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Environmental predictability and the cost of imperfect information: influences on offspring size variability

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ABSTRACT

We examined the potential influence of mean egg size and environmental predictability on the variation of egg size within and among female brook trout, *Salvelinus fontinalis*. First, we examined egg size variability as a means of balancing the costs of imperfect information and unequal allocation among eggs, predicting that egg size variability will increase as optimal egg size decreases. In the first empirical test of the imperfect information hypothesis, we found support for this prediction, with the variability of egg sizes within females decreasing as mean egg size increased in every population ($n = 10$) and year ($n = 13$) examined. Second, we tested the hypothesis that inter-clutch variability in egg size increases as environments become less predictable. When we compared the variability in egg sizes among females across populations and years, we found greater variability in the mean egg size among females in less predictable environments. Finally, we tested the hypothesis that intra-clutch variability increases as environments become less predictable. When we compared the mean variability in egg size within females across populations and years, we found greater variability in egg sizes within females in less predictable environments. Support for these three hypotheses suggests that there is less egg size variability, both within and among females, when environments are more predictable, and that females use variability in egg size to offset the cost of imperfect information when producing smaller eggs.

Keywords: brook trout, egg size variability, environmental predictability, imperfect information, life-history decisions, *Salvelinus fontinalis*.

INTRODUCTION

The assumption that resources are allocated evenly among offspring is common to many optimal egg size models (e.g. Smith and Fretwell, 1974; Ware, 1975; Kaplan and Cooper, 1984; Forbes, 1991; Lalonde, 1991). However, this is generally not observed in nature. Egg size has been observed to vary among females based on, for example, habitat and latitude in parasitic trematodes (Poulin and Hamilton, 2000), female condition in common eiders, *Somateria mollissima* (Hanssen *et al.*, 2002), maternal and grand-maternal age in mice (Wang and vom Saal, 2000), female size, food availability, diet, oviposition host, maternal

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density, season, temperature, paternal investment and predation risk in arthropods (for a review, see Fox and Czesak, 2000), and based on season, temperature, moisture, irradiance, photoperiod, nutrients, defoliation and seed predation in plants (see references in McGinley *et al.*, 1987). Within females, variability in egg size has been attributed to female age in arthropods (Fox and Czesak, 2000), pond type (temporary *vs* permanent) in treefrogs of the genus *Hyla* (Crump, 1981), male attractiveness in mallards, *Anas platyrhynchus* (Cunningham and Russell 2000), and egg predation risk in acanthosomatid bugs (Kudo, 2001). In fishes, egg size is rarely, if ever, constant, varying significantly within and among females in the same population (Wootton, 1984, 1998). Most studies of egg size in fishes have been limited to mean egg size, addressing questions about egg size variability at the species and population levels, and differences in mean egg size among females and among years. Variability in egg sizes within a single clutch has largely been ignored, being primarily limited to the verbal arguments of Capinera (1979) and the theoretical work of McGinley *et al.* (1987), who predicted that intra-clutch variability is optimal only under a very limited set of circumstances (see below).

In this study, we examined the allocation of resources among eggs within individual female brook trout, *Salvelinus fontinalis*, from Newfoundland, Canada. Our aim was to determine if unequal allocation (i.e. egg size variability) can be explained as an adaptive response and, if so, whether the predictions forthcoming from adaptive hypotheses (Table 1) are supported by the allocation decisions of female brook trout. Within this context, we evaluated the following hypotheses pertaining to the adaptive significance of egg size variability.

Physiological constraint hypothesis

Unequal allocation may not be adaptive and yet still be observed if the allocation of resources among offspring is itself not a plastic life-history trait, but is ‘noise’, caused by a physiological or developmental inability to allocate resources evenly. Given that the distribution of resources to developing eggs appears to depend on the position of the egg

Table 1. Hypotheses and their predictions

Hypothesis	Prediction
1. Physiological constraint	Unequal allocation of resources within a clutch increases with gonad size
2. Imperfect information	Unequal allocation of resources within a clutch decreases with increasing mean egg size
Environmental predictability	
3. Inter-clutch variability	Among-female egg size variability will decrease as the environment becomes more predictable
4. Mean egg size	Mean egg size will increase as the environment becomes more predictable
5. Intra-clutch variability	Within-female egg size variability will decrease as the environment becomes more predictable

relative to blood vessels in the ovary (Mejen, 1940, cited by Kamler, 1992), the proportion of developing eggs distally positioned from blood vessels may differ between small and large ovaries. Assuming that the density of blood vessels decreases as gonad size increases, we expect a positive relationship between gonad size and within-female variation in egg size (Prediction 1, Table 1), reflecting an unequal allocation of resources among offspring.

Imperfect information hypothesis

In general, we predict that females will produce many small offspring when conditions are expected to be favourable or good, and fewer large offspring when conditions are expected to be unfavourable or poor, given that offspring survival is generally size-dependent, particularly under poor conditions, with smaller offspring exhibiting lower survival (Bagenal, 1969; Hutchings, 1991; Einum and Fleming, 1999, 2000; Good *et al.*, 2001). This prediction, however, incorporates the implicit assumption that females can reliably assess the conditions into which their offspring will hatch. A growing body of evidence suggests that energetic allocations to offspring can be phenotypically plastic, and that females may be able to predict future environmental conditions and modify their egg size decisions accordingly. In fish, such proposed egg size modifications have been based on, for example, temperature (Pacific herring, *Clupea harengus pallasi*: Tanasichuk and Ware, 1987; eastern mosquitofish, *Gambusia holbrooki*: Meffe, 1990), food availability (guppies, *Poecilia reticulata*: Reznick and Yang, 1993) and maternal growth history (Atlantic salmon, *Salmo salar*: Jonsson *et al.*, 1996; brown trout, *Salmo trutta*: Lobon-Cervia *et al.*, 1997; grayling, *Thymallus thymallus*: Haugen, 2000; walleye, *Stizostedion vitreum*: Johnston and Leggett, 2002). These modifications to egg size have generally been consistent with our expectations, with females producing more smaller eggs when temperatures are warmer, food availability is higher and when females have experienced superior growth.

But what if females misjudge future larval conditions? Then, females will experience the cost of imperfect information, manifested by the reduced fitness associated with making erroneous decisions. For example, if a female produces eggs that are larger than the optimal size, then her fitness is reduced because she could have produced more offspring (due to the egg size–number trade-off). Alternatively, if a female produces eggs that are smaller than the optimal size, then her fitness is reduced by the poor survival and fitness of her offspring (due to size-dependent survival). We propose that unequal allocation, or the production of variable egg sizes, is a strategy that females can use to offset the cost of imperfect information. However, unequal allocation has its own costs and benefits and is not expected to offset the cost of imperfect information under all conditions. The benefit of unequal allocation is the increase in fitness derived when expectations about future conditions are incorrect and unequal allocation produces some offspring that fair better and increase maternal fitness. The cost of unequal allocation is the reduction in fitness from producing some non-optimal egg sizes when expectations about future conditions are correct.

Under what conditions might the benefit of unequal allocation exceed the cost of unequal allocation? When females expect a good larval environment and are producing small eggs, the cost of imperfect information can be very large, possibly complete reproductive failure, and unequal allocation can save the reproductive event by producing some larger eggs that survive under the less favourable conditions. Conversely, when females expect a poor larval environment and are producing fewer large eggs, the cost of imperfect information can be relatively small – that is, the female could have produced a few more offspring. Since larvae from large eggs survive very well in good environments, the cost of unequal allocation when correctly expecting poor larval conditions is likely to exceed any benefits under imperfect information. Thus, we expect females to use an unequal allocation strategy to offset the cost of imperfect information when future conditions are expected to be good and the optimal egg size is small. When females expect future conditions to be poor and the optimal egg size is large, we expect females to minimize egg size variability to avoid the cost of unequal allocation. The prediction we will test is that females reduce egg size variability as the optimal egg size increases, resulting in a negative relationship between egg size variability and mean egg size (Prediction 2, Table 1).

Environmental predictability hypothesis

Kaplan and Cooper (1984) used a decision theoretic approach to explore the benefits of ‘adaptive coin-flipping’, a process in which females ‘flip a coin’ weighted by the probability of each larval environment, and produce all their eggs optimally sized for the selected environment. The result is greater inter-clutch variability in less predictable environments (Prediction 3, Table 1), assuming that all females use the same ‘adaptive coin-flipping’ strategy. This approach still incorporates the assumption that females produce a constant egg size within a clutch.

It is generally expected that environmental unpredictability will cause females to hedge their bets (*sensu* Seger and Brockmann, 1987) and distribute resources less evenly among offspring (e.g. Capinera, 1979; Crump, 1981; Poulin and Hamilton, 2000). However, these expectations are based on intuition and verbal arguments. McGinley *et al.* (1987) modelled the effect of temporal variation on egg size variation and found that variability among eggs should generally be minimized. The production of variable egg sizes within a clutch was only found to be optimal when smaller egg size is optimal, but not necessarily affected by environmental predictability. Lalonde (1991) examined the effect of environmental predictability on optimal egg size, assuming equal allocation among eggs. He found that, as environmental predictability decreases (increasing variability with no change in mean expectation), the optimal egg size for iteroparous organisms should decrease. If both Lalonde’s (1991) and McGinley and co-workers’ (1987) models are correct, then we can expect that, as environmental predictability decreases, optimal egg sizes should also decrease (Prediction 4, Table 1; Lalonde, 1991) and the production of variable sized eggs within clutches should become optimal (McGinley *et al.*, 1987). These arguments lead us to predict that egg size variability should increase as environmental predictability declines (Prediction 5, Table 1).

METHODS

Data collection

Brook trout were collected, immediately before spawning, from 10 different populations in two areas of Newfoundland, over 3 years. In 1987 and 1988, fish were sampled from the Cape Race area of the Avalon Peninsula (Cape Race River 1987, Cripple Cove River 1987 and 1988, Drook River 1987, Freshwater River 1987 and 1988, Watern Cove River 1987 and 1988, Whalens River 1987 and Wrights River 1987). In 1998, fish were sampled from the Indian Bay area (Alleys Pond, Fourmile Pond and Southern Pond). Thus, from the 10 populations, there were 13 population-year samples. Each female was sampled for length (mm), total weight (g), gonad weight (g) and fecundity. In addition, scales (1987 and 1988 data) or otoliths (1998 data) were removed for age determination, and 10 eggs were randomly chosen from each female and measured for diameter (mm). Additional information on the study populations and methods of data collection may be found in Hutchings (1993, 1996) for the Cape Race area and in Adams (1999) and Adams and Hutchings (in press) for the Indian Bay area populations.

Data analysis

For each female, we calculated mean egg volume (mm^3) and three different measures of the allocation of resources among eggs: coefficient of variation (CV), providing a measure of relative variability (Hilborn and Mangel, 1997); skew (g_1), where a positive g_1 value represents a right-skewed distribution and a negative g_1 value represents a left-skew (Zar, 1984); and kurtosis (g_2), where a positive g_2 value represents leptokurtosis and a negative g_2 value represents platykurtosis (Zar, 1984). Egg volume was calculated for each egg sampled, assuming that eggs were a sphere: volume = $(\text{diameter})^3 \cdot \pi/6$. For all analyses, length, gonad weight, fecundity and egg volume were natural log-transformed. The gonadosomatic index (GSI) was calculated as gonad weight/total weight.

To test the underlying assumption of an egg size–number trade-off, and to test the physiological constraint and imperfect information hypotheses, we used a general linear model (GLM) approach, including population and year as fixed effects and gonad weight and mean egg volume as covariates. We started with a complete model (all main effects and interactions included) and used backwards elimination to remove sequentially the non-significant terms with the least explanatory ability.

To test the environmental predictability hypotheses, egg volumes were first standardized according to the equation

$$y_{\text{st}} = y_{\text{ob}} - \left(a + \sum_i b_i x_i\right) + \bar{y}$$

where x_i are the variables to which y is standardized, y_{ob} is the observed value of y, y_{st} is the standardized value of y, $\bar{y}$ is the mean value of y, and a and b_i represent the coefficients for the regression between y_{ob} and x_i. The coefficients of variation for egg size, within and among females, were then regressed against environmental predictability (defined below). All regressions were weighted by sample size.

Estimating environmental predictability

When choosing how to allocate resources among eggs, the important part of the environment for a female fish to predict is the larval environment into which her offspring will hatch. To determine if an environment is predictable, we need to know what cues a female uses to predict larval environmental quality. For salmonids, there is reason to believe that females use their own growth history to assess the growth environment of their offspring (Jonsson *et al.*, 1996; Lobon-Cervia *et al.*, 1997; Morita *et al.*, 1999; Haugen, 2000). To determine the predictability of the environment, we require data on larval growth to test the correlation between maternal growth and the larval growth of her offspring, strong correlations being indicative of high environmental predictability. Unfortunately, we do not have the data required to quantify the strength of this association.

As an alternative, we considered Berrigan and Seger's (1998) proposition that when life-history decisions must be made before the relevant conditions can be assessed with full accuracy, the use of cues that are not fully reliable will cause increased spread in the allometric relationships and a regression towards the mean. Thus, we can expect predictable environments to produce tighter allometric relationships than unpredictable environments. Based on this reasoning, we used the residual mean square error (MSE) term, representing the tightness of allometric relationships, as our measure of environmental predictability. Increased residual mean square error would indicate decreased predictability. To estimate environmental predictability, we first regressed mean egg volume on maternal length, and then ranked the inverse of mean square error for each population-year to get a measure of relative predictability.

RESULTS

Egg size–number trade-off

Implicit to all models of optimal egg size is the assumption that a trade-off exists between egg size and fecundity (Table 2). Support for this assumption was evident in all populations and years studied ($R^2 = 0.97$, $F_{33,577} = 675.21$, $P < 0.001$) and significant differences existed among populations. The trade-off is of the general form:

$$F \propto \frac{G}{E_v}$$

where F is fecundity, G is gonad weight and E_v is egg volume.

Unequal allocation

The mean coefficient of variation of egg volume within a female's clutch varied among populations from a low of 5.6% in Watern Cove River in 1988 to 16.1% in Watern Cove River in 1987. Among individuals, the coefficient of variation varied from 3.7% (a female from Freshwater River in 1988) to 61.7% (a female from Watern Cove in 1987). Although the distribution of egg volumes within a female's clutch is symmetric (*t*-tests, all $P > 0.05$), 10 of 13 population-years had positive g_1 values (binomial test, $P = 0.046$) and all 5 with 95% confidence intervals that did not overlap zero were positive (binomial test, $P = 0.031$; Table 3). When all females were pooled, the allocation of resources among eggs within females was right skewed (Table 3). All population-years, and all females pooled among populations, exhibited platykurtotic distributions of egg volumes within females. Among populations, g_2 values ranged from −2.63 to −3.79, the pooled g_2 value was −3.31 and none of the 95% confidence intervals included zero (binomial test, $P < 0.001$; Table 3).

The coefficient of variation of egg volume was influenced by mean egg volume, with significant differences among populations and years ($R^2 = 0.62$, $F_{13,598} = 73.57$, $P < 0.001$; Table 4a). As predicted by the imperfect information hypothesis, mean egg volume had a negative effect on egg size variability in all populations and years studied (Table 4b, Fig. 1) and the 95% confidence intervals for these slopes did not include zero for 10 of 13 population-years studied (binomial test, $P = 0.046$). Gonad weight did not have an effect on the coefficient of variation of egg volume ($F_{1,597} = 0.048$, $P = 0.83$), explaining less than 0.008% of the variation unexplained by the described model.

Table 2. Results of the analysis for each population-year between the natural log of fecundity (ln$F$), gonad weight (ln$G$) and mean egg volume (lnE_v): (a) statistical results, (b) parameter estimates for each population-year for $F = \alpha G^{\beta(1)} E_v^{\beta(2)}$

(a)	Model term	d.f.	F	P	ES[a]
	Population	9,577	4.90	<0.001	0.071
	ln$G$	1,577	2441.93	<0.001	0.809
	lnE_v	1,577	526.04	<0.001	0.477
	Population × year	3,577	13.96	<0.001	0.068
	Population × ln$G$	8,577	3.33	0.001	0.044
	Population × lnE_v	9,577	4.17	<0.001	0.061
	Year × ln$G$	1,577	16.02	<0.001	0.027

(b)	Population-year	n	α	β_1[b]	β_2
	Alleys Pond 1998	32	**655**	**0.964**	**−0.909**
	Cape Race River 1987	50	**228**	**0.857**	**−0.605**
	Cripple Cove River 1987	40	**249**	**0.832**	**−0.661**
	Cripple Cove River 1988	48	**272**	**0.985**	**−0.661**
	Drook River 1987	52	**231**	**0.907**	**−0.595**
	Fourmile Pond 1998	31	**439**	**0.957**	**−0.791**
	Freshwater River 1987	56	**416**	**0.971**	**−0.766**
	Freshwater River 1988	58	**342**	**1.124**	**−0.766**
	Southern Pond 1998	25	**1256**	**0.996**	**−1.111**
	Watern Cove River 1987	66	**129**	**0.680**	**−0.423**
	Watern Cove River 1988	52	**128**	**0.833**	**−0.423**
	Whalens River 1987	50	**330**	**0.940**	**−0.733**
	Wrights River 1987	52	**168**	**0.894**	**−0.521**

Note: **Bold** values indicate parameter estimates where the 95% confidence intervals (not presented) do not include zero (or 1 for the α's).

[a] Effect size measures the proportion of the variation explained by the model term after all other terms have been included in the model.

[b] All β_1 parameter estimates were not significantly different from 1.

Even though the distribution of egg volumes within females was not skewed, the skew in egg volume (g_1) was significantly influenced by gonad weight, mean egg volume and population ($R^2 = 0.13$, $F_{21,591} = 4.12$, $P < 0.001$). Skew tended to increase with gonad weight and decrease with increasing mean egg volume.

Kurtosis in egg volume was only affected by population ($R^2 = 0.88$, $F_{10,601} = 448.45$, $P < 0.001$). Neither gonad weight ($F_{1,600} = 1.18$, $P = 0.28$) nor mean egg volume ($F_{1,600} = 0.36$, $P = 0.55$) had significant effects, explaining only 0.2% and 0.1% of the remaining variation, respectively.

Environmental predictability

Egg volumes were standardized for comparison among population-years. A regression of egg volume as a function of GSI and maternal age described the pooled data from all population-years well ($R^2 = 0.72$, $F_{2,608} = 797.51$, $P < 0.001$), so that standardized egg volume (E_{st}) can be calculated as:

Table 3. Mean skew (g_1) and kurtosis (g_2) for each population-year, and for all population-years pooled, with 95% confidence intervals (CI)

Population-year	*n*	g_1 (95% CI)	g_2 (95% CI)
Alleys Pond 1998	32	**0.33** (0.03, 0.64)	**−2.63** (−3.20, −2.07)
Cape Race River 1987	50	0.02 (−0.15, 0.19)	**−3.31** (−3.58, −3.04)
Cripple Cove River 1987	40	**0.24** (0.07, 0.41)	**−3.39** (−3.85, −2.92)
Cripple Cove River 1988	48	−0.09 (−0.23, 0.04)	**−3.59** (−3.82, −3.36)
Drook River 1987	52	0.12 (−0.03, 0.26)	**−3.44** (−3.69, −3.19)
Fourmile Pond 1998	31	**0.34** (0.06, 0.62)	**−2.86** (−3.47, −1.89)
Freshwater River 1987	56	0.02 (−0.14, 0.18)	**−3.45** (−3.67, −3.23)
Freshwater River 1988	58	−0.05 (−0.13, 0.04)	**−3.79** (−3.94, −3.65)
Southern Pond 1998	25	0.18 (−0.13, 0.49)	**−2.63** (−3.37, −1.89)
Watern Cove River 1987	66	**0.23** (0.09, 0.37)	**−3.38** (−3.71, −3.05)
Watern Cove River 1988	52	−0.01 (−0.13, 0.10)	**−3.57** (−3.78, −3.35)
Whalens River 1987	50	0.10 (−0.11, 0.32)	**−3.16** (−3.67, −2.64)
Wrights River 1987	52	**0.23** (0.03, 0.42)	**−2.99** (−3.39, −2.59)
All pooled	612	**0.12** (0.07, 0.16)	−**3.31** (−3.41, −3.21)

Note: **Bold** values indicate population-years where the 95% confidence intervals do not include zero.

$$E_{\mathrm{st}} = E_{\mathrm{ob}} - 237.5\ \mathrm{GSI}^{1.03}\ \mathrm{e}^{0.087 \cdot \mathrm{Age}} + 30.62$$

where E_{ob} is the observed egg volume and 30.62 is the mean egg volume for all measured eggs across all population-years. Each of the 10 measured eggs were standardized, and a mean and coefficient of variation of standardized egg volume were calculated for each female.

Variability in egg volume among females in a population, measured as the coefficient of variation of mean standardized egg volumes among females ($\mathrm{CV_a}$), decreases as environmental predictability increases ($\ln \mathrm{CV_a} = -0.85 - 0.089 \cdot \mathrm{Predictability}$; $R^2 = 0.67$, $F_{1,11} = 22.83$, $P = 0.001$; Fig. 2). Environmental predictability did not have a significant effect on the mean standardized egg volume (E_{st}) produced in any population-year ($\ln E_{\mathrm{st}} = 3.54 - 0.012 \cdot \mathrm{Predictability}$; $R^2 = 0.18$, $F_{1,11} = 2.44$, $P = 0.15$).

The mean within-female coefficient of variation of standardized egg volume ($\mathrm{CV_w}$) decreased as environmental predictability increased ($\ln \mathrm{CV_w} = -1.67 - 0.083 \cdot \mathrm{Predictability}$; $R^2 = 0.49$, $F_{1,11} = 10.39$, $P = 0.008$; Fig. 3). Even though there may be a trend towards positive skew in the allocation of resources among eggs within females, environmental predictability had no effect on the symmetry of allocation ($g_1 = 0.08 + 0.0035 \cdot \mathrm{Predictability}$; $R^2 = 0.008$, $F_{1,11} = 0.0087$, $P = 0.77$). Environmental predictability was not a significant predictor of differences in the kurtosis of the within-female distribution of egg volumes among population-years ($g_2 = -3.1 - 0.028 \cdot \mathrm{Predictability}$; $R^2 = 0.097$, $F_{1,11} = 1.18$, $P = 0.30$).

DISCUSSION

Female brook trout adjust the allocation of resources among eggs in response to unpredictable environmental conditions and to offset the cost of imperfect information. We found no evidence that egg size variability is a physiological constraint of the size of the gonads in which eggs develop. We found that egg size variability decreased when mean egg size

Table 4. Results of the analysis, for each population-year, between the natural log of the coefficient of variation of egg volume (lnCV) and mean egg volume ($\ln E_{\mathrm{v}}$): (a) statistical results, (b) parameter estimates for each population-year for $\ln \mathrm{CV} = \alpha + \beta \ln E_{\mathrm{v}}$ ($\alpha = -1.63$ for all population-years)

(a)	Model terms	d.f.	*F*	*P*	ES[a]
	$\ln E_{\mathrm{v}}$	1,598	30.83	<0.001	0.049
	Year × $\ln E_{\mathrm{v}}$	2,598	323.02	<0.001	0.519
	Population × year × $\ln E_{\mathrm{v}}$	10,598	4.54	<0.001	0.071

(b)	Population-year	*n*	β[b]	Lower 95% CI	Upper 95% CI
	Alleys Pond 1998	32	−0.104	−0.210	0.001
	Cape Race River 1987	50	**−0.148**	−0.288	−0.009
	Cripple Cove River 1987	40	**−0.204**	−0.357	−0.051
	Cripple Cove River 1988	48	**−0.327**	−0.460	−0.195
	Drook River 1987	52	**−0.195**	−0.338	−0.051
	Fourmile Pond 1998	31	−0.094	−0.200	0.012
	Freshwater River 1987	56	**−0.143**	−0.282	−0.003
	Freshwater River 1988	58	**−0.309**	−0.439	−0.179
	Southern Pond 1998	25	**−0.082**	−0.150	−0.015
	Watern Cove River 1987	66	−0.117	−0.259	0.025
	Watern Cove River 1988	52	**−0.346**	−0.449	−0.244
	Whalens River 1987	50	**−0.144**	−0.285	−0.003
	Wrights River 1987	52	**−0.195**	−0.302	−0.089

[a] Effect size measures the proportion of the variation explained by the model term after all other terms have been included in the model.

[b] **Bold** values indicate slopes that are significantly different from zero.

increased, as predicted by the imperfect information hypothesis. Environmental unpredictability was associated with increases in both within- and among-female egg size variability but did not have a significant effect on mean egg size. As far as we know, this is the first test of the imperfect information hypothesis, and the first test of the influence of environmental predictability on within-female egg size variability for any species of fish.

Previous research on the influence of environmental predictability on egg size variability is limited. Kaplan and Cooper's (1984) prediction that among-female variability should increase in less predictable environments has been supported by studies of eastern mosquitofish (Meffe, 1990) and parasitic trematodes (Poulin and Hamilton, 2000). The prediction that within-female variability in egg size should increase with decreased environmental predictability has only been tested by Crump (1981), who found support for this prediction among five species of treefrogs in Ecuador. While researchers studying fish egg sizes have acknowledged within-clutch variability (e.g. Meffe, 1990; Einum and Fleming, 2000), we are unaware of any attempts to explain this variability.

Our measure of environmental predictability is not an ideal measure for two reasons. First, it is based on a theory that has not been tested. Therefore, the strength of our conclusions about the influence of environmental predictability is limited by our confidence in this measure. For this reason, we used a rank scale to look at relative predictability and

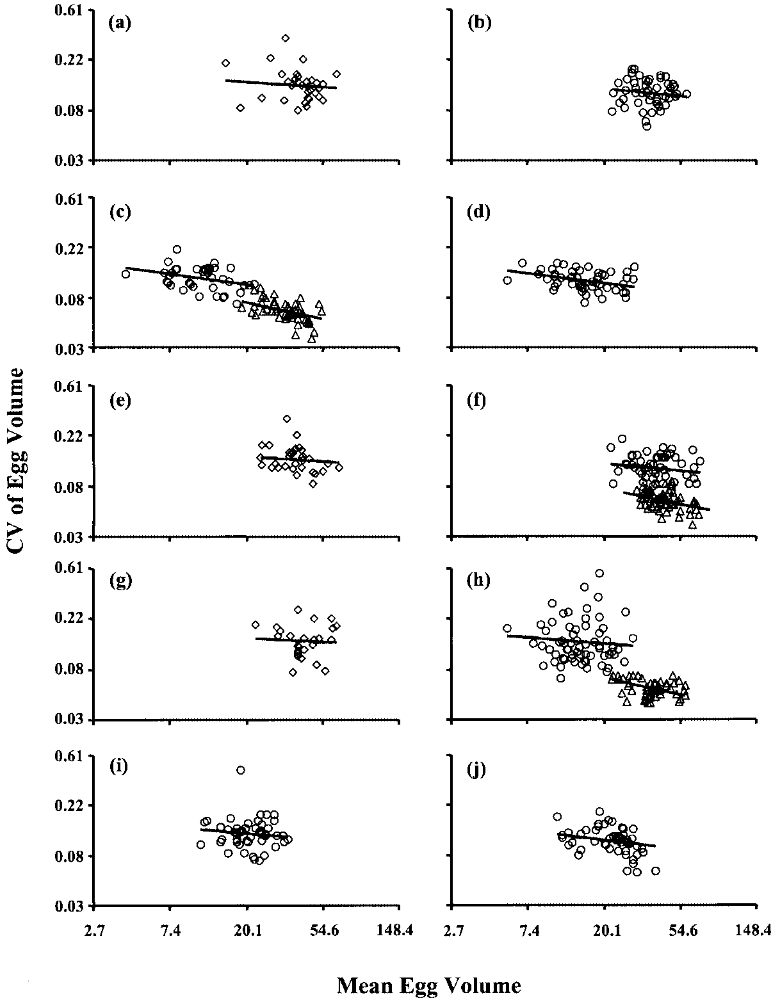

Fig. 1. Coefficient of variation (CV) in egg volume as a function of mean egg volume for: (a) Alleys Pond 1998; (b) Cape Race River 1987; (c) Cripple Cove River 1987 and 1988; (d) Drook River 1987; (e) Fourmile Pond 1998; (f) Freshwater River 1987 and 1988; (g) Southern Pond 1998; (h) Watern Cove River 1987 and 1988; (i) Whalens River 1987; and (j) Wrights River 1987. ◇, 1998; △, 1988; ○, 1987. Lines drawn based on the parameter estimates presented in Table 4.

used weighted regressions, which provided a more conservative test of the hypotheses. Second, our measure of predictability does not measure the predictability of the environment directly. Unfortunately, to measure predictability directly we would need to know what cues female brook trout use to predict future environmental conditions. Simply measuring fluctuations in environmental conditions is not sufficient to address the question of predictability. An environment may fluctuate drastically. For example, temperatures may swing by as much as 40°C between summer and winter; however, these changes in

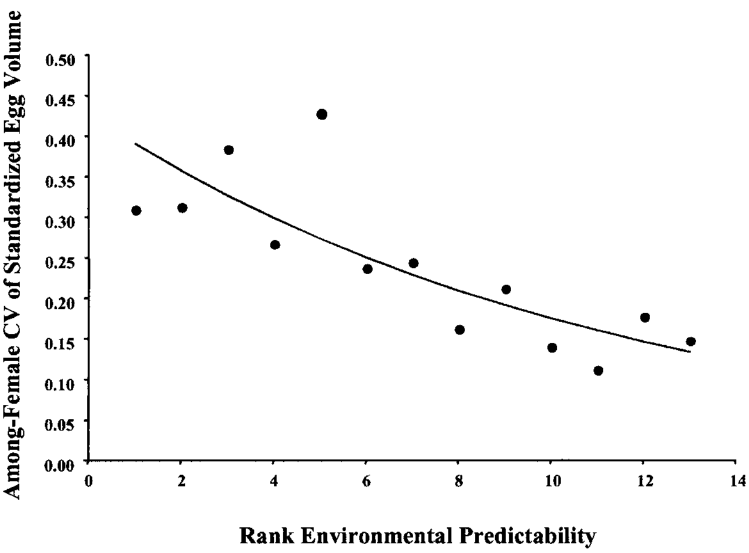

Fig. 2. Among-female coefficient of variation (CV_a) of egg volume, standardized for the gonadosomatic index and maternal age, for each population-year regressed against rank environmental predictability. Line shows the regression: $\ln CV_a = -0.85 - 0.089 \cdot \text{Predictability}$.

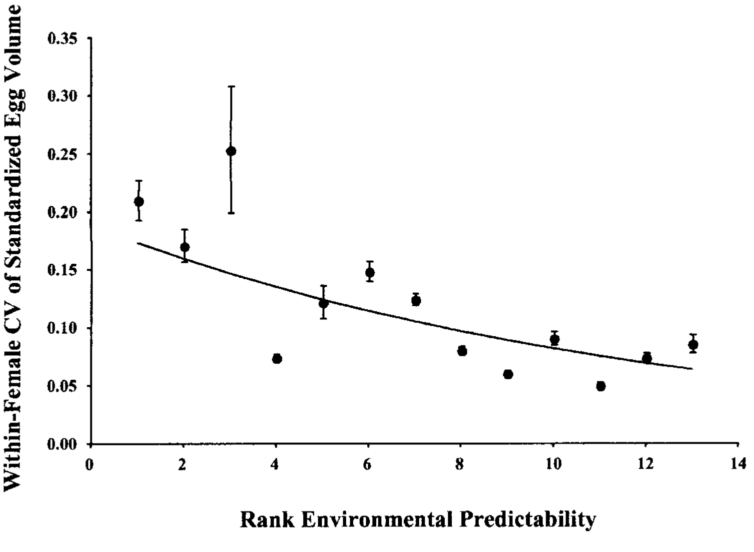

Fig. 3. Within-female coefficient of variation (CV_w) of egg volume, standardized for the gonadosomatic index and maternal age, for each population-year regressed against rank environmental predictability. Error bars represent one standard error. Line shows the regression: $\ln CV_w = -1.67 - 0.083 \cdot \text{Predictability}$.

temperature can be predictable. So, fluctuations alone do not imply unpredictability. Previously, researchers have used habitat characteristics such as temporary versus permanent ponds (Crump, 1981), contrasting thermal conditions (Meffe, 1990) and aquatic versus terrestrial habitats (Poulin and Hamilton, 2000) that do not apply to brook trout. Poulin and Hamilton (2000) also considered latitude. If we expect environments to become more variable at higher latitudes, and we assume this variability correlates with unpredictability, then we can expect to see more variability in egg sizes at higher latitudes. Indian Bay is farther north than Cape Race and there is more variability in egg sizes in the Indian Bay populations than the Cape Race populations, both among ($t_{11} = 2.2$, $P = 0.05$) and within females ($t_{11} = 5.5$, $P < 0.001$). This is consistent with our results; however, as argued above, variable environmental conditions do not necessarily equate with unpredictable environmental conditions.

The increased variability among females when environments are less predictable may be an example of Kaplan and Cooper's (1984) 'adaptive coin-flipping'. However, to be strictly consistent with their model, females would allocate resources evenly among eggs and use the 'coin-flip' to determine the egg size. We observed too much intra-clutch variability in egg size to be consistent with this view, and the intra-clutch variability was not simply a physiological constraint. So, why does variability among females increase in less predictable environments? It is probably a by-product of the uncertainty associated with less predictable environments. As the future condition of the environment becomes less certain, expectations will differ among females. If females are attempting to optimally size their eggs for future environmental conditions, differing expectations about those future conditions will result in an increase in variability among females in the mean egg sizes they produce. As with Kaplan and Cooper's (1984) model, variability among females is not itself an adaptive response, but is instead a necessary result of the uncertainty associated with an unpredictable environment.

Contrary to Lalonde's (1991) prediction for iteroparous organisms, environmental unpredictability did not result in smaller eggs. It is possible that the cost of reproduction for female brook trout is so great that they make reproductive decisions as if they were semelparous. In this case, Lalonde's model would predict an increase in egg size in unpredictable environments. However, previous research on some of the Cape Race populations does not support such a possibility (Hutchings, 1993). Instead, our data suggest that egg size may increase as environmental predictability decreases, which is consistent with observations of guppy decisions. Reznick and Yang (1993) subjected guppies to treatments in which food availability was either constant or variable. Guppies that experienced a change in food availability, which would increase uncertainty about future conditions, produced larger offspring. It may be that when faced with uncertainty about the future, females prepare for the worst and make decisions that minimize the cost of being wrong.

Our results are consistent with the hypothesis that females attempt to predict the environmental conditions into which their offspring will emerge. Previous research on egg size decisions suggests that females use these expectations to adjust the size of their eggs and offspring (e.g. Tanasichuk and Ware, 1987; Meffe, 1990; Reznick and Yang, 1993; Jonsson *et al.*, 1996; Lobon-Cervia *et al.*, 1997; Haugen, 2000; Johnston and Leggett, 2002). Our results contribute to this perspective by showing that females also adjust the allocation of resources among eggs within a clutch in response to these expectations. We conclude that egg size variability, both within and among females, declines when environmental predictability increases, and that females use variability in egg size to offset the cost of imperfect information when producing smaller eggs.

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