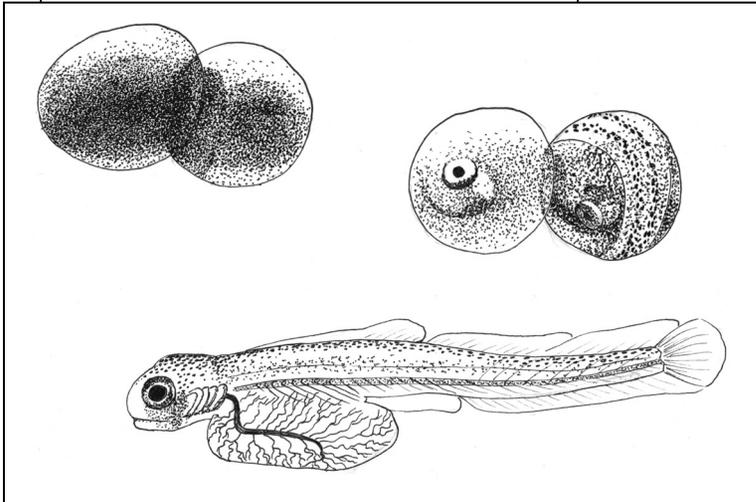


Evolution of Egg Size and Number

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Early stage eggs, eyed eggs, and an alevin

4

Reproductive traits are strong determinants of fitness and should thus be associated with intense selection. One important component of this selection is the period following fertilization of the ova. In a wide range of organisms, particularly those with high numbers of offspring, early life stages experience massive mortality (e.g., Fortier and Leggett 1985; Brosseau and Baglivo 1988; Iverson 1991). Thus, if phenotypic variation is present, the potential for selection on juveniles may exceed that at any other stage of life. Although some phenotypic variation may be caused by genetic variation among the juveniles themselves, the importance of maternal effects (particularly through egg size) has become increasingly apparent (reviewed by Roff 1992; Bernardo 1996a; Mousseau and Fox 1998a,b). It is now clear that egg size is an important fitness component, with offspring fitness after hatching tending to increase with increasing egg size (e.g., Roff 1992, pp. 348–352; Sinervo et al. 1992; Hipfner and Gaston 1999; Einum and Fleming 2000a).

All else being equal, and barring density-dependent effects, the fitness of a female should increase with increasing egg number. However, egg size not only influences offspring fitness but also the number of offspring a female can produce. The most popular reasoning is that (1) a female has only a limited amount of energy resources available for egg production (or space to hold eggs in her body cavity), and (2) for a given energetic investment (or amount of space), an increase in egg size will inevitably cause a decrease in egg number. Due to this tradeoff, the size of eggs imposes a constraint on egg number (e.g., Rohwer 1988; Elgar 1990; Sinervo and Licht 1991), resulting in negative phenotypic and genetic correlations between these traits in many organisms (Roff 1992, p. 357), including salmonids (e.g., Jonsson and Jonsson 1999; Kinnison et al. 2001).

Egg size thus presents breeding females with an evolutionary dilemma, arising because maximization of both numbers of eggs and offspring fitness (which is size-dependent) is not attainable. Because egg size is inherently linked to egg number, the evolution of each cannot be considered in isolation. Here we outline general theoretical models for the evolution of egg size and number (Sections 1.1–1.5), and show how research on salmonids has provided critical empirical tests of these models (Sections 1.1–1.5). Due to our empirical focus on salmonids, we use terms such as “egg” and “hatching,” but the theoretical framework also applies to other organisms. We close with a consideration of how egg size evolves on a macro-evolutionary scale (i.e., among species), and suggest that further progress can be made by simultaneously considering multiple features of an organism’s biology that are likely to influence egg size evolution.

Several issues should be addressed before proceeding. First, our approach is primarily based on traditional optimization theories, because these have stimulated much empirical work, and have been pivotal in our understanding of egg size and number variation. Yet, alternative approaches may be relevant in some systems. For example, if selection is frequency-dependent or density-dependent, the optimal value may fluctuate over time, making an evolutionary stable strategy (ESS) approach appropriate (Sinervo et al. 2000). Furthermore, variation within populations may be non-adaptive if caused by mutational input and

genetic drift. Fortunately, most optimization theories are built on explicit testable assumptions, and provide qualitative predictions regarding the nature of variation (e.g., correlations with environment conditions), enabling rigorous tests.

Second, the optimization approach assumes that optimal values are achieved, and that there are no constraints (e.g., mechanical or genetic) preventing adaptation (other than any constraints explicitly included in a model). Although this may be an inaccurate assumption in many cases, the relative success of the optimization approach, at least qualitatively, suggests that such constraints may rarely be strong enough to prevent trait values from approaching optimal values. We discuss such constraints in Sections 3.1 and 3.2.

Third, in empirical and theoretical studies of selection one must determine whether or not offspring fitness components should be assigned to parental fitness (Wolf and Wade 2001). If the component of offspring fitness is controlled largely by the mother (i.e., maternal effect), then it will be appropriate to incorporate this component into maternal fitness. This may not be true if both (1) the offspring fitness component is strongly influenced by the offspring's own genotype (i.e., direct effect), and (2) there is a genetic correlation between the maternal trait and the direct effect (Wolf and Wade 2001). For example, if juveniles originating from large eggs are also genetically superior, then incorporating the offspring fitness component into maternal fitness may yield somewhat incorrect conclusions regarding the evolutionary dynamics of egg size. In empirical studies this potential problem can be solved by manipulating the trait in question and thereby controlling for such correlations (Sections 2.1–2.2).

1. Theory

The idea that some tradeoff must exist between egg size and number can be traced back at least to Lack (1947a) and Svårdson (1949). Lack discussed how clutch size evolves in altricial birds (i.e., birds where offspring are fed by parents). His hypothesis was that clutch size is determined by the number of young that parents can raise to independence. Although he was mainly concerned with the level of resources provided to each young *after* hatching, the main argument remains the same for provisioning before hatching; an increase in number of offspring for a constant level of total investment cannot occur without a cost to individual offspring fitness. Similarly, Svårdson (1949) realized that there must be a balance between the number and size of eggs in fishes. Based on observations suggesting that larger eggs give rise to larger larvae, which have better survival prospects, he proposed that there must be a premium on large eggs, which must tend to decrease egg number. These verbal models were important contributions toward an increased interest in reproductive allocation (e.g., Kendeigh et al. 1956; Olsson 1960; Bagenal 1969; Blaxter 1969; Klomp 1970). Then, a mathematical model on reproductive allocation was published by Smith and Fretwell (1974). This model has been incredibly influential (more than 750 citations over 15 years, ISI Web of Science), in part by sparking an

explosion of theoretical efforts to better understand the evolution of egg size and number. These efforts have remained a prominent area of life history theory (e.g., Brockelman 1975; Parker and MacNair 1978; Parker and Begon 1986; Lloyd 1987; McGinley et al. 1987; Morris 1987; Sargent et al. 1987; McGinley 1989; Geritz 1995; Hutchings 1997; Forbes 1999; Hendry et al. 2001b; Sakai and Harada 2001). We start our discussion of theoretical models by presenting the analysis of Smith and Fretwell (1974). We then consider how the basic theoretical framework has been extended by subsequent models.

1.1. The Smith–Fretwell Model

Smith and Fretwell (1974) set out to solve the problem of the allocation of a fixed quantity of resources into offspring. They assumed (1) a tradeoff between egg size and number, (2) the currency being maximized through selection is maternal fitness (i.e., number of grandchildren), and (3) the pattern of allocation does not influence survival or future reproduction of the mother. Thus, for a given breeding event, maternal fitness (W) depends on the number of offspring produced and the mean fitness of offspring. This can be expressed as:

$$W(M, m) = \frac{M}{m} \times f(m) \quad (1)$$

where M represents the total amount of resources invested into egg production (e.g., total ovary mass in oviparous fishes), and m represents the amount of resources invested into each egg. Thus, M/m equals the number of eggs produced. $f(m)$ is a function describing how offspring fitness depends on egg size.

Smith and Fretwell (1974) assumed that $f(m)$ is an asymptotic function with some minimum viable egg size (Figure 4.1a). Two suggested explicit functions for $f(m)$ are:

$$f(m) = 1 - \exp[-(m - m_{min})] \quad (2)$$

and

$$f(m) = 1 - \left(\frac{m_{min}}{m}\right)^a \quad (3)$$

where m_{min} is the minimum viable egg size, and a is a constant determining the rate at which the function approaches the asymptote (Parker and Begon 1986; McGinley et al. 1987). Thus, offspring fitness is maximized (but with ever-diminishing proportional increases) as egg size approaches infinity. This is not the case for maternal fitness. The optimal egg size with respect to maternal fitness (m^*) can be found by setting $dW/dm = 0$ and solving for $m = m^*$:

$$m^* = \frac{f(m)}{f'(m)} \quad (4)$$

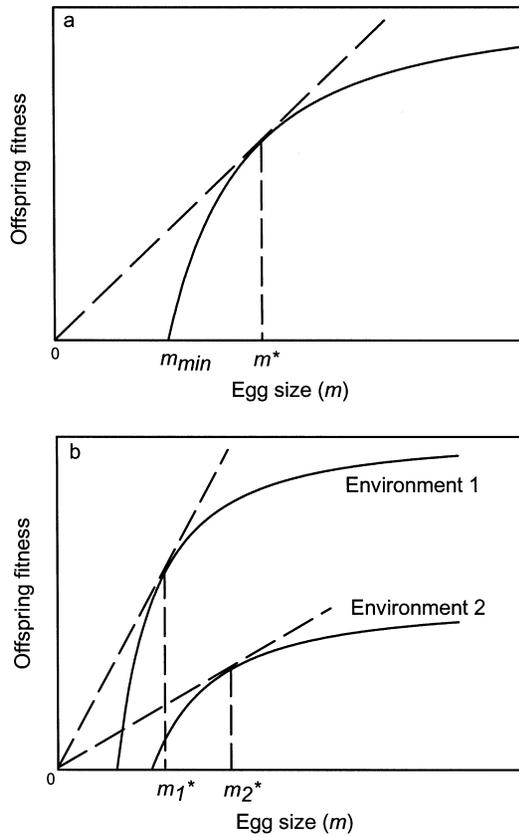


Figure 4.1. (a) The hypothetical asymptotic relationship between egg size and offspring fitness as suggested by Smith and Fretwell (1974). m^* denotes the optimal egg size that maximizes maternal fitness and m_{min} denotes the minimum viable egg size. The optimal egg size can be obtained by drawing a tangent to the function from the origin as done here, or by determining where the derivative of the function relating maternal fitness to egg size equals zero (see Figure 4.4). (b) Due to better environmental conditions, maximum relative fitness is higher and minimum viable egg size smaller in environment 1 than in environment 2. As a result, the optimal egg size in environment 1 (m_1^*) is smaller than in environment 2 (m_2^*).

This is the well-known marginal value solution (Charnov 1976), and the result can also be obtained graphically (Figure 4.1a). An important point is that because $f(m)$ is independent of M (i.e., no density-dependent effects on $f(m)$), so too is the optimal egg size (m^*), and the resulting ratio (M/m^*) determines the optimal egg number. As we shall see in Section 1.4, relaxing the assumption of no density dependence can change the outcome.

The simple structure of the Smith–Fretwell model makes it tractable for extensions beyond predicting a single optimal egg size and number in a single population. It has therefore had an enormous impact on life history theory but

empirical tests have been rare. In Section 2.1, we outline such a test using a phenotypic manipulation of egg size in Atlantic salmon.

1.2. Optimal Egg Size and Environment Quality

According to the basic Smith–Fretwell model, all females reproducing in a particular environment should produce identical egg sizes. However, different environments may have different relationships between egg size and offspring fitness (i.e., variable $f(m)$). Any changes in this function have implications for Equation (4), and thus for optimal egg size. This means that the model has the potential to predict not only evolutionary stable egg sizes within a population, but also adaptive variation among populations. In general (although not always—see Section 1.3), the Smith–Fretwell framework predicts that as the quality of the environment experienced by offspring decreases, optimal egg size should increase (Figure 4.1b; McGinley et al. 1987). In Section 2.2, we outline empirical tests of this prediction using experiments on brook charr and brown trout.

1.3. Opposing Selection Stages

The Smith–Fretwell model has commonly been used to consider contributions to offspring fitness after hatching. In some organisms, however, egg size may also influence offspring fitness *before* hatching. For example, predation on pelagic eggs in marine environments has been suggested to select against small sizes (Rijnsdorp and Jaworski 1990). Egg size may also influence development, with larger eggs sometimes requiring more time from fertilization to hatching or yolk absorption (Sibly and Monk 1987; Einum and Fleming 2000a; but see Hutchings 1991; Hendry et al. 1998; Einum and Fleming 1999). Accordingly, if the egg stage is a “safe harbor” with low mortality, and an increase in egg size reduces the duration of the later high-risk juvenile stage, selection should favor large eggs (Williams 1966b; Shine 1978). Conversely, in organisms that experience high intrinsic mortality during the egg stage there may be selection for small, fast-developing eggs. These examples suggest selection for egg size before hatching, and that selection pressures may sometimes oppose each other during different developmental stages (e.g., large eggs may provide a negative contribution to offspring fitness before hatching, but a positive contribution after hatching). Such opposing selection pressures at different life history stages may be common in nature (Schluter et al. 1991).

A recent analysis examining how opposing selection pressures may shape egg size evolution is given by Hendry et al. (2001b). They considered a situation where offspring fitness and egg size were negatively correlated before hatching, but positively correlated after hatching. A negative pre-hatching survival/size relationship could occur for many reasons. In particular, egg size in aquatic organisms has been assumed to be negatively correlated with survival before hatching because levels of dissolved oxygen may constrain egg size (Krogh 1959). The reasoning here is that as egg size increases, the volume of the egg (and thus its oxygen demand) increases faster than the surface area (over which

oxygen diffusion occurs). This assumption had been widely stated but never been empirically tested at the time Hendry et al. (2001b) developed their model. A recent experiment designed to test the assumption, however, found the opposite effect: large eggs survived *better* than small eggs when challenged with low dissolved oxygen (Einum et al. 2002). Furthermore, egg surface area increased faster than oxygen consumption with increasing egg size, suggesting that the ability of eggs to acquire the necessary oxygen for metabolism actually increased with increasing egg size (Einum et al. 2002). Thus, modifications to existing expectations and theories appear necessary. Hendry and Day (2003) have shown that this new evidence can be accommodated by the general theoretical approach of Hendry et al. (2001b).

For now we will continue with the traditional reasoning that large eggs suffer disproportionately in low dissolved oxygen, because it is instructive even if ultimately incorrect. For a given level of oxygen, a maximum viable egg size may exist, and with increasing oxygen this maximum size may increase. In the model of Hendry et al. (2001b), the overall individual offspring fitness function ($f(m)$) consisted of two components:

$$f(m) = f_{pre}(m) \times f_{post}(m) \quad (5)$$

where the first and second components describe the relationship between egg size and fitness before hatching and after hatching, respectively (Figure 4.2a). The post-hatching fitness function (f_{post}) followed Equation (3). The pre-hatching fitness function (f_{pre}) was modeled as:

$$f_{pre}(m) = k \left[1 - \left(\frac{m}{km_{max}} \right)^b \right] \quad (6)$$

where m_{max} is the maximum viable egg size, b is a constant determining the shape of the function, and k is a constant related to the quality of the incubation environment. Thus, by varying the value of k , Hendry et al. (2001b) could solve for optimal egg sizes in different pre-hatching environments (Figure 4.2b).

One result emerging from this analysis was that an increase in pre-hatching environment quality (caused by differences among populations or female phenotypes) should cause an increase in the optimal egg size (Figure 4.2c). Thus, this model predicts that if the quality of the incubation environment influences pre-hatching fitness (all else being equal), populations experiencing low-quality incubation environments (i.e., low levels of dissolved oxygen) should produce small eggs. In Section 2.3, we outline a correlative study on sockeye salmon that provides support for this model. However, the above logic and results need to be reconsidered if the assumption that large eggs suffer more than small eggs in low dissolved oxygen proves incorrect (Einum et al. 2002; Hendry and Day 2003).

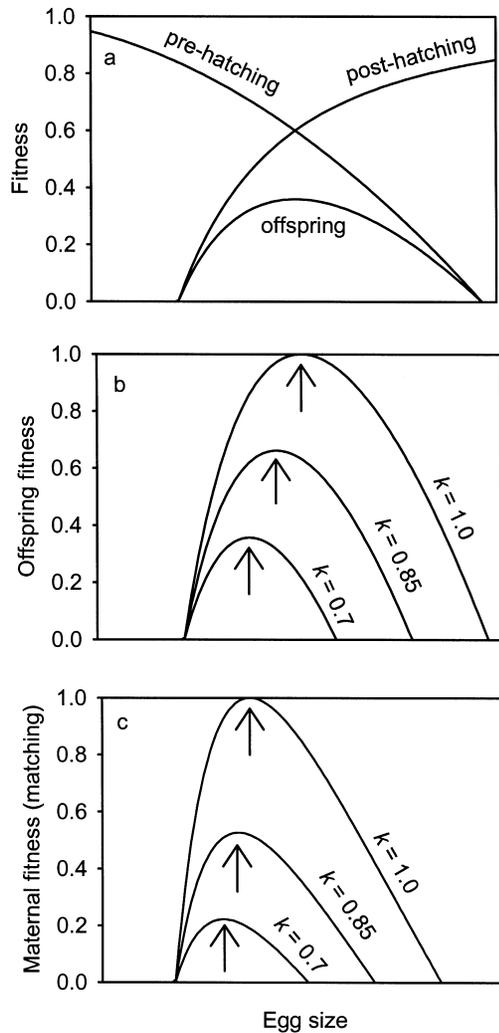


Figure 4.2. The relationship between egg size, offspring fitness, and maternal fitness in a situation of opposing selection pressures (e.g., negative relationship between egg size and offspring fitness before hatching, but a positive relationship after hatching). a) Pre-hatching and post-hatching fitness functions and the corresponding offspring fitness for a range of possible egg sizes. (b) Offspring fitness functions (rescaled to a maximum of 1.0) under three different incubation environment qualities (k , see Equation (6) in text; increasing k corresponds to increasing incubation environment quality). (c) Maternal fitness (rescaled to a maximum of 1.0) for females of three different sizes, when their eggs incubate in different pre-hatching environments (i.e., female size is positively correlated with incubation environment quality). Arrows indicate egg sizes that maximize maternal fitness. Modified from Hendry et al. (2001).

1.4. *Phenotype-Specific Optimal Egg Size*

Classic optimality models predict that a single optimal egg size maximizes maternal fitness in a given environment. Why then do we so commonly observe extensive egg size variation among individuals within populations? This observation is clearly at odds with the classic models, and calls for an explanation (Bernardo 1996b). Several competing hypotheses have been advanced. First, if environment quality varies through the breeding season, optimal egg size may vary accordingly (e.g., Bagenal 1971; Kerfoot 1974; Chambers 1997). This hypothesis cannot, however, explain the variation in a population at a given time. Second, egg size may be constrained in small females due to morphological features found in some taxa (e.g., pelvic girdle size; Congdon et al. 1983; Sinervo and Licht 1991). This constraint seems unlikely in organisms without such features, such as salmonids (see Section 3.1). Third, if females have imperfect information about optimal egg sizes, selection may favor increased variation in egg size both within and among females (Koops et al. 2003).

A quite different set of arguments, all based on extensions of the Smith–Fretwell model, rest on the assumption that shapes of the egg size/offspring fitness function depend on maternal phenotype. For example, larger females are expected to produce larger and/or more eggs due to higher total amounts of reproductive effort, and this in turn may influence the egg size/offspring fitness function. Parker and Begon (1986) developed a series of models examining how social interactions among siblings and non-siblings may influence rules of allocation among females of different sizes. McGinley (1989) took a different approach, wherein the number of offspring may influence the egg size/offspring fitness function through effects on levels of predation. These two models and others demonstrate the theoretical potential for adaptive variation in egg size within populations. More specifically, they predict that optimal egg size should increase with increasing gonad investment under negative density dependence caused by sibling competition or predation (i.e., larger clutches experience higher levels of competition or predation). In these cases, the reduction in egg number with an increase in egg size is more than compensated by the combined effects of reduced density dependence among offspring and their increased size-dependent fitness (see also Hendry and Day 2003).

A common feature of the Parker and Begon (1986) and McGinley (1989) models is that the selective pressures for variable egg sizes (i.e., individuals adjust their egg size to optimize fitness) occur after hatching. Sargent et al. (1987) suggested an alternative hypothesis. They assumed that survival of juveniles could be described by the Smith–Fretwell model (i.e., survival increases with egg size), but that increasing egg size increased egg or larval mortality. This negative effect of increased egg size could occur either by (1) an increase in instantaneous mortality, or (2) an increase in developmental time while keeping instantaneous mortality constant. Under both of these scenarios, females that were able to reduce egg or larval mortality through parental care should also produce large eggs.

The idea that optimal egg size can be shaped by egg mortality was further investigated by Hendry et al. (2001b). In Section 1.3 we discussed how their model identified pre-hatching environment quality as a potential evolutionary force shaping egg size. They suggested that this could have implications for variation in optimal egg size within populations in the case of a positive correlation between maternal phenotype and environment quality. Hendry et al. (2001b) referred to such situations as “phenotype/habitat matching,” and pointed out that such matching can occur in certain organisms (e.g., when female phenotype influences incubation environments indirectly through interference competition, or directly through parental care). To examine if this could select for intrapopulation variation in egg size, they developed a model where matching occurs (larger females provide higher quality incubation environments), larger females have greater gonad investment, and offspring fitness is described by Equations (3), (5) and (6) (i.e., offspring fitness is related to egg size negatively before hatching and positively after hatching). Their model predicted that larger females should produce larger eggs (Figure 4.2c). In addition, it predicted that increasing female size should result in a greater proportional increase in egg number than in egg size because egg number shows a linear relationship with maternal fitness, whereas egg size does not. Finally, because it is female size and not gonad investment that determines environment quality, egg size should not increase with relative gonad investment (i.e., ovary mass adjusted for body size).

In Section 2.4, we outline a study that provides correlative evidence for these hypotheses in a variety of salmon populations. However, Hendry et al. (2001b) relied on the assumption that larger eggs are selected against in low dissolved oxygen conditions, whereas Einum et al. (2002) showed that the opposite may be true. Hendry and Day (2003) have recently shown that inverting the traditional assumption according to the new results of Einum et al. (2002) yields the following predictions. First, larger females should produce larger eggs if (1) they place their eggs in lower quality environments (i.e., less dissolved oxygen), which seems unlikely but has been suggested by Holtby and Healey (1986), or (2) they place their eggs in higher quality environments but this improvement in habitat quality is less than the decline habitat quality owing to the larger clutch sizes of larger females (i.e., negative density dependence). Testing these new predictions will require additional empirical study.

1.5. Non-Equilibrium and Non-Optimal States

We have thus far discussed the evolution of egg size and number from the perspective of optimality. The Smith–Fretwell model, and other models that derive from its basic premise, describe evolution under a simplified set of ideal conditions. For example, these models generally imply evolution over unlimited time frames, with consistent environment quality and selection through time, and with ample genetic variation. However, equilibrium and optimal conditions may not be achieved under some circumstances. For example, most new popu-

lations are likely established with trait values that are not at their optimal (or equilibrium) state, and many extant populations have been exposed to altered environment conditions that may influence $f(m)$. It should be possible to gain some insights into non-equilibrium and non-optimal states by examining perturbed or introduced populations where ancestral genotypes interact with new selective regimes. In Section 2.5, we discuss experimental and correlative work that provides insights into non-equilibrium/non-optimal aspects of egg size and number in chinook salmon.

2. Empirical Tests of the Theory

The theoretical treatment of egg size/number evolution has flourished in the wake of Smith and Fretwell (1974) but empirical tests have lagged behind, and some authors have questioned the validity of optimality models for examining egg size evolution (e.g., Sinervo et al. 1992; Bernardo 1996b). As in other fields of science, models are valuable for deriving testable predictions, but without rigorous tests, they remain purely theoretical.

Salmonids are particularly suitable for empirical tests of existing egg size/number theory. First, the predictive power of the Smith–Fretwell model and its extensions depends on multiple offspring among which resources are divided. The potentially high egg number and its great range in salmonids (hundreds to many thousands, see Table 1 in Hutchings and Morris 1985; Stearns and Hendry 2003—*this volume*) makes them a powerful system for testing these models. Second, salmonids lack post-hatching parental care, which would otherwise complicate patterns of optimal reproductive allocation (Trivers 1974). Third, salmonid development from fertilized egg to adult can be divided into discrete stages, and these stages may be exposed to different and even opposing selection pressures. Fourth, salmonids form well-defined populations with limited degrees of gene flow among them (Quinn 1993; Hendry et al. 2003a). These populations inhabit a range of biotic and abiotic environments, which sets the stage for adaptations to local conditions (review: Taylor 1991b). Fifth, salmonid eggs are large and variable relative to other fishes (Wootton 1984; Hutchings and Morris 1985; Beacham and Murray 1993; Fleming 1998), suggesting considerable potential for egg size variation to influence offspring and maternal fitness. Finally, salmonids are recreationally and commercially important and so (1) a vast amount of data has been collected on their life history and its genetic basis, and (2) numerous translocations have occurred providing seminatural experiments in the evolution of populations faced with altered selective regimes.

As a result of their suitability for studies of egg size and number, salmonids have been extensively used both in field studies and experiments. In the following, we show how each of the theoretical issues outlined in Sections 1.1–1.5 has been examined using research in salmonids.

2.1. The Smith–Fretwell Model: a Test Using Phenotypic Manipulations in Atlantic Salmon

Empirical tests of the Smith–Fretwell model have been rare for wild populations. One exception is a recent study of Atlantic salmon (Einum and Fleming 2000a). A previous study had demonstrated that juvenile body size at emergence from nests was an important determinant of early survival (Einum and Fleming 2000b), probably because larger juveniles have improved competitive ability, increased resistance to starvation, and/or reduced risk of predation (Bagenal 1969; Hutchings 1991; Kristjánsson and Vøllestad 1996; Einum and Fleming 1999; Heath et al. 1999). However, no manipulations had been performed to establish whether this was a causal effect of egg size, or due to correlations between size and other traits.

To isolate the effects of egg size *per se*, Einum and Fleming (2000a) manipulated egg size by rearing parents to adulthood in captivity, a procedure that can result in some females producing more variable egg sizes than in the wild (CV = 18.5% versus 4.0% for wild fish, Einum and Fleming 2000a). Such variation in egg size appears to be independent of genetic effects, or other characteristics of the oocytes themselves, and may arise owing to variation in the position of the egg relative to blood vessels in the female ovary (Einum and Fleming 1999). A sample of small eggs and large eggs was obtained from each of eight females, producing a total of 16 groups that differed substantially in egg size (small eggs were on average 31.4% lighter than their large siblings), and allowing a test for causal relationships between egg size and offspring fitness (e.g., Wade and Kalisz 1990; Sinervo and Svensson 1998). The different groups were allowed to develop naturally in artificial nests, and emerging juveniles were group marked and released into a stream. Body size and survival was assessed by extensive sampling 28 and 107 days after median emergence. The results were then used to test the assumptions and predictions of the Smith–Fretwell model, including: (1) egg size determines juvenile body size, (2) the relationship between egg size and juvenile fitness (measured as survival) will be positive but asymptotic, and (3) egg size will evolve to maximize maternal fitness. Thus, the predicted optimal egg size that would maximize maternal fitness, based on the experimental data, should match the mean egg size observed in the natural population.

Juvenile body size at emergence from the gravel, and at the two subsequent sampling periods, was positively related to egg size (Figure 4.3), supporting the first implicit assumption of the Smith–Fretwell model. Estimated selection intensities indicated strong directional selection toward larger egg size, with respect to offspring fitness. Furthermore, significant stabilizing selection for maternal fitness acted directly to reduce the variance in egg size. This means that females producing eggs that were too small or too large would have reduced fitness. The relationship between egg size and the proportion of fry recaptured (a measure of survival) was best described by asymptotic regressions in accordance with the second assumption of the Smith–Fretwell model (Figure 4.4). Finally, the optimal egg size estimated from these data corresponded to the mean egg

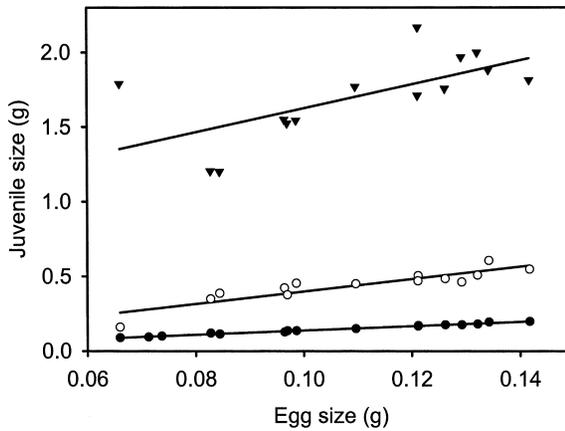


Figure 4.3. The relationship between Atlantic salmon egg and juvenile size (wet mass) at emergence (filled circles, $y = 1.4x$, $r^2 = 0.99$), at 28 days after median emergence (open circles, $y = 4.2x$, $r^2 = 0.81$), and at 107 days after median emergence (triangles, $y = 0.8 + 8.0x$, $r^2 = 0.43$). Each data point represents the mean value from one nest.

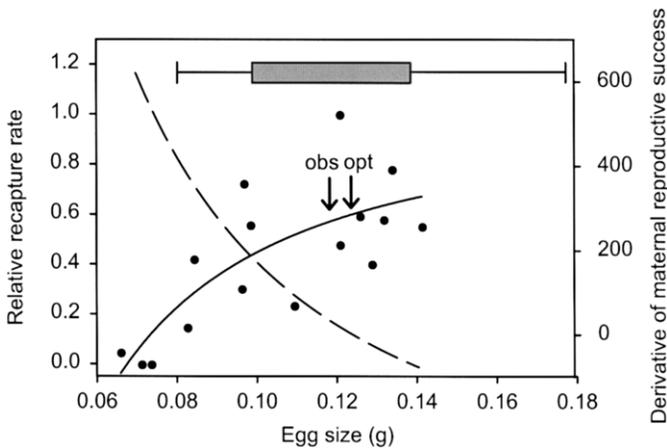


Figure 4.4. The relationship between egg size and the relative recapture rate of juvenile Atlantic salmon 28 days after median emergence. A similar relationship was found after 107 days. Each data point represents mean values for one nest. The asymptotic function relating offspring recapture rates to egg size (solid line) is estimated according to Equation (3), where $m_{min} = 0.068$ g and $a = 1.507$ ($r^2 = 0.59$). The dashed line represents the derivative of the function relating maternal reproductive success to egg size. The derivative equals zero for the egg size that maximizes maternal reproductive success (opt). Observed mean (obs) and the standard deviation and range (box plot at top) of egg size in the native population is indicated. From Einum and Fleming (2000a).

size observed in the natural population. This result indicates that mean egg size in Atlantic salmon has evolved primarily to maximize maternal fitness, and acts via effects on offspring fitness. The close fit between predictions and observations demonstrates that the Smith–Fretwell model represents an important contribution toward understanding egg size and number evolution.

2.2. Optimal Egg Size and Post-Hatching Environment

Quality: Experimental Tests

In our above treatment of the Smith–Fretwell model, we showed how it can be used to predict differences in egg size among populations if they experience different environments, and if the egg size/offspring fitness function depends on those environments (Figure 4.1b). Environment quality obviously differs among populations. For example, growth rates during the first year of life vary more than twofold among Norwegian populations of brown trout, primarily as a phenotypic response to differences in water temperature (Jensen et al. 2000). However, it is less obvious that the egg size/offspring fitness function depends on environment quality.

Two studies have tested for an effect of environment quality on the egg size/offspring fitness function in salmonids. The first compared survival of juvenile brook charr originating from different egg sizes (Hutchings 1991). Twenty-seven different egg size groups, each consisting of 20 juveniles, were derived from females in three different populations and reared separately in aquaria at two different food levels (high and low). A comparison of regressions between egg size and juvenile survival for the high and low food levels showed that survival generally increased with increasing egg size, but that the effect depended on environment quality. Specifically, the slope relating egg size to survival was steeper for small eggs than for large eggs, suggesting that juveniles from small eggs do just as well as those from large eggs when conditions are favorable. Thus, due to a tradeoff between egg size and egg number, the optimal egg size was smaller in the high-quality environment, as predicted from Section 1.2.

The second study compared growth of juvenile brown trout originating from small and large eggs (Einum and Fleming 1999). Growth rate has implications for later body size and is thus considered to be closely related to fitness in organisms with indeterminate growth. Egg size was manipulated as described in Section 2.1, and siblings from small and large eggs were reared together in seminatural enclosures, allowing competitive interactions. This design addressed two issues not considered in Hutchings' (1991) study: (1) it controlled for genetic correlations between egg size and other traits by comparing siblings from different-sized eggs, and (2) it included effects of competitive asymmetries (i.e., juveniles from small eggs competed with those from large eggs), which should be common in the wild. In this experiment, siblings from large eggs outgrew those from small eggs, but as predicted, the magnitude of this effect depended on environment quality, with the relative advantage of large juveniles decreasing with increasing environment quality (Figure 4.5). These results argue

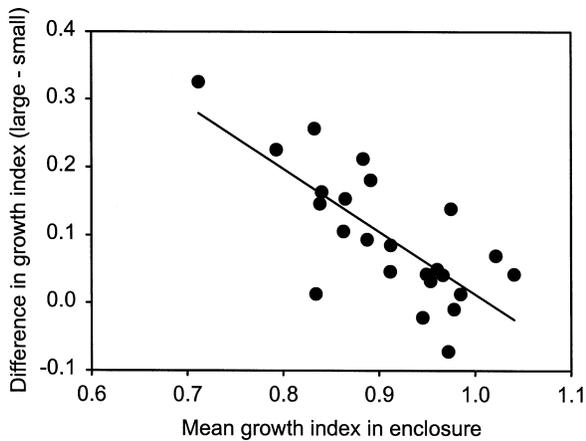


Figure 4.5. The relationship between mean growth index (growth rates relative to maximum growth for given size and temperature) of an enclosure, and the difference in growth index between sibling brown trout originating from large and small eggs and reared in competition ($y = 0.94 - 0.92x$, $r^2 = 0.56$). Each data point represents the mean value for one enclosure. The effect of egg size on relative growth decreases as environment quality increases. Modified from Einum and Fleming (1999).

that the optimal egg size will be smaller where the environment experienced by juveniles is of higher quality.

These two studies show that the egg size/offspring fitness function depends on environment quality. Thus, variation among populations in environment quality may promote divergent local adaptation. Is there any empirical evidence for such adaptation? Generally, demonstrating local adaptation is a laborious task (Rose and Lauder 1996), and no explicit tests of the above hypothesis have been performed for salmonids. However, correlative studies lend circumstantial support. Fleming and Gross (1990) found that among 17 populations of coho salmon, egg number increased and egg size decreased with increasing latitude. They suggested that this pattern might be explained by the existence of concurrent clines in competition for prey or size-selective predation (if competition or size-selective predation decrease with latitude). Alternatively, optimal egg size may be small at low temperatures (higher latitudes) because conversion efficiency (i.e., offspring mass/egg mass ratio) increases as incubation temperatures decrease (Heming 1982). In other words, the egg size required to produce a given optimal offspring size (i.e., maximizing maternal fitness) is smaller at lower temperatures.

Other sources of support for dependence of the egg size/offspring fitness function on environment quality come from within-population studies of Atlantic salmon (N. Jonsson et al. 1996), brown trout (Lobón-Cerviá et al. 1997) and white-spotted charr (Morita et al. 1999). In these studies, females that experienced high growth rates as juveniles produced smaller eggs as adults. This might represent an adaptive phenotypically plastic response to early growth

conditions. Assuming that mothers can use the growth they experience as juveniles as a clue to the conditions their offspring will experience, they might adjust egg size according to the expected optimal value in that environment. Thus, females that experience higher growth as juveniles may benefit from producing larger numbers of small eggs. Similar correlations between growth rate and egg size has been found among populations of Japanese masu salmon (Tamate and Maekawa 2000).

Finally, two other recent studies are relevant but are treated here in brief because they were published after the completion of this chapter. First, Heath et al. (2003) showed that smaller egg sizes evolve in hatchery salmon because the relationship between egg size and offspring survival is weaker than in the wild. Second, Koops et al. (2003) showed that more variable environments and smaller eggs are associated with increased variability in egg size. This pattern is in part a function of variation in the egg size/fitness function.

2.3. *Opposing Selection Stages: Pre-Hatching Mortality May Select for Small Eggs*

The evolution of egg size is commonly thought to be driven by variation in post-hatching fitness. However, egg mortality may be caused by many factors (disease, predation, physical disturbance, temperature, dissolved oxygen, gravel size) and can be very high (Chapman 1988). For example, Bradford (1995) found that the average survival-to-emergence of pink salmon, chum salmon, and sockeye salmon was only 7%. Quinn et al. (1995) tested the hypothesis that selection during incubation may influence egg size by examining variation among 18 populations of sockeye salmon in two Alaskan lake systems. The populations all experience similar oceanic conditions, migrate at similar times and for similar distances, and have the same rearing environment for their offspring (large oligotrophic lakes). Thus, variation in egg size among populations was most likely attributable to variation in the incubation environment. One feature of the incubation environment that varies among these populations is the size of the spawning and incubation gravel (geometric mean gravel size varies 30-fold). Quinn et al. (1995) compared the average egg size of the populations to the average gravel size of their spawning sites.

As predicted, mean egg sizes, and egg sizes adjusted to a common female length, were positively correlated with geometric mean gravel size (Figure 4.6), and with other measures of gravel size (Quinn et al. 1995). It thus appears that pre-hatching mortality in sockeye salmon influences the evolution of egg size, and does so most strongly in the smallest gravels. One hypothesis for the positive correlation between egg size and gravel size was that smaller gravels reduce oxygen availability, which then selects against large eggs because they are less able to obtain the oxygen they need (Quinn et al. 1995). As noted above, however, a recent experiment suggested that large eggs are actually favored when challenged with low dissolved oxygen (Einum et al. 2002). Thus, a positive relationship between egg size and gravel size may arise for some other reason. Alternatives suggested by Quinn et al. (1995) are (1) size-selective predation on

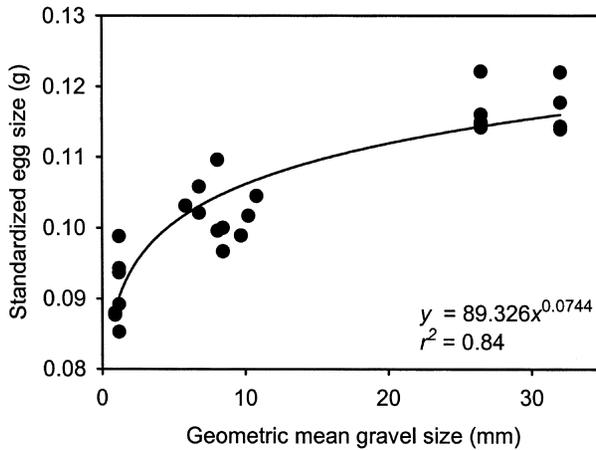


Figure 4.6. The relationship between standardized egg size (wet mass, adjusted to a common female length of 450 mm) and the size of incubation gravels for Alaskan populations of sockeye salmon. Multiple points for a given gravel size represent samples from the same population in different years. Data from Quinn et al. (1995).

eggs by gape-limited fishes (particularly sculpins) may favor larger eggs in larger gravels where sculpins can gain access to the incubating eggs, and (2) larger juveniles may become trapped when trying to emerge through smaller gravels.

2.4. Phenotype-Specific Optimal Egg Size

As we saw in Section 1.4, several existing models predict a correlation between optimal egg size and female phenotype within populations. Hendry et al. (2001b) suggested that their environment matching model was particularly well suited for salmonids, where large females are better competitors and obtain preferred nesting sites of higher quality (van den Berghe and Gross 1989; Foote 1990; Fleming and Gross 1994). According to their model, this should select for (1) a positive correlation between female size and egg size, (2) a greater proportional increase in egg number than in egg size with an increase in female size, and (3) a positive correlation between relative (i.e., adjusted to a common female size) gonad investment and relative egg number but not relative egg size. Hendry et al. (2001b) tested these predictions using empirical data from 101 populations of five species (43 populations of four species had data for both egg size and number). First, egg size was significantly positively correlated with body length within 47 of 61 populations having egg size data, supporting prediction 1. Second, the proportional increase in egg number was greater than the proportional increase in egg size within 37 of 43 populations having both types of data (Table 4.1), supporting prediction 2. Third, females with greater relative investment produced more but not larger eggs within all three collections having appropriate data, supporting prediction 3.

Table 4.1. Relationships between female length and egg size (mass) and egg number for studies of salmonid fishes.

Species	Egg size vs. body length				Egg number vs. body length				Paired t	
	Pops (fish)	Slope (S.D.)	r^2 (S.D.)	Pops sign.	Pops (fish)	Slope (S.D.)	r^2 (S.D.)	Pops sign.	Paired N ($S < N$)	t (P)
Sockeye salmon	14 (1755)	1.25 (0.18)	0.19 (0.15)	4	14 (4731)	1.86 (0.31)	0.31 (0.14)	14	14 (11)	2.64 (0.01)
Sockeye salmon	8 (202)	1.05 (0.31)	0.39 (0.16)	8	10 (160)	2.03 (0.30)	0.61 (0.16)	10	8 (8)	7.63 (<0.001)
Masu salmon	7 (153)	1.01 (0.93)	0.27 (0.30)	3	7 (149)	1.94 (0.90)	0.35 (0.23)	5	7 (5)	1.78 (0.04)
Coho salmon	22 (495)	1.15 (0.66)	0.32 (0.20)	2	17 (330)	2.28 (0.51)	0.68 (0.18)	16	14 (13)	5.75 (<0.001)

Columns indicate the number of discrete populations (Pops), with the total number of fish in parentheses, the slope coefficient averaged across populations (slope), r^2 averaged across populations, and the number of populations with significant relationships (Pops sign.). The second last column gives the number of populations for which both egg size and egg number slopes were available (Paired N), with the number of populations in which the egg number slope was greater in parentheses. The last column provides the t statistic for paired sample t-tests of the difference in slope between egg size and egg number, both with respect to body length. Data from Hendry et al. (2001b).

How confident can we be that the proposed environment matching model is responsible for the observed correlation between female size and egg size? Both the sibling competition model (Parker and Begon 1986) and the predation model (McGinley 1989) are in some respects similar in their predictions. Both predict an increase in egg size with female size, and unless female size influences the egg size/offspring fitness function too strongly, they also predict that the proportional increase should be greater for egg number than for egg size. In one respect, however, these models differ from that of Hendry et al. (2001b); whereas the environment matching model assumes the effect of female body size on offspring fitness is caused by maternal behavior, the sibling competition and predation models assume an effect of egg number per se on offspring fitness. As a result, the sibling competition and predation models predict a positive correlation between relative gonad investment and relative egg size. That is, if a female produces large gonads relative to her body size, she should also produce large eggs relative to her body size. This prediction contrasts with the environment matching model, which predicts no such correlation, and conflicts with the available empirical data (Hendry et al. 2001b). The observed relationship between female size and egg size in salmonids therefore seems to fit the environment matching model of Hendry et al. (2001b).

However, the above results may be a case of getting the right answer for the wrong reason. The recent experimental evidence suggesting that large eggs actually have an advantage in low dissolved oxygen (Einum et al. 2002) counters one of the assumptions of Hendry et al. (2001b), and suggests that positive egg size/female size correlations may arise for another reason. For example, larger females may actually provide incubation environments of lower quality because they lay larger clutches, which have greater total oxygen demand. Under these conditions, larger females should produce larger eggs if larger eggs are better able to cope with lower dissolved oxygen. Indeed, Hendry and Day (2003) have shown that this prediction follows when the results of Einum et al. (2002) are incorporated into the theoretical modeling approach of Hendry et al. (2001b). Furthermore, Einum et al. (2002) have shown that larger females should be favored to produce larger eggs because doing so reduces oxygen demand per unit of clutch mass.

2.5. Non-Optimal States: Micro-Evolution in New Zealand Chinook Salmon

Trait values of new or disturbed populations will often not be at their equilibrium or optimal values. The rate at which traits in the population will then approach the new equilibrium (and potentially optimal) values will depend on the nature of selection, genetic variation, and gene flow. The time required to reach approximate equilibrium values for traits such as egg size and number is not known but significant deviations from equilibrium conditions, and hence strong selection, are likely for the newest of populations. For this reason, historical and experimental introductions provide useful systems for examining rates and patterns of evolution on contemporary time frames (review: Hendry and

Kinnison 1999; Kinnison and Hendry 2001; Reznick and Czhambor 2001; Stockwell et al. 2003).

Chinook salmon introduced to New Zealand have recently been the subject of intensive research (e.g., Kinnison et al. 1998a; 2001; Quinn et al. 2001b; Unwin et al. 2003). All of the present day populations are descended from upper Sacramento River (California, USA) “fall-run” fish introduced into a single river system on the South Island of New Zealand between 1901 and 1907 (McDowall 1994). Thus, any genetic differences existing among the extant New Zealand populations have evolved on a time scale of around 30 or fewer generations. Kinnison et al. (2001) examined how the cost of freshwater migration by adults might influence the evolution of egg size and number in these new populations. In particular, they first predicted that an increasing cost of migration would result in a proximate cost to tissue energy reserves and gonad investment. To test this prediction, they released smolts from the same families from two sites with different migratory rigor, and then measured ovarian traits of maturing females returning to each site.

The experimental manipulation of migratory rigor (100 km and 430 m elevation vs. 17 km and 17 m elevation) resulted in a 17% reduction in metabolizable muscle mass and a 14% reduction in mean egg size and total ovarian mass (Kinnison et al. 2001; Figure 4.7). Altered costs of migration are thus one cause of immediate changes in ovarian investment (particularly egg size). The interesting question then becomes: are these changes non-equilibrium and non-optimal, and how do they influence the evolution of egg size? A comparison of egg size, number, and total ovarian mass for two established New Zealand populations with different migratory rigor (100 km and 430 m elevation, vs. 60 km and 200 m elevation) confirmed the above proximate cost of migration:

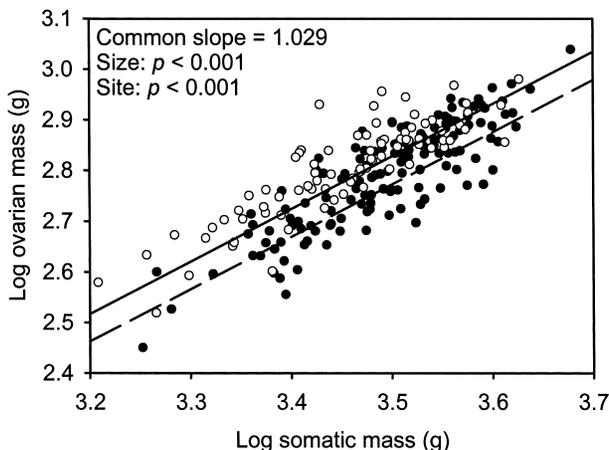


Figure 4.7. The cost of migration on ovarian investment shown by log ovary mass relative to log somatic mass for 3-year-old female chinook salmon from the same families returning after a long freshwater migration (filled circles—100 km, 430 m elevation) or a short freshwater migration (open circles—17 km, 17 m elevation). Dashed and solid lines represent the predicted ANCOVA relationships.

wild-caught females had a lower ovarian mass and smaller eggs in the longer migrating population (Kinnison et al. 1998a). When these same two populations were then reared under common-garden conditions, however, the farther migrating population had a 6.4% larger ovarian mass, suggesting evolutionary compensation for the proximate cost of their longer migration (Kinnison et al. 2001). Interestingly, the compensation came largely in the form of increased egg number rather than egg size.

Kinnison et al. (2001) suggested several possible reasons for why egg number evolved more quickly than egg size, despite the obvious proximate cost of migration on egg size and not egg number. First, evolutionary constraints, particularly those resulting from genetic correlations, may be important. In general, ovary mass shows higher genetic correlations with egg number than with egg size (Su et al. 1997; Kinnison et al. 2001), suggesting that an evolutionary increase in ovary mass should be accompanied by an initial increase in egg number rather than egg size. This effect would suggest that the smaller egg size in the longer migrating population is actually suboptimal, and that with enough time, it might increase to some new and larger equilibrium value. Second, optimal egg size may actually be smaller in longer migrating populations. For example, migration may diminish energy reserves available to females for the production of high-quality nest sites. If so, the model of Hendry et al. (2001b) (Section 1.3) would predict a decrease in optimal egg size as migratory costs increase. Another possibility is that there may be consistent correlations between distance from the ocean and environment variables that influence optimal egg size (Section 2.2).

Kinnison et al. (2001) also examined egg size and number variation among North American populations of Pacific salmon. They obtained estimates of mean egg size and number (most corrected for female size) for five geographic groups of populations in three species. Each group consisted of between four and 14 populations that enter fresh water at essentially the same location but that migrate different distances. For all five groups, the ratio of egg number to egg size increased with increasing migratory distance, driven by a strong tendency for egg size to decrease and egg number to remain relatively constant or increase (Figure 4.8). Other authors have also found that egg size decreases with increasing migratory difficulty (Beacham and Murray 1993; Healey 2001). This pattern parallels the costs of migration and evolutionary compensation for those costs in New Zealand. However, total egg production (ovary mass) tends to remain negatively correlated with migration distance (see also Fleming and Gross 1989; Beacham and Murray 1993; Healey 2001), suggesting that full compensation for migratory costs does not occur.

It remains unknown whether the observed patterns among indigenous populations reflect optimality or constraints. If they reflect constraints, then optimality may be very slow to evolve or may never be attained. If smaller egg size with more difficult migrations is actually adaptive, attention should be focused on determining how factors related to migration alter fitness functions. The quantitative precision of optimality theory in explaining the range of egg size variation among indigenous salmon populations awaits further empirical confirmation. Ultimately, deviations from optimality predictions may serve as a basis

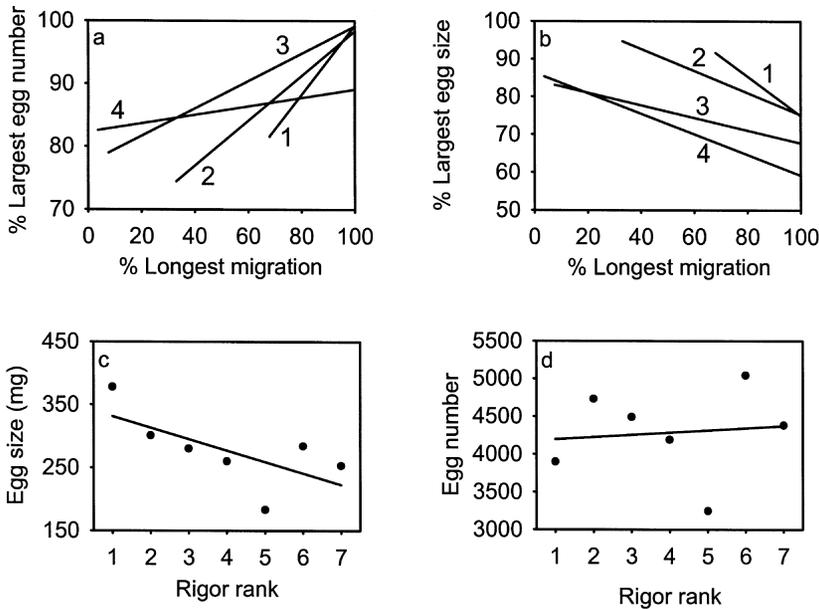


Figure 4.8. Relationships between migratory distance (rigor) and reproductive investment (egg size and egg number) for chinook, sockeye, and coho salmon from five geographic population groups. For (a) and (b), graphs represent regression lines through population values in which each population's mean egg size, mean egg number, and migration distance is converted to a percentage of the largest population mean value for that group. Trait values are standardized to a common body size in each population grouping. (1) Fraser River coho (a: $r = 0.68$, b: $r = -0.75$), (2) Puget Sound coho (a: $r = 0.71$, b: $r = -0.89$), (3) Fraser River sockeye (a: $r = 0.27$, b: $r = -0.82$) and (4) Fraser River chinook salmon (a: $r = 0.51$, b: $r = -0.34$). For (c) ($r_s = -0.71$) and (d) ($r_s = 0.14$), regressions for Columbia River chinook salmon are presented (with individual population points) relative to an *a priori* ranking of migratory rigor taking into account migration distance and seasonality effects on time spent in the river. Data from Kinnison et al. (2001).

for determining when more complex evolutionary interactions are at play. Salmon adapting to hatchery environments provide another opportunity to examine what happens when selection on egg size or number is changed. Heath et al. (2003) have shown that egg size decreased rapidly in a hatchery environment, presumably because selection for larger eggs was weaker than in the wild but selection for more eggs was not.

3. How Do We Proceed from Micro- to Macro-Evolutionary Theory?

The Smith–Fretwell model and its extensions have been important in shaping our understanding of variation in egg size and number within and among popu-

lations. Some effort has also been devoted to understanding variation among higher phylogenetic groups (e.g., Ware 1975; Kölding and Fenchel 1981; Hutchings and Morris 1985; Sargent et al. 1987; Visman et al. 1996; Fleming 1998). This endeavor is particularly challenging because the life history of an organism (used here in the broad sense to include behavior, morphology, and other aspects of biology) likely influences the relationship between egg size and fitness. In this section, we posit factors that may be responsible for observed variation in egg size among species, pointing out aspects that may be particularly important in salmonids. This is not meant to be an exhaustive consideration, but rather a summary of several factors that may explain some of the variation. Our starting point is a consideration of constraints on egg size evolution. We then move to factors that might influence egg size evolution according to the Smith–Fretwell framework (including effects of egg size on survival before and after hatching). Finally, we consider how other life history traits may evolve to maximize fitness within the limits set by various constraints on egg size.

3.1. Mechanical Constraints

Adult body size will ultimately constrain egg size. In its simplest form, this constraint sets an upper limit on egg size because a female only has a given amount of resources (and space in her body cavity) available for egg production. Thus, even if all resources are allocated to one offspring, it can still only be of a certain size. This inevitability was taken to absurdities in a tongue-in-cheek parody of the so-called adaptationist program: “Why are juveniles smaller than their parents?” (Ellstrand 1983). Such constraints would only be important for organisms producing small clutch sizes, and thus not salmonids. Additional constraints may arise because of design limits on the structures used for oviposition or parturition. For example, in most tetrapods, eggs or neonates must pass through the pelvic girdle, which faces competing selection for locomotory function. Similarly, many insects employ specialized ovipositors with design constraints associated with the egg-laying substrate. In theory, such constraints could also apply to species laying multiple eggs during a given reproductive event.

In salmonids and most other fishes, bony girdles do not completely enclose the oviposition canal and thus such constraints seem unlikely. This conclusion is supported by the observation that although non-anadromous salmonids are much smaller than their anadromous counterparts, their egg sizes are fairly similar (Hendry et al. 2003b—*this volume*). For example, although mature non-anadromous *O. nerka* (kokanee) may be one-third the length of anadromous *O. nerka*, their egg diameters differ by only about 4% (Wood and Foote 1996). If any mechanical constraints actually exist in female salmon they would most likely relate to overall ovary size. For example, larger ovaries will compete with organs for space in the body cavity and may reduce swimming ability and predator avoidance (see Miles et al. 2000 for locomotor constraints in lizards).

Sinervo and Licht (1991) argued that physical constraints exist in lizards based on experiments where they enlarged eggs by removing parts of the clutch

during vitellogenesis, and found that such females often could not successfully oviposit. It is also interesting, however, that the optimal egg size expected in the absence of failed oviposition seemed to match the mean egg size in wild populations (Sinervo et al. 1992), suggesting that there is little if any post-oviposition selection for larger eggs. Thus, the question of whether egg size really is constrained by design limits on structures used for oviposition or parturition remains unanswered.

3.2. Genetic Constraints

Optimality theories assume that genetic architectures allow the traits under consideration to evolve to a value maximizing maternal fitness. Under certain circumstances this may not be realistic. The most obvious genetic constraint is a paucity of additive genetic variation, which would reduce evolutionary responses to phenotypic selection. However, heritabilities and additive genetic variance for life history traits in animals are generally extensive (Mousseau and Roff 1987; Houle 1992). Estimates of the heritability of egg size in salmonids vary widely but are often quite high (e.g., 0.60, Su et al. 1997; 0.78, Kinnison et al. 2001), suggesting that genetic variation will not appreciably limit the evolution of egg size.

A second genetic constraint is the presence of genetic correlations. Such correlations can be caused by linkage disequilibrium (i.e., genes determining two traits are closely located on the chromosome and certain allele combinations are more common than others), in which case they will likely be transient, or by pleiotropy (i.e., two traits are determined by the same genes), in which case they may be permanent. In this latter case, selection on one trait causes simultaneous changes in another trait, and they cannot evolve independently to their individual optima.

Given these potential complications, are the optimality approaches in this chapter likely to be fair approximations of what is really occurring in the wild? Ultimately, evolutionary constraints on egg size can best be demonstrated by showing that observed mean egg sizes do not maximize maternal fitness. However, as we discuss further at the end of this chapter, such demonstrations may be difficult to obtain if evolutionary changes in other traits “adapt” the organism to its constrained egg size, in which case the observed egg size may be optimal even where significant constraints are present.

3.3. Adaptations to Pre- and Post-Hatching Environment

Selective pressures potentially imposed by the pre-hatching environment were initially discussed in Sections 1.3 and 1.4. In those sections, we focused on the model of Hendry et al. (2001b) concerning oxygen limitations faced by eggs, and the relationship between sockeye salmon egg size and spawning gravel size (Quinn et al. 1995). Hendry et al. (2001b) also attempted to explain variation in the strength of relationships between female size and egg size among species. Using data from 181 freshwater fish species, they found that positive correlations

between female size and egg size were more common in fish where female size was likely to influence the quality of the incubation environment (e.g., females construct nests). They argued that in these species, larger females could provide better oxygen conditions for their eggs, allowing the evolution of larger egg size. Again, however, this analysis rested on the assumption that large eggs suffer disproportionately in low dissolved oxygen, and subsequent work has found that the effect may actually be the opposite (Einum et al. 2002).

Thus, we may need to seek other explanations for this variation. In a comparative study of 119 fish species, Einum and Fleming (2002) found that intra-population variation in egg size was most pronounced in fish with demersal eggs and larvae, where offspring environment is likely influenced by maternal phenotype, and least so in fish with pelagic eggs, which experience a relatively stochastic spatial distribution during incubation. These results indicate that there is selection favoring within-population variation in egg size in species where maternal phenotypes can influence the offspring environment. Furthermore, fish with demersal eggs and pelagic larvae did not differ from those with pelagic eggs, indicating that this selection may occur mainly post-hatching. However, at least for salmonids, oxygen limitations during incubation have the potential to select for variation within populations, although for a different reason than previously thought (Einum et al. 2002; Section 2.4). Pre-hatching environments may also pose many other forms of selection on egg size. For example, small eggs may be *favored* in some organisms to promote passive dispersal or reduce predation (e.g., Hammond and Brown 1995; Moegenburg 1996). Selection during this stage may therefore shift optimal egg size considerably from that expected based only on the post-hatching period.

Variation in post-hatching fitness functions are probably also important and here we list five potentially important factors. First, the abundance and size distribution of food may influence how starvation rates are related to egg size. If food abundance is low, it has been hypothesized that selection will favor large, developmentally advanced young (Itô 1980; Itô and Iwasa 1981). Some evidence from experimental work within salmonid populations supports this idea (Hutchings 1991; Einum and Fleming 1999). The size distribution of prey may also influence starvation rates relative to egg size. If small eggs produce larvae that are too small to exploit the available prey items, this may set a lower limit to egg size. If we assume that the types of food possibly exploited by offspring (e.g., carnivorous versus herbivorous diet) are under stronger phylogenetic constraints than egg size, organisms must adapt their egg size, feeding structures, or feeding style, to the available prey size and numbers.

Second, from a game theory perspective (Maynard Smith 1982), interference competition may select for large and developmentally advanced offspring if the outcome of competition is phenotype-dependent. The outcome of agonistic interactions often depends on body size (e.g., Johnsson et al. 1999; Cutts et al. 1999b), and in certain biological systems this may select for large eggs (e.g., species with territorial juveniles).

Third, if predation rates are size-dependent, this may shape the egg size/offspring fitness function. Such size-selective predation appears common in

many systems (e.g., Connell 1970; Caldwell et al. 1980; Palmer 1990; Moegenburg 1996). For a given intensity of size-selectivity, the potential for effects of predation on the evolution of egg size depends on the level of predation that juveniles commonly experience, which may vary among taxa.

Fourth, if the number of offspring strongly influences offspring fitness through effects on competition among siblings or predation (density dependence), this may favor larger eggs (Section 1.4, Parker and Begon 1986; McGinley 1989). We suggest that this effect may be particularly evident when comparing (1) organisms with different levels of dispersal during egg and larval stages, and (2) organisms with and without parental care. In the first scenario, organisms with high degrees of dispersal will have little opportunity for intra-clutch interactions in comparison with organisms where siblings show less dispersal. In the second comparison, particularly if parental care must be divided among offspring (e.g., feeding), producing too many eggs will be disadvantageous, and more resources should go into each egg. Evidence for such patterns is given by Sargent et al. (1987), who showed that fishes with parental care produce larger eggs (although their explanation was related to development time and egg mortality, see Section 1.4).

Finally, abiotic environment conditions may influence the egg size–offspring fitness function. For example, seasonal migrations may set a constraint on the minimum offspring size if juveniles must reach a certain size at a given time to be able to complete such migrations. Hydrodynamic stress may also select for large offspring to avoid dispersal if large juveniles are better able to withstand such stress. For example, juveniles from species of darters (*Percidae*) hatching from larger eggs drift in the water column less than those hatching from smaller eggs (Paine 1984). This may be the reason for the pattern observed in stream-living darters, where a high degree of gene flow among populations is associated with high egg numbers and small egg sizes (Turner and Trexler 1998).

3.4. Predictions and Perspectives

One may wish to speculate about causes of variation in egg size among salmonid species. In particular, the different North American Pacific salmon species provide a tempting target. These are similar in many aspects of their biology, such as patterns of adult migration, semelparity, spawning season, nest defense after spawning, and geographic distribution. Yet, they vary considerably in egg size and number (Table 4.2), and in some factors that may influence their evolution. Here we make some suggestions as to what selective factors may have played a role in this variation, if only to illustrate the complexity associated with such an endeavor.

As discussed in Sections 1.3 and 1.4, female size may have implications for the quality of the incubation environment and the intensity of sibling interactions. Thus, it is not surprising that chinook and chum salmon, being generally larger than the other species, also produce larger eggs (see also Fleming 1998). However, this can not be the whole story, because whereas sockeye salmon are larger than pink salmon, they produce substantially smaller eggs (Table 4.2). We

Table 4.2. Egg size (wet mass, means and ranges of population means), egg number (mean of population means), and general behavioral and life history traits of North American Pacific salmon.

Salmon species	Mean female body size (mm)	Post-emergent behavior	Egg size (mg)	Egg number
Sockeye	530–690	Lake rearing, shoaling	105 (69–132)	3500
Pink	460–560	Downstream migration to estuaries	162 (136–197)	1800
Coho	590–700	River rearing, initial aggregations, later territorial	188 (91–297)	3000
Chum	550–780	Downstream migration to estuaries	239 (164–282)	3200
Chinook	480–1030	Downstream migration to estuaries (ocean type) or river residence (stream type)	251 (138–378)	4300

Data from Groot and Margolis (1991) and Fleming (1998). Exceptions can be found to each of the generalizations about post-emergent behavior.

suggest two possible explanations for this pattern. First, whereas juvenile pink salmon disperse to estuaries at emergence, juvenile sockeye salmon rear in lakes. Levels of size-selective predation may thus be higher in pink salmon (although this has not been tested). Second, whereas pink salmon fry experience strong osmoregulatory stress as they reach the highly saline marine environment, sockeye salmon fry that rear in lakes do not. Effects of such stress are thought to depend on juvenile size because larger size generally confers better osmoregulatory ability (McCormick and Saunders 1987). These factors may be among those that place a premium on large eggs in pink salmon, relative to sockeye salmon.

It is also interesting that coho salmon produce much larger eggs than sockeye salmon despite their similar body sizes. Selection for large eggs in coho salmon may come about through effects on competitive abilities. Whereas juvenile sockeye salmon shoal in lakes, coho salmon are territorial in streams during their juvenile stage (Groot and Margolis 1991), and this potentially selects for large juvenile size.

The consideration of any one factor influencing egg size/offspring fitness relationships in isolation is clearly not sufficient to explain the observed variation in egg size among Pacific salmon. Abiotic, physiological, and ecological factors may all be necessary parts of any conceptual model predicting variation among higher phylogenetic groups. Although the number of factors influencing egg size evolution (including any constraints) and interactions among these makes such a research project immensely challenging, it also makes it interesting.

Considerations of the evolution of optimal egg size tend to be biased toward an expectation that egg size evolves to match other aspects of an organism's life history. An alternative view is that many features of an organism's life history actually evolve to suit a particular egg size that is otherwise determined by constraints. Perhaps the size of lizard eggs *was* constrained by pelvic girdle size during earlier evolutionary stages (Section 3.1), but other aspects of their life history have now evolved to suit that egg size. Although there is no doubt that egg size has evolved to different evolutionary stable states within taxonomic groups (e.g., Pacific salmon, see Table 4.2), simultaneous evolution in other traits has occurred. Focusing on the evolution of egg size alone biases us toward considering only part of what "optimality" may entail. In fact, instead of asking "which came first, the chicken or the egg?" (see Shykoff and Widmer 1998 for comparative method solution) perhaps we should be asking "which evolved most, the chicken or the egg?" Carefully designed experiments may be of aid in the search for possible evolutionary changes that could create coadaptations with egg size. Furthermore, comparative studies using a phylogenetic approach that simultaneously consider evolutionary changes in multiple traits (e.g., Crespi and Teo 2002) could possibly identify instances where constraints on egg size appear to have governed the evolution of other traits.