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FITNESS CONSEQUENCES OF VARIATION IN EGG SIZE AND FOOD ABUNDANCE IN BROOK TROUT *SALVELINUS FONTINALIS*

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Abstract.—Relationships between egg size and juvenile survival in brook trout, *Salvelinus fontinalis*, were determined experimentally at two levels of food abundance and then incorporated into a model that related maternal fitness to egg size and food supply. Egg volume was positively correlated with juvenile size at hatching and size at yolk sac resorption but had no significant effect on embryonic survival or development time. Juvenile survival was linearly related to egg size throughout the first 50 days of exogenous feeding at high and low food levels. The effects of egg size and food abundance on juvenile survival were not additive. Decreased food abundance significantly increased mortality among the smallest eggs but had a negligible effect on the largest eggs. Model simulations indicate that maternal fitness is a curvilinear function of egg size and that food supply influences both the height and the shape of the function. The fitness functions provide empirical support for the hypothesis that selection favors an increase in offspring size with reductions in resource abundance.

Key words.—Brook trout, egg size, fitness, food abundance, life history, Salmonidae, *Salvelinus fontinalis*, variation.

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The evolution of offspring size and number depends on the relationship between offspring size and offspring fitness and on the influence this relationship has on parental fitness (Svårdson, 1949; Lack, 1954; Smith and Fretwell, 1974). If offspring fitness is independent of offspring size, then the evolutionarily stable strategy (ESS; sensu Maynard Smith, 1982) of investment per offspring should be to maximize the number of offspring, each approaching the physiologically minimum size, within a brood (Brockelman, 1975). However, if offspring fitness increases with offspring size, then the ESS of investment per offspring is attained when the proportional gain in offspring fitness from an increment in parental investment equals the proportional parental loss in offspring numbers (Lloyd, 1987). If selection optimizes parental investment per offspring, then offspring size may be more or less constant within populations (Smith and Fretwell, 1974; Morris, 1987).

The general conclusion that natural selection optimizes offspring size has been questioned (e.g., Sargent et al., 1987) be-

cause of the considerable variation in offspring size in many organisms. Such intrapopulation variability is common within species of salamanders (Kaplan, 1980), frogs (Crump, 1981), fish (Marsh, 1986) and plants (Michaels et al., 1988). Another confounding influence is the positive correlation between maternal size and offspring size in some fish (Hutchings and Morris, 1985), reptiles (Pimental, 1959), and amphibians (McGinley, 1989).

Inter- and intrapopulation variation in offspring size has several explanations. Variability per se has been explained as an adaptation to a variable environment (Capinera, 1979). Kaplan and Cooper (1984) predicted that variable environments should select for variable offspring size (but see McGinley et al., 1987). Sargent et al. (1987) attributed increases in fish egg size with increasing maternal size to the larger female's increased ability to provide parental care. Parker and Begon (1986) argued that if the intensity of sibling competition is an important determinant of offspring survival, then larger females, having more resources for reproduction, should produce larger eggs than smaller females. Sibly and Calow (1983) predicted that increased food abundance should lead to increased offspring number but decreased offspring size. In large part,

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these alternative explanations reduce to differences in the assumed relationships among offspring size, parental fitness, and the environment.

The relative merit of alternative hypotheses for the evolution of offspring size and offspring number cannot be fully assessed without empirical data on offspring size-fitness functions. My objectives were to derive empirically relationships between offspring size and both offspring and maternal fitness in the brook trout (Salmonidae: *Salvelinus fontinalis*) and to show how these relationships change between environments that differ in food abundance.

MATERIALS AND METHODS

Sexually mature male and female brook trout were collected from three rivers near Cape Race, southeastern Newfoundland, Canada, in October 1988 and transferred to holding facilities at the Ocean Sciences Centre near St. John's. Eggs from 66 broods (15 from Freshwater River, 27 from Cripple Cove River, and 24 from Watern Cove River) were fertilized artificially (within-population crosses). Broods were placed in four vertical incubation chambers receiving a continuous flow of water at 7.5°C.

A dissecting microscope fitted with an eyepiece micrometer was used to measure the egg diameters and the offspring lengths (both to the nearest 0.01 mm) of 10 randomly chosen individuals in each brood. Mean egg diameter for each brood was determined when the eggs were placed in the incubation chambers. Mean size at hatching was calculated after all eggs in a brood had hatched and again at the time of yolk sac resorption. Survival was estimated during three stages of embryonic development: (1) fertilization to eyed stage, (2) eyed stage to hatching, and (3) hatching to resorption of yolk sac.

The influence of egg size on juvenile survival was assessed following yolk sac resorption. Twenty-seven of the 66 broods (6 from Freshwater, 12 from Cripple Cove, and 9 from Watern Cove) were transferred to 16 38-liter aquaria in a temperature- (11°C) and photoperiod- (10L:14D) controlled room. Twenty fish from each brood were placed in one-half of each aerated aquarium (halves separated by gray plastic). Broods were fed

twice daily either a high (0.010 g per fish) or a low (0.005 g per fish) ration of dry pellet food (BioDiet®). The high ration corresponds to the *ad libitum* feeding level recommended by Leitritz and Lewis (1976). Survival was monitored 20, 30, 40, and 50 days following yolk sac resorption. Survivorship was measured as the number of individuals alive in a brood at the end of a given time interval relative to the number alive at the beginning of that time interval. I analyzed for tank effects by raising four replicates of 20 individuals from one brood (Cripple Cove population) in aquarium sections randomly located throughout the room and feeding them the high ration.

Data were analyzed with parametric statistical tests. Differences in embryonic development and survival within and among populations were evaluated with a one-way analysis of variance. Survival data were transformed (arcsine) as recommended by Sokal and Rohlf (1981) for proportions. Egg size was expressed as egg volume [volume = $(\pi)(\text{diameter})^3/6$], a more appropriate measure of egg energy content and of offspring fitness than egg diameter (Wootton and Evans, 1976). Pearson moment correlation coefficients were calculated for all bivariate associations between egg size and all developmental and survival characteristics. Interpopulational comparisons were made to assess the generality of the observed survival probabilities and developmental rates and their associations with egg size. A Model I regression analysis was used to describe juvenile survival probabilities as a function of egg size. Slope homogeneity of the regressions of juvenile survival on egg size at each food level was analyzed using an analysis of covariance. The effect of aquarium origin on juvenile survival was analyzed with a *G* test.

RESULTS

Effects of Egg Size on Embryonic Survival and Development

Embryonic developmental characteristics and survival probabilities are presented in Table 1. Mean egg size ranged from 4.12 to 5.22 mm among broods. Egg size differed significantly ($P < 0.001$) among broods within populations [Freshwater: $F(14, 135)$

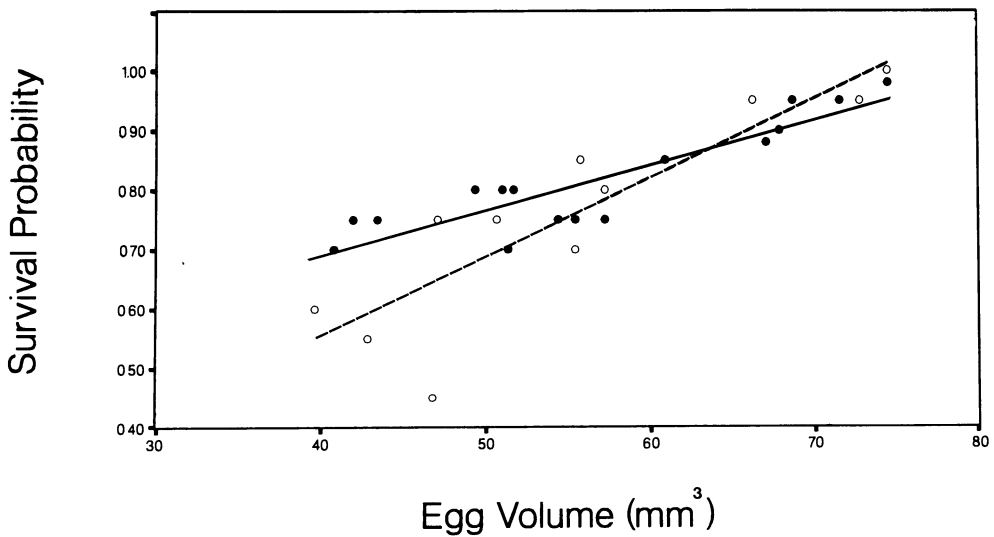


FIG. 1. Relationship between juvenile survival at 20 days and egg size at high (closed circles) and low (open circles) levels of food. Data points correspond to broods reared in separate aquaria. (For reference, egg volumes of 30 and 80 mm³ correspond to egg diameters of 3.80 and 5.26 mm, respectively.)

= 134.51; Watern Cove: $F(23, 216) = 118.44$; Cripple Cove: $F(26, 243) = 82.17$] but not among populations [$F(2, 63) = 0.67$; $P = 0.52$]. Egg number per brood ranged from 12 to 343.

Embryonic survival did not differ significantly among populations during any of the three developmental stages (Table 1). (These data are probably underestimates because unfertilized eggs could not be distinguished from fertilized eggs until the eyed stage of development.) Pooling data among populations, egg size was uncorrelated (1) with embryonic survival to the eyed stage ($r = -0.04$; $P = 0.73$), (2) with survival from the eyed stage to hatching ($r = 0.05$; $P = 0.71$), and (3) with survival from hatching to yolk sac resorption ($r = -0.11$; $P = 0.38$).

In all populations, egg size was positively associated with size at hatching and size at yolk sac resorption (r ranged from 0.55 to 0.76). Neither size at hatching [$F(2, 63) = 1.34$; $P = 0.27$] nor size at yolk sac resorption [$F(2, 63) = 0.08$; $P = 0.92$] differed among the three populations.

Time from fertilization to hatching (developmental time) averaged 75.8 ± 2.2 days and did not differ significantly among populations [$F(2, 63) = 1.14$; $P = 0.33$]. Egg size was uncorrelated with developmental time (pooled $r = -0.16$; $P = 0.19$) and ac-

counted for no more than 7% of the variation in developmental time in any of the populations.

Effects of Egg Size and Food Supply on Juvenile Survival

Juvenile survival was positively correlated with egg size during the first 20 days of exogenous feeding at both low ($r = 0.88$; $P < 0.001$; $N = 11$ broods) and high ($r = 0.87$; $P < 0.001$; $N = 16$) food levels (Fig. 1). The slopes of the linear regressions relating juvenile survival to egg size were not the same for the two food levels ($F = 5.66$; $P = 0.02$). Decreased food abundance resulted in significantly higher mortality for the smallest eggs and a negligible difference in mortality for the largest eggs.

The influence of egg size and food supply on juvenile survival persisted through the first 50 days of exogenous feeding at both low ($r = 0.81$; $P = 0.001$; $N = 8$ families) and high ($r = 0.77$; $P = 0.001$; $N = 13$) food levels. The slopes of the regressions relating juvenile survival to egg size for each ration did not differ between the 20- and 50-day intervals (low ration: $F = 0.02$, $P = 0.89$; high ration: $F = 0.17$, $P = 0.68$). The lack of slope heterogeneity between the food levels at the 50-day interval ($F = 2.01$; $P = 0.17$) can be attributed to small sample sizes

TABLE 1. Embryonic development and survival for three populations of brook trout (data are means \pm standard deviations; number of broods/females = N). Asterisks indicate whether within-population differences in body size, developmental time, or survival are significantly associated with egg size.

Trait	Population		
	Freshwater ($N = 15$)	Cripple Cove ($N = 27$)	Watern Cove ($N = 24$)
Egg size (mm)	4.80 \pm 0.33	4.70 \pm 0.27	4.72 \pm 0.30
Egg number	47 \pm 25	190 \pm 79	55 \pm 28
Maternal size (mm)	109 \pm 15	185 \pm 31	129 \pm 11
Size at hatch (mm)	17.0 \pm 1.5*	17.0 \pm 1.0**	16.6 \pm 1.2**
Size at yolk sac resorption (mm)	21.8 \pm 1.0*	22.0 \pm 1.9*	22.2 \pm 1.5*
Time to hatching (days)	75.3 \pm 3.0	75.8 \pm 2.1	76.0 \pm 1.7
Survival (proportion)			
Preeyed stage	0.84 \pm 0.08	0.91 \pm 0.10	0.91 \pm 0.08
Eyed to hatch	0.98 \pm 0.02	0.96 \pm 0.05	0.96 \pm 0.05
Hatch to yolk sac resorption	0.90 \pm 0.16	0.98 \pm 0.04	0.98 \pm 0.03

* $P < 0.05$.

** $P < 0.01$.

(a technical failure in the air supply to six aquarium sections resulted in the death of several fish in six broods 28 days after the beginning of the experiment). Daily mortalities during the first 50 days of exogenous feeding were incurred by the smallest or next to smallest sibling within each brood. Tank effects did not contribute to variation in juvenile survival [$G = 0.43$, $df = 3$, $P > 0.10$].

Interactive Effects of Egg Size and Food Supply on Maternal Fitness

Maternal fitness per brood can be approximated by

$$w_{ijk} = (m_{ij})(l_{ik}) \quad (1)$$

where m_{ij} is the expected number of eggs of size i that can be produced in a gonad of weight j , l_{ik} is the survival probability for eggs of size i in environment k (i.e., environments differing in food supply), and w_{ijk} represents the fitness of females producing eggs of size i , in a gonad of weight j , in environment k .

I considered fecundity to be primarily a function of egg size and gonad weight. There is empirical field evidence of a trade-off between egg size and egg number in the Cape Race populations (Hutchings, 1990). Partial correlation coefficients between egg size and egg number (controlling for gonad weight) are negative in Freshwater (-0.75 , $P < 0.001$, $N = 55$), Cripple Cove (-0.60 , $P < 0.001$, $N = 45$), and Watern Cove (-0.68 , $P < 0.001$, $N = 49$) populations. Because

the rate of increase in reproductive biomass (egg number \times mean egg volume for each female) with gonad weight is equal among populations (Hutchings, 1990), I used one population to illustrate the fitness consequences of producing eggs of different sizes in different food environments. Expected fecundities for eggs of different sizes in Cripple Cove females were calculated from a multiple regression equation which described fecundity (m) as a function of gonad weight (j) and egg volume (i), $m_{ij} = 28.3j - 2.7i + 83.6$ (where $j = 6.01$ g, the population mean).

Juvenile survival probabilities (l_{ik}) were calculated from the linear regression equations, which related the probability of survival in environment k to egg volume i for low ($k = 1$) and high ($k = 2$) food levels. These equations, $l_{i1} = 0.013i + 0.026$ and $l_{i2} = 0.008i + 0.378$, were those determined experimentally for juveniles during their first 20 days of exogenous feeding (the only period during which egg size influenced survival significantly).

The simulations indicate that fitness is a curvilinear function of egg size and that food supply influences both the height and the shape of the function (Fig. 2). For eggs less than 5.15 mm in diameter, reduced food supply has a negative impact on maternal fitness. The convergence in fitness at egg sizes greater than 5.15 mm reflects the minimal effect that food supply has on the survival of juveniles produced from large eggs

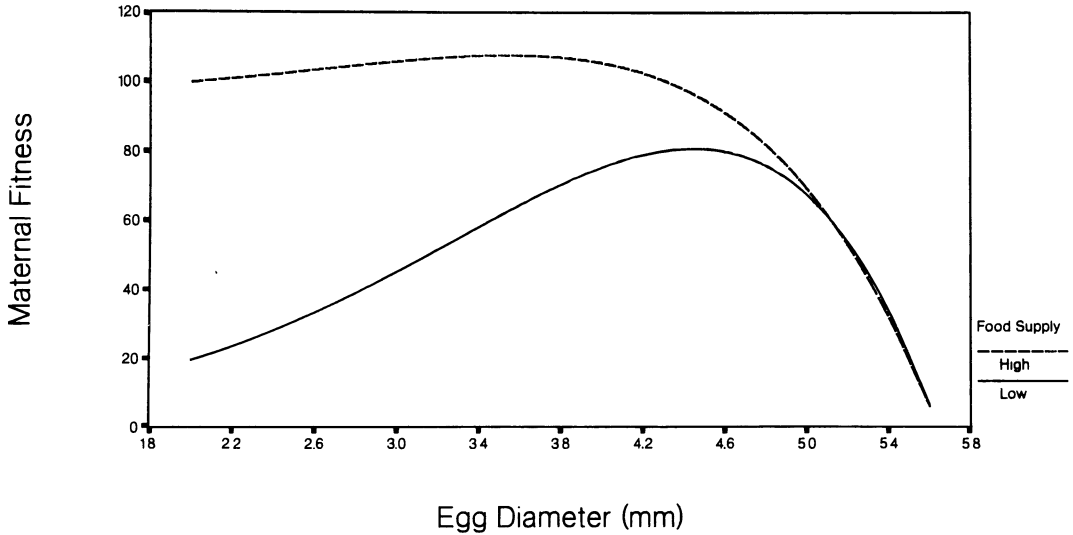


FIG. 2. Simulated relationship between maternal fitness (w in Eq. (1), standardized for gonad size) and egg size in high and low food environments.

(cf. Fig. 1). The egg size that maximizes the number of surviving juvenile offspring (i.e., the optimal egg size) increases from 3.6 mm at the high food level to 4.4 mm at the low food level.

DISCUSSION

The study provides empirical support for the hypotheses that natural selection favors an increase in offspring size with reductions in resource abundance (Smith and Fretwell, 1974; Kaplan and Cooper, 1984) and that better offspring growing conditions favor an increase in offspring number per brood (Sibly and Calow, 1983; Morris, 1987). For brook trout, decreased food abundance selects for the production of smaller numbers of larger eggs. Large juveniles hatch from large eggs and large juveniles have higher survival in early life than do small juveniles. Although food supply was manipulated for juveniles only in this study, experimental evidence indicates that salmonid egg size may be unaffected by adult food availability. Scott (1962) reported that egg size did not differ between groups of rainbow trout, *Oncorhynchus mykiss*, fed either a restricted diet or *ad libitum* although females in the former group produced fewer eggs per unit body mass.

The nonadditive effects of food abundance and egg size on juvenile brook trout survival, coupled with the maternal trade-

off between offspring size and number, results in different optimal egg sizes for environments that differ in food abundance. Environmental interactions on the relations between offspring size and survival-related traits are necessary for the evolution of environment- or population-specific offspring size optima. Empirical evidence of such interactions is also available for amphibians. Kaplan (1985) reported nonadditive effects of egg size and food abundance on time to metamorphosis in the California newt, *Taricha torosa*. A significant developmental time \times ovum size interaction on offspring survival has recently been found in the Oriental fire-bellied toad, *Bombina orientalis* (R. H. Kaplan, unpubl.).

The empirically based fitness functions derived here incorporate the commonly assumed tradeoff between offspring size and number, and they depend on linear associations between offspring survival and offspring size. However, theoretical formulations generally assume that the function relating offspring size to survival within a population or a species is either concave (Smith and Fretwell, 1974; Winkler and Wallin, 1987) or logistic (Sargent et al., 1987; Lloyd, 1987). These functions include asymptotic values for which survival changes relatively little with changes in offspring size. But it may not be reasonable to expect such asymptotic offspring sizes to exist under

natural conditions. Under stabilizing selection, only a limited range of offspring size is expected, e.g., around the inflection point of a logistic function. This would result in an approximately linear relation between offspring survival and offspring size when data are obtained from natural populations.

In brook trout, the production of fewer eggs may be the primary evolutionary cost to the production of larger eggs. Sargent et al. (1987) posited that increased mortality during the egg stage, through increased instantaneous egg mortality or increased developmental time, represents an evolutionary cost to large eggs. In the present study, embryonic survival and developmental time to hatching were uncorrelated with egg size. The independence of egg mortality and egg size may have been due to nonlimiting supplies of oxygen in the incubation chambers. In substrate where oxygen is limited, large coho salmon (*O. kisutch*) eggs suffer higher mortality than small eggs (van den Bergh and Gross, 1989). However, if females select the substrate and, indirectly, select the oxygen regime into which they bury their eggs, then oxygen limitation may not represent an important cost to the production of large eggs. Developmental time during yolk resorption has been reported to increase with increasing egg size in chinook salmon, *O. tshawytscha* (Rombough, 1985). However, such a developmental cost may be compensated by increased mobility of larger juveniles resulting in feeding prior to complete yolk sac resorption (personal observation, present study). Although not denying the potential importance of developmental delays associated with large eggs, their effect on fitness may be minimal relative to the survival benefits accrued at the juvenile stage.

The data presented here further document the survival advantages of large size in early life in many animals [e.g., fish (Bagenal, 1969; Marsh, 1986), amphibians (Berger and Uzzell, 1977)] and in some plants (Black, 1958; Schaal, 1980). For brook trout, the proximate advantages are probably related to behavior. Intraspecific interactions among juvenile trout are governed by size-dependent dominance hierarchies (Grant, 1990). The agonistic behavior of large, dominant individuals limits the food consumption of smaller subordinates and can

significantly reduce the latter's fitness (e.g., the smallest individuals within broods experienced the highest mortality in the present study). Juveniles from large eggs had higher survival probabilities when competing with other large individuals than did juveniles from small eggs competing with other small juveniles. Because greater energy reserves in larger individuals can reduce susceptibility to starvation (Bagenal, 1969; Marsh, 1986), subordinates within groups of large juveniles are probably better able to withstand the physiological stress imposed on them by intraspecific competition than are subordinates within groups of small individuals.

The influence of egg size on offspring survival and maternal fitness may have been underestimated here because the results were based on competition among siblings of the same egg size. In natural populations, it is likely that nonsiblings from eggs varying by 1 mm or more in diameter compete for food and space (cf. Gibson, 1988). This should accentuate the fitness differential between large and small juveniles (Parker and Begon, 1986; Parker et al., 1989).

Interactive effects of the environment on the relation between offspring size and maternal fitness can significantly influence the evolution of offspring size and offspring number in organisms inhabiting spatially and temporally heterogeneous environments. The results suggest that when the environment changes little from year to year, selection should favor the production of a single egg size within a brood. The extent to which offspring size is optimized in natural populations may largely depend on environmental variability and on its influence on the relation between offspring size and offspring survival (Kaplan and Cooper, 1984; McGinley et al., 1987).

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