

Egg-size evolution in aquatic environments: does oxygen availability constrain size?

Sigurd Einum¹*, Andrew P. Hendry² and Ian A. Fleming³

¹Norwegian Institute for Nature Research, Tungasletta 2, NO-7485 Trondheim, Norway

²Redpath Museum and Department of Biology, McGill University, 859 Sherbrooke Street West, Montreal, PQ, H3A 2K6, Canada

³Coastal Oregon Marine Experiment Station and Department of Fisheries and Wildlife, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365, USA

Selection against large eggs has been proposed for aquatic environments, putatively because large eggs should have more difficulty obtaining the required oxygen. Here, we use brown trout (*Salmo trutta*) eggs to provide an experimental test of this hypothesis. At high levels of dissolved oxygen (14 mg l⁻¹), egg survival was high and independent of egg size. At low oxygen levels (2.3 mg l⁻¹), survival decreased overall, and was higher for large-egged than small-egged siblings. Thus, contrary to conventional expectation, low oxygen levels selected for large rather than small eggs. A second experiment using Atlantic salmon (*S. salar*) eggs indicated that oxygen consumption increases relatively slowly with increasing egg mass (allometric constant = 0.44). The failure of the conventional ‘bigger is worse during incubation’ hypothesis may thus be due to the erroneous assumption that oxygen consumption increases at a greater rate with increasing egg mass than does the egg surface area that is available for oxygen diffusion. We also demonstrate, using data from Atlantic salmon, that nest-specific oxygen consumption decreases with increasing egg size, but that this effect is more pronounced for large than for small females. This may help to explain the positive correlation between adult body size and egg size observed in fishes that cluster their eggs.

Keywords: maternal effects; offspring size; fecundity; selection; incubation; metabolic rate

1. INTRODUCTION

The advantages to juveniles of originating from large eggs have been demonstrated repeatedly in a wide range of taxa: juveniles from large eggs typically have increased survival and growth (reviewed by Roff 1992; Mousseau & Fox 1998). Why then do we not see the evolution of ever-increasing egg size? One reason is that optimal egg size should maximize maternal fitness rather than offspring fitness (Smith & Fretwell 1974; Einum & Fleming 2000). As maternal fitness is the product of the number of offspring and their average fitness, and because an increase in egg size necessitates a decrease in egg number (for a given total level of investment into egg production), a trade-off exists between these two traits (Roff 1992). If the relationship between egg size and offspring fitness is asymptotic, an intermediate egg size will maximize maternal fitness (Smith & Fretwell 1974; Einum & Fleming 2000).

The Smith–Fretwell model assumes that the only cost of increasing egg size is its negative effect on egg number, and therefore maternal fitness. However, subsequent work has indicated that offspring fitness itself may sometimes be negatively correlated with egg (or seed) size (e.g. Hammond & Brown 1995; Seymour & Bradford 1995; Donohue & Schmitt 1998; Kaplan 1998; Lee & Strathmann 1998). For organisms whose eggs incubate in water, it has been suggested that such an effect should occur because the larger embryos of large eggs have more difficulty obtaining the oxygen needed to meet their meta-

bolic demands (Krogh 1959). The basis for this hypothesis is that a given increase in egg diameter will lead to a greater increase in egg volume or mass (which determines oxygen requirements) than in egg surface area (which determines oxygen acquisition ability).

This assumed negative effect of egg size on egg survival rates under low oxygen conditions has never been tested directly. Van den Berghe & Gross (1989) came closest by reporting that large coho salmon (*Oncorhynchus kisutch*) eggs had lower survival rates than small eggs in poor incubation conditions (i.e. lots of fine sediments). However, they did not actually measure the dissolved oxygen levels experienced by the eggs, and could not disentangle the effects of egg size *per se* from other potentially confounding maternal and genetic effects (e.g. large females, which produce larger eggs, may have inherently higher metabolic rates than small females). Despite the lack of a formal empirical test, the ‘bigger is worse during incubation’ hypothesis has been repeatedly invoked in general theoretical models of egg-size evolution (e.g. Sargent *et al.* 1987; Hendry *et al.* 2001), as well as in adaptive interpretations of natural egg-size variation (e.g. Holtby & Healey 1986; Fleming & Gross 1990; Quinn *et al.* 1995; Seymour & Bradford 1995; Jonsson & Jonsson 1999; Kolm 2001).

The ‘bigger is worse during incubation’ hypothesis implicitly assumes that oxygen consumption increases proportionally with egg volume (or mass). If this ratio is not constant, the effect of increasing egg size on oxygen requirement relative to accessibility may be different from that typically assumed. This can be shown by expressing the ratio between the volume (V) and the surface area (S) of a sphere as

* Author for correspondence (sigurd.einum@nina.no).

$$\frac{V}{S} = \frac{\frac{4}{3}\pi r^3}{4\pi r^2}, \quad (1.1)$$

where r is the radius. The ratio can be modified to reflect oxygen requirements (VO_2) by incorporating a constant a (the intercept in a log-log relationship) and a scaling factor b , which determines how VO_2 changes with the changing egg volume

$$\frac{VO_2}{S} = \frac{a(\frac{4}{3}\pi r^3)^b}{4\pi r^2}. \quad (1.2)$$

As b decreases below 1, the effect of an increase in radius on the required rate of oxygen uptake per unit of surface area decreases. If b is less than $2/3$, an increase in egg size will actually cause a decrease in the VO_2/S ratio, and oxygen will become the limiting factor sooner for small eggs than for large eggs, contrary to conventional thinking. Intraspecific estimates of b appear to be absent for aquatic eggs, whereas interspecific estimates for amphibian eggs indicate $b = 0.52–0.62$ (Seymour & Bradford 1995). These estimates are close enough to $b = 2/3$ to indicate that estimating the intraspecific relationship for eggs may be critical to determining whether we should theoretically expect large or small eggs to be at a greater disadvantage under low oxygen conditions.

Salmonid fishes provide a good system to study factors influencing egg-size evolution. First, egg size varies greatly among species, and among and within populations (e.g. Fleming & Gross 1990; Beacham & Murray 1993; Quinn *et al.* 1995). Second, positive effects of increasing egg size on post-hatching juvenile performance (i.e. size, survival and growth) are well documented (e.g. Hutchings 1991; Einum & Fleming 1999, 2000). Third, salmonid eggs can experience levels of dissolved oxygen that are low enough to cause substantial mortality (Lacroix 1985; Chapman 1988; Peterson & Quinn 1996; Rubin & Glimsäter 1996). Fourth, the ‘bigger is worse during incubation’ hypothesis has been at the root of several generally accepted explanations for covariation between life-history traits in this taxa (e.g. Van den Berghe & Gross 1989; Fleming & Gross 1990; Hendry *et al.* 2001). We therefore experimentally tested this hypothesis by exposing sibling brown trout (*Salmo trutta*) eggs of differing size to low levels of dissolved oxygen, and by examining variation in survival to the juvenile stage. We then conducted a companion experiment using Atlantic salmon (*S. salar*) eggs to estimate the scaling factor b in the relationship between egg size and oxygen consumption.

2. MATERIAL AND METHODS

(a) Oxygen challenge

Ten female brown trout, reared to maturity in captivity at the Norwegian Institute for Nature Research (NINA) Station (southwestern Norway, $58^\circ 59' N$, $5^\circ 58' E$), were artificially spawned and their eggs fertilized by ten males (one-to-one mating) on 10 November 2000. Such captive rearing has previously been shown to enhance within-female variation in egg size in a portion of the population, while keeping the fat and protein percentages constant, enabling a comparison of siblings originating from small and large eggs (Einium & Fleming 1999, 2000). Egg size in wild Atlantic salmon and brown trout typi-

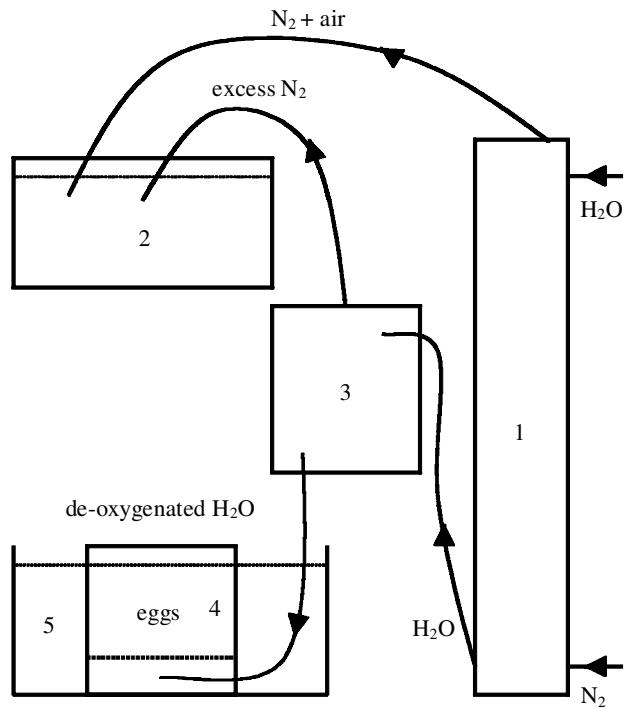


Figure 1. Experimental apparatus used for the exposure of brown trout eggs to low levels of dissolved oxygen. Nitrogen gas was pumped into the bottom of a vertical column (1) through a diffuser and left the system through a tube at the top, before entering a water bath (2). Water entered the column at the top and ran out at the bottom to a water distribution tank (3) where the excess nitrogen was released. De-oxygenated water flowed through a tube to one of five containers (4) where the water was allowed to overflow into hatchery troughs (5).

cally shows little variation within females, but the captive rearing artificially increases this variance ($CV = 2.8–4.7\%$ versus $8.1–18.8\%$ in the high variation females (Einium & Fleming 1999, 2000)). Variability in egg size within females has been thought to be related to the position of the egg relative to blood vessels in the female ovary during development (Kamler 1992), and it is probably this effect that is amplified in the captive environment. The different family groups were incubated at ambient river temperatures in separate perforated plastic boxes in the hatchery.

At the eyed stage (when the eyes of the embryo are clearly visible), close to hatching (20 January 2001, 408 degree-days after fertilization, *ca.* 150 eggs from each family were randomly chosen and transferred to five individual 5 litre circular containers (each divided into two sections, allowing for two families). Brown trout eggs under similar temperature regimes typically hatch in *ca.* 430 degree-days (Einium & Fleming 1999), after which the larvae remain in the gravel for another 200–300 degree-days until the yolk sac is absorbed and exogenous feeding is initiated. During the larval stage they can move in response to oxygen conditions (see references in Hendry *et al.* (2001)). Well-developed eyed eggs were used for our experiment because dissolved oxygen requirements increase as the embryos develop, and this stage is thus critical for the effects of oxygen on survival (e.g. oxygen consumption in chum salmon (*Oncorhynchus keta*) eggs increased from 0.000 93 to 0.005 21 mg per egg per hour throughout incubation (Alderdice *et al.* 1958)). Eyed eggs are also relatively insensitive to mechanical disturbance, so they

could be handled without causing harm (Johnson *et al.* 1989). The remaining eggs (*ca.* 200 per family) were kept in the original boxes as controls. Water was supplied to the experimental groups from a standard oxygen-stripping column that uses a flow-through of nitrogen gas to displace the dissolved oxygen (figure 1). This is a common approach in studies of dissolved oxygen effects on salmonid egg survival (e.g. Alderdice *et al.* 1958; Silver *et al.* 1963; Shumway *et al.* 1964). Each experimental egg container received de-oxygenated water through a tube at the bottom, and the eggs rested on a perforated plastic plate that was raised 5 cm above the bottom. Oxygen levels were maintained at 2.3 mg l^{-1} (s.d. = 0.78, range = 1.0–5.4) for 117 h, at an average temperature of 3.1°C (s.d. = 0.4) (i.e. 18% saturation). Pilot experiments had established that this reduction in oxygen levels (compared with ambient levels of *ca.* 14 mg l^{-1}) was sufficient to produce moderate levels of increased mortality. This oxygen level is also within the range embryos experience in the wild (chum salmon: $2\text{--}10 \text{ mg l}^{-1}$ at spawning and declining throughout incubation (Peterson & Quinn 1996)).

Following exposure to low oxygen levels, small and large eggs were separated by eye (intermediate-sized eggs were not used) from each family and treatment group (i.e. low oxygen exposed versus controls), producing 19–58 eggs in each of the 40 groups (10 small control, 10 large control, 10 small exposed, 10 large exposed). These groups were then incubated in separate boxes in well-oxygenated water. The number of eggs for each group was chosen so that the total biomass for the four groups in each family did not differ (control small = $4.64 \pm 0.85 \text{ g}$, control large = $4.67 \pm 0.83 \text{ g}$, exposed small = $4.65 \pm 0.86 \text{ g}$, exposed large = $4.66 \pm 0.83 \text{ g}$; d.f. = 3, $\chi^2 = 1.08$, $p = 0.782$, Friedman test for related samples). Within a family, large eggs were on average 36.8% heavier than small eggs in the control groups (mean \pm s.d.; small = $100.9 \pm 6.8 \text{ mg}$, large = $138.0 \pm 10.3 \text{ mg}$; $t_9 = 9.59$, $p < 0.001$, paired samples *t*-test), and 34.3% heavier in the exposed groups (small = $101.4 \pm 5.9 \text{ mg}$, large = $136.2 \pm 10.0 \text{ mg}$, $t_9 = 10.79$, $p < 0.001$). The difference in mass between small and large eggs within families did not differ between the control and exposed groups ($t_9 = 1.56$, $p = 0.154$, paired samples *t*-test). Mortality was most pronounced during and after hatching, and thus survival was measured from the start of the manipulation to the end of the larvae stage (i.e. exhaustion of yolk reserves, 20 April 2001, 695.5 degree-days after fertilization). Similar delayed mortality responses to hypoxia have been reported in previous studies (Gottwald 1965), and probably occur because damage inflicted on morphological structures or physiological processes may not cause mortality until those structures or processes are needed later in development.

Surviving and deformed juveniles were counted and then dried (24 h, 65°C) and weighed ($\pm 0.1 \text{ mg}$). Deformed juveniles were considered mortalities, because they had serious morphological deficiencies, were immobile and would not have survived exogenous feeding. Survival and deformity rates (percentage of initial egg number) were arcsine transformed prior to statistical analyses.

(b) Oxygen consumption

Eight female Atlantic salmon, reared in the same way as the brown trout described earlier, were artificially spawned on 28 November 2001. At the eyed stage (23 February 2002), groups of 10 small and 10 large eggs from each female were separated by eye (intermediate-sized eggs were not used) and weighed ($\pm 0.1 \text{ mg}$). Within a family, large eggs were on average 43.0%

heavier than small eggs (mean \pm s.d.; small = $129.3 \pm 19.3 \text{ mg}$, large = $182.0 \pm 13.0 \text{ mg}$; $t_7 = 9.84$, $p < 0.001$, paired samples *t*-test). The different groups (16 total, 10 eggs per group) were placed in 285 ml plastic containers filled with fresh water ($11.2 \text{ mg O}_2 \text{l}^{-1}$) and sealed with lids. The sealed containers were then submerged in a flow-through tank for 125 h, and turned upside down every 8 h to avoid the build up of oxygen gradients. Water temperature during the experiment was $4.4 \pm 0.2^\circ\text{C}$. At the end of the 125 h period, the containers were removed from the tank, unsealed and tested for oxygen content using an Oxyguard Handy Mk III oxygen meter (Dynamic Aqua-Supply Ltd). These measurements were used to calculate the oxygen consumption per egg per hour for the groups. Five empty containers served as controls, and these established that oxygen levels remained constant in the absence of eggs and that the decrease in the treatments was due to metabolism by the eggs.

We also examined the relationship between egg mass and the oxygen diffusion rate per unit surface area that was required to sustain the observed oxygen consumption. This was done for different egg masses by calculating:

- (i) egg volume as $V(\text{cm}^3) = \text{mass (g)} - 0.00884$ (Fleming & Ng 1987);
- (ii) surface area as $S = 4\pi(3V/4\pi)^{2/3}$; and
- (iii) the corresponding oxygen consumption using the empirical relationship between egg mass and oxygen consumption.

3. RESULTS

(a) Oxygen challenge

The initial differences in egg size were reflected in the final dry weight of the resulting juveniles, with those from large eggs being on average 41.8% heavier than those from small eggs in the control groups (mean \pm s.d.; small = $24.4 \pm 1.9 \text{ mg}$, large = $34.6 \pm 3.5 \text{ mg}$; $t_9 = 10.29$, $p < 0.001$, paired samples *t*-test), and 41.2% heavier in the low-oxygen-exposed groups (small = $24.3 \pm 1.8 \text{ mg}$, large = $34.3 \pm 3.1 \text{ mg}$; $t_9 = 14.09$, $p < 0.001$).

Mortality occurred during hatching and the larval stage. The overall mean survival rates (by female and treatment, small and large eggs pooled) were significantly lower in exposed groups than in the control groups (exposed = $58.9 \pm 22.3\%$, control = $96.0 \pm 3.0\%$; $t_9 = 7.16$, $p < 0.001$). In the control groups, the small and large eggs did not differ in survival rates (figure 2, small = $94.6 \pm 5.4\%$, large = $98.0 \pm 2.2\%$; $t_9 = 1.22$, $p = 0.252$). In the exposed groups, small eggs had a significantly lower survival than large eggs (figure 2; small = $47.2 \pm 30.2\%$, large = $74.9 \pm 23.9\%$; $t_9 = 2.70$, $p = 0.025$).

The frequencies of deformed juveniles were significantly higher in the exposed groups than in the control groups (exposed = $5.0 \pm 2.2\%$, controls = $0.8 \pm 1.2\%$; $t_9 = 5.42$, $p < 0.001$). However, the frequency of deformities did not differ between small and large eggs in the control groups (small = $1.2 \pm 1.7\%$, large = $0.3 \pm 0.8\%$; $t_9 = 2.20$, $p = 0.055$) or the exposed groups (small = $5.5 \pm 4.6\%$, large = $4.6 \pm 5.5\%$; $t_9 = 0.29$, $p = 0.781$).

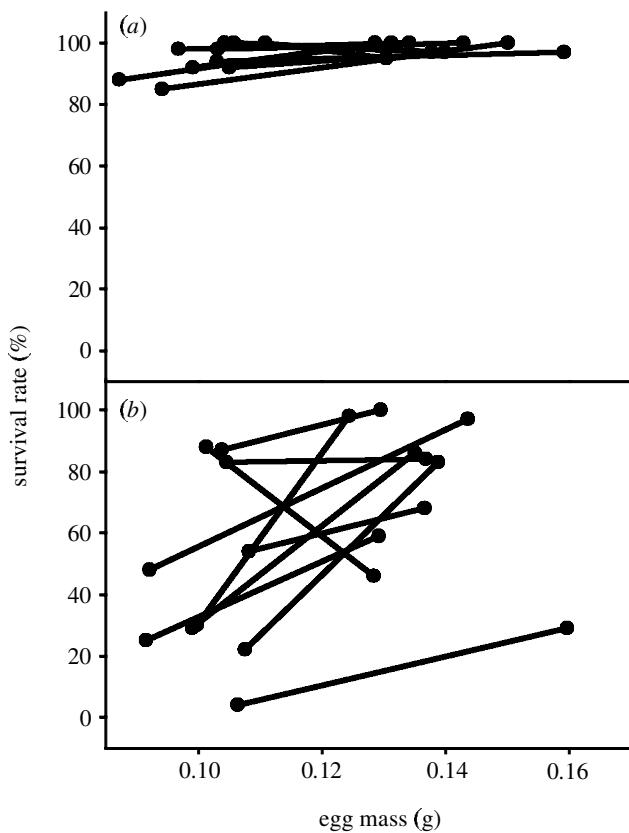


Figure 2. The relationship between mean egg mass and survival rate of eyed eggs from 10 female brown trout when reared under (a) high and (b) low levels of dissolved oxygen. Pairs of differently sized egg groups from the same families are connected by lines.

(b) Oxygen consumption

By the end of the 125 h isolation period, the oxygen content in the egg containers had decreased from 11.2 to $8.2 \pm 0.3 \text{ mg l}^{-1}$. The oxygen consumption increased with increasing mean egg size, and the scaling factor b was estimated at 0.44 (figure 3), which is sufficiently low to cause the required oxygen diffusion rate per unit of surface area to decrease with increasing egg mass (figure 4).

4. DISCUSSION

The present study demonstrated that egg size and levels of dissolved oxygen interact to influence egg survival. Under high oxygen levels (close to 100% saturation), no differences in survival rates were observed between small and large eggs, whereas under temporary exposure to reduced oxygen (18% saturation), small eggs had significantly lower survival rates than large eggs.

Our findings are in opposition to conventional, but untested expectations that low dissolved oxygen should select for smaller eggs. This conventional expectation was based on the (also untested) assumption that oxygen consumption increases proportionally with egg volume (i.e. scaling factor $b = 1$). Through direct measurement of oxygen consumption by eggs of different sizes, we found instead that the appropriate scaling factor, b , was 0.44. This scaling factor indicates that low dissolved oxygen should actually select for larger eggs (see § 1). Thus, our survival experiment and our oxygen consumption experi-

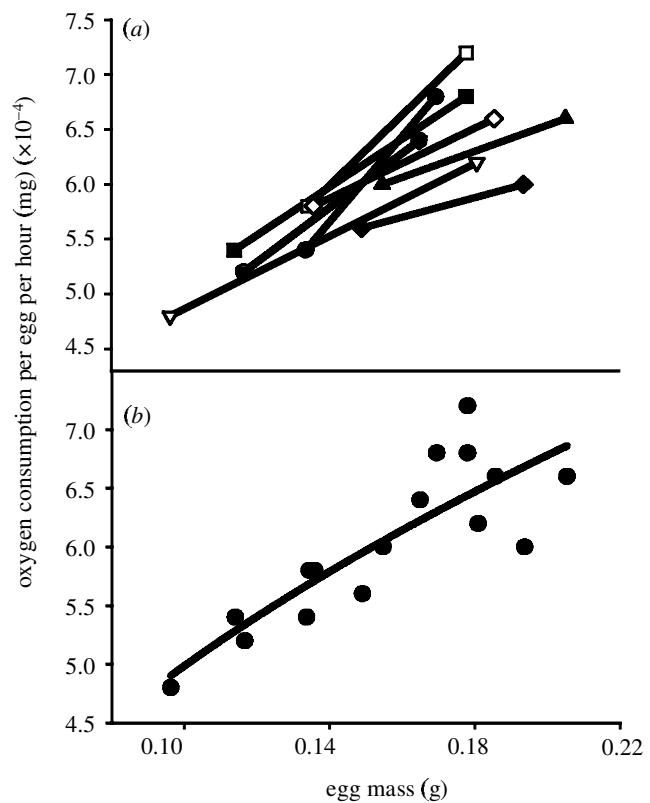


Figure 3. The relationship between egg mass and oxygen consumption. Oxygen consumption was measured for 10 eggs in each of two groups (large and small eggs) from each of eight Atlantic salmon females. In (a) different females are represented by different symbols. In (b) a power function is fitted to the entire dataset (oxygen consumption = $a \times \text{egg mass}^b$, $a = 0.0014 \pm 0.0002$, $b = 0.4434 \pm 0.0771$, $r^2 = 0.72$, $p < 0.001$).

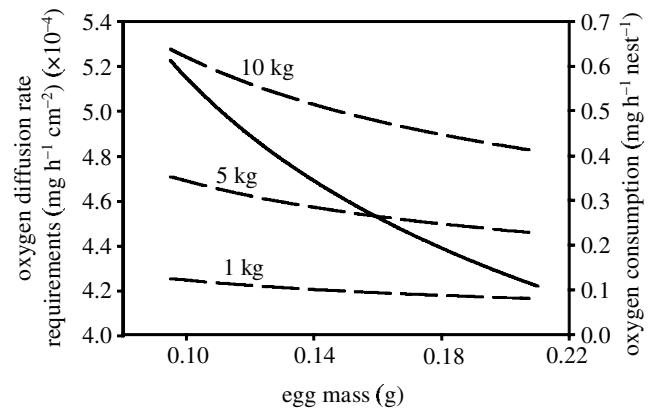


Figure 4. The estimated relationship between egg mass and oxygen diffusion rate requirements per unit of surface area for Atlantic salmon (solid curve), and the estimated relationship between egg mass and oxygen consumption per nest for females of differing body size (dashed curves). The slopes of the latter relationships increase with increasing female size.

ment corroborate each other in suggesting that the conventional expectations were exactly opposite to the true relationships. The lower than expected increase in oxygen consumption with increasing egg size may arise because much of the variation in egg size just prior to hatching is

the result of variation in yolk mass rather than body tissue mass (Beacham *et al.* 1985).

An alternative explanation for the results of our survival experiment is that selection against small eggs under low oxygen conditions is caused by the reduced ability of these eggs to cope with the stress of low oxygen (perhaps because they have lower energy stores (Einium & Fleming 1999)). Under this scenario, selection against small eggs is unrelated to the *V/S* ratio. The current experiment cannot distinguish between this scenario and the above *V/S* ratio scenario for why small eggs had lower survival under low dissolved oxygen. However, it does conclusively show that the conventional rationale (bigger is worse in low dissolved oxygen because of *V/S* constraints) is contradicted by several lines of evidence.

The present findings call for a re-examination and re-interpretation of previous work. For example, the positive correlation between egg size and gravel size in sockeye salmon (*Oncorhynchus nerka*, Quinn *et al.* 1995) may not be caused by oxygen constraints on large eggs in fine gravels, but rather by selection against small eggs caused by gape-limited egg predators that can only penetrate large gravel (Phillips & Claire 1966; Foote & Brown 1998), or by selection against large individuals that might become entombed in fine gravel (Koski 1981; Tappel & Bjornn 1983). Our results also have particular relevance to the observation that egg size commonly increases with female body size (reviewed by Roff 1992). For aquatic animals that build nests for their eggs, it has been argued that large parents can provide better-oxygenated environments for their eggs, and thus should be less susceptible to the previously assumed constraint on egg size (e.g. Van den Berghe & Gross 1989; Hendry *et al.* 2001; Kolm 2001). Our experiments indicate that this hypothesis is incorrect; if oxygen levels are sufficiently low to cause egg mortality, and large females provide better-oxygenated environments, the selective effect would be in the opposite direction, with small females being selected to produce larger eggs. A. P. Hendry and T. Day (unpublished data) have confirmed that this new prediction is consistent with Hendry *et al.*'s (2001) theoretical model, after the assumptions of that model are made consistent with empirical results from the present study.

A related issue that has previously received little attention is the effect of female size on clutch size, and thus oxygen consumption within nests (but see Lee & Strathmann 1998). Large female salmonids produce a greater total biomass of eggs, and despite constructing more nests (Fleming 1998) still deposit a greater biomass per nest than do smaller females (Atlantic salmon, based on excavation of nests from experimental studies: average egg biomass (g) per nest = $13.17 + 0.01 \times$ body mass (g), $r^2 = 0.52$, $N = 60$, $p < 0.001$; I. A. Fleming, unpublished data). Thus, the eggs of large females potentially face greater competition for oxygen within nests than do those of small females. Using the above relationship between biomass per nest and female body size, and the allometric equation relating oxygen consumption to egg size, we calculated the relationship between egg size and oxygen consumption rates per nest for females of differing body size. This exercise revealed that the magnitude of reduction in total oxygen consumption per nest due to increasing egg size varied indirectly with female body size (figure 4). As

larger females deposit a larger biomass per nest, a given increase in egg size causes a larger absolute reduction in egg number, and hence oxygen consumption, in these rather than in small females. An increase in egg size would therefore be more effective in reducing oxygen consumption in nests of large females than in those of small females. This effect, combined with the greater resistance of large eggs to anoxic conditions, may shift the selective optimum towards larger eggs for larger females.

A recent comparative study of fish egg size indicated that selection favouring within-population variation may occur primarily post-hatching (Einium & Fleming 2003). Thus, the prediction that large females benefit in terms of egg survival by producing larger eggs should be examined in future empirical studies. Yet although selection on egg size during the post-hatching period is probably strong and appears to follow the asymptotic shape suggested by the Smith-Fretwell model (Einium & Fleming 2000), the present study clearly demonstrates the scope for pre-hatching selection to influence egg-size evolution. Due to the specific nature of our experiment, we caution that the generality of our selection results should be examined for a wider variety of experimental conditions and organisms. Results obtained using other species or longer-term exposure (or at different stages) to other oxygen levels may differ. However, for salmonids and perhaps for other organisms, many of the arguments relating to pre-hatching selection on egg size under anoxic conditions have been based on untested and apparently erroneous assumptions.

The authors thank J. G. Backer, T. Husebø and the rest of the staff at the NINA Research Station, Ims, Norway, for assistance with the experiments, and H. J. Fyhn, N. B. Metcalfe and two anonymous referees for valuable comments. Financial support was provided by PhD and post-doctoral scholarships from the Norwegian Research Council to S.E. and research funding from NINA to S.E. and I.A.F.

REFERENCES

- Alderdice, D. F., Wickett, W. P. & Brett, J. R. 1958 Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. *J. Fish. Res. Bd Can.* **15**, 229–249.
- Beacham, T. D. & Murray, C. B. 1993 Fecundity and egg size variation in North American Pacific salmon (*Oncorhynchus*). *J. Fish Biol.* **42**, 485–508.
- Beacham, T. D., Withler, F. C. & Morley, R. B. 1985 Effect of egg size on incubation time and alevin and fry size in chum salmon (*Oncorhynchus keta*) and coho salmon (*Oncorhynchus kisutch*). *Can. J. Zool.* **63**, 847–850.
- Chapman, D. W. 1988 Critical review of variables used to define effects of fines in redds of large salmonids. *Trans. Am. Fish. Soc.* **117**, 1–21.
- Donohue, K. & Schmitt, J. 1998 Maternal environmental effects in plants: adaptive plasticity? In *Maternal effects as adaptations* (ed. T. A. Mousseau & C. W. Fox), pp. 137–158. Oxford University Press.
- Einium, S. & Fleming, I. A. 1999 Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. *Proc. R. Soc. Lond. B* **266**, 2095–2100. (DOI [10.1098/rspb.1999.0893](https://doi.org/10.1098/rspb.1999.0893).)
- Einium, S. & Fleming, I. A. 2000 Highly fecund mothers sacrifice offspring survival to maximise fitness. *Nature* **405**, 565–567.
- Einium, S. & Fleming, I. A. 2003 Does within-population variation in fish egg size reflect maternal influences on optimal values? *Am. Nat.* (In the press.)

- Fleming, I. A. 1998 Pattern and variability in the breeding system of Atlantic salmon (*Salmo salar*), with comparisons to other salmonids. *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1), 59–76.
- Fleming, I. A. & Gross, M. 1990 Latitudinal clines: a trade-off between egg number and size in pacific salmon. *Ecology* **71**, 1–11.
- Fleming, I. A. & Ng, S. 1987 Evaluation of techniques for fixing, preserving and measuring salmon eggs. *Can. J. Fish. Aquat. Sci.* **44**, 1957–1962.
- Foote, C. J. & Brown, G. S. 1998 Ecological relationship between freshwater sculpins (genus *Cottus*) and beach-spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Can. J. Fish. Aquat. Sci.* **55**, 1524–1533.
- Gottwald, S. 1965 The influence of temporary oxygen deprivation on embryonic development of rainbow trout (*Salmo gairdneri* Rich.). *Z. Fish. Deren Hilfswiss.* **13**, 63–84.
- Hammond, D. S. & Brown, V. K. 1995 Seed size of woody-plants in relation to disturbance, dispersal, and soil type in wet neotropical forests. *Ecology* **76**, 2544–2561.
- Hendry, A. P., Day, T. & Cooper, A. B. 2001 Optimal size and number of propagules: allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. *Am. Nat.* **160**, 387–407.
- Holtby, L. B. & Healey, M. C. 1986 Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **43**, 1946–1959.
- Hutchings, J. A. 1991 Fitness consequences of variation in egg size and food abundance in brook trout *Salvelinus fontinalis*. *Evolution* **45**, 1162–1168.
- Johnson, S. C., Chapman, G. A. & Stevens, D. G. 1989 Relationships between temperature units and sensitivity to handling for coho salmon and rainbow trout embryos. *Prog. Fish-Cult.* **51**, 61–68.
- Jonsson, N. & Jonsson, B. 1999 Trade-off between egg mass and egg number in brown trout. *J. Fish Biol.* **55**, 767–783.
- Kamler, E. 1992 *Early life history of fish: an energetics approach*. London: Chapman & Hall.
- Kaplan, R. H. 1998 Maternal effects, developmental plasticity, and life history evolution: an amphibian model. In *Maternal effects as adaptations* (ed. T. A. Mousseau & C. W. Fox), pp. 244–260. Oxford University Press.
- Kolm, N. 2001 Females produce larger eggs for large males in a paternal mouth-brooding fish. *Proc. R. Soc. Lond. B* **268**, 2229–2234. (DOI 10.1098/rspb.2001.1792.)
- Koski, K. V. 1981 The survival and quality of two stocks of chum salmon (*Oncorhynchus keta*) from egg deposition to emergence. *Rapp. Cons. Explor. Mer* **178**, 330–333.
- Krogh, A. 1959 *The comparative physiology of respiratory mechanisms*. Philadelphia, PA: University of Pennsylvania Press.
- Lacroix, G. L. 1985 Survival of eggs and alevins of Atlantic salmon (*Salmo salar*) in relation to the chemistry of interstitial water in redds in some acidic streams of Atlantic Canada. *Can. J. Fish. Aquat. Sci.* **42**, 292–299.
- Lee, C. E. & Strathmann, R. R. 1998 Scaling of gelatinous clutches: effects of sibling competition for oxygen on clutch size and parental investment per offspring. *Am. Nat.* **151**, 293–310.
- Mousseau, T. A. & Fox, C. W. 1998 *Maternal effects as adaptations*. Oxford University Press.
- Peterson, N. P. & Quinn, T. P. 1996 Spatial and temporal variation in dissolved oxygen in natural egg pockets of chum salmon, in Kennedy Creek, Washington. *J. Fish Biol.* **48**, 131–143.
- Phillips, R. W. & Claire, E. W. 1966 Intragravel movement of the reticulate sculpin, *Cottus perplexus* and its potential as a predator on salmonid embryos. *Trans. Am. Fish. Soc.* **95**, 210–212.
- Quinn, T. P., Hendry, A. P. & Wetzel, L. A. 1995 The influence of life history trade-offs and the size of incubation gravels on egg size variation in sockeye salmon (*Oncorhynchus nerka*). *Oikos* **74**, 425–438.
- Roff, D. A. 1992 *The evolution of life histories; theory and analysis*. New York: Chapman & Hall.
- Rubin, J.-F. & Glimsäter, C. 1996 Egg-to-fry survival of the sea trout in some streams of Gotland. *J. Fish Biol.* **48**, 585–606.
- Sargent, R. C., Taylor, P. D. & Gross, M. R. 1987 Parental care and the evolution of egg size in fishes. *Am. Nat.* **129**, 32–46.
- Seymour, R. S. & Bradford, D. F. 1995 Respiration of amphibian eggs. *Physiol. Zool.* **68**, 1–25.
- Shumway, D. L., Warren, C. E. & Doudoroff, P. 1964 Influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. *Trans. Am. Fish. Soc.* **93**, 342–356.
- Silver, S. J., Warren, C. E. & Doudoroff, P. 1963 Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos at different water velocities. *Trans. Am. Fish. Soc.* **92**, 327–343.
- Smith, C. C. & Fretwell, S. D. 1974 The optimal balance between size and number of offspring. *Am. Nat.* **108**, 499–506.
- Tappel, P. D. & Bjornn, T. C. 1983 A new method of relating size of spawning gravel to salmonid embryo survival. *N. Am. J. Fish. Mgmt* **3**, 123–135.
- Van den Berghe, E. P. & Gross, M. R. 1989 Natural selection resulting from female breeding competition in a pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution* **43**, 125–140.