MATERNAL EFFECTS ON OFFSPRING SIZE: VARIATION THROUGH EARLY DEVELOPMENT OF CHINOOK SALMON

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Abstract.—We performed two breeding experiments with chinook salmon (*Oncorhynchus tshawytscha*) to explore maternal effects on offspring size. We estimated the magnitude of maternal effects as the differences between sire-offspring and dam-offspring regression slopes. Early in life, offspring size is largely influenced by maternal size, but this influence decreases through early development, with the maternal effect becoming negative at intermediate offspring ages (corresponding to a period of reduced growth of progeny hatching from large eggs) and converging on zero as offspring age. Also, egg size was positively correlated with early survival, but negatively correlated with maternal fecundity.

Key words.—Compensatory growth, fecundity, growth, optimality, salmon, selection, survival.

In most organisms, progeny phenotypes tend to be influenced more by the genotype or environment of their mother than by the genotype or environment of their father. This large effect of maternal (relative to paternal) genotype or environment is generally referred to as a maternal effect (Falconer 1965; Mousseau and Fox 1998) or, when mediated by maternal environmental conditions, as an inherited environmental effect (Rossiter 1996). Within the last decade, theoretical studies considering maternal effects have demonstrated that they can have important ecological and evolutionary consequences (Mousseau and Dingle 1991a,b; Reznick 1991; Riska 1991; Fox 1994). For example, maternal effects can generate time-lags in population dynamics in which dynamics in a future generation are influenced by the environmental conditions experienced in the current generation (e.g., Rossiter 1996). Maternal effects can also accelerate or impede evolutionary responses to natural selection, and characters influenced by maternal effects may experience time-lags in responses to selection, respond in a maladaptive direction, or may continue to respond even after selection has been relaxed (Kirkpatrick and Lande 1989; Cheverud and Moore 1994). When maternal effects are mediated by maternal genotype they may themselves be genetically variable and thus capable of evolving (Wade 1998; Fox et al. 1999). As a result, many maternal effects appear to have evolved as adaptations for dealing with environmental variation (reviews in Mousseau and Fox 1998). However, despite their potential ecological and evolutionary importance, most researchers consider maternal effects in studies only to avoid overestimating genetic variances and avoid confusing environmentally based maternal effects with genetic effects (Falconer 1989; Rossiter

1996; Shaw and Byers 1998). Thus, little is actually known about the biology of maternal effects.

Variation in propagule size is one of the best understood mechanisms by which variation among females influences the phenotypes of progeny. Female gametes are generally substantially larger than male gametes, the size of a developing embryo is influenced largely by the size of the egg it developed from, and not the size of the sperm that fertilized the egg (Chambers and Leggett 1996; Visman et al. 1996; Heath and Blouw 1998). Thus, early in development variation in size among individuals tends to be influenced primarily by genetic or environmental variation among their mothers, rather than their fathers (Falconer 1989; Fox 1994; Bernardo 1996a; Heath and Blouw 1998). However, despite this large maternal effect on body size early in development, maternal effects on progeny size tend to be relatively undetectable by the time progeny mature—progeny tend to mature at a size that is relatively intermediate between the size of both parents (Kinghorn 1983; Mousseau and Dingle 1991a; Fox 1994; Bernardo 1996b; Fox and Savalli 1998; but see Silverstein and Hershberger 1992). This implies that the relative importance of maternal effects versus genetic effects changes throughout development. Yet, because we generally examine only propagule (e.g., egg or seed) and adult size, little is known about how the relative importance of maternal effects changes throughout intermediate stages of development or about how progeny compensate for large maternal effects to eventually attain a genetically targeted size (Fox 1997).

There are two mechanisms by which individuals can compensate for small size at hatching: they can either extend development (increase development time) or increase their growth rate (presumably by either increasing feeding rates and/or increasing conversion efficiency). In some insects, progeny extend development to compensate for small size at hatching (e.g., Fox 1994, 1997). However, in some other organisms development time is constrained. For example,

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chinook salmon (*Oncorhynchus tshawytscha*) must undergo a size-dependent physiological change (smolting) before leaving their natal streams for salt water. The timing at which salmon leave their natal stream (smolt) is constrained to a small window and is triggered by photoperiod and water temperature (Clarke and Shelbourn 1985; Clarke and Hirano 1995). Fry that are below the critical body size for smolting suffer high mortality when exposed to salt water in the laboratory; however, little is known concerning relative survival in the wild (Clarke and Hirano 1995). Thus, extending development time to compensate for small size is not considered an option for juvenile salmon. Nonetheless, whereas egg and hatchling size in salmon are influenced primarily by maternal size (i.e., there is a large maternal effect; Sargent et al. 1987; Bernardo 1996a; Chambers and Leggett 1996; Heath and Blouw 1998), body size is influenced almost equally by both maternal and paternal size when fish eventually migrate to salt water (see Kinghorn 1983; Withler et al. 1987; Heath and Blouw 1998) demonstrating that progeny do compensate for large maternal effects. However, the pattern and mechanism of this compensation is unknown.

We describe two breeding experiments in which we explore how the relative importance of maternal effects and genetic effects on body size change through the development of juvenile chinook salmon (*O. tshawytscha*). We then examine the mechanism producing the change in the relative importance of maternal effects. We find that the influence of maternal effects on progeny size decreases throughout development until variation in progeny body size is explained equally by variation among both male and female parents. Variation in growth rates accounted for the declining importance of maternal effects. Interestingly, progeny appeared to initially overcompensate for the maternal effect: At intermediate ages, progeny hatching from small eggs were actually larger than those hatching from larger eggs, thus resulting in a negative maternal effect (Janssen et al. 1988).

MATERIALS AND METHODS

Chinook Salmon Life History

The early life history of chinook salmon consists of two discrete developmental stages that serve as useful benchmarks for temporal variation in body size of juvenile salmon (Healey 1991). The first stage, in which individuals obtain all resources from maternal reserves, is referred to as the preemergence stage. The second stage, in which individuals feed exogenously, is referred to as the postemergence stage. Eggs are laid in the interstitial spaces of a gravel stream bed, where they are fertilized by males prior to be being covered. Following hatch, the larvae (alevins) remain in the interstitial spaces of the stream bed and obtain nutrition from their yolk-sac without feeding exogenously. Thus, eggs and larvae exhibit no exogenous feeding and together represent the preemergence stage. When the yolk is depleted, individuals (fry) emerge from the gravel and begin exogenous feeding; they enter the postemergence period. The timing of the emergence in Pacific salmon is mostly determined by incubation temperature; however, fry from large eggs have been shown to emerge somewhat later than those from small eggs reared at the same temperature (Rombough 1985; but see Beacham et al.1985). Although fish are reared under artificial conditions in our experiments, we use the pre- and postemergence distinction here because it represents a significant and clearly defined change in juvenile life history.

Mating Experiment

To compare the relative influence of maternal versus paternal body size on progeny size and growth rate, we performed two full-sib mating experiments in which the relationship between parental and progeny size was quantified through development.

In the fall of 1994, 60 male and 60 female chinook salmon of varying sizes (0.8–7.4 kg) and ages (males: two and three years; females three and four years) were taken from a commercial salmon farm and randomly mated to produce 60 full-sib families. In the fall of 1996, 80 male and 80 female salmon of varying sizes (0.7–6.6 kg) and ages (female: three years; males: two and three years) were also mated to produce 80 full-sib families. In both experiments, fertilized eggs were incubated at 10°C in separate vertical-stack incubation trays with water flow of 15 l/min. Eggs that had died were counted at the beginning of the "eyed-egg" stage (visible eye-spot on the developing embryo in the egg; ≈ 25 days postfertilization at 10°C) and 1000 live eggs were retained for the balance of the experiment. Eggs hatched at ≈ 50 days of age. Larvae were reared at a constant 10°C in the same vertical-stack incubation trays until they began exogenous feeding, after which they were reared as family groups in 200-L tanks at a controlled density (800–1000 individuals per tank) at a constant 10°C. Eyed eggs and larvae were screened weekly for mortality. Although considerable variation in survival among family groups was observed, most mortality occurred prior to the eyed stage, and thus did not strongly affect fry rearing density. No correlation between fry rearing density and growth was observed ($P > 0.10$). No record of mortality was kept after the beginning of exogenous feeding (beginning at ≈ 105 days).

In both 1994 and 1996 a random subsample of the offspring from each full-sib family was group weighed twice during the egg stage; once at fertilization ($n = 20$ per family) and once just prior to hatch at ≈ 45 days postfertilization ($n = 100$ per family). Eggs were dried on paper towels to reduce adherent water. In 1994, families were also weighed after the initiation of exogenous feeding (beginning of the postemergence stage) and the juvenile fish were weighed approximately weekly (between 12 and 30 per family) until ≈ 200 days after egg hatch. Fish were not weighed during the larval stage in 1994. In 1996, however, families were weighed once during the larval stage (at 78 days postfertilization; $n = 15$ per family) and once just after the onset of exogenous feeding (at 105 days; $n = 15$ per family). Although some variation in the time of the onset of exogenous feeding was observed, no record was kept of exact date for specific families. Reported time of onset of exogenous feeding (see Figs. 1 and 2) is the time at which an estimated 50% of the families had depleted all of their yolk-sac. Logistic difficulties precluded reliable weight measurements for postemergent fry in the 1996 experiment. All fish were patted dry prior to weighing.
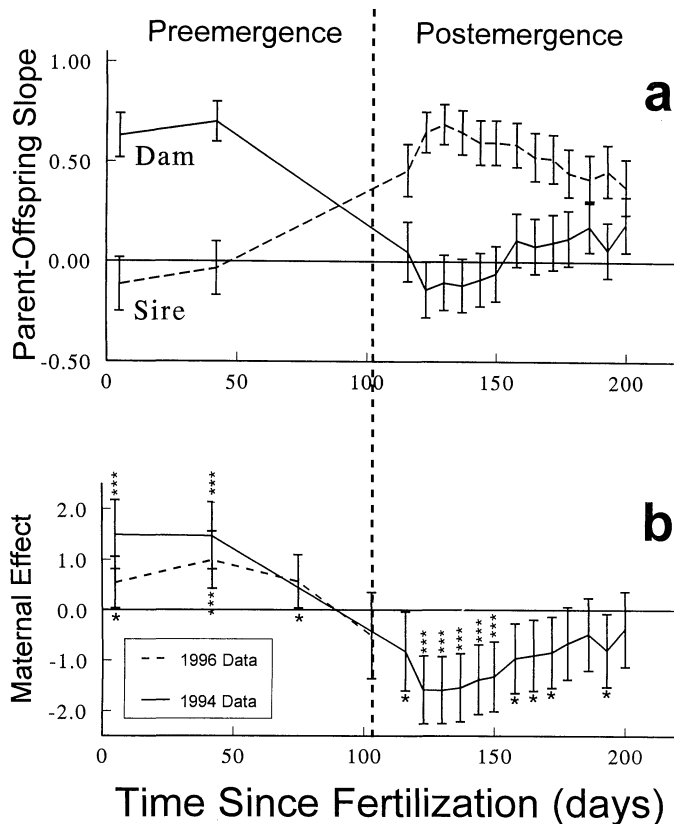
FIG. 1. Parent-offspring regressions and estimated maternal effects for chinook salmon. (a) Sire-offspring (dashed line) and dam-offspring (solid line) regression slopes ($\pm$ 2 SEM) from the 1994 experiment (n = 60 full-sib families). In 1996, the slope of the dam-offspring regressions were significant greater than zero for three of the four sampling dates (mean $\pm$ 1 SEM: day 0 = 0.48 $\pm$ 0.20; day 45 = 0.65 $\pm$ 0.18; day 78 = 0.50 $\pm$ 0.20; day 104 = 0.36 $\pm$ 0.25), whereas the slopes of the sire-offspring regressions were not significantly different from zero for any of the four sampling dates (mean $\pm$ 1 SEM: day 0 = 0.21 $\pm$ 0.22; day 45 = 0.15 $\pm$ 0.22; day 78 = 0.21 $\pm$ 0.23; day 104 = 0.01 $\pm$ 0.32). (b) Estimated maternal effects ($\pm$ 95% confidence limits) for egg and juvenile stages from both 1994 and 1996 experiments. The vertical dashed line indicates the change from preemergence (prior to exogenous feeding) to postemergence (subsequent to exogenous feeding) life stages. ***P < 0.001; **P < 0.01; *P < 0.05.

Statistical Analysis

To estimate the relative influence of maternal versus paternal body size on the size of their progeny and to quantify changes in this influence throughout development, we regressed mean offspring size against the size of each of their parents (parent-offspring regressions; Falconer 1989; Roff 1998). When all individuals are measured at the same age (both parents and offspring) and the variation in body size is the same within each sex, twice the slope of the parent-offspring regression is an estimate of the heritability (h^2) of body size and the difference between the dam-offspring and sire-offspring slopes is an estimate of the magnitude of the maternal effect. In our study, however, parents and their offspring were not measured at the same age (parents were mature and of variable age, offspring were measured throughout development). Thus, these parent-offspring regressions likely
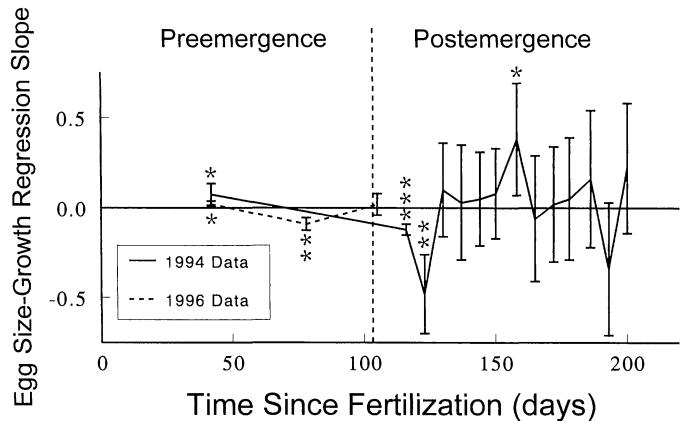

FIG. 2. Calculated slopes ($\pm$ 2 SEM) for the regression of relative growth rate versus mean eyed-egg weights for the 1994 and 1996 experiments. The vertical dashed line the change from preemergence (prior to exogenous feeding) to postemergence (subsequent to exogenous feeding) life stages. ***P < 0.001; **P < 0.01; *P < 0.05.

underestimate the true heritabilities (due to high V_E among parents). However, the difference in slopes is still a useful measure of the relative effect of maternal versus paternal body size on the size of their progeny—when maternal effects are very large progeny will resemble their mother and not their father (sire-offspring slope $\ll$ dam-offspring slope) and when maternal effects are not present progeny will resemble both of their parents equally (equal slopes). The degree to which progeny resemble the phenotype of their mothers, rather than that of their fathers, is thus an estimate of the relative maternal effect, and was estimated by subtracting twice the slope of the sire-offspring regression from twice the slope of dam-offspring regression (Falconer 1989; Roff 1998). We tested the null hypothesis of equal slopes for the dam-offspring and sire-offspring regressions using a homogeneity of slopes analysis (Zar 1974). The 95% confidence limits of the difference in linear regression slopes was calculated following Zar (1974).

Because the slope of the regression is influence by the variance in body size, which varied with progeny age and differed between the sexes of the parents, the slope of the sire-offspring regression is expected to be different from the dam-offspring regression regardless of genetic or maternal effects. To make all regression slopes directly comparable, mean progeny and parental weights were standardized to a mean of zero and variance of one (by first subtracting the mean for that sample and dividing this difference by the sample variance). This correction was applied separately to each age class and separately to the sire and dam weights. Because sexing immature salmon is destructive, we could not separate male and female progeny in our analyses. However, in two previous experiments juvenile sex was determined using a PCR-based genetic sex marker (Devin et al. 1994; Heath et al. 1994; Heath et al. 1996) and no difference in the mean or variance of body weight was observed between the sexes (D. D. Heath, unpubl. data).

To investigate whether growth varied among families, and whether this variation could explain the observed relation-

ships between parents and their offspring, we estimated relative growth rates for each family in the 1994 experiment. Relative growth rate (RGR_{1-2}) was calculated as $RGR_{1-2} = (Wt_2 - Wt_1)/(Wt_1 \times time)$, where Wt_1 and Wt_2 are the mean weights at two successive sampling dates and time is the number of days between the two sampling dates. Relative growth rate is a good estimate of growth in fish for short time periods (Heath et al. 1991). We then regressed RGR on eyed-egg weight for all families in the 1994 and 1996 experiment to examine the relationship between relative growth rate and egg weight.

To examine the influence of egg size on early survival, we tested the hypothesis that mean family survival during the preemergence period increased with mean eyed-egg weight (Spearman rank-sum correlations; examined for both years). For the 1996 experiment we also examined the relationship between lifetime fecundity and egg size by first calculating relative fecundity for each female by dividing each female's lifetime fecundity by her body weight. We used relative fecundity to correct for the well-known effect of body size on the number of eggs produced in fish (see Roff 1992). Relative fecundity was then regressed against mean eyed-egg weight. Fecundity data were not collected in the 1994 experiment.

RESULTS

The size of eggs that females laid was highly positively correlated with the size of the females (Fig. 1a; dam-offspring regression: $R^2 = 0.48$, $P < 0.001$ and $R^2 = 0.42$, $P < 0.001$ for 1994 and 1996, respectively), but not with the size of their mates (sire-offspring regression: $R^2 = 0.001$, $P > 0.05$ and $R^2 = 0.021$, $P > 0.05$). As expected, this resulted into a highly significant effect of maternal (but not paternal) size on larval body size at 45 days postfertilization (Fig. 1a). After 45 d post-fertilization, the effect of maternal body size (relative to paternal size) began to decrease, and by day 116 postfertilization progeny began to resemble the phenotype of their fathers (Fig. 1a). Interestingly, progeny appeared to developmentally overcompensate for the large effect of maternal size—by day 105 postfertilization (i.e., postemergence) variation among progeny tended to reflect variation among their fathers more than their mothers (Fig. 1a), resulting in a maternal effect that became significantly negative (Fig. 1b).

Although variation in body size of progeny of intermediate ages reflected that of only one of their parents, progeny body size gradually converged on the size expected when there is no maternal effect—by age 180 days there was no detectable difference between the sire-offspring and dam-offspring slopes (Fig. 1a) such that the estimated maternal effect on body size was not statistically different from zero. By day 200 (the end of the experiment) maternal effects were negligible (Fig. 1b) and the parent-offspring regression slopes were 0.19 ($\pm$ 0.14, dam) and 0.38 ($\pm$ 0.14, sire). Assuming that the parent-offspring slopes have by this time converged on a steady value, an estimate for the narrow-sense heritability (h^2) of body size in chinook salmon would be approximately 0.57 $\pm$ 0.28. This estimate of the heritability of body size in juvenile salmonids is somewhat higher than published estimates (Gjedrem 1983; Kinghorn 1983).

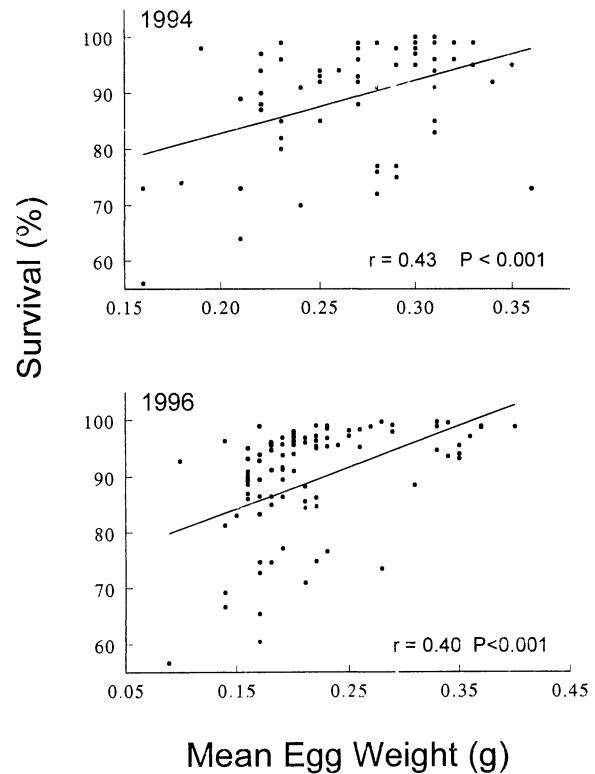The changes in relative growth rate observed throughout

FIG. 3. Early survival (preemergence) of chinook salmon plotted against mean eyed-egg weight in 1994 and 1996. Points represent mean survival per family from egg fertilization to the initiation of exogenous feeding. Each family is a single datapoint ($n = 80$ and $n = 60$ in 1994 and 1996, respectively). Lines represent best-fit linear regressions, but analysis was based on rank-sums (Spearman rank-sum correlations, $P < 0.001$ for both years).

development of chinook salmon (Fig. 2) roughly corresponded to the pattern observed for maternal effects (Fig. 1b). Progeny hatching from large eggs initially grew slightly faster than progeny hatching from small eggs, presumably due to increased water absorption because larvae are not feeding exogenously at this stage. This pattern did not extend past the early larval stage, that is, progeny from large eggs actually grew slower than progeny hatching from small eggs. By day 130, however, any relationship between egg size and relative growth rate largely disappeared (Fig. 2).

In both experiments, eyed-egg size was positively correlated with larval survivorship between egg hatch and the initiation of exogenous feeding: Larvae hatching from larger eggs survived better than those hatching from smaller eggs (Fig. 3; Spearman rank-sum correlations, $P < 0.001$ for each year). There was also a significant trade-off between egg size and female fecundity (Fig. 4): Females that laid larger eggs laid substantially fewer eggs than females laying smaller eggs (after correcting for body size; data available for 1996 experiment only). Approximately 60% of the observed variation in relative fecundity could be explained by mean eyed-egg weight.

DISCUSSION

In many organisms, maternal effects on progeny body size are fairly large early in development (because mothers make
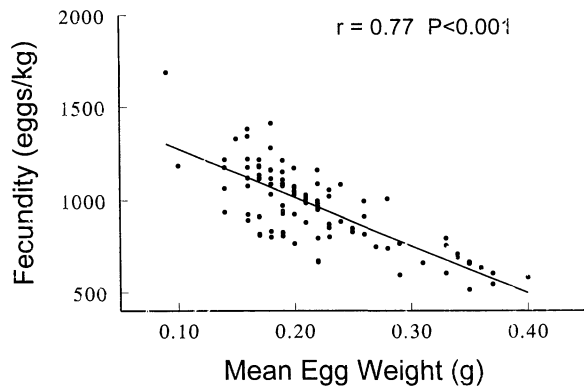
FIG. 4. Relative fecundity of females plotted against mean eyed-egg weight for 80 full-sib chinook salmon families (1996 experiment). Relative fecundity was calculated as the number of eggs produced divided by the weight of the female. The regression equation is: relative fecundity $= 1539 - 2597$ (egg weight).

eggs), but are negligible by the time progeny mature (e.g., Fox 1994, 1997; reviews in Mousseau and Fox 1998). This suggests that, as progeny age, the relative impact on body size of maternally derived resources decreases, while expression of the offspring genome increases in importance (Kaplan 1987; see Heath and Blouw 1998). Here we have examined how the importance of maternal effects changes throughout the development of the progeny. Our results show that change in the influence of maternal effects on offspring size is not a straightforward monotonic decline, as often assumed (see Reznick 1991; Fox 1997; Fox and Savalli 1998), but rather includes significant sign changes (i.e., a negative maternal effect; Janssen et al. 1988). Although our analysis involved only offspring body size, it is reasonable to expect that the maternal effect on other traits may also change over time in an unexpected manner.

The significant negative maternal effect observed in our study appears to be a result of differences in growth rate among families hatching from different size eggs. At the beginning of the postemergence period (initiation of external feeding), progeny hatching from small eggs grew faster (higher RGR) than progeny hatching from large eggs (Fig. 2). This corresponded to the start of the negative maternal effect (Fig. 1b), thus suggesting a cause-and-effect relationship. We suspect this change in growth rate and the resulting negative maternal effect may result from two possible mechanisms: (1) differential feeding behavior whereby small progeny attempt to compensate for their small size; and/or (2) progeny from small eggs emerge earlier than those from large eggs and thus have a longer exogenous feeding time. Chinook salmon juveniles must undergo a complex physiological change associated with their move from freshwater to saltwater habitat (smoltification). They are thus under strong selection to grow to meet the minimum smoltification size threshold. An optimization model for predation risk versus growth effort (foraging effort) predicts that families of chinook salmon with small initial size will accept higher predation risk to gain a growth advantage via more aggressive foraging (Ludwig and Rowe 1990; Rowe and Ludwig 1991; Abrams and Rowe 1996). This could be realized by the small fish either increasing their foraging aggressivity or by early

emergence from the gravel; in either case, the small fish would be exposed to higher predation risk, but would gain a growth advantage. Clearly, such foraging/emergence behavior within the hatchery environment would not incur any increase in predation risk, but would elevate growth rate. Thus, Ludwig and Rowe's (1990) model provides a conceptual explanation for the unusual growth pattern that we observed (Fig. 2) and the evolutionary basis of the negative maternal effect. Our hypothesized mechanisms for the negative maternal effect demonstrated here can easily be tested, because they predict that families of chinook salmon with smaller mean eyed-eggs size should feed more aggressively and/or emerge earlier than those with large egg sizes.

Propagule size has been shown to have important fitness consequences (Bell 1980; Reznick 1991; Roff 1992; Fox 1994; Quinn et al. 1995; Bernardo 1996a,b) for a large variety of organisms. Large egg and/or juvenile body size in fish is associated with higher survival (see Reznick 1991; Heath and Blouw 1998), faster growth (Gall 1974; Pitman 1979; Wallace and Aasjord 1984; Reznick 1991), and better swimming performance (Bams 1967; Ojanguren et al. 1996). The positive correlation between survival and egg weight reported here is evidence that there is a selective advantage to laying large eggs even within the near-optimal hatchery environment. However, our results likely underestimate the fitness advantage that progeny hatching from large egg size would experience in a natural rearing environment. It is generally accepted that large propagule size is most advantageous in suboptimal or highly variable environments (Parker and Begon 1986; Elgar 1990; Reznick 1991; Roff 1992; C. W. Fox, unpubl). Also, if our interpretation of growth rate patterns is correct, progeny hatching from small eggs must risk higher predation in an attempt to compensate for their small body size if they are to smolt in time for their migration to salt water. In addition to this survival-based selection for large eggs, our data also demonstrate a substantial cost to females of laying large eggs—females that lay large eggs must necessarily lay fewer eggs than an equal-sized female laying smaller eggs (i.e., a trade-off between egg size and fecundity; Fig. 4). This trade-off has been observed in a number of other species and is thought to be a major contributor to the evolution of egg size (see Roff 1992; Visman et al. 1996). Thus, egg size in chinook salmon likely represents a balance between selection for large eggs (via effects on progeny survival) and selection for small eggs (via fecundity selection and a trade-off between egg size and number). This relationship is complicated by the substantial increases in fecundity realized by females who sexually mature at older ages and are thus considerably larger; however, these females also suffer increased mortality during their additional year(s) at sea (Healey 1991).

In summary, we have investigated changes in the relative importance of maternal effects through the early development of juvenile chinook salmon. We found that, as expected, the contribution of maternal effects to progeny body size generally decreases through development. However, this decrease is not monotonic. Instead, it includes significant sign changes, so that we observed a period in which progeny generally exhibited a phenotype opposite that of their mother (progeny hatching from eggs laid by large mothers are smaller

than progeny hatching from eggs laid by small mothers, a negative maternal effect). This result appears to be caused by changes in the growth rate of progeny—following the initiation of exogenous feeding, progeny hatching from small eggs tended to grow faster than progeny hatching from large eggs. This growth pattern could result from two mechanisms: progeny from small eggs feed more aggressively than those from large eggs and/or progeny from small eggs emerge sooner and thus begin exogenous feeding before the progeny from large eggs. Both of these hypothesized mechanisms would lead to increased risk of predation for the progeny from small eggs. The exploration of these hypothesized mechanisms of growth compensation in juvenile salmon will be the subject of future research.

ACKNOWLEDGMENTS

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HYBRID DYSFUNCTION IN FIRE-BELLIED TOADS (*BOMBINA*)

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Abstract.—Reproductive isolation between two taxa may be due to endogenous selection, which is generated by incompatibilities between the respective genomes, to exogenous selection, which is generated by differential adaptations to alternative environments, or to both. The continuing debate over the relative importance of either mode of selection has highlighted the need for unambiguous data on the fitness of hybrid genotypes. The hybrid zone between the fire-bellied toad (*Bombina bombina*) and the yellow-bellied toad (*B. variegata*) in central Europe involves adaptation to different environments, but evidence of hybrid dysfunction is equivocal. In this study, we followed the development under laboratory conditions of naturally laid eggs collected from a transect across the *Bombina* hybrid zone in Croatia. Fitness was significantly reduced in hybrid populations: Egg batches from the center of the hybrid zone showed significantly higher embryonic and larval mortality and higher frequencies of morphological abnormalities relative to either parental type. Overall mortality from day of egg collection to three weeks after hatching reached 20% in central hybrid populations, compared to 2% in pure populations. There was no significant difference in fitness between two parental types. Within hybrid populations, there was considerable variation in fitness, with some genotypes showing no evidence of reduced viability. We discuss the implications of these findings for our understanding of barriers to gene flow between species.

Key words.—Amphibia, hybrid zone, natural selection, reproductive isolation, speciation.

Despite more than a century of deliberation on the origin of species, evolutionary biologists remain undecided as to the mechanisms by which reproductive isolation is generated. Whether geographic isolation, or allopatry, is a prerequisite to speciation has been hotly debated (cf. Mayr 1963 and Bush 1975, 1994), and there is not even consensus as to the nature of the reproductive isolation that accumulates in allopatric populations. If two allopatric populations have diverged such that they remain reproductively isolated on secondary contact, is this because of adaptation to alternative environments (exogenous selection; Moore and Price 1993), incompatibilities between respective genomes (endogenous selection), or both?

These issues can be addressed when previously allopatric populations come into contact and display only partial reproductive isolation, resulting in hybrid zones where the homogenizing effects of dispersal and recombination are counterbalanced by natural selection. It has previously been argued that the majority of such hybrid zones are maintained by selection against hybrid genotypes (Barton and Hewitt 1981; 1985), with reproductive isolation being generated by

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