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LETTER

Costs of reproduction can explain the correlated evolution of semelparity and egg size: theory and a test with salmon

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Abstract

Species' life history traits, including maturation age, number of reproductive bouts, offspring size and number, reflect adaptations to diverse biotic and abiotic selection pressures. A striking example of divergent life histories is the evolution of either iteroparity (breeding multiple times) or semelparity (breed once and die). We analysed published data on salmonid fishes and found that semelparous species produce larger eggs, that egg size and number increase with salmonid body size among populations and species and that migratory behaviour and parity interact. We developed three hypotheses that might explain the patterns in our data and evaluated them in a stage-structured modelling framework accounting for different growth and survival scenarios. Our models predict the observation of small eggs in iteroparous species when egg size is costly to maternal survival or egg number is constrained. By exploring trait co-variation in salmonids, we generate new hypotheses for the evolution of trade-offs among life history traits.

Keywords

Costs of reproduction, demography, iteroparity, life history theory, offspring size, salmon, semelparity.

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INTRODUCTION

Life history traits play a fundamental role in determining individual fitness and population dynamics. Diversity in these traits reveals how life history strategies help species cope with environmental challenges. An important aspect of this diversity is the difference between species that reproduce once and die (semelparous) and those that reproduce more than once (iteroparous). Semelparity can be more advantageous than iteroparity when survival is low or when reproduction itself is sufficiently costly to survival (Williams 1957, 1966; Charnov & Schaffer 1973; Bell 1980; Young & Augspurger 1991). Reproductive strategies also range from producing many small or few large progeny (Smith & Fretwell 1974; Stearns 1992). The evolution of life history diversity along these axes involves trade-offs among age at maturation, egg number, egg size and parity (number of reproductive bouts) (Adler *et al.* 2014). In order to predict the evolution of life histories in fishes that have indeterminate growth and/or migration among habitats, this classic theory has to be reconciled with the details of development, growth and survival. We combine comparative data analyses and demographic models to investigate the evolution of correlations among offspring size, number and parity in salmonid fishes, which have well-documented variation in these traits. By using a combination of data and theory, we present a novel perspective on the effects of growth and migration on the evolution of life histories of fishes, which represent the greatest diversity in life history traits of all vertebrates.

An influential theory predicts offspring size and number will evolve to maximise the number of surviving offspring (Smith & Fretwell 1974). Accordingly, the optimal offspring size, x_{SF} (SF for Smith–Fretwell), depends on the shape of the offspring survival function, which is determined by the environment (Rollinson & Hutchings 2013; Kindsvater & Otto 2014). Females with more resources produce more offspring of the optimal size. When mothers can survive to reproduce again, however, their reproductive budget also evolves to balance the trade-off between current reproduction and maternal survival. If reproduction is very costly to maternal survival, females may delay reproduction altogether (Proaktor *et al.* 2008; Miller *et al.* 2012). When offspring survival is independent of maternal age and female survival does not depend on the size of her offspring, trade-offs between offspring size and number and trade-offs between current and future fitness have been treated as if they are independent. In other words, iteroparous females might produce fewer offspring in order to survive to reproduce again, but prior theory does not predict co-variation in offspring size with parity (Smith & Fretwell 1974; Stearns 1992).

The remarkable diversity in life histories of salmon, trout, charr and relatives (Salmonidae) offers the opportunity to study the evolution of parity, offspring size and number, and refine theories of parity and offspring size by addressing the influence of growth after maturity and mortality associated with migration. In Pacific salmon, lengthy migrations and the difficult transition from the ocean to freshwater before reproduction are energetically costly and decrease adult survival,

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potentially explaining the evolution of semelparity in this lineage (Williams 1966; Groot & Margolis 1991; Cooke *et al.* 2004; Evans *et al.* 2011). The environment faced by juveniles determines offspring fitness; in turn, variation in early survival drives the diversity of salmonid life histories. Furthermore, there is an empirical correlation between semelparity and salmonid egg size (Crespi & Teo 2002), which is also related to differences in maturation and body size (Fleming & Gross 1990; Einum & Fleming 2000; Crespi & Teo 2002; Sloat *et al.* 2014). Migration costs, sexual selection or environmental variability have been hypothesized to explain these patterns (Crespi & Teo 2002; Einum & Fleming 2007), but how these mechanisms might operate remains unclear. Here, we analyse trait co-variation at the population level (using 363 populations representing 13 species) to understand the correlations among life history traits across salmonids in greater detail than previous studies, which used species' means for each trait. We then develop three hypotheses for the joint evolution of egg size and semelparity motivated by our statistical analyses, and explore them using demographic models. Through this combined statistical and theoretical approach, we gain novel insights into how the details of development and physiology could interact with external selective forces to shape the evolution of complex life histories.

SALMONID DATA ANALYSIS

Methods

We analysed published life history trait data for salmonids (Supporting Information: Data Table 1). We included data sets that reported egg size or egg number, body length, parity (0: iteroparity, 1: semelparity) and migration behaviour (0: residency, 1: anadromy). Egg sizes were converted to standard units (wet mass; see Supporting Information). Because latitude (a proxy for temperature) is related to egg size in salmonids (Fleming & Gross 1990) and may be related to other traits, we included latitude as a covariate.

In salmon, parity and anadromy are correlated: many iteroparous populations are non-migratory and most semelparous populations have anadromous females. However, our data set includes 32 non-migratory (resident) populations of semelparous Sockeye Salmon (Kokanee, *Oncorhynchus nerka*) and Masu Salmon (*O. masou*) and 45 anadromous iteroparous populations of Brown Trout (*Salmo trutta*) and Dolly Varden (*Salvelinus malma*); we plot the reproductive traits of these species in Fig. S1.

We conducted statistical analyses in R (R Core Team 2015). We used linear mixed-effects models, including nested random effects of species within genus around the intercept and fixed effects of body size, parity, anadromy and latitude. Our response variables were either egg size or egg number. We examined residuals to ensure the data were normally distributed. We log-transformed body size, egg size and number: for all analyses we examined residual plots to check model assumptions.

We considered the top set of models with AIC weights that summed to 0.95 (95% confidence set). We used model averaging to estimate coefficients and errors for each predictor (using the *MuMIn* package; Barton 2013).

RESULTS

For egg size, our global model including body length, parity, anadromy and latitude, as well as all interactions between body length, parity and anadromy was the top model, but there were alternative models in the 95% confidence set (Table 1a). As expected, egg size was positively related to both latitude and body size (Table 2a). All else being equal, semelparity had a positive effect and anadromy had a negative effect on egg size. These direct effects were not significant on their own because of a strong three-way interaction between body length, anadromy and parity (Table 2a). The egg size of iteroparous migrants increased less steeply with body length (Fig. 1a). The predicted egg size was always smaller for iteroparous species than for semelparous species, for both resident and migratory populations.

Egg number increased with body length, rising from under 100 for Brook Trout (*Salvelinus fontinalis*) to over 15 000 for Atlantic Salmon (*Salmo salar*; Fig. 1b). The size–fecundity relationships of semelparous and iteroparous species in Fig. 1b were strikingly similar. Again, body length, parity, anadromy and their interactions, as well as latitude, were included in the top model set (Table 1b). The averaged coefficients of the 95% confidence set of models suggest that body length and the interaction between body length and parity had a positive effect on egg number, but there was a negative effect of the three-way interaction between body length, anadromy and semelparity (Table 2b). The other interactions had a great deal of uncertainty associated with their estimates (Table 2b). Figure 1b shows the differences between iteroparous and semelparous species were much less pronounced for egg number than for egg size.

While the set of models in Table 1 incorporates genus and species identity in the random effects (Tables S1, S2), these models do not fully account for the phylogenetic relationships among populations. We conducted a phylogenetic least squares regression (using *ape*; Paradis 2012), using mean values for each of the 13 species, ignoring variation among populations in egg size and migratory behaviour, because there is no population-level phylogeny. Although semelparity still had a positive effect on egg size, only the positive relationship between female size and egg number was significant (Table S3). Because semelparity evolved only once (in the ancestor of *Oncorhynchus*; Fig. S2; Crete-Lafreniere *et al.* (2012)), our ability to confirm that parity is causatively related to egg size is limited. Keeping this caveat in mind, we turn to theoretical models to determine whether and when correlations between parity and egg size, such as those observed in Fig. 1, are expected to evolve.

Model description

We develop a stage-structured model for which we can vary key parameters, such as the background mortality rate, growth rate or the shape of trade-off functions, in order to ask when correlations between parity, offspring size and number are predicted to evolve. We assume throughout that traits evolve to maximise the long-term population growth rate, λ (Charlesworth 1994), although similar results are likely to hold if juvenile survival depends on density (see

Table 1 Candidate models relating body length, parity, anadromy and their interactions to (a) egg size and (b) egg number, accounting for latitude. We used the natural log of egg size, number and body length. We standardised continuous predictor variables (body length and latitude) by centring them and dividing by two standard deviations. Parity and anadromy are binary categories: species are either semelparous or iteroparous; populations are anadromous or resident. Additive effects among predictor variables are coded as +; interactions between predictors are coded as ×. K is the number of parameters in each model, ΔAICc is the difference in AICc values between model i and the best model of those considered and w_i is the probability that a model is the best model of the set. All models within the 95% confidence set (i.e. cumulative sum $w_i > 0.95$) are included in the table

Response	Model	K	Log likelihood	AICc	ΔAICc	w_i
(a) Egg size	Body length + Parity + Anadromy + Latitude + Body length × Parity + Body length × Anadromy + Parity × Anadromy + Body length × Anadromy × Parity	12	−41.41	108.35	0	0.57
	Body length + Parity + Anadromy + Latitude + Body length × Anadromy	9	−45.82	110.52	2.17	0.19
	Body length + Parity + Anadromy + Latitude + Body length × Parity + Body length × Anadromy + Anadromy × Parity	11	−43.93	111.16	2.81	0.14
	Body length + Parity + Anadromy + Latitude + Body length × Parity + Body length × Anadromy	10	−45.40	111.87	3.52	0.1
					Total:	1
b) Egg number	Body length + Parity + Anadromy + Body length × Parity + Body length × Anadromy + Anadromy × Parity + Body length × Anadromy × Parity	11	−28.97	81.22	0	0.60
	Body length + Parity + Anadromy + Latitude + Body length × Parity + Body length × Anadromy + Anadromy × Parity + Body length × Anadromy × Parity	12	−28.71	82.94	1.71	0.26
	Body length + Parity + Anadromy + Anadromy × Parity	8	−34.53	85.76	4.53	0.06
	Body length + Parity + Anadromy + Body length × Anadromy + Anadromy × Parity	9	−33.94	86.74	5.51	0.04
					Total:	0.96

Table 2 Standardised coefficients describing the main effects of predictor variables and their interactions (Table 1) on (a) egg size and (b) egg number. The coefficients and 2.5 and 97.5% confidence intervals for each of the fixed effects are reported. Model coefficients were averaged using the natural average method, which weights parameter values by the summed model weights, w_i (Grueber *et al.* 2011)

Response	Parameter	Coefficient	2.5%	97.5%
(a) Egg size	Intercept	4.04	3.67	4.42
	Body length	0.62	0.34	0.91
	Latitude	0.31	0.19	0.42
	Anadromy	−0.05	−0.28	0.17
	Semelparity	1.15	−0.12	2.42
	Body length × Anadromy	−0.73	−1.14	−0.32
	Body length × Semelparity	0.02	−0.76	0.79
	Anadromy × Semelparity	−0.26	−0.71	0.19
	Body length × Anadromy × Semelparity	1.03	0.11	1.95
(b) Egg number	Intercept	7.39	7.12	7.67
	Body length	2.50	2.21	2.78
	Latitude	0.03	−0.06	0.13
	Anadromy	−0.09	−0.34	0.16
	Semelparity	−0.24	−2.49	2.01
	Body length × Anadromy	0.13	−0.24	0.51
	Body length × Semelparity	0.55	0.05	1.05
	Anadromy × Semelparity	0.27	−0.05	0.59
	Body length × Anadromy × Semelparity	−1.04	−1.69	−0.39

Kindsvater & Otto 2014). Parameters are described in Table S4. Fig. 2a is a simple representation of our model, with multiple size classes and mature stages. Females of stage i survive with probability p_i, which can be constant, or a function of reproductive effort ($R_{i,}$), egg size ($X_{i,}$), or both $[p_i(R_{i,}\ x_i)]$. We also assume there is a fixed cost R_0 to fitness that comes from the physiological toll of preparing for reproduction, including moving from the ocean to freshwater. Reproductive fitness m_i in each stage i is the product of offspring number n_i, and each offspring's probability of survival $f_i(x_i)$, such that $m_i = n_i\ f_i(x_i) = [(R_i{-}R_0)/x_i]\ f_i(x_i)$. Throughout, we assume that larger offspring survive better $[df_i(x_i)/dx_i > 0]$, although the function could theoretically have different shapes (Fig. 2b).

We introduce three hypotheses, described in detail below, which potentially explain the variation in offspring sizes between semelparous and iteroparous fish. We initially consider that offspring survival $f_i(x_i)$ may depend on both maternal stage and parity (Hypothesis 1). We then explore how egg size and number both evolve with parity to give a total reproductive budget of $R_i = R_0 + n_i x_i$ at stage i (Hypothesis 2). Finally, we hold egg number fixed for females of a given size and explore the evolution of egg size with parity (Hypothesis 3).

We first evaluate whether these three hypotheses can explain correlations between semelparity and egg size using matrix models. These models allow individuals to remain in a stage with probability σ_i. Allowing for an indefinite number of life

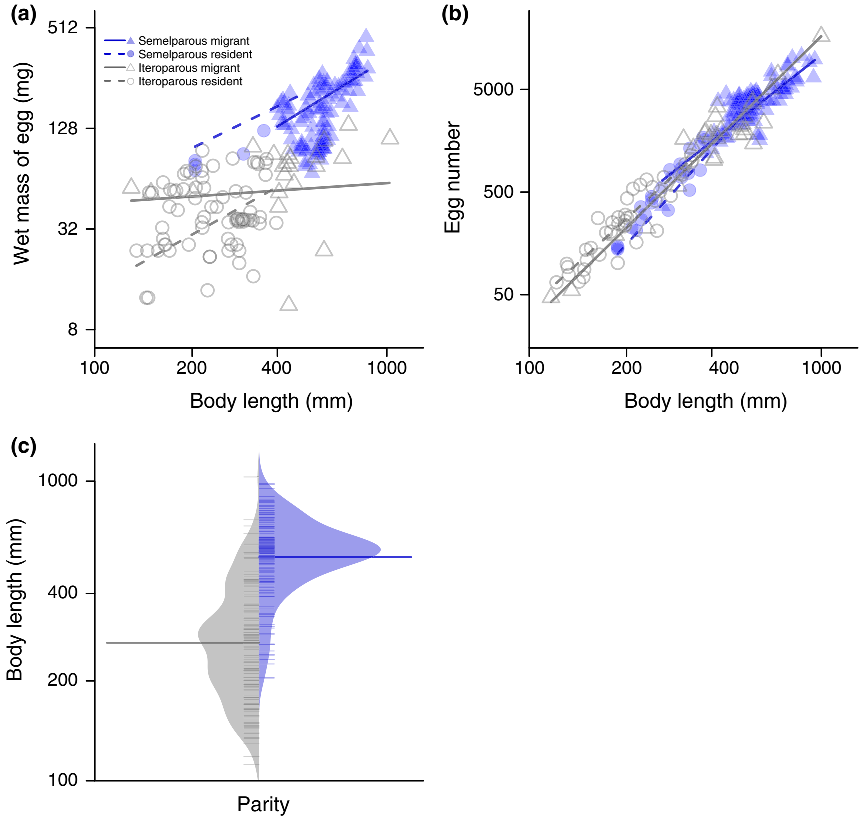

Figure 1 Relationships among body size, egg size and egg number for semelparous and iteroparous populations of salmonid fishes. Each point represents a population; triangles are migratory populations. (a) Egg size by body size. The lines are the top model predictions using restricted maximum likelihood estimation (REML; incorporating random effects) for the four possible life histories (Table 2a). The relationship between egg size and body length differs between semelparous and iteroparous life histories in a manner that depends on migration, resulting in the significant three-way interaction in Table 2a. (b) Egg number by body size. As in (a) the lines are the top model predictions using REML and incorporating random effects for the four possible life histories. (c) Distribution and mean body lengths of spawning individuals by parity (blue is semelparous; grey is iteroparous).

stages, the population changes according to the transition matrix

$$\mathbf{M} = \begin{pmatrix} \sigma_1 p_1 + m_1 & m_2 & m_3 & \dots & m_\omega \\ (1-\sigma_1)p_1 & \sigma_2 p_2 & 0 & \dots & 0 \\ 0 & (1-\sigma_2)p_2 & \sigma_3 p_3 & \dots & 0 \\ \dots & \dots & \dots & \dots & 0 \\ 0 & 0 & 0 & \dots & \sigma_\omega p_\omega \end{pmatrix}, \qquad (1)$$

where we census immediately before reproduction. Using standard matrix algebra, we can determine the effect of a change in a stage-specific rate on the population growth rate, λ, given by the leading eigenvalue of **M** (Otto & Day 2007; Kindsvater & Otto 2014). In the Discussion, we explore the implications of these models in light of the empirical patterns observed in salmonids.

HYPOTHESIS 1: ITEROPAROUS SPECIES PRODUCE JUVENILES THAT SURVIVE BETTER AT SMALLER SIZES

The first hypothesis for the correlation between parity and egg size is simply that the juvenile survival function, $f_i(x_i)$, differs systematically between iteroparous and semelparous species such that smaller and larger eggs are favoured respectively. That is, egg size evolves to different Smith–Fretwell optima, defined as the point x_{SF} at which dm_i/dx_i equals zero. With $m_i = [(R_i - R_0)/x_i]\ f_i(x_i)$, this point occurs when $df(x_i)/dx_i = f(x_i)/x_i$, which does not depend on the total reproductive budget R_i or the cost of migration R_0. Without changes in reproductive budget, egg number will be inversely correlated with egg size. For example, differences in stream characteristics could generate these differences in offspring fitness functions (Rollinson & Hutchings 2013). Another possibility is that females that have previously reproduced make better nesting or mate choices and thus increase the survival of their eggs. Doing so would likely reduce the optimal egg size (e.g., shifting from solid to dashed curves in Fig. 2b). In this case, we would also predict that iteroparous species produce smaller eggs as they age and gain experience.

HYPOTHESIS 2: SMALLER EGG SIZE INCREASES MATERNAL SURVIVAL IN ITEROPAROUS SPECIES

We next consider the case where juvenile survival depends on egg size but does not otherwise depend on maternal age or parity [i.e. $f_i(x_i) = f(x_i)$]. We then determine the life history that maximises λ when both egg size and egg number are free to evolve. We again find the conditions required for egg size and parity to co-evolve, assuming that iteroparous species will become semelparous if reproducing only once yields the high-

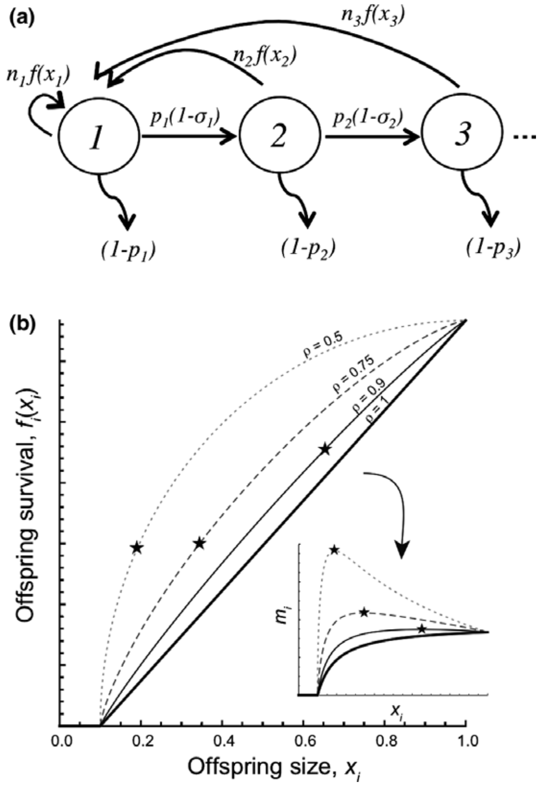

Figure 2 (a) Example life history with multiple reproductively mature stages (size classes). Individuals survive and grow from one stage to the next with probability $p_i\,(1 - \sigma_i)$. The number of surviving offspring per female in stage i is given by $m_i = n_i\, f(x_i)$. (b) Examples of the offspring survival function, $f(x_i)$, using eqn S2 with different values for the shape parameter, ρ. When multiplied by the number of eggs, n_i, these functions give the number of surviving eggs per female, m_i (arrow to inset plot). Here, we have assumed that $n_i = [R_i - R_0]/x_i$, so that larger eggs result in fewer eggs (as in Hypothesis 1). The Smith–Fretwell optimum x_{SF} for each function is marked with a ★.

est population growth rate λ. We start by calculating the growth rate for the simplest case of semelparity, where R_i is zero except at a given age a. In this example, we assume $\sigma_i = 0$, so females cannot return to a stage; we relax this assumption in the SI *Mathematica* File.

Semelparity

With semelparity, the eigenvalue of **M** simplifies to:

$$\lambda_a = \sqrt[a]{n_a\, f(x_a) \prod_{i=1}^{a-1} p_i} \tag{2}$$

The leading eigenvalue is then maximised when females devote all available resources to reproduction, such that maternal survival past the age of reproduction drops to zero ($p_a = 0$). Assuming that total reproductive investment, R_a, and egg size, x_a, are free to evolve independently, then the total reproductive investment, R_a, evolves up to the point that survival past reproduction is zero and egg size again evolves to the Smith–Fretwell optimum ($x_a = x_{\mathrm{SF}}$). We assume that females never make eggs so large that egg size alone drives their survival to zero.

With a semelparous life history, the relationships between maternal survival, migration costs, fecundity and offspring survival determine whether it is better to reproduce in the first year ($a = 1$) or delay maturation ($a > 1$). Specifically, the age of maturity evolves towards the value of a that yields the highest λ_a. If a species grows little over time so that the maximum age-specific fitness [$m_i = n_i\, f(x_i)$] is similar for all ages, semelparous females that reproduce in their first year will have the greatest fitness. Alternatively, if we assume that body size and fecundity increase with age (as in most fish), delayed semelparous strategies can evolve, with the length of the delay increasing with background survival, p_i. For example, a semelparous fish will evolve to reproduce in the second year when:

$$n_1\, f(x_1) < \sqrt{n_2\, f(x_2)\, p_1} > \sqrt[3]{n_3\, f(x_3)\, p_1 p_2} \tag{3}$$

When eqn 3 is satisfied, the benefits of growing and reproducing in the second year outweigh the benefits of reproducing in the first year, as well as the advantages of growing for yet another season to reproduce in the third year. This result recapitulates classic life history theory for the evolution of semelparity (e.g. Charnov & Schaffer 1973; Young & Augspurger 1991).

Iteroparity

We next consider the fitness of reproduction in multiple years, asking when iteroparous life histories are favoured over semelparous life histories and what the consequences are for egg size. When both total investment and offspring size can evolve, in some cases population growth rate is maximised by an intermediate amount of reproduction at age i (allowing mothers to survive to reproduce again). This occurs when both:

$$\frac{\partial\lambda}{\partial R_i} = \frac{\vec{v}\,\frac{d\mathbf{M}}{dR_i}\,\vec{u}}{\vec{v}\,\vec{u}} = 0 \text{ and } \frac{\partial\lambda}{\partial x_i} = \frac{\vec{v}\,\frac{d\mathbf{M}}{dx_i}\,\vec{u}}{\vec{v}\,\vec{u}} = 0 \tag{4}$$

(Otto & Day 2007), where element u_i of the column vector $\vec{u}$ represents the fraction of the population at stage i at the stable age-distribution, v_i of the row vector $\vec{v}$ represents the reproductive value of females of stage i and $\vec{v}\,\vec{u}$ is the average reproductive value of the population (all of which are positive in age-structured models). Allowing maternal survival to depend on total reproductive effort and offspring size, $p_i(R_i, x_i)$, and recalling that $m_i = n_i\, f(x_i) = [(R_i - R_0)/x_i]\, f(x_i)$, the derivatives in eqn 4 can be carried out to give:

$$\frac{\partial\lambda}{\partial R_i} = \frac{u_i\, v_1}{\vec{v}\,\vec{u}} \left(\frac{f_i(x_i)}{x_i} + \psi_i\, \frac{\partial p_i}{\partial R_i}\right) \tag{5a}$$

$$\frac{\partial\lambda}{\partial x_i} = \frac{u_i\, v_1}{\vec{v}\,\vec{u}} \left(\frac{(R_i - R_0)}{x_i}\,\frac{df(x_i)}{dx_i} - \frac{(R_i - R_0)}{x_i^2} f(x_i) + \psi_i\, \frac{\partial p_i}{\partial x_i}\right) \tag{5b}$$

where ψ_i is the expected reproductive value of a surviving female at the next time step, relative to the reproductive value of juveniles:

$$\psi_i = \sigma_i\, \frac{v_i}{v_1} + (1 - \sigma_i)\, \frac{v_{i+1}}{v_1} \tag{6}$$

When reproducing females have no future reproductive value ($\psi_i = 0$), eqn 5a is positive, indicating that reproductive effort will evolve to its maximum (i.e. terminal investment). In this case, eqn 5b is maximised at the Smith–Fretwell offspring size, echoing the results for semelparity.

With some future reproductive value ($\psi_i > 0$), however, reproductive investment at stage *i* evolves to a lower level in order to increase female survival (i.e. reproductive effort decreases when the parenthetical term in eqn 5a is negative because of its negative impact on maternal survival, $\partial p_i/\partial R_i$). Similarly, as long as female survival decreases with increasing offspring size ($\partial p_i/\partial x_i < 0$), eqn 5b is optimised at an offspring size that lies below the Smith–Fretwell optimum. As the costs of migration increase, delayed maturation evolves, because the fitness gained from reproducing early is discounted by R_0. However, R_0 has little effect on the egg size that evolves (SI *Mathematica* File).

Thus, if iteroparity does evolve and larger egg size reduces maternal survival, offspring size is predicted to be smaller than x_{SF} and hence smaller than egg sizes of semelparous species, all else being equal. In this case, we also predict that egg size in iteroparous species will increase towards x_{SF} whenever reproductive value decreases with age (Kindsvater & Otto 2014).

There is one main caveat to this explanation for the correlation between semelparity and large eggs. Namely, maternal survival must be sensitive to egg size beyond the effect of total reproductive investment. If female survival depends only on R_0 and R_i, then $\partial p_i/\partial x_i = 0$ in eqn 5b and iteroparous species should also produce offspring of size x_{SF}. While there is some evidence for the costs of egg size to females in other vertebrates (Williams 2005), further work is needed to determine if this is a plausible scenario in salmonids.

HYPOTHESIS 3: SMALLER EGGS REDUCE TOTAL REPRODUCTIVE INVESTMENT IN ITEROPAROUS SPECIES

We now address our third hypothesis for the correlation between parity and egg size, which assumes that fecundity is more constrained than egg size for females of a given age or size. We modify Hypothesis (2) such that females can alter total reproductive investment by adjusting offspring size, with offspring number n_i held fixed for females in stage *i*.

Semelparity

In the semelparous case, the eigenvalue is determined by eqn 2. Total reproductive investment, R_a, will evolve to the point where female survival goes to zero ($R_{max,a}$), with females evenly dividing the resources that remain after the fixed cost of reproduction among the n_i offspring. Egg size no longer evolves to the Smith–Fretwell optimum but to $x_{max,a} = (R_{max,a} - R_0)/n_a$. Again, the optimal age of maturity depends on the relationships between age and fecundity (n_a), offspring survival [$f(x_{max,a})$], physiological costs of reproduction (R_0) and maternal survival. These relationships can be determined numerically by evaluating eqn 2 (SI *Mathemtica* File).

Iteroparity

Iteroparous life histories are favoured over semelparity if investing in small eggs yields reasonably high survival for both mother and offspring. Assuming offspring number n_i is fixed for females in stage *i*, we can use either $\partial\lambda/\partial R_i$ or $\partial\lambda/\partial x_i$ in eqn 4 to find the optimal life history [relating the two using $(R_i - R_0)/x_i = n_i$]. Focusing on offspring size, we find that x_i evolves according to the sign of:

$$\frac{\partial\lambda}{\partial x_i} = \frac{u_i\, v_1}{\vec{v}\,\vec{u}}\left(n_i\,\frac{df(x_i)}{dx_i} + \psi_i\,\frac{dp_i}{dx_i}\right) = \frac{u_i\, v_1}{\vec{v}\,\vec{u}}\; n_i\left(\frac{df(x_i)}{dx_i} + \psi_i\,\frac{dp_i}{dR_i}\right) \tag{7}$$

Again, when there is no future reproductive value ($\psi_i = 0$), $\partial\lambda/\partial x_i$ is positive and offspring size will evolve to be the same size in iteroparous and semelparous females, given the resources available after paying the upfront cost of reproduction, R_0.

With some future reproductive value ($\psi_i > 0$), offspring of iteroparous females is again predicted to be smaller. Essentially, females that can potentially reproduce again invest in smaller offspring to ensure their own survival, reaching an evolutionary stable strategy where the costs in offspring fitness, $df(x_i)/dx_i$, exactly balance the future fitness gains through maternal survival, $\psi_i\, dp_i/dR_i$.

OPTIMAL REPRODUCTIVE STRATEGIES FOR SPECIES WITH SALMONID-LIKE LIFE HISTORIES

Our first hypothesis was that egg size varies simply due to differences in the relationship between egg size and juvenile fitness, $f_i(x_i)$ (Fig. 2b). To evaluate the second and third hypotheses, however, we must numerically evaluate the optimal strategy, considering semelparous and iteroparous life histories, as well as early and delayed ages of maturation. To do so, we assumed specific functional forms for juvenile survival, growth, maternal survival and upfront migration costs (described in Supporting Information and SI *Mathematica* file). Then, we used the models described above to find the optimal life history. We assume a strictly age-structured population ($\sigma_i = 0$), although numerical analyses including stage structure ($\sigma_i = 0.1$) yield similar results (SI *Mathematica* file); thus our conclusions are robust to differences in the duration of different life stages.

Figure 3 illustrates the optimal egg size, parity and maturation age for different background survival rates and functional forms of the trade-off relating egg size to maternal survival. Although Fig. 3 assumes no fixed costs of migration ($R_0 = 0$), a very similar picture emerges with $R_0 > 0$ (SI *Mathematica* file). We evaluate the optimal life histories predicted by both the second (Fig. 3a) and third (Fig. 3b) hypotheses. In both cases, iteroparity evolves when a female's survival remains high despite reproduction. This occurs when background survival is sufficiently high and maternal survival is a concave function of egg size. When background survival is low or egg size strongly decreases maternal survival, semelparity evolves (Fig. 3). Semelparous species reproduce in the first year when background survival is low, but delay maturity for increasingly long periods as background survival rises (Fig. 3). Regardless of their age or size at reproduction, semelparous females produce larger eggs than iteroparous females in their first reproductive bout. The difference in egg sizes increases with background survival (Fig. 3). Thus, both our second and third hypotheses could account for the finding that iteroparous species produce smaller eggs than semelparous species (Fig. 3). This result is robust to several alternative model parameterisations (SI *Mathematica* File).

We conclude that the timing and investment in reproduction will be highly sensitive to the risk of mortality, the costs of migration and reproduction, any extra costs of investing in egg size and offspring fitness $f(x_i)$ (Table 3).The benefits of delaying reproduction (in order to grow and thereby increase fecundity) are balanced against the risk of mortality. After maturity, producing smaller eggs can be advantageous if it improves the female's chance of reproducing again, especially when it only decreases offspring fitness by a small fraction (see also Kindsvater & Otto 2014). We do not predict any difference in egg size between iteroparous and semelparous females, assuming all else is equal, unless there is a cost to mothers of investing in eggs above and beyond her total reproductive investment (Hypothesis 2), or unless clutch size is less evolvable than egg size (Hypothesis 3). We expect the greatest differences in egg size between iteroparous and semelparous females when background survival is high (Fig. 3) and when the number of surviving offspring, m_i, is relatively insensitive to adjustments in egg size, which occurs when ρ is near one (see inset Fig. 2b;

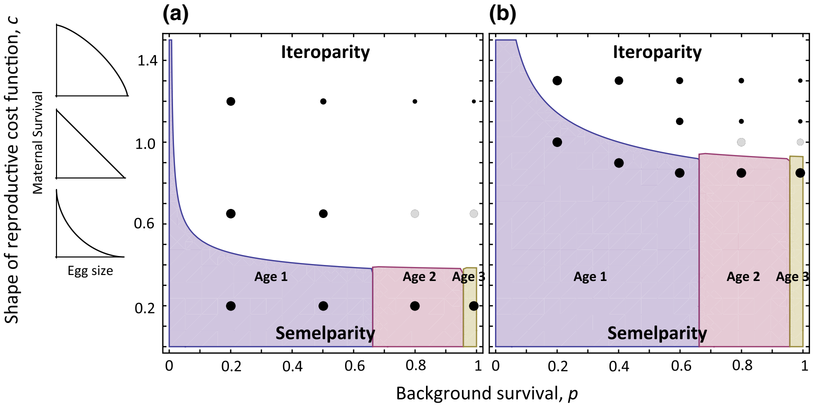

Figure 3 The evolution of semelparity, iteroparity and egg size. The optimal life history is shown when (a) egg size and total reproductive effort both evolve (Hypothesis 2) and (b) egg size evolves while egg number is constrained (Hypothesis 3). The diameter of each dot corresponds to the egg size predicted for the combination of maternal survival parameters [x-axis: background survival; y-axis: shape of the maternal survival curve as a function of egg size, (a) c_x or (b) c, inset graphs]. When female survival declines with egg size (smaller c), semelparity is favoured (shaded regions) and females produce the maximum egg size possible (egg sizes scaled separately in each plot). As the trade-off becomes less severe or background survival increases, iteroparity evolves (white regions) and egg size decreases. Grey dots indicate when the optimal iteroparous strategy involves delayed maturity. Specific functions and parameter values are given in the Supporting Information.

Table 3 Summary of the assumptions, predictions and evidence for each of the three hypotheses addressed with the stage-structured model

Hypothesis	Assumptions	Predictions	Evidence from salmonids (Fig. 1; Tables 1 and 2)
1	Iteroparous and semelparous salmonids have different offspring fitness functions $f_i(x_i)$	No clear prediction for the evolution of egg size with semelparity. Egg number should decrease if optimal egg size increases, unless reproductive effort differs with parity. If juveniles of experienced (older) females have higher growth rates, larger eggs are optimal for younger iteroparous females	None. Egg number allometry is similar in iteroparous and semelparous species. Young iteroparous females have smaller eggs (Einum & Fleming 2000), counter to the prediction
2	Egg size and number are free to evolve, but both decrease the female's chance of surviving to reproduce again. All females have the same $f_i(x_i)$	Semelparity evolves when mortality and costs of reproduction are high. Young iteroparous females evolve smaller eggs when per-egg costs reduce female survival	Mixed. Young iteroparous females have smaller eggs than older females (Fleming 1996) or semelparous species. Migrating females produce smaller eggs, given the same body size, suggesting eggs could be costly. Yet this hypothesis does not predict similar egg number allometry for semelparous and iteroparous species.
3	Egg size is free to evolve, but number is set according to female size, i.e. early on in the female's reproductive cycle. All females have the same $f_i(x_i)$	Semelparity evolves if mortality and costs of migration and reproduction are high. Young iteroparous females evolve smaller eggs to improve maternal survival	Consistent. Semelparous females have large eggs; young iteroparous species decrease egg size, not number; migrating females produce smaller eggs, given the same body size, and parity does not have a strong effect on the egg number-body size relationship

compare Fig. 3a with $\rho = 0.9$ to Fig. S4a with $\rho = 0.75$); this result is similar to the pattern in Kindsvater & Otto (2014). The variability in egg sizes within and among salmonid populations suggests that while selection is undoubtedly acting on egg size, the offspring fitness surface may be a relatively flat function of size (Rollinson & Hutchings 2013).

DISCUSSION

Life history theory has made fundamental contributions to our understanding of the evolutionary processes generating diversity. Where trait data do not fit current predictions, we have the opportunity to develop a deeper understanding of the processes underlying this diversity. We therefore developed a comprehensive framework for evaluating the evolution of offspring size and number when reproduction trades off with female survival, applying this framework to understand the evolution of salmonid life histories. Reproduction is costly for anadromous salmonids, as their life history requires a physiologically taxing transition between the ocean and freshwater and can entail long migrations. The transition between cool saline oceanic water to warm freshwater, long rivers and steep elevation changes in Northern Pacific rivers could explain the evolution of semelparity, but it is not clear whether this would also affect offspring size. Empirically, we confirmed that egg size not only varies between iteroparous and semelparous salmonids, but it is also affected by migration and body size. By contrast, egg number shows surprisingly little variation between semelparous and iteroparous populations or between resident and migratory (anadromous) populations for females of a given body size (Fig. 1b). We thus developed a stage-structured modelling framework to explore the co-evolutionary link between parity and egg size.

We considered three hypotheses for the unexplained correlation between parity and egg size.

Hypothesis 1: Juvenile survival could depend on parity if iteroparous and semelparous offspring experience different environments, leading to differences in the trade-off between size and number. This could also occur if iteroparous offspring benefit from the size or experience of older mothers.

Hypothesis 2: Egg size could affect female survival, above and beyond the cost of total reproductive effort, such that producing smaller eggs improves the survival of iteroparous females.

Hypothesis 3: Iteroparous species can more readily evolve reduced egg size than egg number when reallocating resources from reproduction to survival. These three hypotheses are not mutually exclusive.

We can evaluate these hypotheses in the light of our analyses of salmonid life history data (Table 3). If Hypothesis (1) was true, we would expect semelparous species to produce fewer eggs than iteroparous species, unless reproductive effort also changes. Surprisingly, there is little effect of parity on egg number (Fig 1b), and changes in reproductive effort are expressed in egg size. Similarly, Hypothesis (2) does not fully explain Fig. 1b; it predicts iteroparous species will produce smaller eggs but it fails to account for the similarity in egg number between semelparous and iteroparous species. If the pattern in Fig. 1b reflects a constraint on egg number for females of a given body size, Hypothesis (3) then predicts that semelparous species will invest all remaining resources in egg size. To explain the relationship of egg size with maternal body size (Fig. 1a), larger females must have relatively more resources to devote to each egg. This prediction could be tested experimentally by manipulating growth and determining whether both egg size and egg number increase with body mass.

While all three hypotheses could be contributing to the patterns in our data, we think the third hypothesis is most compelling, as it is consistent (by assumption) with the tight empirical relationship between egg number and body size, regardless of parity (Table 3). This begs the question of why egg number would be constrained. Females could have greater flexibility in egg size than number because egg number is determined several months before females begin their migration (Tyler *et al.* 1994; Patterson *et al.* 2004). This detail of developmental timing also could explain intra-population variation in reproductive allocation across years: female Sockeye Salmon have smaller eggs, but not fewer, during high streamflow years with more challenging migrations (Braun *et al.* 2013). This pattern suggests that either females producing large eggs do not survive to reproduce in high-flow years or that females adjust egg size according to the difficulty of their migration. Similarly, in Brown Trout populations with sympatric anadromous and resident females, residents have larger eggs than anadromous females the first time they spawn, suggesting that young anadromous females reduce egg size to improve their own survival (Jonsson & Jonsson 1999; Olofsson & Mosegaard 1999). Finally, Sockeye females that migrate farther inland or to higher elevations also produce smaller eggs than females spawning closer to the river delta (Crossin *et al.* 2004). This could reflect variation in the optimal egg size in different environments, but it is also consistent with more evolvable egg sizes than numbers.

Some predictions of our theoretical model motivate further research. Semelparous species tend to be larger than iteroparous species when they reproduce (Fig. 1c), which suggests that they grow for a longer period before maturation. We cannot determine if their larger body size arises from delayed maturation (as predicted by our model) or if it simply reflects a difference in juvenile growth rates. The correlation between semelparity, delayed maturation and larger size warrants investigation. Research on Steelhead/Rainbow Trout (*O. mykiss*), which mature at varying ages and may be either migratory or not, could potentially distinguish between these hypotheses by comparing egg sizes of residents and migratory forms of this species.

In addition to changes in egg size and size at reproductive maturity, semelparous salmon have more exaggerated secondary sexual traits, and longer periods of parental care, than their iteroparous relatives (Sargent *et al.* 1987; Quinn & Foote 1994). Increased allocation to these costly traits may have evolved in the semelparous species because they have fully sacrificed future survival. The costs of these traits, in addition to egg size, could increase as salmon face environmental changes that affect growth and survival (Mangel 1994). For example, if warming waters increase migration costs (Hinch & Martins 2011), the toll of these traits may decrease fitness in semelparous species, while previously iteroparous species may be able to reproduce only once. Given that there is only one evolutionary transition from iteroparity to semelparity in salmonids, more data are needed from other taxa to better understand the evolution of correlated changes in reproductive traits in general. The approach taken here could be applied to other taxa to infer the evolutionary forces that have led to variation in life histories and predict their responses to environmental change.

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AUTHOR CONTRIBUTIONS

H.K.K., D.C.B. and J.D.R. designed the study. D.C.B collected the data. D.C.B. and H.K.K. conducted the statistical analyses. H.K.K. and S.P.O. conducted the theoretical analyses. H.K.K., D.C.B., S.P.O. and J.D.R. wrote the paper.

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