
Environmental unpredictability and offspring size: conservative versus diversified bet-hedging

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ABSTRACT

Classic life-history theory and extensions thereof can readily explain variation in egg size among populations and individuals. However, most such models assume that there is some degree of predictability in offspring environment. Offspring provisioning when environments vary unpredictably is more problematic and may lead to bet-hedging (i.e. reducing variance in fitness). Bet-hedging may involve the production of fewer and larger offspring (conservative) or of variable-sized offspring (diversified). The use of diversified bet-hedging theory to explain within-clutch variation is common but controversial, and simulation models have shown that the fitness benefits of such variability depend critically on the shape of the egg size–offspring fitness curve. Here, we use one of the few empirically derived egg size–offspring fitness functions (from Atlantic salmon) in conjunction with simulations to examine the plausibility for the evolution of such bet-hedging strategies. We show that conservative bet-hedging can be a viable strategy for dealing with unpredictable environments, while diversified bet-hedging is rarely selectively advantageous (i.e. only under extremely variable environments), and then only for purely annual organisms. This is supported by empirical evidence from iteroparous Atlantic ($n = 37$ populations) and semelparous Pacific ($n = 26$ populations) salmon where less than 3% of the variation in egg size among wild fish is due to within-clutch variability. Only under novel (rare) rearing conditions, such as captive rearing to maturity in freshwater, was a significant increase in within-clutch variation observed. These patterns in conjunction with the modelling results indicate that within-clutch variation, at least in salmon, is more likely a reflection of the direct influences of the rearing environment on a female's ability to allocate resources evenly than of evolutionary adaptation. Future work in the area of egg size evolution in unpredictable environments may benefit from a stronger focus on conservative rather than diversified bet-hedging.

Keywords: environmental variation, life-history evolution, *Oncorhynchus*, physiological constraints, *Salmo salar*.

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INTRODUCTION

Classic life-history theory predicts that in a given predictable environment, a single egg size will evolve that maximizes fitness and, by extension, that variation in egg size among populations is a reflection of environmental differences (Svårdson, 1949; Smith and Fretwell, 1974). Egg size variation may also exist among individuals *within* populations, and a suite of theoretical models suggest that such variation may be adaptive if the egg size–offspring fitness function differs among individuals (Parker and Begon, 1986; Sargent *et al.*, 1987; McGinley, 1989; Hendry *et al.*, 2001). This is likely if maternal phenotype influences offspring habitat quality, as recently supported by a comparative study of egg size variation within fishes (Einum and Fleming, 2002). Egg size may also vary between reproductive bouts within females as a response to temporal changes in the environment and/or changes in accessibility to different environments (Kerfoot, 1974; Kaplan and Cooper, 1984; Chambers and Leggett, 1996; Fox and Czesak, 2000).

Application of the above models assumes that there is some degree of predictability in offspring environment, which may not be unreasonable in many cases. Offspring provisioning when environments vary unpredictably, however, is more problematic, and may lead to bet-hedging. In brief, bet-hedging theory suggests that under certain conditions genotypes with a reduced arithmetic mean fitness may be at an evolutionary advantage if this is associated with a reduced temporal variation in fitness (reviewed in Philippi and Seger, 1989). That is, it may be better to have at least some success each year (or generation) than having high success in some years and complete failure in others. Two types of bet-hedging strategies exist: conservative and diversified. In terms of offspring provisioning, conservative bet-hedging corresponds to producing fewer but larger offspring than would be the optimum in a stable environment with the same long-term mean quality. This strategy provides greater reproductive success during poor years (because larger eggs are more successful during poor conditions; e.g. Einum and Fleming, 1999), but less success during good years (when the optimal egg size is smaller). In contrast, diversified bet-hedging is achieved by increasing the phenotypic variance among individual offspring to ensure that at least some of them are successful (Philippi and Seger, 1989). Thus, in terms of offspring provisioning, this would correspond to producing variable egg sizes within a clutch.

Can diversified bet-hedging provide an explanation for the existence of egg size variation within a female's clutch? Or is such within-clutch variation a physiological/developmental constraint in a female's ability to allocate resources evenly? Some authors have argued that females should produce variable egg sizes any given year in an unpredictable environment (Capinera, 1979; Crump, 1981). Most recently, Koops *et al.* (2003) reported considerable differences in within-clutch egg size variation among populations of a salmonid fish, brook trout (*Salvelinus fontinalis*), with variation being positively correlated with a surrogate measure of environmental unpredictability. In contrast, McGinley *et al.* (1987), using simulation models, concluded that a single offspring size is often the optimal parental investment strategy under such conditions. Only under rare conditions did environmental heterogeneity favour the production of variable offspring. Koops *et al.* (2003) also found that within-clutch variability in egg size decreased as mean egg size increased among and within populations, and proposed that variability in good environments (i.e. when the optimal egg size is small) is adaptive. The reasoning behind this is that when females produce small eggs, the potential cost (in terms of reduced reproductive success) of

misjudging future environmental conditions is larger than when females produce large eggs. By contrast, other authors have used verbal arguments to claim that within-clutch variability is non-adaptive (e.g. Fox and Czesak, 2000). Thus, the issue of whether such variability is adaptive remains controversial.

A key determinant of whether within-clutch variability is advantageous is the shape of the relationship between egg size and offspring fitness (McGinley *et al.*, 1987). Unfortunately, little quantitative information exists about the functional relationship between egg size and offspring fitness, and this has made it difficult to quantitatively examine the adaptive advantage of within-clutch variability for any organism. Such a relationship, however, has recently been established for a population of Atlantic salmon, *Salmo salar* (Einum and Fleming, 2000). Here, we use this empirically derived egg size–offspring fitness function in conjunction with simulations to test whether unpredictable environments should select for conservative and/or diversified bet-hedging with respect to egg size. Moreover, we present empirical data on within-clutch egg size variability for Atlantic and Pacific (i.e. *Oncorhynchus kisutch*, *O. keta* and *O. tshawytscha*) salmon reared under different environments to examine the degree of, and variation in, within-clutch variability in egg size.

METHODS

Model

Offspring fitness (f) is a function of egg size (m):

$$f(m) = 1 - (m_{\min}/m)^a$$

where $m_{\min}$ is the minimum viable egg size and a is a constant (e.g. Smith and Fretwell, 1974; McGinley *et al.*, 1987; Einum and Fleming, 2000). Using parameter values derived for Atlantic salmon ($a = 1.507$ and $m_{\min} = 0.068$; Einum and Fleming, 2000), we modelled mean and temporal variability in environmental quality by varying the mean and variability in $m_{\min}$ (cf. McGinley *et al.*, 1987). We adjusted mean $m_{\min}$ down (good environment) or up (poor environment) relative to the empirical value (0.068 g) by 25 and 50% (mean $m_{\min} = 0.027, 0.049, 0.084$ and 0.098 g) to provide a broad range of environmental qualities over which to examine affects. The corresponding optimal egg sizes were calculated according to Einum and Fleming (2000) and used in the simulations. We simulated temporal environmental variability about the mean by letting $m_{\min}$ be random normally distributed with a coefficient of variation (CV) of 0, 10, 20, 30, 40 or 50%. Given that the empirically derived ratio of $m_{\min}$ to mean egg size in Atlantic salmon is 0.56 (Einum and Fleming, 2000), a CV of 30% must be considered large (and probably rare), causing total reproductive failure during some years. Thus, the range of CVs chosen (0–50%) is likely to encompass the range of possible scenarios in extant populations. In theory, it is possible that the value of a , which determines the steepness of the function, varies across environments as well. However, for a given range of egg sizes, $m_{\min}$ determines the proximity of this range to the asymptote of the egg size–offspring fitness curve and, in effect, the steepness of the relationship between egg size and fitness. In accordance with McGinley *et al.* (1987), we therefore chose to keep a constant while varying $m_{\min}$.

For each combination of mean and variation in $m_{\min}$, we simulated different within-clutch egg size distribution scenarios, with egg size being random normally distributed around the

corresponding optimum with $CV = 0, 20, 40$ and 60% (encompassing reported ranges; Koops *et al.*, 2003). We determined mean reproductive success ($RS = f(m) * M/m$, where M is total gonadal mass, set to 100 g per individual) under each scenario for 100 phenotypically homogenous populations over 100 years, and used the geometric mean RS over the 100 years as the measure of fitness for each population. The geometric mean RS is the least conservative measure of fitness when testing for the adaptive value of bet-hedging, because complete failure in any single year causes the overall RS to go to zero (equivalent to the population going extinct). However, for organisms that are iteroparous and/or have overlapping generations (e.g. salmonid fishes, such as Atlantic salmon and brook trout), the arithmetic mean discounted by the variance among years ($\text{mean} - [\text{variance}/2 * \text{mean}]$) may be a more appropriate fitness measure than the geometric mean (Lacey *et al.*, 1983).

Egg size data

We collected egg samples from Atlantic salmon in Norway from 20 wild, two sea-ranched (hatchery), 12 captive freshwater-reared and three captive saltwater-reared populations (see Appendix). Wild fish were caught and stripped at ovulation at local hatcheries, and scale analyses were performed to remove farm females from the material. Sea-ranched populations were reared captive in freshwater at the NINA Research Station, Ims, southwestern Norway, and then released as smolts (i.e. juvenile seaward migratory stage) to rear naturally in the ocean before returning as adults to the River Imsa, where they were sampled. Captive freshwater populations were the offspring of wild adults that had been brought into the gene bank facility at Haukvik, central Norway (18 populations) or the NINA Research Station (two populations), and whose eggs and offspring had been incubated and reared to adulthood in freshwater. Captive saltwater populations included two wild-origin populations and one aquaculture strain that were reared initially in freshwater and then transferred as smolts to sea-pens of a commercial fish farm in southwestern Norway, where they were reared until maturity. Data for coho salmon (*O. kisutch*) derive from Fleming and Gross (1990) and represent 13 wild and eight sea-ranched populations from Washington state, USA and British Columbia, Canada (Lorenzetta Creek excluded because individual egg size measures were missing). Egg samples from chum salmon (*O. keta*) were collected from two wild (Blaney [$n = 9$ females] and Worth [$n = 17$] Creeks) and two hatchery (Chehalis [$n = 6$ females; Fleming and Ng, 1987] and Chilliwack [$n = 3$]) populations within the Lower Fraser River drainage, Canada. Chinook salmon (*O. tshawytscha*) eggs were sampled from the Quinsam Hatchery, Vancouver Island, Canada ($n = 15$ females).

Ten eggs from each female were weighed individually for calculation of the mean and CV of egg size. The coefficient of variation was arcsine-transformed before analysis and where the data did not meet the requirements for parametric analysis, non-parametric tests were used.

RESULTS

Model results

In stable environments, selection always resulted in a decrease in reproductive success (RS) with increasing amounts of within-clutch variation in egg size (Fig. 1). Moreover,

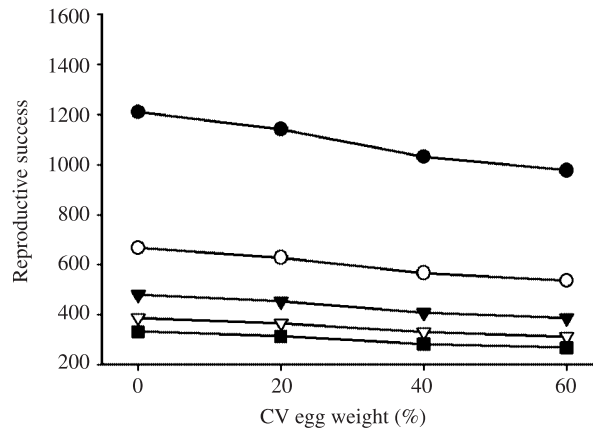


Fig. 1. Reproductive success as a function of within-clutch egg size variation (CV egg weight) in temporally stable environments of differing qualities. Environmental quality, as described by the minimum viable egg size ($m_{\min}$), increases from the bottom to the top line [$m_{\min} = 0.027$ (●), 0.049 (○), 0.068 (▼), 0.084 (▽) and 0.098 (■)].

the decrease in RS with increasing egg size variation was similar across the different environmental qualities (19.3% decrease from CV = 0 to 60% for all values of $m_{\min}$). The addition of temporal environmental variability (i.e. variability about the mean $m_{\min}$) caused a decrease in RS under all egg size variation scenarios (Fig. 2a). In a stable or moderately fluctuating environment (CV $m_{\min} = 0$ –20%), RS always decreased with increasing variation in egg size. In highly fluctuating environments (CV $m_{\min} = 30$ –50%), geometric mean RS increased initially with increasing egg size variation, suggesting that variable egg sizes may be advantageous in such extreme conditions (Fig. 2a). However, using the arithmetic mean RS discounted by the variance, which is more appropriate for iteroparous organisms and/or those having overlapping generations, any advantage of variable egg size disappeared (Fig. 2b).

To examine whether variable environmental conditions select for larger eggs in organisms that are iteroparous and/or have overlapping generations, we used our baseline environmental parameters ($a = 1.507$, $m_{\min} = 0.068$) and calculated the arithmetic mean RS discounted by the variance among years for 100 populations over 100 years under different combinations of mean egg size (range: 0.100–0.400 g, increments of 0.005 g) and CV of $m_{\min}$ (range: 0–50%, increments of 1%). This simulation demonstrated that variable environments select for larger eggs than the optimum in a stable environment with identical long-term average environmental conditions (Fig. 3). For example, at CV of $m_{\min} = 50\%$, the optimal egg size was 0.145 g, in contrast to the optimal value of 0.125 g in a stable environment. The corresponding gain in reproductive success by increasing egg size in this example was about 5% (420 vs 400).

Our simulations show that within-clutch variability in egg size is only selectively advantageous when environmental conditions are highly variable (and unpredictable) and the geometric mean RS is the appropriate measure of fitness (Fig. 2). However, even under such constrained circumstances, an alternative strategy would be to produce a single size of egg that is larger than the optimum predicted in a stable environment with identical

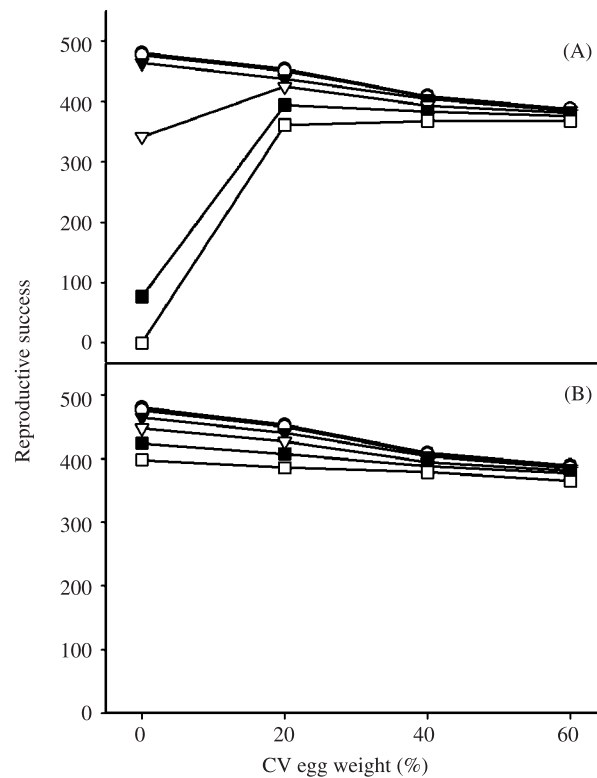


Fig. 2. (A) Geometric mean reproductive success and (B) arithmetic mean reproductive success discounted by temporal variance as a function of within-clutch egg size variation in environments of differing temporal variability. Temporal variability in environmental conditions increase from the top to the bottom line [mean $m_{\min}$ = 0.068; CV $m_{\min}$ = 0% (●), 10% (○), 20% (▼), 30% (▽), 40% (■) and 50% (□)].

long-term mean conditions. To examine this we used one of the environmental conditions that selected for variable egg size (mean $m_{\min}$ = 0.068, CV $m_{\min}$ = 40%; see Fig. 2a), and calculated the geometric mean RS of 100 populations over 100 years under different combinations of mean (range: 0.100–0.400 g, increments of 0.005 g) and CV (range: 0–40%, increments of 1%) of egg size. The combination of mean and CV of egg size that maximized RS under these conditions was 0.150 g and 5%, respectively (Fig. 4). There was a strong effect of mean egg size on RS around this optimum and a weaker effect of CV. For CV = 0, the geometric mean RS at this mean size (RS = 392 for egg size of 0.150 g) was 734% larger than that at the optimal egg size in a stable environment with the same mean quality (RS = 47 for egg size of 0.125 g). For mean egg size = 0.150, the difference in geometric mean RS at CV = 0 and 5% was only 10% (392 vs 431). Thus, for strictly annual organisms in highly variable environments, there is a high premium on producing larger eggs, and a somewhat smaller premium on producing more variable eggs than in stable environments. The pay-off of employing these strategies in semelparous organisms is larger than the more modest effect iteroparous organisms can obtain by increasing egg size in variable environments (Fig. 3).

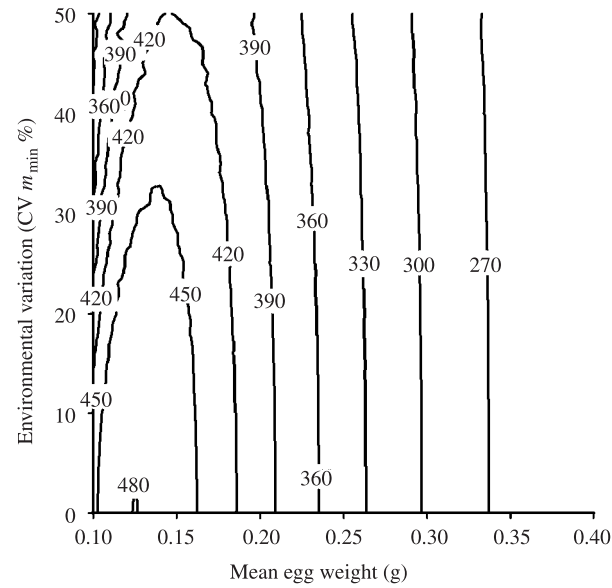


Fig. 3. Arithmetic mean reproductive success discounted by the variance among years under different combinations of mean egg size (in the absence of within-clutch egg size variation) and environmental variation. Mean $m_{\min} = 0.068$.

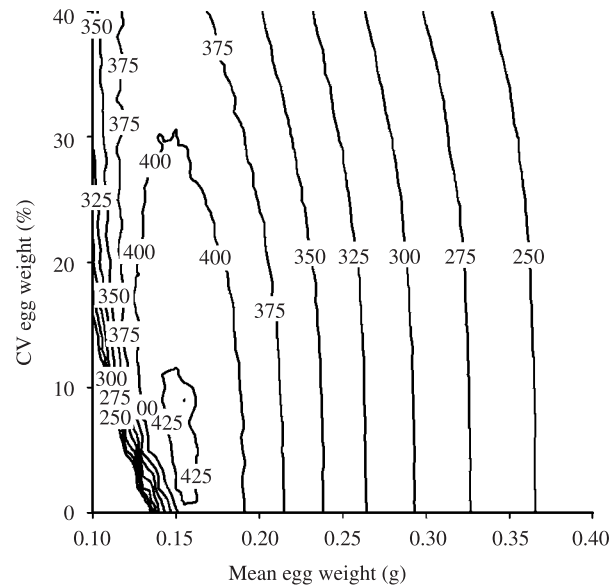


Fig. 4. Geometric mean reproductive success in a temporally variable environment under different combinations of mean and within-clutch variation in egg size. Mean $m_{\min} = 0.068$, CV $m_{\min} = 40\%$.

Variation in mean and CV of egg size among populations and environments

Mean egg size differed significantly among populations within both wild ($F_{19,271} = 12.35$, $P < 0.001$) and captive freshwater-reared populations of Atlantic salmon ($F_{11,195} = 3.74$, $P < 0.001$). Moreover, median within-clutch CV of egg wet weight differed among wild (Kruskal-Wallis tests; wild: $\chi^2 = 45.38$, d.f. = 19, $P = 0.001$) but not freshwater-reared populations ($\chi^2 = 14.15$, d.f. = 11, $P = 0.225$). There were pronounced differences in CV of egg weight between the two environments, with the mean of median CVs for freshwater-reared populations being 1.7 times greater than that of wild populations (Fig. 5; wild: 3.68 ± 0.58 ; freshwater-reared: 6.14 ± 1.04 ; Mann-Whitney U -test; $n = 32$, $Z = 4.59$, $P < 0.001$). Moreover, less than 3% of the variation in egg size of wild females was due to within-clutch variability, while 26% of that of captive females was due to within-clutch variability. The CVs of sea-ranched (hatchery) and captive saltwater-reared Atlantic salmon populations were similar to those of wild populations (Fig. 5). These results are further substantiated if we compare directly the two populations that were reared in all four environments (Imsa and Lone). Both populations showed significant differences among

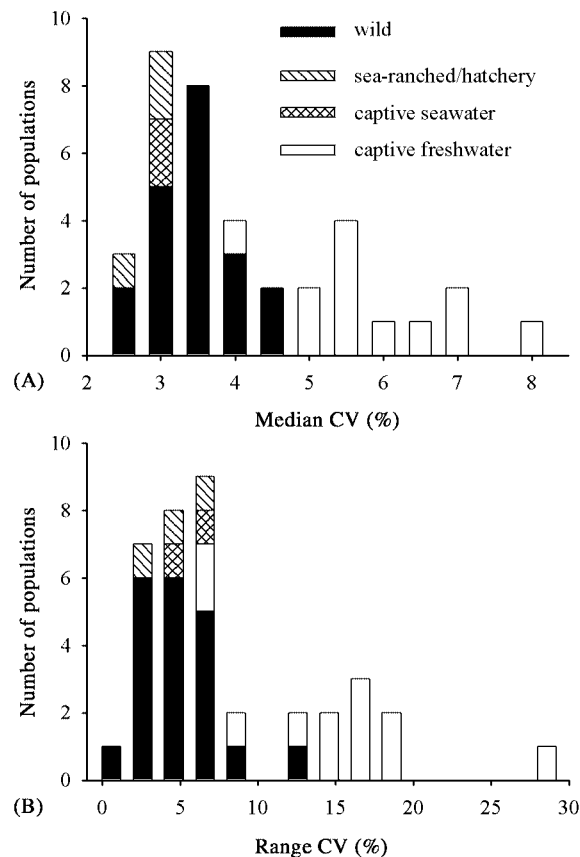


Fig. 5. Distribution of (A) median and (B) range of within-clutch variation in egg size of wild, sea-ranched/hatchery, captive seawater and captive freshwater populations of Atlantic salmon.

environments (Imsa: $\chi^2 = 22.61$, d.f. = 3, $P < 0.001$; Lone: $\chi^2 = 10.05$, d.f. = 3, $P = 0.018$), with freshwater-reared being more variable than all other environments in both populations ($P < 0.004$ and $P < 0.028$ in all contrasts for Imsa and Lone, respectively). There were no differences among the other three types (Imsa: $\chi^2 = 0.07$, d.f. = 2, $P = 0.965$; Lone: $\chi^2 = 0.01$, d.f. = 2, $P = 0.995$).

The patterns of within-clutch egg size variation for Pacific salmon were similar to those of wild and sea-ranched Atlantic salmon populations (Fig. 6). There was no significant difference in the within-clutch CV of egg weight (arcsine-square root transformed) between wild and sea-ranched coho salmon populations (nested ANOVA, females nested within type: $F_{1,20} = 1.79$, $P = 0.194$). Moreover, chum and chinook salmon populations, while too few in number to test statistically, appear to follow a similar pattern (Fig. 6). There were significant differences among coho and chum salmon populations in both mean (coho: $F_{20,488} = 16.02$, $P < 0.001$; chum: $F_{3,31} = 5.39$, $P = 0.004$) and within-clutch CV of egg size (coho: $F_{20,488} = 4.75$, $P < 0.001$; chum: $F_{3,31} = 5.04$, $P = 0.006$). However, within-clutch variability explained less than 1% of the total egg size variability for coho (0.4%), chum (0.5%) and chinook salmon (0.4%).

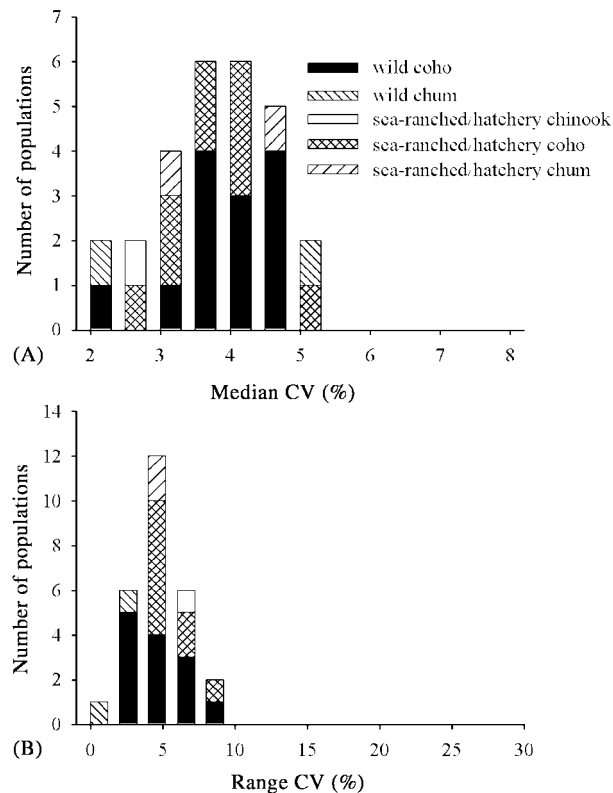


Fig. 6. Distribution of (A) median and (B) range of within-clutch variation in egg size of Pacific salmon. Wild and sea-ranched/hatchery coho salmon, wild and sea-ranched/hatchery chum salmon, and sea-ranched/hatchery chinook salmon populations.

DISCUSSION

Our simulations indicate that conservative bet-hedging (i.e. production of fewer and larger eggs than the optimum in stable environments) can be a viable strategy for dealing with variable (and unpredictable) environments. By contrast, diversified bet-hedging (i.e. within-clutch variation in egg size) can be selectively advantageous only under very restricted conditions. Neither good nor variable environments select for within-clutch egg size variability in organisms that have asymptotic egg size–offspring fitness curves similar to that estimated for Atlantic salmon and which are iteroparous and/or have overlapping generations. For purely annual organisms, some fitness advantage can be accrued from producing variable egg sizes in highly variable environments. However, these are minor compared with those obtained through the production of eggs larger than the optimum under stable environments. The selective advantage of producing larger eggs in variable environments for annual organisms is similar to that found by Lalonde (1991), who used a hypothetical asymptotic egg size–offspring fitness function to model effects of environmental variability. Lalonde's (1991) model, however, did not simultaneously consider the effect of varying egg size within clutches as we have done here. Our results show that when both are allowed to evolve simultaneously, the greatest fitness benefit to females in variable environments derives from the production of larger, rather than more variable eggs.

Koops *et al.* (2003) found that within-clutch variability in egg size decreased as mean egg size increased among and within populations of the iteroparous brook trout and suggested that within-clutch variability increased as environments became less predictable. Two hypotheses were proposed to explain these patterns. First, the 'imperfect information hypothesis' proposed that when females expect future conditions to be poor and the optimal egg size is large, egg size variability should be minimized to avoid the cost of unequal allocation. Second, the 'environmental predictability hypothesis' proposed that the optimal egg size should also decrease as environmental predictability decreases and the production of variable sized eggs within clutches should become optimal. These propositions contrast with our theoretical results, and two potential factors may be responsible for this discrepancy. First, the egg size–offspring fitness function for brook trout in the wild may not be asymptotic. However, it is unlikely that it would differ substantially in shape (i.e. not asymptotic) from that of Atlantic salmon, a closely related species occupying broadly similar juvenile habitat (i.e. north temperate streams and rivers). Moreover, there is little evidence that large eggs of salmonid fishes, including brook trout, incur a disadvantage (e.g. Hutchings, 1991; Einum and Fleming, 1999; Einum *et al.*, 2002). Thus, the general findings of our model should be applicable to brook trout as well.

Alternatively, the observations of Koops *et al.* (2003) may reflect pure phenotypic responses to environmental conditions or physiological status rather than evolutionary adaptations. Our results indicate that environmental conditions may have strong direct effects on egg size variability. Within-clutch variation differed among populations in the wild, although it explained little of the overall egg size variability (< 3% for Atlantic and < 1% for Pacific salmon). Captive rearing of salmon to maturity in freshwater (done at two independent sites), however, generated a significant increase in within-clutch variation (Fig. 5) and was responsible for explaining a greater percentage (26%) of the overall variability. This environmentally driven increase in within-clutch variation was most clearly illustrated by paired comparison of populations reared under both conditions. Moreover, there was no significant among-population difference in within-clutch variation for

captively reared fish despite significant differences in mean egg size, suggesting that the effect was common to the environment rather than specific to the population (i.e. an adaptation). It might be argued that the freshwater-reared populations, having experienced artificially high levels of food abundance, should produce small and variable eggs according to the imperfect information hypothesis. However, if this were the case, then seawater-reared populations should also show increased within-clutch variability, but they do not. Thus, unpredictability in food abundance cannot explain these observations. We suggest that the observations of Koops *et al.* (2003) may reflect purely physiological constraints in the ability to produce equally sized eggs, which may be influenced by the females' physiological status or the environment.

Invoking verbal arguments to explain observed within-clutch egg size variation as adaptive is not uncommon (e.g. Capinera, 1979; Crump, 1981; Lips, 2001). However, we believe that such arguments may oversimplify the situation, especially given the non-intuitive way in which such variation may influence an organism's fitness. Models with clearly stated assumptions and reasonable estimates of the egg size–offspring fitness function may be more informative for developing predictions about the adaptive value of within-clutch egg variability. If egg size–offspring fitness curves are similar to those of Atlantic salmon, evolution of within-clutch egg size variation as an adaptive response to environmental variation appears unlikely for iteroparous organisms and/or those having overlapping generations. Even for strictly annual organisms, the greatest fitness benefit to females in variable environments derives from the production of larger, rather than more variable eggs. There were also some benefits of producing larger eggs in variable environments for iteroparous organisms. Thus, future work in the area of egg size evolution in unpredictable environments may benefit from a stronger focus on conservative rather than diversified bet-hedging.

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APPENDIX

Populations of Atlantic salmon used (river names, counties) and their sample size (n = number of females sampled)

Population	n	Population	n
Wild		Sea-ranched	
Aagårdselva, Østfold	5	Imsa, Rogaland	88
Alta, Finnmark	12	Lone, Hordaland	11
Åselva, Nordland	19		
Audna, Vest-Agder	20	Captive freshwater	
Bjerkreim, Rogaland	20	Aureelva, Møre & Romsdal	10
Daleelva, Hordaland	5	Byaelva, Nord-Trøndelag	9
Daleelva, Sogn & Fjordane	5	Driva, Møre & Romsdal	8
Eira, Møre & Romsdal	12	Eidsdal, Sogn & Fjordane	23
Etne, Hordaland	8	Figga, Nord-Trøndelag	20
Glomma, Østfold	13	Fjelna, Sør-Trøndelag	8
Håelva, Rogaland	20	Imsa, Rogaland	21
Imsa, Rogaland	16	Måna, Møre & Romsdal	28
Jølstra, Sogn & Fjordane	13	Ogna, Nord-Trøndelag	20
Jørpelandselva, Rogaland	20	Rauma, Møre & Romsdal	25
Korsbrekkelva, Møre & Romsdal	12	Usma, Møre & Romsdal	11
Lone, Hordaland	17	Valldal, Møre & Romsdal	24
Nausta, Sogn & Fjordane	7		
Numedalslågen, Vestfold	14	Captive seawater	
Oselva, Hordaland	14	Imsa, Rogaland	53
Vikja, Møre & Romsdal	5	Lone, Hordaland	7
		Aquagen (commercial strain)	8

