

Egg Size, Female Effects, and the Correlations Between Early Life History Traits of Capelin, *Mallotus villosus*: An Appraisal at the Individual Level¹

R. Christopher Chambers, William C. Leggett, and Joseph A. Brown

ABSTRACT: The authors examined the within-individual correlations between egg quality (quantified by yolk volume) and early life history traits in capelin, *Mallotus villosus*. The commonly reported generalization—large eggs produce large larvae that subsist longer on endogenous energy reserves—was not supported by our analysis. Post-hatching lifespan of unfed larvae did not vary with initial egg yolk volume, yolk-sac volume at hatching, or size at hatching. The only correlate of post-hatching lifespan was a direct relationship with oil globule volume at hatching. Size and age at hatching covaried directly, but hatching later exacted a cost on yolk reserves. Significant female influences on these early life history traits of offspring were found. Initial egg yolk volume and oil globule volume at hatching contributed most to the rejection of the null hypothesis of no female effect. None of the early life history traits examined was correlated with female size, but female condition and lipid indices were directly correlated with average initial yolk volume.

Most individuals in marine fish populations die before feeding begins (Hewitt et al. 1985; Ware and Lambert 1985; McGurk 1986; Taggart and Leggett 1987a). Central to much of Reubin Lasker's work was the role of timing in survival during these early life stages. This was explicit in his early papers on temperature-dependent developmental rates (Lasker 1962, 1964; Zweifel and Lasker 1976) and became an implicit part of his "stable oceans hypothesis" (Lasker 1975,

1981, 1985), which postulates that coincidence in the timing of physical oceanographic conditions favoring food production and the timing of first feeding in fish larvae is critical to larval survival. Peterman and Bradford (1987) recently evaluated interannual variability in both the frequency of turbulence-generating winds and the survival of northern anchovy, *Engraulis mordax*, larvae and found an inverse relationship between these two events.

Temporal matching of resources and consumers is one of degree as timing of early life history (ELH) events varies even under constant conditions (Chambers and Leggett 1987, 1989; Chambers et al. 1988). Knowledge of the within-population variation in ELH traits is, therefore, crucial for estimating the number of larvae that establish feeding, and thus retain the potential for recruitment to the fishery. To Lasker's credit, his temperature-dependent development experiments in sardines, *Sardinops sagax*, were conducted on individual embryos isolated in incubation chambers in order "to assess their individual variability of development and growth" (Lasker 1964, p. 399). While variability in hatching age within and across temperatures is apparent from Lasker's plot of age at hatching of individual sardines versus temperature, the potential relevance of this variability to survival was not discussed further.

Variable provisioning of energy reserves to embryos is one of several mechanisms that could generate variability in size at hatching, in size and age at first feeding, in ability to withstand starvation, and, consequently, in survival to and during the critical switch from endogenous to exogenous nutrition. It is often reported that larger eggs produce larger larvae that subsist longer without food (e.g., Blaxter and Hempel 1963). Although this has become doctrine in reviews of marine fish early life histories (Blaxter 1969, 1988; Hempel 1979; Hunter 1981; Rothschild 1986), at least one of three caveats applies to work that has led to this generalization. 1) Eggs were grouped either by size (e.g., small vs.

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R. Christopher Chambers, William C. Leggett, Department of Biology, McGill University, 1205 Ave. Dr. Penfield, Montreal, Quebec, Canada H3A 1B1. and Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1C 5S7.

Joseph A. Brown, Department of Biology, McGill University, 1205 Ave. Dr. Penfield, Montreal, Quebec, Canada H3A 1B1; present address: Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1C 5S7.

large) or source (e.g., full-sibling groups) and the analysis of the influence of egg size on ELH traits was conducted among these groups. Correlations, when reported, were based on the average trait values in these groups. Such analyses obscure variation in and correlation between traits at the individual level—where natural selection acts. 2) Simple correlations were calculated. These may reflect the response of two traits to a third covarying trait rather than appraise the influence implied. 3) Egg size was confounded with other factors not explicitly considered (e.g., different source populations, seasons of spawning, years, and ages of females). The influence attributed to egg size is, therefore, equivocal. These are important limitations. The estimates of relationships between egg size and subsequent ELH traits so derived cannot be presumed to be of the same magnitude or statistical significance as those from within-individual observations. The conclusions of previous studies must be viewed as provisional demonstrations of associations of egg size with the ELH traits considered.

The extent to which relationships exist at the individual level between egg size, hatchling size, and prestarvation lifespan remains unanswered. In this paper we analyze such ELH trait covariation in capelin, *Mallotus villosus*. We address two questions: First, which pairs of ELH traits covary when evaluated at the individual level while (statistically) holding other traits constant? Of particular interest is which, if any, of these traits vary with egg quality. Second, is the pattern of ELH trait variation attributable to maternal influences?

METHODS

Spawning capelin were collected on 23 and 25 June 1988 at spawning sites in eastern Newfoundland, Canada (lat. 49°39'N, long. 52°41'W). These capelin were held in a 1,000 L flow-through tank at the Marine Science Research Laboratory, Logy Bay, Nfld. until 28 June when crosses were performed. Eggs from each of 10 females were fertilized with milt from one male. This provided a range of eggs sizes and created the potential for female effects on ELH traits of offspring while minimizing male influence.

Yolk diameters of 12–15 eggs per female were measured at 20–28 h postfertilization at a magnification of 40×. These embryos were in the blastula stage and their yolks remained approximately spherical. Embryos were then trans-

ferred individually to separate wells of 12-well tissue culture plates. These plates served to limit possible interaction among incubating embryos (e.g., bacterial growth on dead eggs) by keeping embryos at least 3.5 cm apart. In total, 142 eggs were housed in 12 plates, each containing 1 or 2 fertilized eggs per female. Each set of 4 plates was submerged to a depth of 10 cm in a separate plastic tank containing static seawater; thus, all embryos in a tank were exposed to the same seawater. This seawater was filtered to 1 μm, sterilized with ultraviolet light, and changed every 2 days to ensure sufficient levels of oxygen for the developing embryos. All three static seawater tanks were placed in a common water table maintained at $9.5 \pm 0.49^\circ\text{C}$ (mean \pm SD). At the late eyed stage, embryos were transferred individually to separate 125 mL glass jars containing 100 mL of filtered, sterilized seawater. Embryos in jars occupied the same location in the water table as they had before transfer. Fluorescent lamps in the laboratory were set to 18 h light, 6 h dark.

Embryos were inspected daily and their day of hatching recorded. Hatchlings were anaesthetized (MS-222, 25 mg/L), measured, revived, and returned to their jars. Total length (TL), length and height of yolk, and diameter of oil globule were measured. Larvae were inspected daily until their death, which was inferred if a larva did not respond to gentle tapping of its holding jar. Deformed hatchlings (3.5%) and those failing to escape the egg membrane (1.4%) were excluded from analyses.

Immediately after spawning, each female was measured (standard length, SL) and frozen. Subsequently, but within 2 months, females were thawed and somatic weights determined. Constant dry weights were achieved after oven drying at 60°C for 48 hours. These dried carcasses were ground and their lipids were extracted by flooding with diethyl ether and decanting (Dobush et al. 1985). Constant lean, dry weights were obtained after three cycles of lipid extraction. Indices of somatic condition (wet weight/SL) and lipid condition (extractable lipid weight/lean dry weight) were calculated for each female.

We analyzed six ELH traits: initial yolk volume (Y1), total length at hatching (TL), yolk volume at hatching (Y2), oil globule volume at hatching (G), age at hatching (H), and posthatching lifespan (L). Initial egg yolk and oil globule at hatching were approximately spherical and we estimated their volumes from their diameters.

Yolk at hatching was approximately a prolate spheroid and we estimated this volume from measurements of length and height of the yolk complement minus the volume of the oil globule it contained.

We used initial yolk volume rather than initial egg volume to quantify egg quality because it better represents the energy content of the egg. We chose posthatching lifespan over the more frequently used time to yolk-sac depletion or time to irreversible starvation ("point-of-no-return", Blaxter and Hempel (1963)), because the latter are much more difficult to determine accurately. We assumed a high correlation between these components of posthatching lifespan for unfed larvae. In support of this assumption we calculated a correlation of $r = 0.88$ ($P < 0.001$) between the interval from hatching to yolk-sac depletion and the interval from yolk-sac depletion to irreversible starvation, using data from 25 marine fish species presented by McGurk (1984).

We accounted for the potential influence of environmental (laboratory) variation on ELH measurements by using location of the embryos and larvae in the water table as a blocking variable. In addition, jars were inspected for hatchlings, and hatchlings were measured, in sequence by block. Block specification thus represented chance differences among the three static tanks; locational differences (which might include effects of slight temperature or light gradients on any of the ELH traits); and effects of unavoidable delays in measuring hatchlings. These delays were caused by the time required to measure the hatchlings. As an extreme example, 30 hours were required to measure all larvae hatching on the modal hatching day.

We employed a two-way randomized block experimental design with female parent as the treatment of interest (i.e., are there significant differences among females in the ELH traits of their offspring?). This design allowed us to determine both the female effect on ELH traits and the within-individual correlations between those traits. The design was unbalanced because the number of eggs used varied (12–15 per female) and some mortality occurred before hatching.

We treated the six traits as a multivariate response and analyzed these as a random-effects multivariate analysis of variance (MANOVA) with the general linear model

$$(Y_1, TL, Y_2, G, H, L) = \mu + \text{female} + \text{block} \\ + \text{female} \times \text{block} + \epsilon.$$

The six ELH traits of the response vector are defined above, μ is the overall mean, *female* codes for females 1–10, *block* codes for tank/location/monitoring order 1–3, and ϵ is random error from the model.

We calculated partial correlations between all pairs of traits from residuals remaining after the effects of block and the remaining four traits (considered for this procedure as covariables) had been statistically removed. We also calculated simple correlations between all pairs of traits based on average group values (common female parent), as has been the practice in previous work. These correlations were compared with the partial correlations to assess differences in estimated correlations based on the two approaches.

We evaluated the female effect on the trait vector with Wilk's lambda criterion (Timm 1975). After rejecting the null hypothesis of no female effect we gauged the contribution of each trait to this result. This was done by examining the magnitude and sign of the correlation between each trait mean and the standardized and adjusted discriminant function that maximized among-female differences (Timm 1975; Wilkinson 1975). We also compared the MANOVA findings with standard *F*-tests and with percentage of the total variance due to female source as calculated from univariate ANOVA's on each ELH trait. We assessed the influence of female condition on the ELH traits of her offspring by estimating the simple correlation between each family-average ELH trait and female size, condition index, and lipid index.

Prior to analysis we log transformed initial yolk volumes and yolk and oil globule volumes at hatching. MANOVA, discriminant analysis, and partial correlations were performed on SYSTAT (Wilkinson 1988) and the variance components were estimated using SAS (SAS Institute, Inc. 1987).

RESULTS

Survival to hatch was over 98%. The quantity of variation in initial yolk volume, age at hatching, and age at death (C.V. (= SD/mean) = 0.15, 0.03, and 0.24, respectively) was comparable to values reported for other species (cf. Chambers et al. 1988). Length, yolk, and oil globule volume at hatching were more variable than expected (C.V. = 0.08, 0.98, and 1.44) owing partly to their rapid change during the 1–2 days after hatching when measurements were taken. By

measuring larvae in block sequence we reduced this variance due to ontogeny in our analyses of correlations and female effects.

Correlations Between ELH Traits

There were seven significant partial correlations between the ELH traits (Fig. 1). These correlations measure whether or not a change in one trait is associated with a change in the other while holding the remaining (four) traits constant. Size, yolk reserves, and age at hatching all covaried directly with initial yolk volume. Hatchling size increased with age at hatching, but yolk reserves at hatching were negatively related to age at hatching. Yolk and oil globule volume at hatching covaried directly. Oil globule volume at hatching was the only trait that covaried with posthatching lifespan; all else equal, larvae with larger oil globules lived longer.

It is important to note the trait pairs that failed to show associations. Oil globule volume at hatching did not vary with initial yolk volume. Length at hatching was independent of yolk or oil globule volume at hatching. Furthermore, posthatching lifespan was not related to initial

yolk volume, length, age, nor yolk volume at hatching.

The correlations between ELH traits based on family averages differed from the partial correlations calculated within individuals (Table 1). The sample size of family groups was small ($n = 10$), hence, caution is required when assessing the pattern that emerged. First, there were no neg-

TABLE 1.—Simple correlations between early life history traits of capelin, *Mallotus villosus*, calculated from family averages (df = 8). * $P < 0.05$, ** $P < 0.01$.

Trait	(1)	(2)	(3)	(4)	(5)	(6)
1) Egg yolk volume	1.00	0.55	0.53	0.36	0.43	0.59
2) Length at hatching		1.00	0.58	0.45	0.32	0.42
3) Yolk volume at hatching			1.00	0.80**	0.08	0.54
4) Oil volume at hatching				1.00	0.13	0.68*
5) Age at hatching					1.00	0.57
6) Posthatching lifespan						1.00

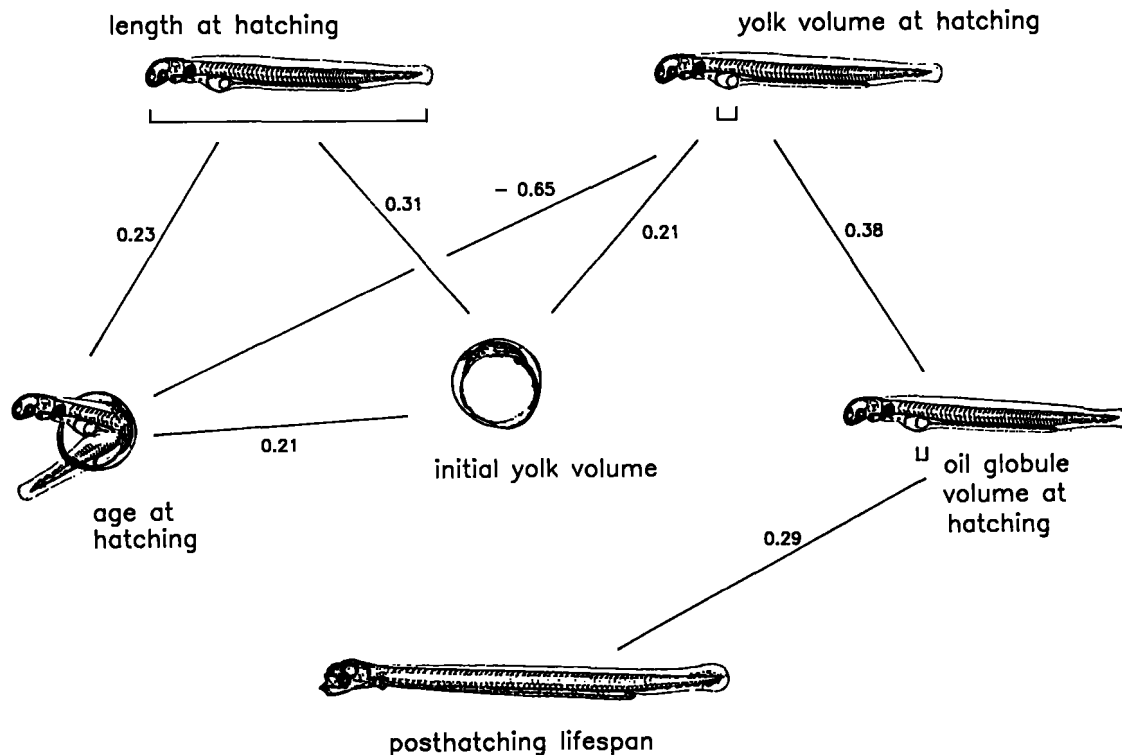


FIGURE 1.—Early life history traits of capelin, *Mallotus villosus*, subjected to analyses and the within-individual partial correlations between traits. Only significant correlations are shown ($P < 0.05$, $df = 126$).

ative correlations between traits. Second, while the correlation between yolk volume and oil globule volume at hatching and between oil globule volume and posthatching lifespan remained significant ($P < 0.05$), the magnitude of the correlations between posthatching lifespan and all other ELH traits approached significance. This pattern of correlations derived from family averages suggests that offspring from eggs with large yolk volumes are larger at hatching, hatch later, have larger yolk reserves and oil globules at hatching, and live longer than do offspring of females producing eggs with less yolk. This pattern is consistent with results of most previous reports based on average trait values.

Female Effects on ELH Traits

Initial egg yolk volume varied among females (Fig. 2). Female identity significantly influenced the set of six ELH traits (Wilk's $\lambda = 0.0001$, $F = 6.1$, $df = 54, 70$, $P < 0.0001$). Initial yolk volume and oil globule volume at hatching were the predominant traits contributing to among-female differences (Table 2). Univariate ANOVAs supported the MANOVA result; all traits varied significantly among females and the percentage of variance due to female was greatest for initial yolk and oil globule volume at hatching (Table 2). None of the family-averaged ELH traits was significantly correlated with female size. However, the average initial yolk volume of the egg

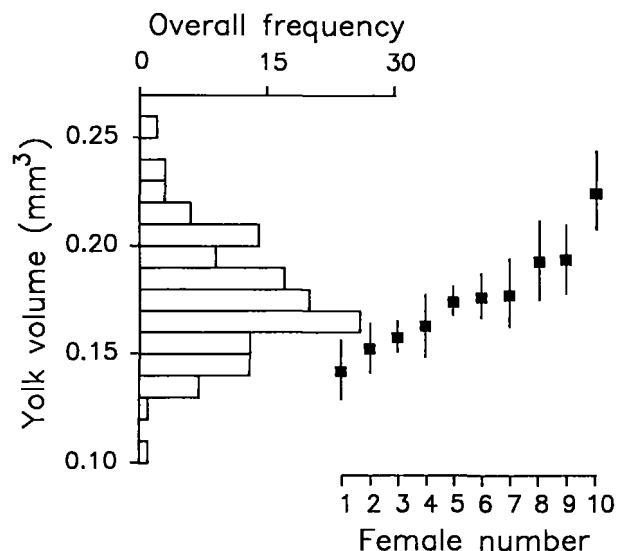


FIGURE 2.—Overall frequency distribution of initial egg yolk volumes and partitioned variation (means \pm 2 SD) of yolk volumes by female for capelin, *Mallotus villosus*. A total of 142 eggs were measured from 10 females. Females are ranked by average yolk volumes of their eggs.

was directly related to condition and lipid indices of the female (Table 2).

DISCUSSION

Correlations Between ELH Traits

Our observations of positive within-individual relationships between initial yolk volume and

TABLE 2.—Contributions of early life history traits (ELH) of capelin, *Mallotus villosus*, to the rejection of the null hypothesis of no female effect, and correlations between these traits and properties of female parents used. (1) Correlations between ELH trait means and the standardized discriminant function that maximized among female differences. (2) Percentage of total variance in each ELH trait due to female effect. Correlation between ELH trait means and female size (3), female condition index (4), and female lipid index (5). The magnitude of the correlation between ELH traits and the discriminant function reflects the contribution of a trait to rejection of the multivariate null hypothesis of no female effect. The eigenvalue associated with this discriminant function accounted for >77% of the variation among the ELH traits. * $P < 0.05$, ** $P < 0.01$.

	Egg yole volume	Length at hatching	Yolk volume hatching	Oil volume hatching	Age at hatching	Posthatch lifespan
1) Discriminant function	0.43	0.15	0.11	0.35	0.10	0.21
2) % variance	71.30	17.21	2.91	66.67	12.01	24.39
3) Female size						
SL	0.36	0.00	0.35	0.30	-0.41	-0.05
Wet somatic weight	0.61	0.18	0.53	0.43	-0.22	0.24
4) Female condition	0.65*	0.22	0.57	0.46	-0.17	0.29
5) Female lipid	0.85**	0.44	0.43	0.31	0.34	0.55

hatchling length, and between initial yolk volume and yolk volume at hatching agree with most previous reports based on grouped data (reviewed in Blaxter 1988). The positive relationship between initial yolk volume and age at hatching differs from the generally reported pattern of no association. Moreover, the increase in length with age at hatching we observed is contrary to that reported by Bengtson et al. (1987) who analyzed daily hatching cohorts within families. Hatching late, however, appears to occur at the expense of yolk reserves (Fig. 1). This negative relationship was not present in the correlations based on family averages (Table 1).

Neither initial yolk volume, length at hatching, nor yolk volume at hatching was related to posthatching lifespan when evaluated within individuals. This contrasts both with our correlations based on family averages and with previous generalizations (from group averages) that large initial egg size leads to hatchlings that survive longer in the absence of food (Blaxter 1988). The only association with posthatching lifespan that we detected was the direct influence of oil globule volume at hatching. Our data indicate that if all else were held constant, an increase in oil globule volume delays the time to starvation of individual larvae. This prolonged posthatching lifespan should increase the chances of encountering suitable food before irreversible starvation and, thus, the chances of survival. Lipids, whether aggregated in oil globules or dispersed throughout the yolk, appear to serve primarily as energy reserves (Blaxter 1969). Conservation of oil globules (relative to yolk) has been reported for species that have oil globules in their yolk sacs (e.g., May 1971; Bagarinao 1986) although oil globules may also serve to regulate buoyancy.

A variety of evidence argues for advantages of large size at hatching (a positive correlate of initial yolk volume). Larger larvae have greater mouth widths (Shirota 1970), have greater success in establishing feeding (Knutson and Tilseth 1985), are more effective predators (Blaxter and Staines 1970; Hunter 1981), consume a greater range of prey sizes (Hunter 1981), and have higher survival when predators are absent (Rosenberg and Haugen 1982; Henrich 1988) or present (Lilleland Lasker 1971; Bailey 1984; Folkvord and Hunter 1986; Purcell et al. 1987). Although many of these studies compared larvae of two or more groups that differed in age as well as size, the results are likely to apply to the finer size differences among contemporaries. Mortal-

ity has also been reported to be size specific and to be concentrated early in the life cycle in natural populations (Crecco et al. 1983; Smith 1985; Rice et al. 1987; Savoy and Crecco 1988).

The cost of producing large eggs is frequently evaluated under the assumption of a trade-off between egg size and egg number (Svardson 1949; Smith and Fretwell 1974). This assumption has led to optimality derivations for balances between size and number of eggs under given conditions. Observed patterns of size and number of eggs among species, populations, or reproductive modes are then evaluated in light of the predicted optima (Ware 1975; Sargent et al. 1987; Tanasichuk and Ware (1987)). The correlations between ELH traits we observed suggest that egg size expresses reciprocity with other ELH traits to which optimality methods may be applied. For example, a corollary of the direct relationship between length and age at hatching in capelin is that an inverse relationship exists between length at and developmental rate to hatching (the reciprocal of age at hatching). If daily mortality rates are greater in the embryonic than in the larval period, an extended embryonic period is seen as a cost of being large at hatching.

This optimality approach is inherently deterministic. It does not explicitly admit within-population and within-female variation in egg size (Fig. 2) and in other ELH traits we observed. Rather, this variation is viewed as failure to achieve the optimal trait value or combination of trait values. In contrast, we consider trait variation itself to be adaptive. For capelin, the emergence of larvae from their intertidal incubation sites into the nearshore water is linked to the episodic occurrence of relatively warm water and nearshore turbulence, generated by onshore winds and coastal water mass exchanges (Frank and Leggett 1981a, 1983; Taggart and Leggett 1987b). The attainment of a developmental stage from which an embryo can be induced to hatch (e.g., through a sudden rise in temperature and/or turbulence) or its nutritional state at the time of emergence, if previously hatched (Frank and Leggett 1982), are important determinants of survival during early pelagic life. However, the intertidal incubation zone is variable for capelin in three fundamental ways. First, temperature directly influences developmental rates of embryos. Local temperatures in the intertidal substrate oscillate up to 10°C (Frank and Leggett 1981b) with tidal cycle. Thus, there are large microsite differences in

temperatures and developmental rates. Second, the small particle substrate to which eggs adhere is motile, mixing in all three dimensions with wave action. Third, onshore winds promote hatching and/or release of larvae from these beaches, yet their frequency is highly variable within and between years (Frank and Leggett 1981a, 1983; Leggett et al. 1984; Taggart and Leggett 1987b). From the maternal perspective, the time of the transition of her offspring from beach residence to the pelagic mode is unpredictable owing to these three sources of variation. It appears unlikely that a single optimal solution exists for developmental rate, size at hatching, or energy reserves. Additional examples of intrapopulation and intraclutch variation in early life history traits, and of theoretical bases for the maintenance of this variation in unpredictable environments, is provided in Capinera (1979) and Kaplan and Cooper (1984).

Female Effects on ELH Traits

Variation in egg quality is a sum of genetic and environmental factors. We have no evidence that egg size is heritable in capelin. We did not detect a male effect or heritable variation in size at hatching in another study involving 11 male capelin each mated with 3 females (Chambers and Leggett unpubl. data), yet there, as here, significant differences among females were evident in both initial egg and hatchling sizes. Our determination of a direct relationship between condition and lipid indices of females, and initial egg yolk volume probably reflects a predominant environmental component to the observed variation in egg quality (yolk volume) and its correlates. The degree of influence from environmental sources of maternal effects on ELH traits probably depends largely on conditions experienced by a female during the time that energy is being acquired and converted towards oogenesis, particularly her feeding rate (Hislop et al. 1978) and encountered temperatures (Tanasichuk and Ware 1987). If so, these largely non-genetic maternal effects have the potential to modulate the expression of critical ELH traits and modify the survival pattern that would otherwise be exhibited if the initial provisioning of yolk reserves were at par throughout the population. Well-endowed individuals could thus be buffered against selection in the yolk-dependent period with, perhaps, residual effects later in larval life. The inverse correlation between size of mother and age at smoltification of her

progeny in sockeye salmon, *Oncorhynchus nerka*, as reported by Bradford and Peterman (1987) may be such a residual effect.

Covariation Within Individuals and Variation Within Groups

Relationships we observed between ELH traits clearly show that simple correlations based on group data may support, but may also be inconsistent with inferences drawn from analyses at the individual level. Only estimates of variation and correlations between traits that are based on individual-level observations are grounded on the same scale that natural selection primarily acts (Sober 1984). Caution must be exercised when extrapolating from group differences or correlations based on averages to influences of one trait on another, to potential advantages conferred on individuals, to dynamics of populations, or to evolution of life histories.

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