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Maternal provisioning of offspring and the use of those resources during ontogeny: variation within and between Atlantic Salmon families

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Summary

1. The size and proximate composition of eggs and alevins (larvae) were measured from six full sibling families of Atlantic Salmon (*Salmo salar*), at six stages between fertilization and first feeding.
2. Egg and alevin size measures (diameter, wet mass, dry mass) and proximate composition attributes (water, protein, fat, energy) were all highly correlated with each other (r = 0·89–0·99), suggesting that each is a reasonable surrogate for any other.
3. Most of the variation in egg size (95·0–97·0%) and composition attributes (95·5–97·9%) was partitioned between, rather than within, females. Most of this variation was attributable to differences in female size, owing to the length of time spent at sea.
4. Fat, protein and energy content varied less on a relative basis (controlling for egg size variation) than on an absolute basis, suggesting that certain combinations of egg attributes are optimal regardless of egg size.
5. Stored fat decreased by 9·6 μg day^{-1} before hatching but increased by 27·4 μg day^{-1} after hatching. The increase after hatching suggests that alevins actively synthesize (probably from protein) and store lipids between hatching and first feeding.
6. Stored protein decreased by 8·8 μg day^{-1} before hatching and by 181·3 μg day^{-1} after hatching. Assuming all metabolic energy was derived from stored protein, metabolic rate increased logarithmically from 0·115 J day^{-1} to 5·43 J day^{-1}. Rates of oxygen consumption estimated from protein loss (6·09–288·9 μl O_2 d^{-1}) were similar to those reported in studies that measured oxygen consumption using respirometry.
7. Alevins appear to convert protein to fat, a change that their mothers were unable or unwilling (in an evolutionary sense) to make. This may reflect the conflicting goals of parents and offspring for maximizing fitness.

Key-words: egg quality, parent–offspring conflict, reproductive investment, *Salmo salar*

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Introduction

Early life is a period of high mortality for a wide variety of organisms, and many adaptations have evolved to minimize losses during this period (Roff 1992). One way for organisms to increase the survival of their offspring, and therefore their own fitness is through parental care (Clutton-Brock 1991; Mousseau & Fox 1998). Here we consider variation in the amount of parental care in Atlantic Salmon (*Salmo salar*), an oviparous fish that does not provide care for eggs after they are fertilized (Fleming 1996).

Maternal provisioning of offspring often has pronounced effects on fitness (Mousseau & Fox 1998; Lindström 1999). In Atlantic Salmon and other oviparous fishes, a critical aspect of maternal provisioning is the size and energy content of eggs. Juveniles originating from larger eggs are larger, and typically have higher growth, survival and fitness (Hutchings 1991; Roff 1992; Heath & Blouw 1998; Einum & Fleming 1999, 2000a). Thus, all else being equal, selection acting on offspring fitness should favour large, energy-rich eggs. Egg size cannot increase without bounds, of course,

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because females can endow their eggs with only finite resources, and because egg size is ultimately constrained by the size of the reproductive tract (Roff 1992, p. 352; Bernardo 1996). Even within these bounds, however, all else is not equal, because mothers and offspring are in conflict as to the optimal amount of allocation into individual eggs (Trivers 1974; Mock & Parker 1997).

From an evolutionary perspective, females should maximize their own fitness rather than that of their individual offspring. This distinction is important because maternal fitness is the product of offspring fitness and the number of offspring produced (Smith & Fretwell 1974). A given unit of parental investment into egg production must be partitioned between individual eggs (e.g. size) and their number. From the perspective of maternal fitness, optimal egg size is that at which the increase in offspring fitness with a further increase in egg size no longer exceeds the increase in maternal fitness that would attend the same proportional investment into egg number (Trivers 1974; Mock & Parker 1997). If offspring are genetically identical, parents and offspring are not in conflict, and optimal egg size is the same from the perspective of maternal or offspring fitness. In sexually reproducing, diploid organisms in outbred populations, however, full siblings are at most an average of 50% related, and so an offspring should attempt to acquire extra resources at some expense to their siblings. In many species, multiple paternity within a brood can be common and relatedness between offspring is correspondingly lower, favouring increasing selfishness of offspring. As a result, optimal egg size and energy content will be greater from the perspective of the offspring than from that of their mother (Trivers 1974; Mock & Parker 1997).

After the initial endowment of an egg with energy stores, offspring can achieve some developmental autonomy (except under the constraints imposed by genomic imprinting; Spencer, Clark & Feldman 1999), and ontogenetic patterns of energy use should be better tailored to the offspring's genotype. Patterns of energy use during development should therefore reflect adaptations maximizing offspring fitness, rather than the brokerage of a compromise between offspring and maternal fitness. One important way that offspring can increase their fitness is by efficiently converting energy stores provided by their mother into somatic tissue, and by preparing themselves for the period of exogenous feeding.

Our goals were to examine variation in maternal provisioning of offspring, and the use of those provisions during ontogeny, allowing insights into the evolution of maternal investment. We assayed characteristics of eggs (term used before hatching) and alevins (term used after hatching but before exogenous feeding) within and between full-sib families of Atlantic Salmon, and then followed changes in these characteristics from fertilization until independent feeding, after which young salmon are referred to as juveniles. Our study differs from those previous in that we (1) consider variation in fat, protein and energy content instead of just egg and alevin size; (2) measure attributes of individual eggs and alevins rather than batches; (3) consider variation both within and between females; and (4) quantify ontogenetic changes in fat, protein and energy content.

EGG SIZE AND QUALITY IN SALMONIDS: SPECIFIC OBJECTIVES

Nearly all studies addressing maternal provisioning and egg quality in fish consider only various measures of egg and alevin size (Brooks, Tyler & Sumpter 1997; Heath & Blouw 1998; Balon 1999). This approach has been defended because (1) many fish eggs are so small that individual energy content cannot be determined reliably (e.g. Parra, Rønnestad & Yúfera 1999); (2) determining energy content kills the embryo, thereby rendering subsequent evaluation of performance impossible; and (3) it seems intuitively reasonable that larger eggs will contain greater energy stores. This approach can be questioned, however, because energy stores or other factors may vary between eggs of a given size (Brooks *et al*. 1997; Balon 1999). A few studies have shown that the total energy content of individual eggs is correlated with their size (e.g. Kristjánsson & Vøllestad 1996), but only two studies have determined the fat, protein and energy content of individual salmonid eggs (Einum & Fleming 1999, 2000a). Our first objective was to test for correlations between various size measures (diameter, wet mass, dry mass) and proximate composition attributes (water, fat, protein, energy).

In salmonids, larger eggs give rise to larger juveniles (e.g. Thorpe, Miles & Keay 1984; Hutchings 1991; Hayashizaki, Hirohashi & Ida 1995), and larger juveniles enjoy increased survival, competitive ability, swimming performance, growth and overall fitness (Bagenal 1969; Ojanguren, Reyes-Gavilán & Braña 1996; Cutts *et al*. 1999a; Einum & Fleming 1999, 2000a). Offspring fitness should therefore exert a strong influence on maternal provisioning, favouring large and energy-rich eggs (unless oxygen availability during incubation is low, see Discussion). However, a strong trade-off between egg size and number within populations indicates that, for a given level of investment into egg production, females producing larger eggs must produce fewer of them (Thorpe *et al*. 1984; Bromage *et al*. 1992; Quinn, Hendry & Wetzel 1995; Jonsson & Jonsson 1999; Heath, Fox & Heath 1999). These conditions set the stage for a classic parent–offspring conflict, one that mothers should dominate because their investment stops at fertilization (before offspring can exert any influence). Recent evidence confirms that average egg size within Atlantic Salmon populations is indeed that which maximizes maternal fitness (Einum & Fleming 2000b).

Variation in salmonid egg size has a genetic, maternal and environmental basis (Thorpe *et al*. 1984; Jonsson,

Jonsson & Fleming 1996; Su, Liljedahl & Gall 1997; Heath *et al*. 1999; Jonsson & Jonsson 1999). Variation between populations can be large, and has been explained by reference to selection imposed by incubation temperature (Fleming & Gross 1990; Jonsson & Jonsson 1999), gravel size (Quinn *et al*. 1995) and migration distance (Beacham & Murray 1993). Variation between years within populations has been explained in some cases as a plastic response to growth conditions experienced by females (Lobon-Cervia *et al*. 1997). Variation between females within populations can be explained in part by body size (larger females produce larger eggs; Quinn *et al*. 1995; Fleming 1996) and growth rate (Morita *et al*. 1999), but much remains unexplained. Finally, variation within females may be small or large, and has not yet been explained. Our second objective was to consider how variation in egg size and proximate composition is partitioned within and between females.

Early salmonid development can be conveniently divided into two intervals – from fertilization until hatching, and from hatching to emergence from the gravel (roughly corresponding to the start of feeding). In Atlantic Salmon, the length of these two intervals depends on temperature, but the period of time from fertilization to hatching is usually about twice that from hatching to emergence (Berg & Moen 1999, and references therein). At emergence, free-swimming juveniles establish territories in streams and their success in doing so depends on time of emergence, metabolic rate and body size (Cutts *et al*. 1999a; Cutts, Metcalfe & Taylor 1999b). Patterns of energy use during ontogeny should prepare juveniles for this demanding period. Our third objective was to examine the differential use of fat, protein and energy during ontogeny. We also converted changes in energy stores to estimates of metabolism for comparison with published values based on respirometry.

Materials and methods

Eggs were collected from Atlantic Salmon captured in the river Stjørdalselva, middle Norway. Female salmon (Table 1) were screened for diseases or lesions (National Veterinary Institute, Trondheim), and to verify that none was an aquaculture net-pen escapee (using morphology and scales). All females were wild except for number 2 (Table 1), which had been released into the river as a smolt. The eggs of each female were fertilized by a different male (i.e. six full-sib families), and were then reared in a hatchery supplied with well-water (3·0–5·0 °C). Eight eggs or alevins were sampled from each of the six families on each of six occasions (Table 2). Eyes were visible in the first week of January (about 249 day–degrees), and hatching took place between 17 March and 1 April (about 520 day–degrees). The last sample was taken immediately before the juveniles were fed for the first time (about 700 day–degrees).

Each egg or alevin was individually weighed at the hatchery (U.W.E., Taiwan; type: NJW-150, precision: ±0·0005 g), placed in a numbered plastic bag and frozen. A Precisa scale (Zürich, Switzerland; type: 100A-300M, precision: ±0·0001 g) was used for subsequent weighing. Callipers were used to measure egg diameters (Smiec, Shanghai, precision 0·02 mm). Proximate composition (fat and protein) of each egg and alevin was determined by fat extraction by a solvent mixture (petrol–ether (five parts) and chloroform (one part)) and combustion (550 °C in 24 h) to determine proteins as described in (Berg & Bremset 1998) and (Einum & Fleming 1999). Total energy for each egg and alevin was estimated by assigning protein a value of 19·7 kJ g^{-1} and fat a value of 39 kJ g^{-1} (Withers 1992).

The solvent mixture used for fat extraction extracts neutral lipids, which function as energy stores; in contrast to polar lipids, which function as structural lipids in membranes and nerve tissues (Dobush, Ankney &

Table 1. Characteristics of females and their eggs (mean ± SD) used for the experiment. Cumulative mortality between hatching and first feeding is shown for each family. Female age is given as freshwater age (winters). seawater age (winters)

	Female 1	Female 2	Female 3	Female 4	Female 5	Female 6
Female characteristics						
Age	3.1	2.1	2.2	3.3	3.2	3.2
Spawn date	6 November	6 November	6 November	6 November	14 November	6 November
Length (cm)	60	68	80	84	85	92
Mass (kg)	1·5	3·5	6·0	6·0	6·0	8·0
Egg characteristics						
Diameter (cm)	0·461 ± 0·033	0·424 ± 0·014	0·595 ± 0·008	0·588 ± 0·009	0·641 ± 0·023	0·570 ± 0·017
Wet mass (g)	0·053 ± 0·005	0·059 ± 0·005	0·136 ± 0·009	0·125 ± 0·004	0·142 ± 0·005	0·111 ± 0·011
Dry mass (g)	0·017 ± 0·001	0·017 ± 0·003	0·045 ± 0·005	0·043 ± 0·002	0·049 ± 0·001	0·038 ± 0·004
Protein (g)	0·015 ± 0·001	0·016 ± 0·001	0·036 ± 0·002	0·037 ± 0·001	0·040 ± 0·001	0·031 ± 0·003
Fat (g)	0·003 ± 0·0004	0·002 ± 0·0002	0·005 ± 0·0004	0·006 ± 0·0003	0·007 ± 0·0003	0·006 ± 0·0007
Energy (kJ)	0·395 ± 0·025	0·390 ± 0·024	0·906 ± 0·057	0·942 ± 0·036	1·071 ± 0·022	0·838 ± 0·080
Cumulative mortality						
To eyed stage (%)	6	1	2	12	1	3
To hatching (%)	28	3	3	15	2	6
To first feeding (%)	35	5	4	19	3	8

Table 2. Sampling dates and developmental notes. Note that family five (from female five) was fertilized 8 days before the other females. This difference was corrected in analyses that used days after fertilization as a continuous variable

Sampling period	Date (d.m.y)	Days after fertilization	Comment
1	21.11.1997	15	
2	12.02.1998	98	Eyed eggs (about 7 January)
3	11.03.1998	125	Just before hatching
4	30.03.1998	144	Newly hatched
5	30.04.1998	175	
6	21.05.1998	196	Immediately before first feeding

Krementz 1985; Randall *et al*. 1991). Extraction with our solvent therefore estimates stored (metabolizable) lipids and will slightly underestimate total lipids (O. K. Berg and B. Henriksen, unpublished data). Repeatability of our proximate analysis was determined using parallel analyses of 19 small pieces (0·05–0·09 g) from a cooked chicken egg yolk. Protein content on a relative basis was 18·3 ± 0·8%, and fat content was 31·4 ± 1·3% (mean ± SD). The small coefficients of variation, 4·4% and 4·1%, respectively, confirmed the repeatability of our methods.

Rates and percentages of change in fat, protein and energy content were calculated to exclude the hatching period (i.e. periods 1–3 *vs* periods 4–6), so losses associated with the hatching itself (e.g. shedding of the egg shell and loss of materials encased in the egg shell but not the embryo) were not included in the estimation of losses caused by metabolism. Assuming a logarithmic increase in protein consumption due to metabolism (based on the daily protein loss during the other periods), the metabolic protein loss between periods 3 and 4 was estimated, and subsequently an 'extra' protein loss of approximately 2·6 mg was estimated. On average, the loss associated specifically with the hatching process (shedding of eggshell, etc.) was about 2·5% of the initial mass of the eggs.

STATISTICAL ANALYSIS

The first objective was to examine relationships between the different variables, including egg size measures (diameter, wet mass, dry mass) and proximate composition attributes (water, fat, protein, energy). To this end, Pearson's correlation coefficients were used for all pair-wise comparisons between variables just after fertilization (sample 1, Table 2). The sequential Bonferroni procedure was used to correct for multiple comparisons ($\alpha/21 = 0{\cdot}002$). Simple linear regressions were used to define predictive relationships between each pair of variables. Two females (1 and 2) were considerably smaller than the other four, owing to their shorter time at sea (Table 1). Pearson's coefficients were therefore used to examine correlations after excluding the two small females.

The second objective was to consider how maternal investment varied within and between females. To this end, variation between families at the first sampling period was tested for using MANOVAs (one for the size measures, a second for the composition attributes; using Wilks' lambda), and one-way ANOVAs (for each variable individually). Variance components (minimum norm quadratic unbiased estimator) were used to determine the percentage of the total variance in each variable that was attributable to differences between females. Owing to the two different size classes of females (Table 1), nested ANOVAs (and MANOVAs) were also used to test for effects of size class and family nested within size class. Variance components were again used to estimate the proportion of variance explained by family, this time nested within size class. The above analyses considered absolute investment into various composition attributes. Relative investment was considered by adding wet egg mass as a covariate to each model. These MANCOVA and ANCOVA models allowed a test for family effects (and effects of family within size class) after controlling for variation in wet egg mass.

The third objective was to consider how embryos used the resources that were allocated to them. To this end, egg and alevin size measures between families and sample periods were compared using two-way, replicated MANOVA (all measures combined) and ANOVA (each measure individually). For these analyses and those following, family was not nested within female size class because the use of family by itself explained the same amount of variation with less complexity. Composition attributes were compared between families and between sample periods using similar models. We were also interested in ontogenetic patterns for relative attributes (i.e. controlling for egg size). Wet egg mass was therefore added as a covariate to each model dealing with composition attributes. We were particularly interested in the interaction between family and sample period (an indication that families used their resources in different ways), and the effect of sample period (an indication that size measures or composition attributes changed over time).

The above analyses revealed significant family and family by sample interactions (see Results). An additional exploratory analysis was therefore performed by dividing the sample periods into two intervals – before hatching (Periods 1–3) and after hatching (Periods 4–6). Linear regressions were used to define relationships between days after hatching (as a continuous variable) and absolute values for fat, protein and energy. These relationships were then used to predict the rate of change in each attribute, and the percentage change over each interval 100 [(initial mass – final mass)/initial mass]. ANCOVA was used to test for differences between the slopes of these relationships within each interval.

For presentation purposes, relative amounts of each composition attribute were also expressed on a mass-specific basis (% water, % fat, % protein, kJ g^{-1}

Table 3. Correlations and predictive equations for different egg size measures and proximate composition attributes at the first sample after fertilization. Pearson's correlation coefficients including eggs from all females are given above the diagonal (correlations excluding females 1 and 2 are given in parentheses). All correlations were highly significant, even after sequential Bonferroni corrections. Regression parameter estimates (α – intercept; β – slope) for using the row trait to predict the column trait are given below the diagonal (using all females, $N_{eggs} = 48$)

	Diameter (cm)	Wet mass (g)	Dry mass (g)	Water (g)	Protein (g)	Fat (g)	Energy (kJ)
Diameter		0·943	0·952	0·931	0·948	0·938	0·958
		(0·762)	(0·727)	(0·739)	(0·721)	(0·763)	(0·818)
Wet mass	$\alpha = -0{\cdot}129$		0·991	0·997	0·990	0·908	0·982
	$\beta = 0{\cdot}428$		(0·929)	(0·983)	(0·488)	(0·914)	(0·836)
Dry mass	$\alpha = -0{\cdot}051$	$\alpha = -0{\cdot}003$		0·977	0·992	0·926	0·988
	$\beta = 0{\cdot}157$	$\beta = 0{\cdot}361$		(0·845)	(0·569)	(0·943)	(0·888)
Water	$\alpha = 0{\cdot}323$	$\alpha = -0{\cdot}004$	$\alpha = -0{\cdot}004$		0·890	0·981	0·970
	$\beta = 3{\cdot}202$	$\beta = 1{\cdot}556$	$\beta = 0{\cdot}556$		(0·422)	(0·852)	(0·767)
Protein	$\alpha = -0{\cdot}038$	$\alpha = -0{\cdot}001$	$\alpha = 0{\cdot}002$	$\alpha = 0{\cdot}006$		0·932	0·995
	$\beta = 0{\cdot}123$	$\beta = 0{\cdot}282$	$\beta = 0{\cdot}776$	$\beta = 2{\cdot}202$		(0·639)	(0·838)
Fat	$\alpha = -0{\cdot}007$	$\alpha = -0{\cdot}000$	$\alpha = 0{\cdot}000$	$\alpha = 0{\cdot}016$	$\alpha = -0{\cdot}001$		0·962
	$\beta = 0{\cdot}022$	$\beta = 0{\cdot}046$	$\beta = 0{\cdot}129$	$\beta = 11{\cdot}206$	$\beta = 0{\cdot}166$		(0·956)
Energy	$\alpha = -1{\cdot}025$	$\alpha = -0{\cdot}013$	$\alpha = 0{\cdot}050$	$\alpha = 0{\cdot}007$	$\alpha = -0{\cdot}002$	$\alpha = 0{\cdot}082$	
	$\beta = 3{\cdot}26$	$\beta = 7{\cdot}37$	$\beta = 20{\cdot}32$	$\beta = 0{\cdot}083$	$\beta = 26{\cdot}18$	$\beta = 141{\cdot}9$	

Table 4. Results of statistical analyses of the partitioning of maternal investment. Egg size measures and egg composition attributes were compared between families (one-way models), and between families nested within female size class (nested models). Egg composition attributes were compared on an absolute basis (no covariate, absolute composition) and on a relative basis (with wet egg mass as a covariate, relative composition). For each effect in each model, the F ratio is given with degrees of freedom as subscripts. The percentage of variance explained by differences between females is also provided for each model (%Var)

	One-way models		Nested models			
Dependent variable	Family		Size class	Family (size class)		Covariate Wet egg mass
Egg size measures	$F_{5,42}$	%Var	$F_{1,4}$	$F_{4,42}$	%Var	
Diameter	153·53***	95·0	37·31**	18·59***	11·0	
Wet mass	261·32***	97·0	49·12**	24·60***	8·8	
Dry mass	219·16***	96·5	64·73**	15·94***	6·6	
Absolute composition	$F_{5,42}$	%Var	$F_{1,4}$	$F_{4,42}$	%Var	
Water mass	221·06***	96·5	39·36**	25·49***	10·7	
Fat mass	172·29***	95·5	20·41*	35·30***	19·1	
Protein mass	371·22***	97·9	61·09**	28·52***	7·3	
Energy	326·25***	97·6	55·56**	27·39***	7·9	
Relative composition	$F_{5,41}$	%Var	$F_{1,37}$	$F_{4,41}$	%Var	$F_{1,41}$
Water mass	6·94***	0·3	0·64	6·56***	0·2	411·51***
Fat mass	49·23***	18·4	0·20	57·12***	19·3	34·93***
Protein mass	21·23***	1·8	10·32**	18·74***	1·3	123·65***
Energy	35·66***	3·7	4·35	35·88***	3·2	109·98***

*$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$.

of energy). Statistical analyses were also performed on these mass-specific values, yielding similar results (not shown) to analyses using wet egg mass as a covariate.

Results

Different egg size measures (diameter, wet mass, dry mass) and proximate composition attributes (absolute water, protein, lipid and energy content) were all highly correlated with each other (Table 3). All correlations remained significant after sequential Bonferroni corrections for multiple tests. Correlations were also strong at each subsequent sampling period (results not shown). Conversion between the different variables can be accomplished using the linear regression coefficients reported in Table 3. When the two smaller females were excluded, correlations were generally weaker but all were still highly significant (Table 3). Overall, each variable was a reasonable surrogate for the others, particularly over a large range of female sizes. Accuracy of predictions will depend on the size range of females, and when the range is small, certain variables are more highly correlated than others (Table 3).

VARIATION WITHIN AND BETWEEN FEMALES

Egg size at the first sampling period varied between families when the three size measures were considered collectively (MANOVA, $F_{34,111} = 34{\cdot}17$, $P < 0{\cdot}001$), and when each was considered individually (Table 4).

When family was nested within female size class, smaller females had significantly smaller eggs (MANOVA, $F_{3,40} = 34{\cdot}17$, $P < 0{\cdot}001$; Table 4) but egg size also varied between families within a size class (MANOVA, $F_{12,106} = 12{\cdot}62$, $P < 0{\cdot}001$; Table 4). Most of the total variance in egg size measures (95·0–97·0%) was attributable to differences between families, but only 8·8–11·0% of the variance was attributable to differences between families nested within female size class. Note that when the two younger females were excluded most of the variation was still attributable to differences between families (diameter = 79·1%, wet mass = 75·2%, dry mass = 67·2%).

Egg composition attributes varied on an absolute basis (i.e. without wet egg mass as a covariate) between families (MANOVA, $F_{15,111} = 76{\cdot}63$, $P < 0{\cdot}001$; Table 4). When family was nested within size class, smaller females had less water, fat, protein and energy (MANOVA, $F_{3,40} = 565{\cdot}33$, $P < 0{\cdot}001$; Table 4) but these attributes also varied between families within a size class (MANOVA, $F_{12,106} = 32{\cdot}37$, $P < 0{\cdot}001$; Table 4). Most of the total variance in egg attributes (95·5–97·9%) was attributable to differences between families, but only 7·3–19·1% of the variance was attributable to families nested within female size class. Note that when the two younger females were excluded from the analysis, most of the variation was still attributable to differences between families (water = 74·9%, fat = 81·0%, protein = 76·8%, energy = 76·4%).

Egg composition attributes varied less on a relative basis (i.e. with wet egg mass as a covariate) than on an absolute basis, a result evident in the significance of wet egg mass (MANCOVA, $F_{3,39} = 241{\cdot}70$, $P < 0{\cdot}001$; Table 4). Each attribute nonetheless varied between families on a relative basis (MANCOVA, $F_{15,108} = 17{\cdot}09$, $P < 0{\cdot}001$; Table 4). When family was nested within female size class, size class had a significant effect for all traits combined (MANCOVA, $F_{3,40} = 565{\cdot}33$, $P < 0{\cdot}001$), as did family nested within size class (MANCOVA, $F_{12,106} = 32{\cdot}37$, $P < 0{\cdot}001$). Considering each attribute individually, size class did not have a significant effect on relative values for three of the four attributes (protein mass being the exception, Table 4) but family nested within size class was still always significant (Table 4). Very little of the variation in relative attributes was attributable to differences between females, indicating that the use of wet egg mass as a covariate effectively mirrored female effects (the least so for protein).

Table 5. Results of statistical analysis of ontogenetic patterns. Two-way ANOVAS were used to test for family, sample period and interaction effects. Proximate composition attributes were compared on an absolute basis (no covariate, absolute composition) and on a relative basis (with wet egg mass as a covariate, relative composition). For each effect in each model, the F ratio is given with degrees of freedom as subscripts. Note that egg diameter was only measured for the three samples before hatching, and so the degrees of freedom for that model were different (family, $F_{5,10}$; sample period, $F_{2,10}$; interaction, $F_{10,126}$)

	Family	Sample period	Interaction	Covariate (wet egg mass)
Egg size measures	$F_{5,25}$	$F_{5,25}$	$F_{25,252}$	
Diameter	141·86***	21·23***	2·02*	
Wet mass	108·43***	8·70***	9·70***	
Dry mass	101·84***	27·72***	8·21***	
Absolute composition	$F_{5,25}$	$F_{5,25}$	$F_{25,252}$	
Water mass	49·49***	20·94***	13·37***	
Fat mass	59·86***	8·79***	5·87***	
Protein mass	89·45***	34·06***	7·51***	
Energy	100·85***	22·45***	7·19***	
Relative composition	$F_{5,25}$	$F_{5,25}$	$F_{25,251}$	$F_{1,251}$
Water mass	1·71	22·00***	12·65***	1741·86***
Fat mass	9·79***	11·65***	4·91**	17·45***
Protein mass	1·34	22·88***	10·82***	68·90***
Energy	2·89*	19·87	9·27***	65·16

*$P < 0{\cdot}05$, **$P < 0{\cdot}01$, ***$P < 0{\cdot}001$.

ONTOGENETIC TRENDS

Egg and alevin size measures varied between families (MANOVA, $F_{15,343} = 91{\cdot}11$, $P < 0{\cdot}001$; Table 5) and sample periods (MANOVA, $F_{6,248} = 19{\cdot}06$, $P < 0{\cdot}001$; Table 5), with a significant interaction (MANOVA, $F_{30,365} = 2{\cdot}29$, $P < 0{\cdot}001$; Table 5). Absolute composition attributes considered collectively varied between families (MANOVA, $F_{15,691} = 140{\cdot}58$, $P < 0{\cdot}001$) and sample periods (MANOVA, $F_{15,691} = 114{\cdot}34$, $P < 0{\cdot}001$), with a significant interaction (MANOVA, $F_{75,748} = 8{\cdot}26$, $P < 0{\cdot}001$). Relative composition attributes, considered collectively, also varied between families (MANCOVA, $F_{15,688} = 16{\cdot}05$, $P < 0{\cdot}001$) and sample periods (MANCOVA, $F_{15,688} = 75{\cdot}58$, $P < 0{\cdot}001$), with a significant interaction (MANCOVA, $F_{75,745} = 6{\cdot}29$, $P < 0{\cdot}001$). In the following, we consider ontogenetic patterns for fat, protein and energy individually.

Fat content considered on an absolute or relative basis varied between families and sample periods, with a significant interaction (Table 5). On average, absolute fat content decreased from just after fertilization ($0{\cdot}0048 \pm 0{\cdot}0019$ g) to just before hatching ($0{\cdot}0027 \pm 0{\cdot}0016$ g), and then increased to just before first feeding ($0{\cdot}0043 \pm 0{\cdot}0020$ g; Fig. 1). Based on regression relationships, eggs lost about 0·01 mg of fat per day, for a total decrease of 27·1% over 110 days, and alevins gained 0·027 mg of fat per day, for a total increase of 102·8% over 52 days (Table 6). Simple simulations were used to test whether the observed increase in fat content after hatching could have been caused by differential mortality. The observed mean and standard deviation were used to generate normal distributions of fat content for 100 simulated alevins in each family, and then the alevins with the lowest fat content were deleted in accord with observed mortality (Table 1). In each case, this simulated selective mortality caused only minor changes in mean fat content for families, and could not account for the observed increase in fat after hatching.

Protein content considered on an absolute basis varied between families and sample periods, with a significant interaction (Table 5). When protein content

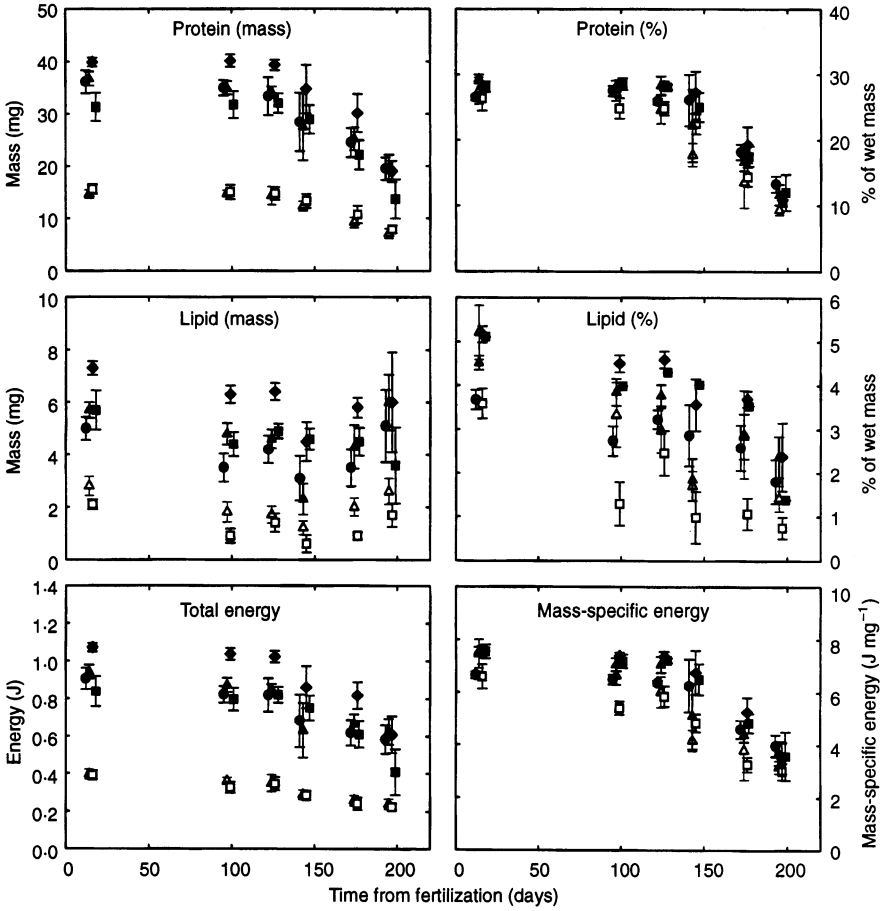

Fig. 1. Ontogenetic trends in protein, fat and energy expressed as absolute values (left three panels) and on a mass-specific basis (right three panels). Error bars depict standard deviations. Note the shift in energy use from before hatching (sample periods 1–3) to after hatching (sample periods 4–6), and the increase in fat mass after hatching. The continual decline in percentage fat reflects an increase in percentage water (not shown). Symbols: △; female 1, □; female 2, ● female 3, ▲ female 4, ◆ female 5, ■ female 6.

Table 6. Ontogenetic trends in fat, protein and energy before hatching (Periods 1–3) and after hatching (Periods 4–6). Parameter values (means ± SD across full-sib families) are for the slope and intercept of each composition attribute (fat, protein, energy) regressed on days after fertilization. ANCOVA statistics indicate results of tests for homogeneity of slopes and intercepts between families (intercepts were only tested when slopes did not differ). The percentage change in each attribute over each stage (% change) was calculated as 100[(final value – initial value)/initial value]

Egg attributes	Before hatching (110 days)			After hatching (52 days)		
		ANCOVA			ANCOVA	
	Value	*F*	*P*	Parameters	*F*	*P*
Fat content						
Slope (μg day^{-1})	–9·6 ± 0·7	0·107	0·991	27·4 ± 29·0	12·4	<0·001
Intercept (mg)	4·82 ± 1·96	407·3	<0·001	–1·23 ± 5·12	–	–
% change	–43·8			+20·0		
Protein content						
Slope (μg day^{-1})	–8·8 ± 11·6	2·5	0·036	–181·3 ± 86·9	7·9	<0·001
Intercept (mg)	29·2 ± 11·2	–	–	50·5 ± 20·7	–	–
% change	–3·8			–28·6		
Energy content						
Slope (J day^{-1})	–0·55 ± 0·25	1·56	0·18	–2·50 ± 2·46	9·8	<0·001
Intercept (10^{-1})	7·63 ± 2·94	964·7	<0·001	9·47 ± 5·45	–	–
% change	–23·0			–16·2		

was considered on a relative basis only the family effect was not significant (Table 5). On average, absolute protein content decreased from just after fertilization (0·0290 ± 0·0104 g) to just before hatching (0·0279 ± 0·0101 g) and then further decreased to just before first feeding (0·0145 ± 0·0058 g). Based on regression relationships, eggs lost about 0·009 mg of protein per day, for a total decrease of 3·3% over 110 days, and alevins lost 0·181 mg of protein per day, for a total decrease of 38·3% over 52 days (Table 6). The daily reduction in protein mass was thus about 20 times higher after hatching than before hatching (Fig. 2). Initial alevin size did not influence the subsequent proportional decrease in protein mass ($\log_e$ protein mass just before first feeding minus $\log_e$ protein mass just after hatching) – two of the females with larger eggs (5 and 6) had larger proportional decreases in protein content (59·9%, 77·1%) and two (3 and 4) had smaller proportional decreases (35·9%, 31·0%) than did the females (1 and 2) with smaller eggs (51·9%, 54·9%).

Energy content considered on an absolute or relative basis varied between families and sample periods, with a significant interaction (Table 5). On average,

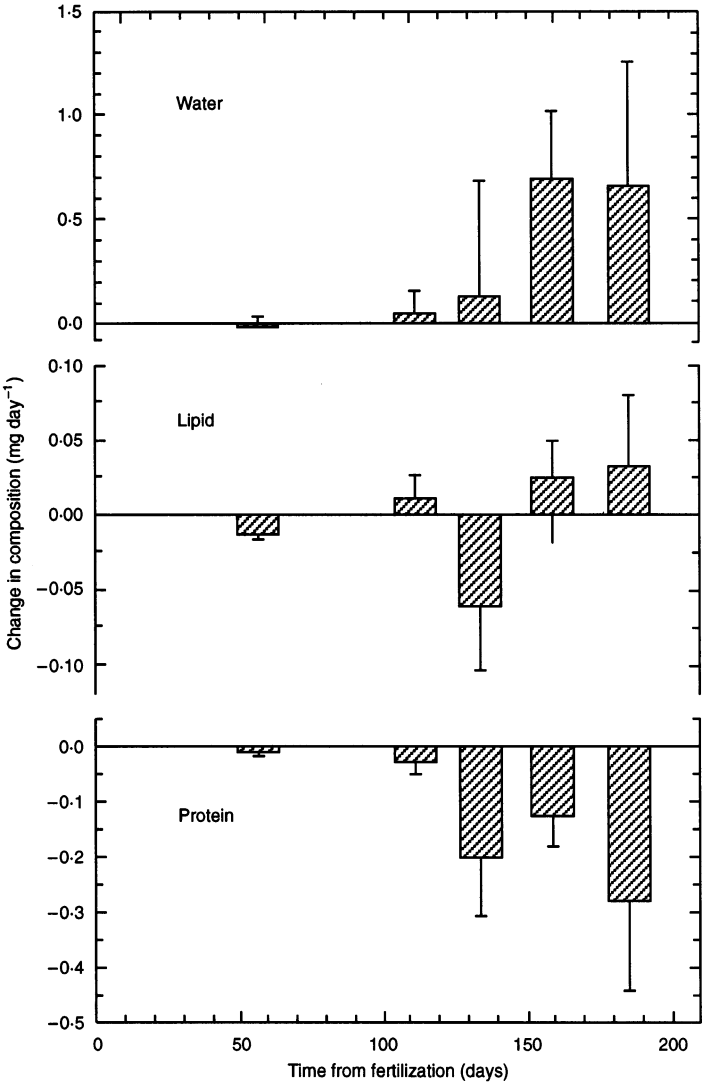

Fig. 2. Mean daily mass changes (mg/day) of water, fat and protein content of salmon eggs and alevins as a function of days after fertilization. The mean time from fertilization to hatching is 135 days.

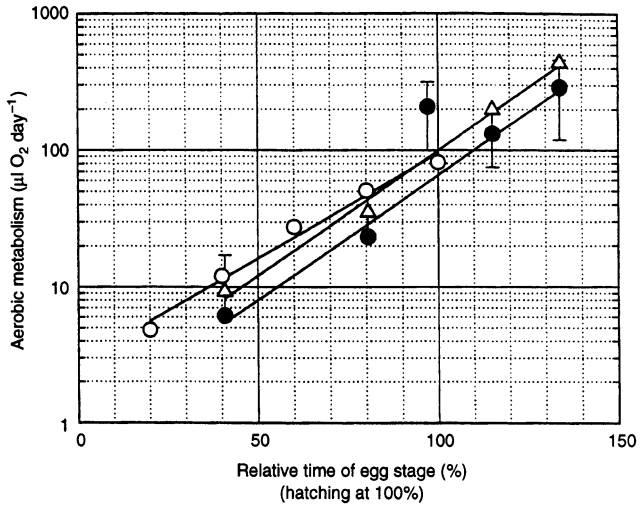

Fig. 3. Aerobic metabolism (expressed as oxygen consumption) of salmon eggs and alevins as a function of time after fertilization, expressed in percentage of the time to hatching. ● Our results – measured at 3·5 °C; ○ published data (mean values) from other studies on *Salmo salar* (measured at 9·5 °C); Privolniew (1938); Hayes (1949); Bøen (1987); △ our results corrected to 9·5 °C using Q_{10}-value of 2·0.

energy content decreased slowly from just after fertilization (0·7570 ± 0·2732 kJ) to just before hatching (0·7008 ± 0·2665 kJ) and then decreased rapidly to just before first feeding (0·4482 ± 0·1847 kJ). Based on regression relationships, eggs lost about 0·550 J of energy per day, for a total decrease of 23·0% over 110 days, and alevins lost 2·50 J of energy per day, for a total decrease of 16·2% over 52 days (Table 6).

METABOLISM

Assuming that all energy necessary for supporting the metabolism of the eggs and alevins was derived from the combustion of stored protein (Fig. 2), daily metabolic rates were calculated. These values increased in direct proportion to the daily protein loss; from 0·115 ± 0·208 J day^{-1} during the initial period to 5·43 ± 3·20 J day^{-1} during the final period. The equivalent aerobic metabolic rates, expressed in rates of oxygen consumption (V_{O_2}), increased from 6·09 ± 11·06 µl O_2 day^{-1} to 288·9 ± 170·2 µl O_2 day^{-1}. These rates were similar (after correction for temperature) to those documented in other studies on Atlantic Salmon eggs, where rates of oxygen consumption were measured directly (Fig. 3).

Discussion

Our study is one of a few for salmonids or other fishes that (1) considered variation in fat, protein and energy content instead of just egg or alevin size; (2) measured attributes of individual eggs and alevins rather than batches; and (3) considered variation both within and between females (full sibling families). Our first finding was that size measures (diameter, wet mass, dry mass) and proximate composition attributes (absolute water, protein, fat and energy) were all highly correlated (Table 3). This finding lessens concerns regarding the use of one measure as surrogate for another, certainly within populations and perhaps also within species. As a caveat, however, correlations were lower when the two smallest females (those spending 12–24 fewer months at sea than the other four females) were excluded from the analysis. Second, egg size measures, protein and fat composition, and energy content varied much more between females than within them. Third, fat, protein and energy varied more on an absolute basis than on a relative basis (i.e. after controlling for egg size variation). Fourth, fat stores were depleted by half between fertilization and hatching, but then doubled between hatching and first feeding. We discuss the last three of these results in the context of our specific objectives, and with an eye toward implications for the evolution of maternal investment. Competing mechanistic hypotheses can be advanced to explain the variation, and we juxtapose the major alternatives in hopes that they will be the focus of future experimental and comparative research.

VARIATION WITHIN AND BETWEEN FEMALES

Absolute egg size, protein and fat composition, and energy stores varied much more between families than within them (Table 4). For example, only 2·4% of the total variation in energy content was attributable to differences between families. Although most of the within-family variation was attributable to the two different size classes of females, family effects were still highly significant even within a size class (Table 4). If the two smaller females were excluded from the analysis, less of the variation (but still most of it) was attributable to differences between families (see Results). The relative lack of variation within families may arise because (1) females cannot vary their allocation between individual eggs, or (2) selection favours a single optimum within families. The first hypothesis invokes a physiological constraint, and is unlikely because egg size and energy content can vary substantially within Atlantic Salmon females under certain experimental conditions (Einum & Fleming 2000a, 2000b). Moreover, unilateral ovariectomy studies indicate that the development rate of individual eggs can vary within females (Tyler *et al*. 1996). The second hypothesis invokes adaptation, and we have no direct evidence to marshal in its support. If correct, however, it suggests that bet-hedging based on egg size or energy content (Roff 1992, p. 388) is not present within the population.

Maternal provisioning of eggs varied less on a relative than on an absolute basis (wet egg mass as a covariate removed most of the between-female variance component; Table 4). This result suggests that (1) different females within a population have limited ability to influence the relative composition of their eggs, or (2) a certain combination of fat, protein and energy is necessary for proper development and that these requirements are relatively consistent between eggs and alevins of different size. The first hypothesis is constraint-based, and the second is adaptive. Diet manipulation often has no effect on the proximate composition of fish eggs (e.g. Kamler 1992; Fletcher & Wootton 1995) but this result cannot by itself discriminate between a constraint and the adaptive buffering of progeny quality by females facing variation in diet.

ARE SMALL EGGS REALLY 'LOW QUALITY'?

Some females in salmonid populations produce eggs traditionally perceived to be of 'low quality' (i.e. small in size and low in total energy). In the present study, females producing the smallest eggs were those that spent the least time at sea (18 months), but egg size and energy content also varied by up to 20% between females within the larger size class (Table 1). In other populations of salmonids, egg size can vary to even greater degrees among females of a common age (e.g. Jonsson & Jonsson 1999). The traditional view of small eggs is that they produce juveniles having lower average fitness. This argument invokes a constraint – some females are supposedly hampered by energetic, physiological, developmental or allometric limitations to such a degree that they cannot produce optimal eggs. An alternative view is adaptive – under some circumstances smaller eggs with less energy may actually be optimal. Diet substantially influences egg size in some studies (e.g. Jonsson & Jonsson 1999) but not in others (e.g. Bromage *et al*. 1992) but these results cannot be used to discriminate between the constraint hypothesis and possible adaptive plasticity in response to growth opportunity. One line of evidence contradicting the constraint hypothesis is that although non-anadromous salmonids are orders of magnitude smaller than their anadromous counterparts, they have only marginally smaller eggs (Berg & Gausen 1988; Wood & Foote 1996).

A possible adaptive mechanism is based on the expectation that optimal egg sizes are smaller for smaller females. The eggs of salmonids are often exposed to low levels of dissolved oxygen during incubation (Peterson & Quinn 1996), which can substantially increase mortality and reduce metabolic efficiency (Chapman 1988). Larger eggs would be at a disadvantage in such environments because they have a lower surface-to-volume ratio (making oxygen transfer more difficult), and yet have greater metabolic oxygen demand. A few studies have provided evidence that smaller females provide poorer incubation environments for their eggs (e.g. van den Berghe & Gross 1989), and as a result optimal egg sizes should be smaller for these females. This hypothesized mechanism has yet to be experimentally demonstrated but has been invoked numerous times as a possible reason for positive correlations between egg size and female size (e.g. van den Berghe & Gross 1989; Fleming & Gross 1990; Quinn *et al*. 1995). For this mechanism to work, a genetically based or environmentally induced adaptive reaction norm must link maternal size and egg size.

ONTOGENETIC TRENDS

Daily energy use was six-fold higher after hatching than before hatching (Table 6), which is not surprising because metabolism will obviously be higher for a late-stage embryo after hatching than for a early stage embryo before hatching. Based on changes in protein stores (Fig. 2), we estimated the aerobic metabolism of eggs and alevins to range from 6 to 289 μl O_2 d^{-1}, increasing logarithmically from fertilization to first feeding (Fig. 3). Although these V_{O2} values are lower than those previously published for Atlantic Salmon (Privolniew 1938; Hayes 1949; Bøen 1987), the difference is likely the result of lower ambient temperatures in our study. Assuming a Q_{10} (the

increase in metabolic rate produced by raising temperature 10 °C) of 2·0, which is at the lower end of the range of normally occurring biological Q_{10} values (Withers 1992), and taking the temperature difference into consideration, our values fall within those published previously (Fig. 3). As the values reported in other studies were based on direct measurements of oxygen consumption, it seems that the metabolic costs of eggs and alevins are met mostly by protein stores.

A small fraction of the protein loss may not have been used for aerobic metabolism, but may instead have been used in the synthesis of lipid. However, we do not know how large this fraction is, nor do we know the exact cost of conversion of protein into lipid in this case. Hence, the estimation of the aerobic metabolism is merely an exercise to show that such calculated rates are very similar to published literature values, suggesting that the aerobic metabolism probably is largely met by protein metabolism.

Our finding that salmonid alevins increase their fat stores after hatching has never to our knowledge been suggested in the literature. We must acknowledge that the generality of this result is unknown, simply because we are the first to measure ontogenetic changes. Patterns of fat use may differ among years, populations and species; and we will not know by how much until comparable studies are conducted. For our system at least, the result seems robust because (1) it was evident for five of the six females; (2) the change was dramatic (fat values doubled after hatching); and (3) it could not be explained by differential mortality (see Results). The increase in fat after hatching must come from an endogenous source because it occurred when the alevins were not feeding. This source could conceivably be structural lipids or synthesis from protein. An origin from protein is more likely because the quantity of structural lipids cannot come close to accounting for the increase in stored lipids (O. K. Berg and B. Henriksen, unpublished data).

The increase in fat stores of alevins between hatching and emergence suggests that fat stores are critical to postemergent survival. Numerous studies have shown that mortality and selection are strongest on Atlantic Salmon immediately after their emergence (e.g. Einum & Fleming 2000a). Emerging juveniles must rapidly establish a territory and defend that territory from other juveniles (Cutts *et al*. 1999a, 1999b). During this period, aggressive interactions between individuals are common and social status determines subsequent growth (Metcalfe, Wright & Thorpe 1992; Cutts *et al*. 1999b). Fat stores during this crucial period may aid survival, competitive ability and growth because fat is an efficient and rapidly mobilized energy source (carbohydrate stores are minimal in fishes). Fat stores at emergence are probably extremely important for Atlantic Salmon juveniles, and the fat placed in eggs by females does not appear to be sufficient for this period. Instead, alevins seem to undertake an inefficient energy conversion (protein to fat) that their mothers were unable or unwilling (in an evolutionary sense) to make.

The conversion of protein to fat that is undertaken by alevins may ultimately reflect the conflicting goals of offspring and their mothers for maximizing reproductive success. Offspring should maximize their own fitness even if it comes at the expense of their siblings (weighted by their average relatedness), whereas mothers should maximize the product of average offspring fitness and offspring number (Smith & Fretwell 1974; Einum & Fleming 2000b). A female's allocation of energy between offspring is therefore expected to be less than that which best suits each individual offspring (Trivers 1974; Mock & Parker 1997). Perhaps females would not be able to make as many eggs if they invested as much fat into each egg as would be optimal from the offspring's perspective. This leaves offspring with the need to make the best of a suboptimal level of parental investment. This intriguing possibility deserves further research.

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