THE IMPLICATIONS OF MATERNAL DECISIONS

FOR OFFSPRING GROWTH AND SURVIVAL

Ian A. Fleming
Norwegian Institute For Nature Research
Tungasletta 2,
N-7485 Trondheim, Norway
Tlf. +47 73801495 Fax +47 73801401
E-Mail Ian.Fleming@Ninatrd.Ninaniku.No

Sigurd Einum
Norwegian Institute For Nature Research
Tungasletta 2, N-7485 Trondheim Norway
Tlf. +47 73801521 Fax +47 73801401
E-Mail Sigurd.Einum@Ninatrd.Ninaniku.No

EXTENDED ABSTRACT ONLY – DO NOT CITE

Many of the factors determining embryo and early juvenile growth and survival are intimately linked to maternal traits in salmonids. Females choose the spawning sites and times, construct the nests and deposit the nutrient-rich eggs. In Atlantic salmon, female breeding success (i.e., number of her embryos surviving to emergence) shows a strong positive relation to body size due in part to increased fecundity. Increased fecundity, however, is only part of the story, because while female fecundity typically increases at a declining rate with body size, breeding success increases exponentially. Thus large females are producing fewer eggs, but are achieving higher breeding success per unit body size than are small females (Fleming 1998). The female through her effects on nest quality and survival largely determines the probability of embryo survival during incubation.

When the eggs hatch, the small juveniles still have a considerable amount of nutrients and energy stored in the yolk-sac, as a result of maternal provisioning. Once the yolk sac is absorbed, the juveniles emerge from the gravel into the open water. Newly emerged fry are poor swimmers and unlike older fry, are negatively buoyant, rapidly returning to the bottom. Thus, initially they do not

go far from the spawning site. In other words, the female's choice of spawning site and time dictates offspring environment and subsequent growth and survival. A female not able to choose and/or fight for a good site will expose her offspring to potentially harsh environmental conditions and thus poor growth and high mortality immediately after emergence. Loss rates during the first weeks thereafter are very high, with 68-88% mortality during the first 17-28 days (Einum and Fleming 2000a,b). Similar patterns have been observed in brown trout, where about 80% of fry rarely feed after emergence, quickly lose weight and drift down-stream during night and die (Elliott 1994). Incubation and early juvenile life are thus periods of intense selection (Einum and Fleming 2000a,b).

Effects of egg size on early offspring survival and growth

By manipulating egg size and thus controlling for maternal trait interactions, we examined the causal consequences of offspring size in a wild population of Atlantic salmon (Einum and Fleming 2000b). The joint effect of egg size on egg number and offspring survival resulted in stabilizing phenotypic selection for an optimal size. The optimal egg size differed only marginally from the mean value observed in the population, suggesting that it had evolved largely in response to selection on maternal rather than offspring fitness. Maximisation of maternal fitness by sacrificing offspring survival may well be a general phenomenon among highly fecund organisms. Egg size may also influence offspring growth. We found distinct reaction norms in the performance of juveniles from small and large eggs in experiments with brown trout, as growth and survival were similar in high quality environments but became increasingly divergent in poorer environments (Einum and Fleming 1999). The existence of such reaction norms indicates that the optimal egg size varies across gradients of environmental quality, and this has likely shaped the evolution of egg size.

Effects of spawning time on early offspring survival and growth

There is indirect evidence that spawning time among females may be affected by competition, with larger, dominant females spawning before smaller, less dominant females (Elliott 1994, Petersson and Järvi 1997). Such differences can directly influence hatching and emergence time, which may have important consequences for offspring performance (e.g., Metcalfe and Thorpe 1992). To quantify the extent to which timing of breeding may ultimately affect fitness, we undertook laboratory and field experiments with Atlantic salmon (Einum and

Fleming 2000a). To control for confounding effects caused by correlated traits, manipulations of the timing of fertilization combined with intraclutch comparisons were used. Mortality was intense and selective during the initial period following emergence from the gravel resulting in a significant phenotypic shift toward an earlier date of emergence. Moreover, timing of emergence had additional consequences for juvenile body size, with late-emerging juveniles being smaller than early-emerging ones at subsequent samplings, both in the wild and in parallel experiments conducted in semi-natural stream channels. This may affect success at subsequent size-selective episodes, such as winter mortality and reproduction. However, further evolution towards earlier emergence is most likely countered by the probability of experiencing unfavourable environmental conditions early in the spring.

The causality of maternal effects (e.g., egg size and spawning time) in our studies indicate that selection on juvenile traits plays an important role in the evolution of maternal traits in natural salmonid populations. Moreover, they indicate that the reproductive potential of females is dictated by much more than simply their fecundity.

References

Einum, S. And I.A. Fleming. 1999. Maternal Effects Of Egg Size In Brown Trout (*Salmo Trutta*): Norms Of Reaction To Environmental Quality. Proc. R. Soc. Lond. B 266:2095-2100.

Einum, S. And I.A. Fleming. 2000a. Selection Against Late Emergence And Small Offspring In Atlantic Salmon (*Salmo Salar*). Evolution 54:628-639.

Einum, S. And I.A. Fleming. 2000b. Highly Fecund Mothers Sacrifice Offspring Survival To Maximise Fitness. Nature (In Press)

Elliott , J.M. 1994. Quantitative Ecology And The Brown Trout. Oxford University Press.

Fleming, I.A. 1998. Pattern And Variability In The Breeding System Of Atlantic Salmon (*Salmo Salar*), With Comparisons To Other Salmonids. Can. J. Fish. Aquat. Sci. 55(Suppl. 1): 59-76.

Metcalfe, N.B. And J.E. Thorpe. 1992. Early Predictors Of Life-History Events: The Link Between First Feeding Date, Dominance And Seaward Migration In Atlantic Salmon, *Salmo Salar* L. J. Fish. Biol. 41(Suppl. B):93-99.

Petersson, E. And T. Järvi. 1997. Reproductive Behaviour Of Sea Trout (*Salmo Trutta*) – Consequences Of Sea-Ranching. Behaviour 134:1-22