus mykiss*

**Camille A. Leblanc · Carl Schreck ·
Bjarni K. Kristjánsson · Skúli Skúlason ·
David L. G. Noakes**

Received: 4 April 2022 / Accepted: 29 November 2022 / Published online: 13 December 2022

Abstract Within-clutch variation in the size or the amount of yolk in the egg has been widely studied because of its importance for both maternal and offspring fitness. In particular, egg size has been used as a proxy for survival in first-feeding salmonids alevins. We tested the hypothesis that egg size has implications for the phenotypes (development, physiology, and behavior) of juvenile steelhead trout (*Oncorhynchus mykiss*) up to 1 year post fertilization in both hatchery and wild fish. Egg diameter was measured for 38 families; the smallest and largest eggs were selected and reared individually to study embryonic development, and then collectively as "small" and "large" egg groups. The development and growth of individual embryos were followed up to first feeding. We showed that hatchery fish have smaller eggs than wild fish, offspring from small eggs grow better during their first year than those from larger eggs, offspring from large eggs hatch later and at a more advanced stage than those from small eggs, and the degree of smolting and saltwater preference differed between hatchery and wild offspring. By looking at not only mean egg size but also individual mediated–egg size phenotypic traits, we show the significant contribution of egg size in promoting phenotypic variation within a population and its potential for among-population variation.

Keywords Egg size · Body size · Life history · Conditional strategy · Parental investment · Growth

Introduction

Hatchery programs for Pacific salmon and steelhead trout *Oncorhynchus* spp. have been developed around the North Pacific Rim to enhance populations in the wild (e.g., Hill et al. 2006; Williams, 2006; Araki et al. 2008). Evidence suggests that fish from hatcheries have lower fitness than wild fish when they

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David L. G. Noakes Deceased.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10641-022-01377-8.

C. A. Leblanc (✉) · B. K. Kristjánsson · S. Skúlason
Department of Aquaculture and Fish Biology, Hólar University, Hólar Í Hjaltadal, Sauðarkrókur 551, Hólar, Iceland
e-mail: camille@holar.is

C. Schreck
Department Fisheries, Wildlife, and Conservation Sciences, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

S. Skúlason
Icelandic Museum of Natural History, Suðurlandsbraut 24, 108 Reykjavik, Iceland

D. L. G. Noakes
Fisheries and Wildlife Department and Oregon Hatchery Research Center, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

breed in the wild (Berejikian and Ford 2004; Araki et al. 2007; 2008). Araki et al. (2007) showed that captivity reduced subsequent reproductive capabilities by ~ 40% per generation in *Oncorhynchus mykiss* when fish are released to the natural environment. These results indicate that there are important genetic and fitness differences between hatchery and wild fish, and that such heritable differences can arise in only a few generations.

Development of gonads and juvenile salmonid development are strongly influenced by abiotic and biotic factors such as photoperiod, temperature, and growth pattern (e.g. Thorpe 1998; Beckman et al. 2003), all of which can differ greatly between hatchery and natural environment, and may therefore explain the differences between hatchery and wild fish. Despite this, little is known about the mechanisms that trigger such differences and how early in life these differences arise (but see Berejikian and Ford 2004). The nature of the difference in egg size between females may be partly explained by differences in age rather than size in both hatchery and wild fish (in *Salvelinus namaycush* (Johnston 2018) and *Salvelinus alpinus* (Lasne et al. 2018)), but this may vary between species where maternal size rather than age is a better determinant of egg size in *O. mykiss* (Johnston et al. 2016). Hatchery fish commonly have smaller eggs than wild fish (Einum and Fleming 2000), and changes in egg size can occur rapidly with domestication or captivity (Heath et al. 2003; Lasne et al. 2018). Several hypotheses have been proposed to explain why hatchery fish produce smaller eggs. Eggs should be smaller when the environment experienced by juveniles is of high quality such as in a hatchery (Hutchings 1991; Einum and Fleming 1999), i.e., females that experience high growth rate as juveniles typically produce relatively high numbers of small eggs as adults (Jonsson et al. 1996; Lobón-Cerviá et al. 1997; Morita et al. 1999; Fleming et al. 1997; reviewed by Einum et al. 2004). In addition, the relationship between egg size and survival is weaker under hatchery conditions than that in the wild (Heath et al. 2003). In salmonids, egg size is known to influence early life history traits (e.g., Pakkasmaa and Jones 2002; Einum et al. 2004), and in some cases such effects may last until after emergence and first feeding (Leblanc et al. 2011; Björklund et al. 2003; Koops et al. 2003; Thorn and Morbey 2018; Self et al. 2018; Cogliati et al. 2018). Generally, juveniles coming from larger eggs are larger than juveniles coming from small eggs (e.g., Hutchings 1991; Einum and Fleming 1999; Heath et al. 1999; Leblanc and Noakes 2012). In steelhead trout, *O. mykiss*, larger eggs produce larger offspring from yolk sac absorption up to 4 weeks after first feeding (Springate and Bromage 1985). However, egg size does not always have direct implications for overall egg quality and early offspring survival (e.g., Krebs et al. 2018). More recently, Self et al. (2018) showed that later in development, juveniles from smaller eggs had higher growth rates than conspecifics from larger eggs. Despite the importance of *O. mykiss* in both aquaculture and fisheries management, no study has yet examined the potential relationships of egg size with embryonic developmental features and phenotypic traits of juveniles that may vary between hatchery and wild fishes.

Within-clutch variation in egg size and other associated phenotypic traits in juveniles may be an important factor in phenotypic divergence between wild and hatchery salmonids. Importantly, if the origin of the fish (wild vs. hatchery) and/or egg size affects early life phenotypes of 1-year-old salmonids, then important changes in life history may occur in only one generation. In other words, the effect of rearing fish in hatchery/captive conditions for 1 year before being released may have rapid impact on reproductive investment (egg size and fecundity), as well as transgenerational effects on growth and behavior of juveniles (e.g., Araki et al. 2008). Here, we assessed how within-female egg size variation can (1) affect embryonic development, early growth, and behavior of individual embryos and juveniles, and then (2) how it can affect subsequent first year of growth and smolting development of steelhead trout of both wild and hatchery origins. First, we tested the hypothesis that within-female egg size variation influences the development of early phenotypic traits and the developmental rate of *O. mykiss*. This was studied in embryos from small and large eggs tracked individually from fertilization to first feeding. We predicted that hatchery eggs would be smaller than eggs from wild parents and that progeny of hatchery fish would grow faster than progeny of wild fish, as in Atlantic salmon *Salmo salar* (Einum and Fleming 1997; Fleming et al. 2002) and brook charr *Salvelinus fontinalis* (Vincent 1960). Furthermore, we predicted that juveniles coming from larger eggs will be larger than juveniles coming from smaller eggs (Einum 2003; Moffett et al. 2006). We also predicted that large fish coming from large eggs would develop more slowly, be more mobile, and feed more and ubiquitously in the water column (Benhaïm et al. 2003; Leblanc et al. 2011). Additionally, we examined the effect of egg size on growth and smolting development (physiology and saltwater preference test) from fish of both hatchery and wild origins. In contrast to our predictions for early development, we did not predict that egg size would affect the growth of 1-year-old fish or their physiological parameters, nor that of salt- or freshwater preference at smolting (e.g., Heath et al. 1999; but see Self et al. 2018). However, we predicted that hatchery steelhead will be larger than wild ones after 1 year raised in hatchery (Blouin et al. 2021). Based on the study of Hill et al. (2006), we predicted that hatchery fish would have reduced ability to regulate ionic concentration when exposed to saltwater, i.e., in a preference test they would be less likely to be found in saltwater.

Methods

Study animals

Returning adult steelhead trout of hatchery and wild origin from the Siletz River (OR, USA) were caught in traps in March 2009 and 2010 as part of the Oregon Department Fisheries and Wildlife (ODFW) monitoring and broodstock programs. “Hatchery” fish were first generation, that is, from wild parents reared at ODFW hatchery for 1 year until released as smolts. For identification, the adipose fins of all hatchery fish were removed before they were released in the river. Hatchery F-1 fish mature in the ocean similarly to wild fish and are caught when returning to the Siletz River (absence of the adipose fin). Wild fish were adult steelhead with intact adipose fins captured at the same times and locations in the ODFW trap on the Siletz River. Based on otoliths reading, most of the females used in this study were spawning for the first time after 2 years at sea. In 2009 and 2010, 59 females from the Siletz River were caught, from which only eight females were second time spawner (Borgerson, pers. comm.).

A total of 41 families were created with a slightly different design for the two years. In 2009, eggs of three females from each origin were fertilized with the milt from five males (hatchery fish) or two males (wild fish), creating 15 and 6 families for hatchery and wild fish respectively. In 2010, 10 single females were crossed with 10 single males from each origin (10 families for each origin). Body mass (to the nearest g) and length (to the nearest 0.1 cm) of parents were measured and two scales were collected to estimate age. We fertilized 60 mL of eggs (approximately 300 to 400 eggs) from each female by mixing with a few milliliters of milt from each male. Three families were discarded because of poor fertilization success (lower than 90%). However, because many of the observations and experiments were performed on developing fish, starting from fertilization up to smolting stage, the levels of replication (that is the number of families) for each test or experiments are not constant, and considerably lower in older fish (see specific tests).

Fertilized eggs were incubated at the Oregon Hatchery Research Center in Heath hatchery trays supplied with oxygen-saturated single pass freshwater from Fall Creek (mean ± SD, 8.2 ± 0.5 °C), and kept in darkness up to emergence (first external feeding). Mortality was assessed weekly, and dead embryos removed manually. When embryos had pigmentation in the eyes, they were visually sorted for smaller and larger eggs within each family (Leblanc et al. 2011), as to retain only these two size classes. Egg size measurements were obtained from 1048 eggs, with 25 eggs measured per size class per family (Table 4 “sorted eggs 2009”).

Egg size and embryo development

Twenty-five fertilized eggs per female were measured to calculate mean egg diameter and variance. Egg diameter was measured on photographs taken 4 h after fertilization (Leblanc et al. 2011). We calculated the mean egg diameter per female and within female variance in egg size for both hatchery and wild fish. Both variables were normally distributed (Shapiro-test: $W_{\text{egg size}} = 0.93$, $p > 0.05$; and $W_{\text{variance}} = 0.89$, $p > 0.05$). We found a strong positive correlation between mean egg size and both female body size (Fig. S1.A; $r = 0.66$, $\text{df} = 38$, $p < 0.001$) and age ($r = 0.63$, $\text{df} = 37$, $p < 0.001$). Within each origin, female body size was more strongly correlated with mean egg size than age. All females were 2 and

3 years old apart from one hatchery female that was 4 (Fig. S1B). Therefore, only female body size was used as a covariate in an ANCOVA testing for differences in egg size, using origin (hatchery vs. wild), year (2009 vs. 2010), and the interaction origin × year, as fixed factors.

We assessed the relationships between egg size, developmental rate, and early growth of individually reared embryos. When embryos had pigment in their eyes, we weighed 10 embryos from each family (to the nearest 0.01 g), measured egg diameters (as described above), and then placed them individually in rearing cells (circular PVC pipes with a mesh bottom: 10 cm Ø and 25 cm height). Cells were placed in a randomized order in 6 covered flow-through tanks (60 × 30 × 14 cm) with constant water flow (mean ± SD 11.4 ± 0.7 °C).

These embryos were observed 1 month after fertilization for developmental features: the number of melanophores on head and trunk, the pigmentation of the eye, the formation of the vitelline vein, and the intensity of blood color (see Table 1). To do so, each embryo was placed in water in a Petri dish and observed under a binocular microscope (20 × magnification). Hatching date was recorded and individual growth rate was estimated as the standard length increment in millimeter per day between hatching and first feeding (similar to Leblanc et al. 2016). Embryos were photographed and weighed at hatching and at first feeding. Standard length (to the nearest 0.01 mm) was measured from the digital pictures using the software SigmaScan Pro 5. After the onset of first feeding, individual fish were reassigned to their family, origin, and egg size groups and reared in group for the rest of the experiment (Fig. 1).

Spearman's correlation was used to test whether egg size was related to early developmental features. Egg weight (mg) was used as an indicator of egg size. We removed the effects of female length by using the standardized residuals from a linear regression of egg weight on female body size. These residuals were used as a measurement of egg size. To test whether female and origin (hatchery vs. wild) affected early development, we used mixed model of covariance (ANCOVA), with female ID nested in origin as a random factor, origin as a fixed factor, and egg size as a covariate.

Individual and group behaviors at first feeding

First feeding juveniles from three hatchery and three wild families (year 2009) were observed to estimate differences in early behavior related to origin and egg size. Within each family, we observed six juveniles coming from smaller eggs and six juveniles coming from larger eggs. Thus, a total of 12 experimental groups ((3 hatchery + 3 wild families) × 2 egg size classes) were observed 2 days after first feeding.

Mobility (stationary and swimming), agonistic interactions (chasing), and feeding behaviors (number of foraging attempts, reaction time, and locations in the water column) of randomly selected individuals were scored from videorecorded sequences (see suppl. material S2 for complete description of the

Table 1 Description of developmental features characterizing early development of steelhead trout embryos and their associated indexes. Modified from Valdimarsson et al. (2002)

Developmental features	Index	Description
Intensity of blood color	0	No red color in the vein
	1	Slight pink color in the vein
	2	Clear red color observed
Formation of vitelline vein	0	Clear vein observed
	1	Clear vein with one ramification across the yolk
	2	Clear vein observed with multiple ramifications
Darkening of eyes	0	Light shadow in eyes
	1	Dark shadow in eyes
	2	Dark-colored cells clearly visible
Number of melanophores	0	No sign of colored cells
	1	Fewer than 10 melanophores visible
	2	Fewer than 100 melanophores visible
	3	More than 100 melanophores visible

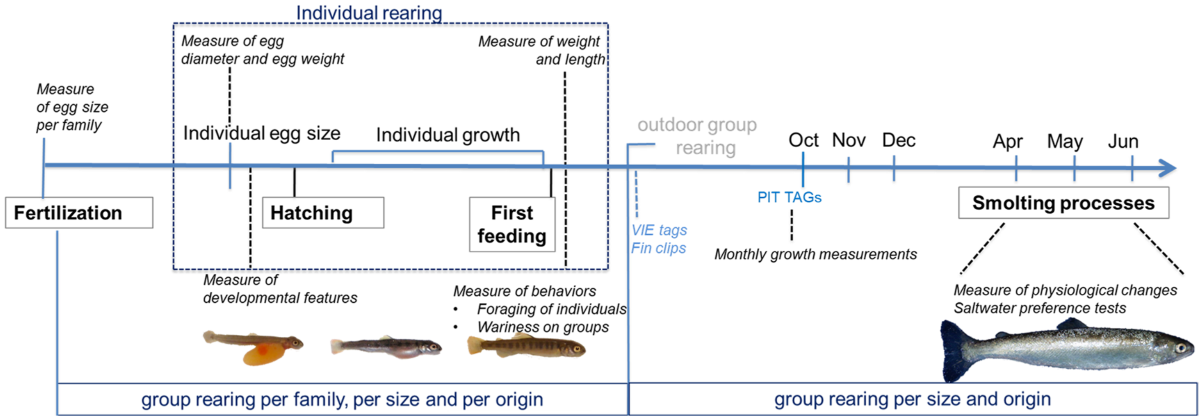

Fig. 1 Schematic of the experiment characterizing the relationship between egg size and multiple phenotypic traits in hatchery and wild juvenile *O. mykiss*

methods). Mobility and foraging behavior of hatchery and wild fish coming from different egg sizes were compared using 2-way ANOVA. Mobility data met the assumptions of ANOVAs but foraging behavior and reaction time data were log-transformed (log $x+1$) to meet the assumption of homogeneity of variances. This transformation still violated the assumption of normality but none of the transformation satisfied both homogeneity of variances and normality. Origin (hatchery vs. wild) and size (smaller eggs vs. larger eggs) and their interaction (origin × size) were the fixed factors in the ANOVA. After transformation, agonistic behavior data still violated both assumptions of normality and homogeneity of variances; thus, independent Kruskal–Wallis tests were performed to assess the effect of origin and the effect of size on agonistic behavior.

In a second experiment, we estimated the fright response and wariness of a group of 20 first feeding fish (replicate), using five replicates of the four treatments (two origin × two egg size groups). Differences in fright response exhibited by fish from each egg size category and each origin were tested in five trials over the week after first feeding (see supplementary material S3. for detailed methods). In brief, we estimated the percentage of fish at the edge of the tray and the elapsed time from disturbance after which the group of fish resumed a random distribution. The percentage of fish at the edge of the tray and time to resume random distribution were compared using a 2-way ANOVA with repeated measures. Time to resume random distribution met the assumptions of ANOVA, whereas percentage of fish at the edge of the tray violated the assumptions of normality and equal variances. Thus, the data were ranked within each observation time before applying the ANOVA with repeated measures. Data were plotted versus time for visualization and to assess if wariness declined with experience.

Smolting and saltwater preference on 1-year-old fish

One-year-old fish were tested for physiological changes, saltwater preference, and behavior at the time of smolting (Fig. 1). One week after first feeding, all families created in 2009 were pooled within each treatment, and juveniles were moved to circular outside tanks (86 cm diameter × 60 cm height) at the OHRC (Noakes and Corrarino 2010). The four treatments were hatchery fish coming from small eggs, hatchery fish coming from large eggs, wild fish coming from small eggs, and wild fish coming from large eggs. Each treatment had three replicate tanks with 50–60 fish per tank. Fish were raised under natural photoperiod and tanks received water from Fall Creek (10.6 ± 1.3 °C). Fish were fed Silver Cup Diet (SCD) of size #0, #1, #2, #3, and #4, and Bio-Oregon 2.0 mm following their growth gain. In October 2009, fish were anesthetized (stage 3 anesthesia; 50 mg/L MS-222 buffered with 125 mg/L $NaHCO_3$) and individually PIT tagged in the body cavity using a beveled edge syringe. A total of 577 fish were PIT tagged (8-mm PIT tags BIOmark; mean ± SD: body weight 11.46 ± 3.36 g and fork length (FL) 100.1 ± 10.7 mm).

Fish were carefully monitored for 24 h after the tagging procedure. Mortality of 1.7% was observed within the first 24 h and 4.8% of the fish lost their tag in following days. Fish were individually measured for weight and FL (to the nearest 0.01 g and 1 mm) every month from October 2009 to March 2010.

In order to assess physiological changes in connection to smolting, 120 fish, i.e., 10 fish from each replicate tank, were euthanized (200 mg/L MS-222 buffered with 125 mg/L $NaHCO_3$ to $pH = 7.0$) at 15-day intervals starting on April 15 until June 6, 2010. This period corresponds to the time when wild smolts from Fall Creek migrate downstream and go through physiological changing relative to smolting (Romer et al. 2013). Fish were classified as either unsilvered (clearly visible parr marks), partially silvered (few parr marks and some silvering), or fully silvered (no parr marks, silvering and dark caudal fin; see coloration index in Birt and Green 1986). Gill tissue was collected. Two to four filaments from the first left arch were collected and placed in ice-cold SEI buffer (250 mM sucrose, 10 mM EDTA, 50 mM imidazole, pH 7.3), frozen on dry ice, and then stored at − 80 °C. Gill samples were assayed for Na^+, K^+ -ATPase activity using standard methodology of McCormick (1993). Blood was collected from the caudal vein using heparinized syringes, and immediately centrifuged (10 min at 3000 *g*) to collect plasma. Plasma was frozen on dry ice, and stored at − 80 °C before being assayed for thyroxine (T_4) concentration using the radioimmunoassay from Dickhoff et al. (1978). A high Na^+, K^+ -ATPase activity and a high T_4 concentration are suggestive of smolting transformation in salmonids (McCormick 1993). Growth and physiological data were compared using a 3-way ANOVA. Origin, egg size classes, sampling time, and their interaction were fixed factors. There was no difference between replicated tanks ($F_{(1,2540)} = 0.21$, $p = 0.64$). When significant interactions were detected, Scheffe post hoc tests were used to assess where the difference originated.

In parallel to bi-monthly physiological assessments of smolts, behavior and saltwater preference tests were carried out once per month. On April 18th, May 10th, and June 6th, 10 naïve fish per treatment group were introduced into the four experimental tanks. Fish were acclimated for 48 h in freshwater (Price and Schreck 2003). Using compartmented fresh and saltwater arenas (Fig. 2), fish were allowed to choose between salt- and freshwater for 2 h after which a partition was placed between the two compartments. Switching behaviors between compartments was recorded using video and the final position of each individual noted. Fish were then removed from the tank for identification and the saltwater compartment flushed with freshwater. Fish were exposed to saltwater every other morning for 12 consecutive days resulting in six repeated trials per treatment. For a full description of the saltwater preference test, see the supplementary material S4 and Fig. 2. When the same group of fish had performed 6 consecutive trials, we estimated the consistency of the choice per individual: saltwater if the fish chose saltwater at least four times out of six, freshwater if the fish chose freshwater at least four times out of six, and no choice if the fish chose three times freshwater and three times saltwater. We compared fish choice across treatments (origin and egg size) using Chi-square tests. Additionally, fish movement data (direction of the switch) were counted from video recordings, every 5 min for a 1-min duration. Data were collected on the first, third, and sixth trials each month for each treatment. Direction of the switch was expressed as fresh- or saltwater switch per fish per hour. Mann–Whitney tests were used to compare switching behavior across treatments and Kruskal–Wallis tests were used to compare switching behavior across time and trials.

Results

Egg size from hatchery versus wild steelhead

After accounting for female size, wild fish had larger eggs than hatchery fish (respectively 6.84 ± 0.40 and 6.56 ± 0.35 mm; $F_{(1,35)} = 27.57$, $p < 0.001$; Fig. 3). This was particularly visible when looking at the median of both wild and hatchery eggs (respectively 7.09 and 6.48 mm; Fig. 3; Table 4). After accounting for female size, variance in egg size tended to be greater in hatchery fish compared to wild fish ($F_{(1,35)} = 2.86$, $p = 0.1$; Fig. 3). Variance in egg size increased with female size ($F_{(1,35)} = 18.92$, $p < 0.001$), but this was driven by hatchery fish (Fig. S1.C), and also differed between years (df = 1 $F_{(1,35)} = 56.56$, $p < 0.001$). The factors origin*year and year did not affect mean egg size ($F_{(1,35)} = 0.08$, $p = 0.777$; and $F_{(1,35)} = 0.96$, $p = 0.335$, respectively).

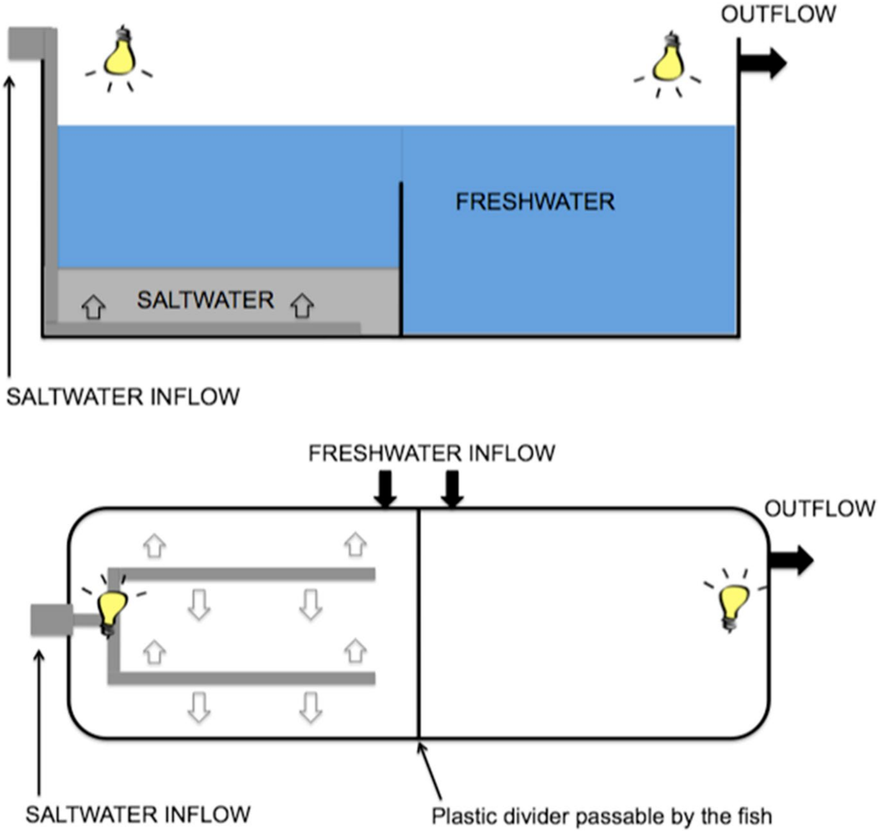

Fig. 2 Diagram of one saltwater preference arena used to assess switching behavior and consistency in saltwater preference in *O. mykiss*. The upper diagram is a side view of the experimental tank and below is a bird view. Plastic arena was 2.2×0.6×0.6 m and was surrounded by a black plastic curtain to prevent disturbance. The pipe from the header tank split into two lines on the bottom of the preference tanks (bottom diagram, gray pipe). Saltwater was slowly introduced through holes drilled every 5 cm in two rows along the sides of the pipes, shown by the open arrows in the bottom view. At the end of the trial, a separator was lowered to isolate fish in side or the other. Light bulbs were suspended above each compartment of the tank. Fresh- and saltwater compartments were interchangeable with independent pipes system (adapted from Price and Schreck 2003)

Development and early growth

Overall, embryos from small eggs developed faster than those from large eggs. Developmental features of embryos observed before hatching were negatively correlated with egg size in both wild and hatchery fish. Melanophores on head and trunk were more developed in smaller eggs from both origins (Table 2). This was also seen in hatching time (dpf), where embryos coming from small egg hatched earlier than embyos from larger eggs. However, this relationship disappeared within each origin group (Table 2). After hatching, growth rate (mm increment per day between hatching and first feeding), weight, and length at first feeding were positively correlated to egg size in both wild and hatchery fish (Table 2).

Before hatching, female identity had an effect on some developmental features such as melanophores on head and body and the darkening of the eye (Table 3). In comparison, the origin of the fish only affected the development of melanophores on the head (Table 3). Hatchery fish took a slightly longer time to hatch than wild ones (respectively 44.9 ± 5.51 vs 43.7 ± 4.18 days; Tables 3 and 4), even after controlling for egg size differences between both origins. Embryos from wild fish were longer, heavier, and grew faster than embryos from “hatchery” fish even after accounting for egg size differences (Tables 3 and 4). After hatching, origin of the mother and female

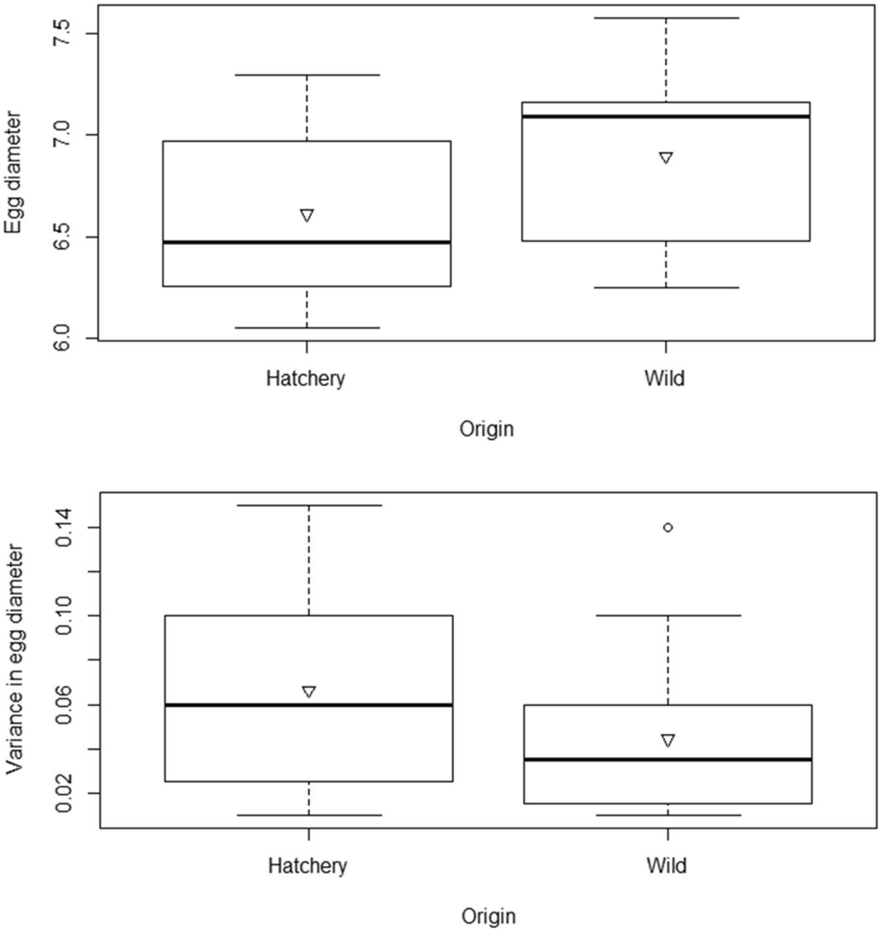

Fig. 3 Mean egg size and within female variance in steelhead trout, *O. mykiss*, from hatchery and wild origin. The upper graph shows the mean egg diameter (mm) per female and the lower graph the variance in mean egg diameter (mm) for a total of 38 families from Siletz River, OR. The bold horizontal line in each box represents the median, the bottom and top edge lines represent the 25th and 75th percentiles respectively, and error bars are the 10th and 90th percentiles. The triangles shows the mean

identity significantly affected growth of embryos and weight and length at first feeding (Tables 3 and 4).

Behaviors at first feeding

Origin and egg size had little influence on the behavior of juveniles at first feeding. Wild fish developing from large eggs fed more at the surface (Table S1), and performed more bottom foraging when compared to both small and large hatchery fish. Small fish developing from small eggs fed more at the bottom than fish from larger eggs (Table S1). Apart from bottom and surface foraging, fish from both origins did not differ in their feeding and swimming behaviors. Only smaller juveniles coming from smaller eggs displayed agonistic behavior (sensu chase; Table S1; protocol in S2).

We assessed group response to a fright event by characterizing the distribution of fish immediately after the fright event and the time to resume a random distribution after the event. On the first fright event, hatchery fish retreated less to the edge than wild fish but over time wariness decreased more rapidly in wild fish than in hatchery fish (Fig. S2). More fish from smaller eggs were seen in the center of the arena on the last 2 days of observation compared to fish from larger eggs (Fig. S2A). Additionally, wild fish took twice as long as hatchery fish to resume random distribution on the first day of observation (Fig. S2B). In the last trial, all groups resume random distribution in about 5 s. However, none of these results was significantly different between treatments (Fig. S2).

Body size, physiology, and saltwater preference tests

Growth increased across time in all treatments (Scheffe post hoc tests: $p < 0.001$; Figs. 4 and 5). After the summer, fish coming from smaller eggs

Table 2 Correlations between embryonic traits and egg size for embryos produced by hatchery-origin and wild-origin female steelhead trout (*O. mykiss*) before and after hatching. Individuals were screened for developmental features before hatching (1 month after fertilization), and after hatching. Spearman's rank correlation coefficients for each measure of development are presented. Data were analyzed independently within each origin and both origins combined "both." Egg size was measured as individual egg weight

Developmental features	Origin	Spearman correlation coefficient	*N*	*p*-value
Before hatching				
Melanophores on the head	Hatchery	−0.534	70	**< 0.001**
	Wild	−0.397	90	**< 0.001**
	Both	−0.524	160	**< 0.001**
Melanophores on the trunk	Hatchery	−0.491	70	**< 0.001**
	Wild	−0.292	90	**0.005**
	Both	−0.462	160	**< 0.001**
Darkening of the eyes	Hatchery	−0.077	70	0.526
	Wild	−0.142	90	0.181
	Both	−0.251	160	**0.001**
Blood color intensity	Hatchery	−0.255	70	**0.033**
	Wild	−0.149	90	0.162
	Both	−0.177	160	**0.025**
Vein ramification	Hatchery	−0.263	70	**0.028**
	Wild	−0.264	90	**0.012**
	Both	−0.270	160	**0.001**
Hatching time (dpf)	Hatchery	0.105	96	0.308
	Wild	0.184	90	0.082
	Both	0.169	186	**0.021**
After hatching				
Growth rate, hatching to first feeding	Hatchery	0.269	87	**0.012**
	Wild	−0.180	90	0.089
	Both	0.407	177	**< 0.001**
Length at first feeding	Hatchery	0.319	85	**0.003**
	Wild	0.057	90	0.596
	Both	0.597	175	**< 0.001**
Weight at first feeding	Hatchery	0.533	85	**< 0.001**
	Wild	0.435	57	**0.001**
	Both	0.715	142	**< 0.001**

The standardized residuals of egg weight from the linear regression model egg weight ~ female fork length were used to account for female effect on egg weight

were increasingly larger than fish coming from larger eggs at each sampling time (October $F_{(1,545)} = 29.66$, $p < 0.001$; November $F_{(1,505)} = 27.56$, $p < 0.001$; December $F_{(1,503)} = 27.27$, $p < 0.001$; February $F_{(1,493)} = 29.38$, $p < 0.001$; March $F_{(1,495)} = 29.44$, $p < 0.001$; Fig. 6). The interaction origin × size × time was close to being statistically significant ($F_{(4,2540)} = 2.30$, $p = 0.057$; Fig. 6). A year after fertilization, hatchery fish were heavier than wild ones ($F_{(1,495)} = 6.29$, $p = 0.012$) due to higher body weight in hatchery fish originating from smaller eggs (Fig. 4). One-year-old juveniles originating from smaller eggs were 18% heavier than fish coming from larger eggs (Fig. 4). This was also observed within both hatchery and wild fish but the difference in body weight between small and large eggs was stronger in hatchery fish (origin × size was significant in March 2010, $F_{(1,495)} = 6.29$, $p = 0.012$; Fig. 4, Table 5). Fork length data showed similar results and are omitted for clarity (but see Table 6 for smolts).

Hatchery fish coming from small eggs were consistently more silvery than wild fish developing from small eggs and hatchery fish developing from large eggs (Scheffe post hoc tests: respectively, df = 135, $p < 0.001$; df = 146, $p < 0.001$; Table 5). Gill Na^+, K^+ -ATPase activity was lower in hatchery fish, but only significant in June (Fig. 5B; Table 5), and lower in larger fish (only significant in late May, see Fig. 5B; Table 5). Over time, thyroxine levels were lower in wild fish than those in hatchery fish and in

Table 3 Embryonic development of hatchery and wild steelhead trout (*O. mykiss*) in relation to female characteristics. Mixed models of covariance on developmental features were performed for each variable. The term female is nested within the origin of the fish (origin): wild or hatchery. Origin was a fixed factor while female (origin) and egg weight were random factors; *n df* and *d df* refer to numerator and denominator degrees of freedom respectively

Developmental features	Factors	n df	d df	*F*	*p*-value
Melanophores on the head	Origin	1	143	9.99	**< 0.001**
	Female(origin)	14	143	4.14	**0.002**
	Egg weight	1	143	53.36	**< 0.001**
Melanophores on the trunk	Origin	1	143	3.04	0.083
	Female(origin)	14	143	2.73	**0.001**
	Egg weight	1	143	22.49	**< 0.001**
Darkening of the eyes	Origin	1	143	0.24	0.624
	Female(origin)	14	143	6.04	**< 0.001**
	Egg weight	1	143	8.34	**0.004**
Blood color intensity	Origin	1	143	0.66	0.417
	Female(origin)	14	143	1.35	0.185
	Egg weight	1	143	3.17	0.077
Vein ramification	Origin	1	143	0.06	0.815
	Female(origin)	14	143	1.12	0.345
	Egg weight	1	143	0.74	0.390
Hatching time (dpf)	Origin	1	166	415.80	**< 0.001**
	Female(origin)	17	166	659.49	**< 0.001**
	Egg weight	1	166	3.01	0.085
Growth rate, hatching to first feeding	Origin	1	157	46.21	**< 0.001**
	Female(origin)	17	157	24.28	**< 0.001**
	Egg weight	1	157	14.78	**< 0.001**
Length at first feeding	Origin	1	155	67.83	**< 0.001**
	Female(origin)	17	155	11.57	**< 0.001**
	Egg weight	1	155	15.09	**< 0.001**
Weight at first feeding	Origin	1	125	117.62	**< 0.001**
	Female(origin)	14	125	22.09	**< 0.001**
	Egg weight	1	125	94.82	**< 0.001**

The standardized residuals of egg weight from the linear regression model egg weight ~ female fork length were used to account for female effect on egg weight

fish coming from large eggs compared to fish coming from small eggs for most of the sampling events (Fig. 5A, Table 5). Heavier hatchery fish (coming initially from small eggs) showed higher thyroxine levels than other groups in April and May (except one sampling point, significant origin × size × time interaction, Table 5, and Fig. 5A).

Fish coming from larger and smaller eggs did not differ in their final choice of salt- or freshwater (df = 2, $\chi^2 = 0.23$, $p = 0.892$) and 28% of fish did not choose consistently fresh- or saltwater. A total of 49% of hatchery fish and only 15% of wild fish chose saltwater consistently (df = 2, $\chi^2 = 21.26$, $p < 0.001$), and 19% of hatchery and 60% of wild fish chose consistently freshwater. Thus, 32% of hatchery fish and 25% of wild fish were not consistent in their salinity choices. Wild fish switched more often to freshwater than hatchery fish (Mann–Whitney: $n = 35$, $U = 72$, $p = 0.007$), but there was no difference between fish coming from larger and smaller eggs (Mann–Whitney: $n = 35$, $U = 140.5$, $p = 0.684$). No significant difference in saltwater switch between hatchery and wild fish (Mann–Whitney: $n = 35$, $U = 119.5$, $p = 0.273$) and between fish coming from larger and smaller eggs was detected (Mann–Whitney: $n = 35$, $U = 138$, $p = 0.636$). There were no differences in fresh- and saltwater switching behavior across time (Kruskal–Wallis: $H_{(2)} = 1.06$, $p = 0.590$; and $H_{(2)} = 1.20$, $p = 0.550$). Switching behavior did not decrease with trials (switch to freshwater $H_{(2)} = 0.79$, $p = 0.675$, and switch to saltwater $H_{(2)} = 0.82$, $p = 0.664$).

Table 4 Summary of maternal, egg, and embryonic traits up to first feeding between hatchery and wild steelhead trout (*O. mykiss*). Hatchery fish were first generation, i.e., from wild parents and reared at ODFW hatchery for 1 year until released as smolts in the river. Both wild and hatchery parents matured in the wild and originated from the same genetic stock (Siletz River, OR). Number of families refers to the total number of crosses at fertilization. Data are mean ± SD; growth rate was calculated as length increment per day between hatching and first feeding. *dpf*, days post fertilization. Statistical differences are indicated only for "sorted eggs" ($^*p \leq 0.05$)

	Hatchery	**Wild**
Number of families	25	16
Female fork length (cm)	66.80 ± 3.94	70.78 ± 5.49
Mean egg size (mm)	6.56 ± 0.35	6.84 ± 0.40
Median egg size (mm)	6.48	7.09
Hatching time (dpf)	44.92 ± 5.51	43.69 ± 4.18
Length at first feeding (mm)	26.89 ± 1.56	28.80 ± 2.60
Weight at first feeding (mm)	19.36 ± 2.62	22.44 ± 5.16
Growth rate (mm/day)	0.34 ± 0.10	0.40 ± 0.10
Sorted eggs (fish from 2009)		
Mean "large" egg size (mm)	6.95 ± 0.42	7.04 ± 0.42
Mean "small" egg size	6.70 ± 0.45	6.53 ± 0.51*

Discussion

This study revealed important relationships between egg size and multiple levels of the phenotype in juvenile steelhead up to smolting. We identified relationships between egg size and early embryonic development, growth, and physiological parameters of both hatchery and wild steelhead trout. Contrary to our prediction, both origin and egg size had an effect on phenotypic traits of 1-year-old fish. We report that hatchery steelhead trout have smaller eggs than wild ones, offspring from small eggs grow better during the first year than those from larger eggs, offspring from large eggs hatch later and at a more advanced stage than those from small eggs, and the degree of smolting and saltwater preference differed between hatchery and wild offspring. Hatchery fish showed lower levels of gill Na^+, K^+ -ATPase activity and higher levels of thyroxine when compared to wild fish raised under the same laboratory condition. These results are consistent with previous studies that found that hatchery fish were larger and had reduced levels of gill Na^+, K^+ -ATPase activity (Hill et al. 2006). However, saltwater preference tests did not follow the physiological data relative to smolting; hatchery fish preferred saltwater whereas wild fish preferred freshwater. Finally, egg size had the largest effect on thyroxine levels of both hatchery and wild fish.

We found that eggs were smaller but more variable for first-generation hatchery-origin females when compared to first-generation wild-origin females, with no differences across years. Here, wild and hatchery parents shared genetic similarities and they only differed in their first year of rearing, i.e., captivity for first-generation hatchery-origin parents and in river for wild-origin parents. The smaller size of wild juveniles compared to hatchery fish has been suggested to be the result of hatchery females experiencing high growth rates as juveniles producing a relatively large number of smaller eggs as adults (Jonsson et al. 1996; Lobón-Cerviá et al. 1997; Morita et al. 1999; Fleming et al. 1997; reviewed by Einum et al. 2004). However, in this study, wild females were of similar size as hatchery females (Table 4). Our results illustrate that rearing the progeny of wild parents for as little time as 1 year in hatchery/captive conditions affects the future reproductive investment of those individuals (smaller and more variable egg sizes) without necessarily affecting their body size at maturity. Importantly, changes in egg sizes can be related to important variations of fitness-related traits early in life such as growth and foraging at first feeding (e.g., Benhaïm et al. 2003; Leblanc et al. 2011). We found that wild females had larger eggs, with less variable egg sizes within a female when compared to hatchery females (Fig. 3). Wild parents produced heavier and longer progeny that grew faster.

One explanation for the observed differences in mean egg size and intra-clutch variability between hatchery and wild-origin fish may be linked to the stability of the environment offspring develop in (Koops et al. 2003). For salmonids, it is hypothesized that females rely on their own growth trajectories, and early life history, to assess the developing environment of their offspring (sensu and citation there in Koops et al. 2003). Following a diversified bet hedging strategy, i.e., increase intra-clutch variation in egg size to maximize chances that some individuals have high fitness (Shama 2015), we would expect that egg size would be larger and less variable in "hatchery" clutches (constant environment) when compared to clutches from wild females (less constant environment) that would be smaller and more variable eggs. However, both mean egg size per female and

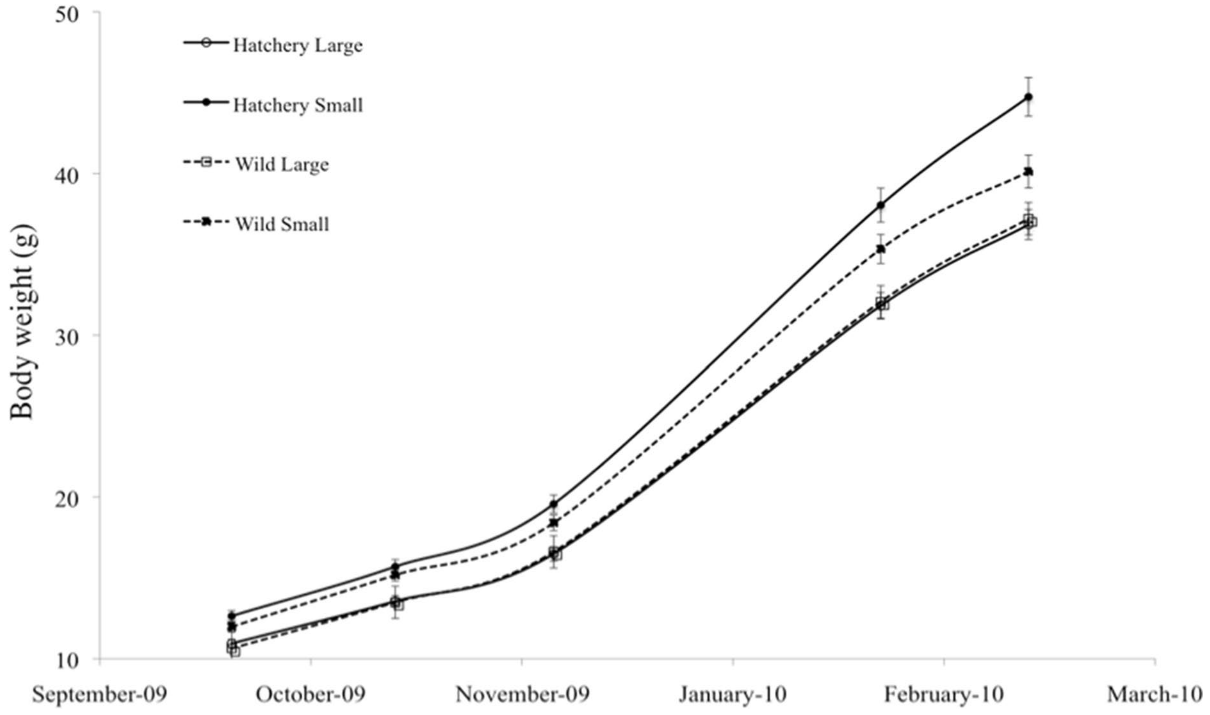

Fig. 4 First year of growth of hatchery and wild steelhead trout originating from small and large eggs raised under semi-natural conditions. "Large" and "small" refer to initial egg size classes within each female. Dashed lines refer to wild fish and solid lines refer to hatchery fish whereas a white circle represents fish from smaller eggs and a black circle fish from larger eggs. Each symbol represents the mean body weight (± SE) of fish within each treatment (3 replicates per treatment)

intra-clutch variation in egg size showed opposite trends in our study, contrasting with findings in other fish species (*Salvelinus fontinalis* Koops et al. 2003; *Gasterosteus aculeatus* Shama 2015). This may indicate that, in steelhead trout, mean egg size and intra-clutch variation in egg size might be governed by other factors such as environmental conditions during gametogenesis or the similarity between mother and offspring embryonic environments (i.e., environmental predictability).

Other environmental factors have the potential to alter egg size of hatchery and wild fish. For example, incubation conditions in hatcheries are usually optimal with most hatcheries using local river water. Therefore, hatchery eggs and embryos are incubated at optimal temperature with saturated water (~100% dissolved oxygen). On the other hand, wild eggs and embryos develop in the gravel with various and/or hypoxic conditions depending on depth of the redd, the egg density, and the amount of sediments. Lower oxygen levels during ontogeny have been associated with egg size of salmonids. In brown trout *Salmo trutta*, higher survival was observed for larger eggs under hypoxic conditions (Einum et al. 2002). Thus, lower oxygen levels during early development of wild fish may result in larger eggs at maturity and could explain the observed differences in egg size between hatchery and wild fish with similar genetic origin.

Smaller embryos coming from smaller eggs developed faster than larger embryos, similarly to Arctic charr *Salvelinus alpinus* (Valdimarsson et al. 2002), and also hatched earlier (Table 2). In invertebrates, egg size is strongly associated with developmental mode: species with small eggs (small amount of yolk) typically have planktonic larvae, disperse, feed on plankton, and then undergo metamorphosis, whereas species with large eggs (large amount of yolk) tend to have no larval period (Moran and McAlister 2009). These two extreme modes of development refer respectively to indirect and direct development (Noakes and Godin 1988). Because egg size reflects the amount of energy available for

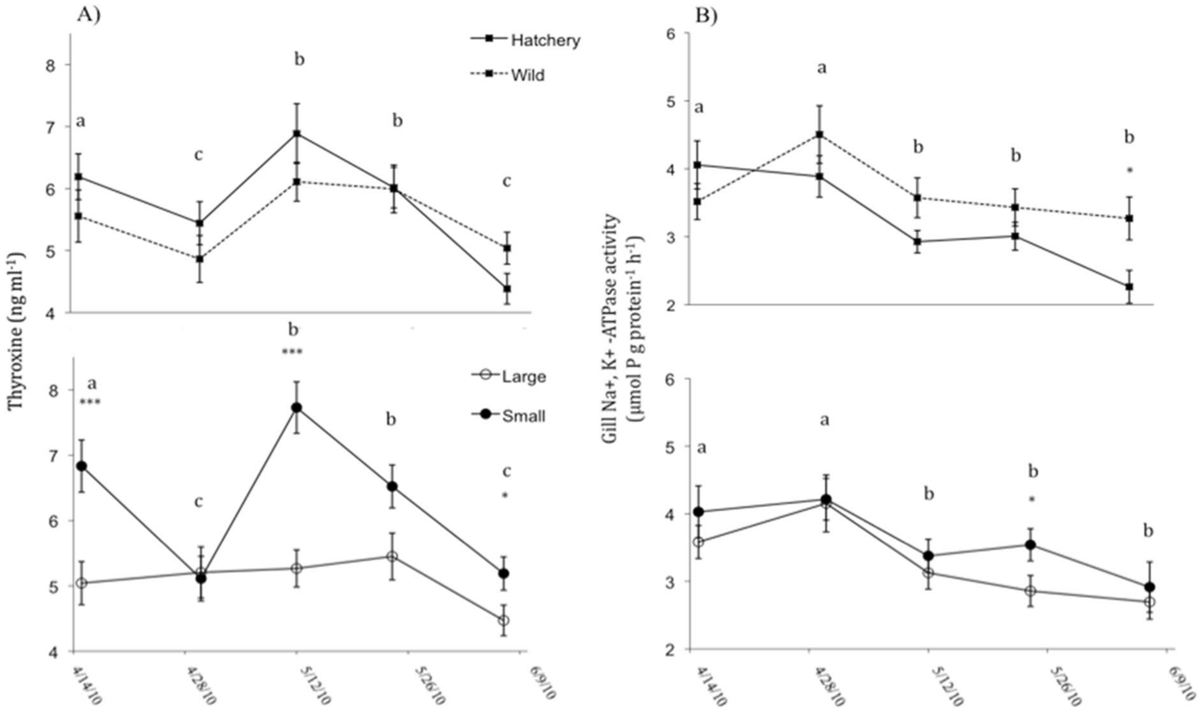

Fig. 5 Physiological parameters of 1-year-old hatchery and wild steelhead trout originating from different egg sizes and reared under semi-natural conditions. Left panel (**A**) shows thyroxine levels (**A**) and right panel (**B**) gill Na +, K + -ATPase activity (mean ± SE). Upper graphs show physiological differences between hatchery (full line) and wild fish (dashed line) and lower graphs show physiological differences between fish coming from large eggs (white circles) and fish coming from small eggs (black circles). Different letters indicate statistical differences ($p < 0.05$) among sampling times (Scheffe post hoc tests). Asterisk indicates statistical differences among origin or size at each sampling time (***$p \leq 0.001$; **$p \leq 0.01$; *$p \leq 0.05$)

Table 5 Phenotypic traits of 1-year-old hatchery and wild *O. mykiss* smolts. Analyses of variance were applied to test for differences in fish body weight, fork length, condition factor, silvery color, gill Na^+, K^+ -ATPase, and thyroxine levels between hatchery and wild (origin) steelhead smolts coming from large and small eggs (size). Fish were raised in hatchery and semi-natural conditions for their first year and sampled 5 times during smolting (time)

Factors		Body weight		Length		Condition factor		Color		ATPase		Thyroxine	
	df	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Origin	1	0.39	0.530	0.04	0.840	3.31	0.070	22.22	**< 0.001**	5.37	**0.021**	1.61	0.205
Size	1	14.37	**< 0.001**	12.61	**< 0.001**	0.27	0.602	13.19	**< 0.001**	4.21	**0.041**	39.51	**< 0.001**
Time	4	7.74	**< 0.001**	5.56	**< 0.001**	7.14	**< 0.001**	6.54	**< 0.001**	6.21	**< 0.001**	8.01	**< 0.001**
Origin × size	1	5.88	**0.015**	3.61	0.058	2.24	0.136	20.32	**< 0.001**	0.48	0.491	2.34	0.127
Origin × size × time	4	1.33	0.251	1.55	0.173	0.51	0.767	0.72	0.609	1.13	0.343	3.93	**0.004**

Levene's tests were performed to check the homogeneity of variances ($p > 0.05$)

embryonic development (Leblanc et al. 2016), egg size variation within a species may indicate different pathways of energy use in embryo development, similar to different patterns of development observed across fish species with different egg sizes (Flegler-Balon 1989) . For embryos of *O. mykiss*, different egg sizes between hatchery and wild fish may reflect differences in patterns of development that are later mirrored by differences in growth and behavior (Self et al. 2018). As predicted, first feeding fish coming from smaller eggs tended to feed more on the bottom whereas first feeding fish from larger eggs tended to feed more at the surface (in Arctic charr; Benhaïm et al. 2003; Leblanc et al. 2011). Wild juveniles from larger eggs tended to forage more at the surface than juveniles from all other treatments. Small fish coming from smaller eggs tended to show more agonistic behavior than larger ones. In polymorphic species like Arctic charr and steelhead trout, differences in feeding tactics between fish coming from small and large eggs could be linked to habitat use and evolutionary processes. Indeed, variation in behavior stemming from even just small size differences at first feeding may influence habitat and food selection that could lead to within and among divergence of populations, especially if there are clear interactions between maternal and genetic effects. However, this will need to be tested in the field. To our knowledge, no data are currently available on mediated egg size foraging/swimming behavior and habitat use of first feeding salmonids.

Interestingly, egg size was associated with absolute growth of embryos and juveniles of steelhead trout up to smolting. At emergence, juveniles coming from larger eggs were larger as classically reported in salmonid species (*Salmo salar* Einum 2003; Moffett et al. 2006; *Salvelinus alpinus* Leblanc et al. 2016). However, this positive relationship between initial egg size and growth observed at emergence turned into a negative relationship after the first summer. Thus, egg size associated with growth of juvenile steelhead trout for more than a few weeks after emergence: juveniles coming from smaller eggs became larger than juveniles coming from larger eggs in both hatchery and wild fish (see also Self et al. 2018). Very few studies have reported long-term relationships of egg size and growth of salmonids (Blanc 2002; Björklund et al. 2003). Two explanations as to why only a few studies have focused on egg size consequences on growth can be provided. First, many salmonid studies indicate that egg size effects on growth disappear quickly after first feeding (genetic and environmental factors become more important than the effect of egg size), but also many, if not most, experiments focusing on the importance of egg size are terminated shortly after first feeding (Srivastava and Brown 1991; Heath et al. 1999). Hence, the long-term effect of egg size may be ignored. The second explanation comes from the variation in egg size itself. Indeed, egg size effects have perhaps received little interest in species where egg size variation within females is not visible and/or where differences in egg size did not appear to affect survival. However, some results indicate that egg size influences on juveniles *O. mykiss* growth lasted longer within families rather than across families (Blanc 2002). An alternative and non-mutually exclusive explanation to the rapid growth in fish coming from small eggs could be linked to yolk limitation and food restriction. This refers to compensatory growth where fishes, after a period of food shortage, exhibit higher growth rate and restore their energy levels and body condition (reviewed in Jonsson and Jonsson 2014). Compensatory growth has been shown in rainbow trout under group-rearing conditions and individual rearing of 40–50gr juveniles (Nikki et al. 2004). The mechanism underlying compensatory growth may be associated with the levels of growth hormone expressions in some fish species (but not all; e.g., *Salvelinus alpinus*; see Beck et al. 2019). In a mouth-breeding cichlid, juveniles originating from small eggs show higher growth hormone receptor expression levels and higher growth rate compared to those from larger eggs (Segers et al. 2012). Therefore, increased growth of juveniles coming from small eggs may be a response to an initial limitation of energy (yolk content) and a strategy to overcome energy thresholds at particular developmental stages such as smolting (see also Jonsson and Jonsson 2014). Our results show that egg size varies across and within *O. mykiss* females, resulting in significant differences in the 1-year growth of fish raised under natural photoperiod and creek water. However, the effect of egg size on phenotypes of individual fish reared in a natural environment still needs to be tested.

Smolting measurements performed in our study were most different between hatchery and wild fish. In comparison, egg size had significant but subtle effects on physiological parameters and color at smolting, those being very likely connected to body size (Table 4). Hatchery steelhead trout are reared for 1 year in freshwater and released as smolts, whereas wild fish usually spend 2 years in freshwater before migrating downstream (Quinn 2005; Romer et al. 2013) . Here, tests clearly indicated a saltwater preference by hatchery fish and a freshwater preference by wild fish, but physiological results indicated a lower osmoregulatory status for hatchery fish. Such mismatch between salinity preference and osmoregulatory status may translate into lower survival of hatchery fish during downstream migration or in the estuary (e.g., Melnychuk et al. 2014). Reduced smolt survival has been linked to decreased osmoregulatory status, hormone levels, and migratory tendency (Hill et al. 2006). Studies have found hatchery coho salmon (*Oncorhynchus kisutch*) smolts to have higher mortality rates in marine environments as well as lower survival rates in the estuary and a longer in-river downstream migration (Chittenden et al. 2008). Thus, the tendency to prefer saltwater combined with a lower osmoregulatory status in hatchery fish may result in lower survival when released as smolts in the river. However, other studies have failed to consistently identify survival differences between hatchery and wild fish (Welch et al. 2004; Johnson et al. 2010). Whether physiological differences and differences in saltwater preference observed in this study are reflected in different subsequent ocean survival between hatchery and wild fish remains to be tested. The mechanisms underlying the differences in physiological parameters observed in this study are not known, and we can only hypothesize that different developmental rates in the first year of growth of hatchery and wild juveniles may result in different smolting times.

We demonstrated that egg size, likely through body size, can affect the phenotypes of juveniles and smolts at multiple levels, with potential consequences for life history. We showed that hatchery fish have smaller eggs than wild fish, offspring from small eggs grow better during their first year than those from larger eggs, offspring from large eggs hatch later and at a more advanced stage than those from small eggs, and the degree of smolting and saltwater preference differed between hatchery and wild offspring. Overall, egg size mediated offspring phenotypes in both hatchery and wild fish during a year, highlighting the importance of egg size in shaping not only early life history traits but also later stages such as reproductive investment. By looking at not only mean egg size but also individual mediated–egg size phenotypic traits, this study demonstrates the significant contribution of egg size in promoting phenotypic variation within a population. Further studies are needed to address the adaptive significance of egg size among and within populations, especially investigating the role of within-clutch variation for phenotypic variation in the wild.

Acknowledgements All care and handling of fish were carried out under the approval of the Institutional Animal Care and Use Committee of Oregon State University (ACUP # 3951). We thank the ODFW North Fork Alsea Hatchery and the Oregon Department of Fish and Wildlife for providing the fish used in this study and the staff at the Oregon Hatchery Research Center for their assistance with care and maintenance of fish. We thank Anup Gurung for helping in PIT tagging fish, John Winkowski for his assistance with running the saltwater tests and smolt sampling, and Rob Chitwood from the Oregon Cooperative Fish and Wildlife Research Unit for providing the experimental tanks for the saltwater tests. Julia Unrein conducted the gill Na^+, K^+ -ATPase assay and Arimune Munakata (Myagi University of Education, Sendai Japan) conducted the thyroxine assay. Antoine Millet, Samantha Beck, Agnes Kera Kreiling, and two anonymous reviewers reviewed an earlier version of the manuscript. Funding was provided by the Icelandic Center for Research (RANNÍS), the Eimskip University Fund at the University of Iceland, and the Leifur Eiríksson Foundation to CAL, and the Oregon Hatchery Research Center, the Oregon Department of Fish and Wildlife, and the Fisheries and Wildlife Department of Oregon State University.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethical approval All care and handling of fish were carried out under the approval of the Institutional Animal Care and Use Committee of Oregon State University (ACUP # 3951). Documentation can be provided upon request.

Conflict of interest The authors have no competing interests that are relevant to the content of this article.Bjarni K. Kristjánsson is on the Editorial Board of *Environmental Biology of Fishes* journal, and is a Guest Editor of this special issue, but he had no involvement in the peer review of this article and had no access to information regarding its peer review.

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