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THE GENETIC BASIS OF LIFE-HISTORY CHARACTERS IN A POLYCHAETE EXHIBITING PLANKTOTROPHY AND LECITHOTROPHY

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Abstract.—The polychaete *Streblospio benedicti* is unusual in that several field populations consist of individuals that exhibit either planktotrophic or lecithotrophic larval development. Planktotrophy in this species involves production of many small ova that develop into feeding larvae with a two- to three-week planktonic period. Lecithotrophy involves production of fewer, larger ova that develop into nonfeeding larvae that are brooded longer and have a brief planktonic stage. Reciprocal matings were performed to investigate genetic variance components and the correlation structure of life-history traits associated with planktotrophy and lecithotrophy. Our objective was to better understand persistence of this developmental dichotomy in *Streblospio benedicti*, and among marine invertebrates in general. Substantial additive genetic variation (75–98% of total) was detected for the following characters at first reproduction: female length; position of the first gametogenic setiger and first brood pouch; ovum diameter; three traits related to fecundity (numbers of ova per ovary, larvae per brood pouch, and larvae per brood); median larval planktonic period and the presence of larval swimming setae; but not for total number of brood pouches; larval length; larval feeding; and larval survivorship. Based on the unusual geographic distribution of development modes in this species, we hypothesize that the developmental traits have evolved in allopatry and have only recently come into contact in North Carolina. The high additive contribution to variance observed for many traits may be inflated due to (a) nonrandom breeding in nature, and (b) examination of only one component of an age-structured population at one time. Nuclear interaction variance and maternal variance accounted for 84% of the total variation in larval survivorship. This observation supports other empirical studies and theoretical predictions that nonadditive components of variance will increase in importance in individual traits that are most closely tied to fitness. A network of life-history trait correlations was observed that defines distinct planktotrophic and lecithotrophic trait complexes. Negative genetic correlations were present between fecundity and egg size, between fecundity and position of the first gametes, and between larval survivorship and median planktonic period. Positive genetic correlations were detected between fecundity and female size at first reproduction and between planktonic period and the presence of swimming setae. Intergenerational product-moment correlations were negative for larval length and fecundity, planktonic period and egg size, female size and larval survivorship, and fecundity and larval survivorship. If the genetic correlation structure observed in the laboratory persists in the field, it may constrain responses of individual characters to directional selection, and indirectly perpetuate the dichotomies associated with planktotrophy and lecithotrophy.

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The traits that define an organism's life history are believed to have coevolved under the influence of natural selection. Efforts to understand this process now involve an interfacing of life-history theory and quantitative genetics. Important questions include the extent to which phenotypic variation in life-history traits is heritable, the extent to which covarying traits are genetically correlated and thus not free to evolve independently, and the interaction of these covariances with the environment (Istock, 1983; Cade, 1984; Loeschcke, 1987; Stearns, 1989*a*, 1989*b*). Individual life-history traits appear to be governed by widespread pleiotropic gene effects, such that the remaining variation among clusters of life-history traits is based on the same individual allelic effects. To date, evidence for these effects has come largely from insects or other terrestrial groups (Dingle and Hegmann, 1982; Loeschcke, 1987).

An unusually dramatic clustering of life-history traits is observed in marine invertebrates. A major dichotomy occurs in development of benthic marine organisms between planktotrophy, in which larvae feed in the water column prior to settlement, and lecithotrophy, in which larvae develop in the benthos or water, but do not feed (see Strathmann, 1985 for a review). This nutritional dichotomy is accompanied by large variations in egg size, fecundity, duration of the planktonic phase, and numerous other

life-history traits (Thorson, 1950; reviewed in Jablonski and Lutz, 1983; Grahame and Branch, 1985). Some of the same tradeoffs believed to be associated with planktotrophy and lecithotrophy, for example, between egg number and egg size, or between fecundity and survivorship, are common in many marine (Christiansen and Fenchel, 1979; Parker and Begon, 1986), freshwater (Duellman and Trueb, 1986), and terrestrial taxa (Harper, 1977; Capinera 1979; Price, 1984). However, the dichotomy between feeding and nonfeeding free-living larval stages is uncommon in most terrestrial and freshwater systems (Strathmann, 1990), except among some anurans (Duellman and Trueb, 1986).

Among certain marine invertebrates (e.g., opisthobranchs, asteroids, polychaetes), it is common for closely related species to exhibit widely varying developmental patterns (Grahame and Branch, 1985). Geographic clines in life-history traits (e.g., egg size) have been documented within a single species (Patel and Crisp, 1960; Lonsdale and Levinton, 1985, 1986). In a few instances single species have been shown to exhibit both feeding and nonfeeding, or planktonic and nonplanktonic larval development (reviewed in Hoagland and Robertson, 1988; Bouchet 1989). This phenomenon was termed poecilogony by Giard (1905).

Much attention to alternative life-history tactics in the marine realm focuses on their far-reaching ecological and evolutionary implications. Planktotrophy and lecithotrophy seem to have little bearing on energy allocation or energetic efficiencies, but the consequences for demographic patterns and dispersal potential are considerable (Strathmann, 1985). Development modes can influence population-level patterns of recruitment, growth and seasonality (Thorson, 1950; Strathmann et al., 1981; Levin, 1984*a*; Chernoff, 1985; Perron, 1986; Levin et al., 1987; Levin and Huggett, 1990), extent of gene flow and differentiation (Burton, 1983; Burton and Swisher, 1984), and on larger time and space scales, geographic ranges, rates of speciation and extinction (Jablonski and Lutz, 1983).

Though a genetic basis is assumed to underlie the life-history differences associated with planktotrophy and lecithotrophy, little is known about the genetic structure of larval development mode and related life-history characters in any marine invertebrate. Trait covariances, which limit the rates and direction of evolution, and form the basis of life-history tradeoffs (Stearns, 1989*a*), have yet to be explored for the trait clusters associated with planktotrophy and lecithotrophy.

Within the Polychaeta, at least five species in the family Spionidae have been reported to produce both planktotrophic and lecithotrophic or direct-developing larvae (Rasmussen, 1973; Simon, 1968; Blake, 1969; Blake and Kudenov, 1981; Levin, 1984*b*; Zajac, 1985; Petch, 1988). Only in *Streblospio benedicti* Webster from North America are eggs of two distinct sizes produced. These egg types are associated with differences in fecundity and in larval trophic mode, size, morphology, planktonic period and survivorship (Levin, 1984*b*). Some females produce several hundred small (70 μm) ova per brood. Larvae developing from small eggs are brooded by the female in dorsal pouches and are released into the plankton at a three- to five-setiger stage (200–250 μm). These larvae are planktotrophic; they are capable of feeding shortly after release and may remain in the water for one to six weeks prior to settlement. Other females produce smaller numbers (10–60/brood) of larger (100–200 μm) ova that develop as lecithotrophic larvae in dorsal pouches to a 12-setiger (600 μm) stage. At the time of release they are competent to settle, but may remain planktonic for a week or more without feeding (Levin, 1984*b*; Levin and Creed, 1986). Total development time and size at settlement are nearly identical for both larval forms; lecithotrophic larvae spend longer in brood pouches and planktotrophic larvae spend longer in the water column. For both morphs, an average of six broods are produced in sequence during a female's lifetime, and development within a single brood is synchronous (Levin et al., 1987).

Previous studies of planktotrophic and lecithotrophic strains of *S. benedicti* from Bogue Sound, North Carolina have shown development mode and associated differences in egg size and fecundity to be independent of seasonal changes in temperature, day length and food availability (Levin and

TABLE 1. Experimental design employed in the study of *S. benedicti* reproductive and developmental traits. Each cell had four to six replicates involving different individuals. Body size and reproductive traits were examined for females mated in this design. Larval characters were examined for the offspring produced by the matings.

	Male			
Female	LL	LP	PL	PP
LL	LL × LL	LL × LP	LL × PL	LL × PP
LP	LP × LL	LP × LP	LP × PL	LP × PP
PL	PL × LL	PL × LP	PL × PL	PL × PP
PP	PP × LL	PP × LP	PP × PL	PP × PP

Creed, 1986; Chu and Levin, 1989). In this paper we examine the genetic basis of life-history traits in this same North Carolina population, where individuals of both reproductive types cooccur, interbreed and produce viable offspring in the field (Levin and Huggett, 1990). A reciprocal mating design was employed to identify the genetic components of phenotypic variance in the developmental polymorphism exhibited by *S. benedicti* and to examine the correlation structure of these components. Our goal was to describe the variation that permits evolution of developmental traits, in an effort to understand how the developmental dichotomy of planktotrophy and lecithotrophy might be maintained in marine invertebrates.

MATERIALS AND METHODS

Experimental Design and Analysis

Lecithotrophic (L) and planktotrophic (P) individuals were selected from the field and used to establish lines representing the two natural population strains we wished to study. Initially, a 2 × 2 reciprocal mating with parental lines L and P was conducted. From the 2 × 2 reciprocal crosses, four types of offspring (LL, LP, PL, and PP) were produced. A 4 × 4 reciprocal mating design was then employed using these four genetic entries (LL, LP, PL, and PP) (Table 1). Each mating type (cross) in the 2 × 2 design had four replications, each involving different individuals (four to six females and four to six males per replication). In the 4 × 4 mating design there was one replication (16 cell means) involving the offspring of four to six females. Size and reproductive characters were examined in the maternal parents used in the 4 × 4 crosses. Larval characters associated with the planktotrophic and lecithotrophic lines were examined for 30–50 of the offspring produced by each replicate cross from the 4 × 4 reciprocal mating design (~200 larvae/mating type) (Table 1). All crosses were carried out by mating individuals selected from parental lines at random.

The diallele cross is an experimental design in which all possible crosses are made among a collection of genetic lines (Sprague and Tatum, 1942; Griffing, 1956; Hinkelmann, 1977), and can be used to obtain information about various types of gene effects for the reference population (Hinkelmann, 1977). Cockerham and Weir's (1977) biomodel of diallele crosses provides a method for estimating maternal and paternal variance components as well as variance components for nuclear genetic effects. If other higher-order interaction effects are not included in the model, the biomodel for the mean observation of *adult traits* in the k-th replicate of the mating between line i and line j (in the 2 × 2 mating design) can be expressed as:

$$y_{ijk} = \mu + n_i + n_j + t_{ij} + m_i + p_j + \epsilon_{ijk} \quad (1)$$

where:

y_{ijk} is the average phenotypic value of individuals from line i × line j in replication k;
μ is the population mean;
n_i is the additive effect of nuclear contribution of maternal line i, $n_i \sim (0, \sigma^2_n)$;
n_j is the additive effect of nuclear contribution of paternal line j, $n_j \sim (0, \sigma^2_n)$;
t_{ij} is the interaction effect of nuclear contributions of line i × line j, $t_{ij} = t_{ji} \sim (0, \sigma^2_t)$;
m_i is the maternal effect of line i, $m_i \sim (0, \sigma^2_m)$;
p_j is the paternal effect of line j, $p_j \sim (0, \sigma^2_p)$;
ϵ_{ijk} is the residual effect, $\epsilon_{ijk} \sim (0, \sigma^2_e)$.

All the effects except the constant μ are independent random effects. The nuclear additive variance (σ^2_n) provides some indication of the heritable component of a particular trait (see discussion below). The interaction variance (σ^2_t) includes variation for dominance, or epistatic effects, or both, and is nuclear in origin. The biomodel assumes there is no correlation between nuclear effects and extranuclear effects. Simulations carried out by Zhu (1989) indicate that this assumption will not cause apparent bias if real correlations exist between nuclear and extranuclear effects. The maternal effects consist mainly of maternal genetic effects, or cytoplasmic effects, or both. The paternal effects are mainly of paternal genetic effects. The maternal (or paternal) common environmental effects were eliminated by the experimental randomization for the crosses and replications. Female size and reproductive characters were analyzed by this biomodel. In this experiment, i, j = 1 represents the line L; i, j = 2 represents the line P; and k = 1, 2, 3, 4 for the four different paternal matings as replications.

An extended biomodel is defined as follows for analysis of the traits of *larvae* produced in the 4 × 4 mating design (Table 1),

$$\begin{aligned} y_{ii'\cdot jj'} = \mu &+ 0.5n_i + 0.5n_{i'} + 0.5n_j \\ &+ 0.5n_{j'} + 0.25t_{ij} + 0.25t_{ij'} \\ &+ 0.25t_{i'j} + 0.25t_{i'j'} + m_{ii'} \\ &+ p_{jj'} + \text{error} \end{aligned} \quad (2)$$

where:

$y_{ii'\cdot jj'}$ is the average phenotypic value of 4 ~ 6 replicates from female ii′ × male jj′;
μ is the population mean;
n_i and $n_{i'}$ are the additive effects of nuclear contribution of maternal entry ii′;
n_j and $n_{j'}$ are the additive effects of nuclear contribution of paternal entry jj′;
t_{ij} is the interaction effect of nuclear contributions from line i × line j, etc.;
$m_{ii'}$ is the maternal genetic effect of entry ii′;
$p_{jj'}$ is the paternal genetic effect of entry jj′; and i, i′, j, j′ = 1 for the contribution from line L or 2 for the contribution from line P.

Variance components were estimated by the MINQUE method (Rao, 1970, 1971) with all the prior values set to one as suggested by Giesbrecht (1985). A MINQUE procedure (J. Zhu and B. Weir, pers. comm.) was used for estimating covariance components between different traits with equal design matrices. The sampling variances of estimated genetic parameters were obtained by the jackknife procedure (Miller, 1974; Efron, 1982). Each mating type (or cell) in Table 1 was the resampling unit for the jackknife procedure. The *t*-test was conducted for testing the null hypotheses of zero variance or covariance components.

The *adult* female reproductive traits were first analyzed by the full biomodel (1). Because both the maternal and paternal variance components were not significant, a reduced model including nuclear effects and maternal effects was used for reestimating. When the maternal variance component was still nonsignificant for all the adult traits, the following reduced model including only nuclear effects was used.

$$Y_{ijk} = \mu + n_i + n_j + t_{ij} + \epsilon_{ijk}. \quad (3)$$

When the *larval* traits were analyzed by the full model (2) with no significant paternal effects, the following reduced model was constructed for analyzing maternal and nuclear genetic effects,

$$\begin{aligned} y_{ii'\cdot jj'} = \mu &+ 0.5n_i + 0.5n_{i'} + 0.5n_j + 0.5n_{j'} \\ &+ 0.25t_{ij} + 0.25t_{ij'} + 0.25t_{i'j} \\ &+ 0.25t_{i'j'} + m_{ii'} + \text{error}. \end{aligned} \quad (4)$$

Covariance components and correlations were estimated for *adult* traits by the reduced model (3) and for *larval* traits by the reduced model (4). Because adult traits and larval traits did not share the same mating design, only Pearson's product-moment correlation coefficients were estimated between adult and larval traits. Significance of these correlations was tested by a *z*-test with Fisher's z′ transformation. Variance and covariance analyses were carried out on cell mean data with a balanced design for all the adult traits and all the larval traits except for larval feeding. There were no larval feeding data for cross LL × PP due to poor survivorship of experimental animals; therefore, variance components for the larval feeding trait were estimated based on the unbalanced data. The covariance components and correlations between larval feeding and all the other traits were also

based on unbalanced data using the MINQUE method.

In this experiment, cross i × i (or ii′ × ii′) is constructed by random mating among different individuals within the same polychaete line (or genetic entry). Thus there is no real full-sib family in this experiment. By the same mating design, all the crosses sharing the same type of maternal or paternal line (or entry) are not the half-sib families. The variance components of the mating design cannot be translated into covariances of relatives. Hence, actual estimates of genetic variance components are not available by this analysis. By the biomodel (1) the total variance of individuals among lines is $\text{var}(y_{ijk}) = V_y = 4\sigma^2_n + \sigma^2_t + \sigma^2_m + \sigma^2_p + \sigma^2_e$. For a real diallele cross mating with noninbred lines ($F = 0$), $4\sigma^2_n$ is an estimator of the additive genetic variance component, and $4\sigma^2_n/V_y$ is an estimator of heritability. In this study, because all crosses were obtained by mating unrelated individuals, we used $4\sigma^2_n/V_y$ as an indicator for proportion of nuclear additive contribution to the total variation. If interbreeding of the experimental lines is not random in nature, our estimates could be inflated.

Data were analyzed untransformed with one exception. The lengths of larvae produced in the 4 × 4 reciprocal crosses were evaluated as a function of larval stage by taking deviations (residuals) from a length-stage regression determined for all larvae (adjusted $R^2 = 0.46$, $P < 0.01$). The labor-intensive nature of the data collection limited us to a small mating design and lowered the probability of detecting significant genetic variation and correlations. For this reason we adopted significance levels including $\alpha = 0.10$, prior to analyzing the results. We recognized this increased the probability of Type I error, but believed this was justified to provide insight regarding potential significance of the estimates.

Culture Methods and Data Collection

Parental worms used in the initial 2 × 2 mating design were settled in the laboratory from larval stages and then were reared in isolation until maturity. Planktotrophic individuals used for the initial reciprocal mating design were offspring of individuals that had been collected from a *Spartina* marsh at Tar Landing in Bogue Sound, NC during Oct. 1984 and reared in the laboratory at 20°C, 35‰ S for four months. Lecithotrophic individuals used for the initial mating were offspring of parents that were either 1) collected about 0.5 km away from Tar Landing during Jan. 1985; or 2) taken from laboratory cultures descended (approximately three generations removed) from October 1983 field collections (0.1 km from Tar Landing) in Bogue Sound.

Individuals raised for use in 4 × 4 crosses (Table 1) were reared according to methods in Levin and Creed (1986). Each worm was isolated approximately one month after settlement (prior to maturity) and then reared in a Petri dish (60 × 15 mm) with sediment and seawater at 20°C until used in crosses. All experimental animals were maintained at LD 12:12 following larval release.

Crosses were made by placing virgin females in a Petri dish with a single male. Each dish contained approximately 6 ml of sediment-seawater slurry (as described above), 15 ml of filtered seawater (30–34‰ S) and an equal volume of air. Once each week the dishes were cleaned by sieving contents though a 300-μm screen, and females were evaluated for reproductive status.

All data were collected for a female's first reproductive event. When the first brood appeared, females were measured for length (mm), number of setigers (polychaete segments bearing setae), position of the first gametogenic setiger, ovum diameter, number of ova/ovary, position and number of brood pouches, number of larvae/brood pouch, and number of larvae/brood. Brooded offspring were released by prodding female brood pouches. Upon release, several larvae from each brood were photographed and examined under the compound microscope for the presence of swimming setae, length (μm), and number of setigers, and then discarded. Larvae within brood pouches develop synchronously; thus, length and developmental stage are nearly identical for larvae from the same brood. Larvae produced in the 2 × 2 mating design were reared in batch culture (by brood) in large crystallizing dishes as described above.

Following release from the female brood pouches, larvae from the 4 × 4 reciprocal crosses (up to 50 per brood) were placed individually in test tubes (13 mm diameter × 100 mm) containing 4.5 ml of filtered seawater and 0.5 ml of sediment on the test tube bottom. Larvae were reared at 20°C and 34‰ S, and were fed mixed phytoplankton cultures. Three times each week larvae were checked visually for evidence of settlement, determined by the presence of a small sediment tube on the test tube bottom. The method and interval for monitoring settlement timing prevented an accurate estimate of size at settlement. Minimum and maximum planktonic periods were the numbers of days after release when the first and last larva in each brood settled. Median planktonic period was estimated to be the time in days (from release) when 50% of the total larvae settling in each brood had done so. Larval survivorship was determined for each brood as the proportion of the 30 to 50 larvae placed in test tubes shortly after release that eventually settled.

For larvae produced in the 4 × 4 crosses, 10 to 15 individuals from each brood were reared in the absence of sediment but were provided with phytoplankton to determine larval trophic mode. These were checked several times each week for the presence of food in their guts, to provide indication of feeding activity. Swimming setae and larval feeding were recorded as present or absent. Our previous surveys suggested that all larvae within a brood exhibit the same trophic mode and setal structures. Because evaluations of larval feeding and setation precluded other measurements such as larval survivorship or planktonic period, we were unable to evaluate larval feeding for all individuals within a brood. If several larvae within a brood were observed to contain phytoplankton within their guts, the replicate cross was defined as producing feeding larvae. Similarly, the presence of several larvae with swimming setae defined the brood as having these structures.

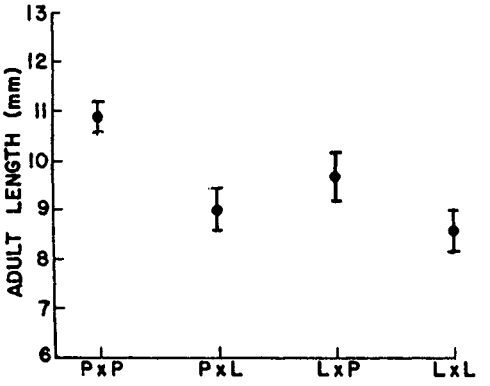
Results

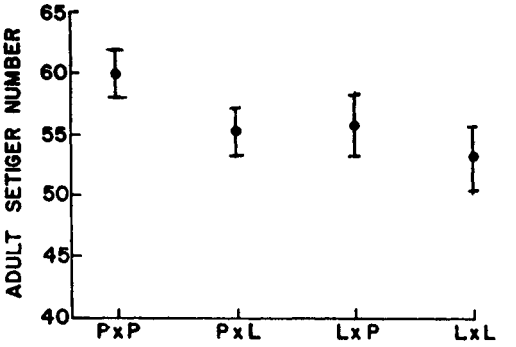
Adult Female Reproductive Characters

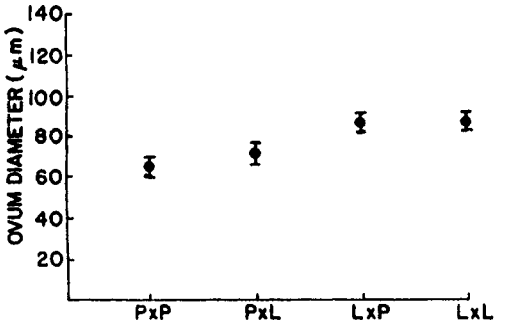
For five of the traits examined, the two measures of female size and the three fecundity-related traits, phenotypic values were highest in females from among the planktotrophic matings (P × P), smallest in females from among the lecithotrophic matings (L × L), and intermediate and similar in the P × L and L × P females (Fig. 1), where the first letter denotes the female line, the second the male line. The reverse was true for the positions of the first gametogenic setiger and the first brood pouch. In the case of ovum diameter, average values were lower in females produced by P × P and P × L crosses and higher and identical in females produced by L × P and L × L crosses (Fig. 1).

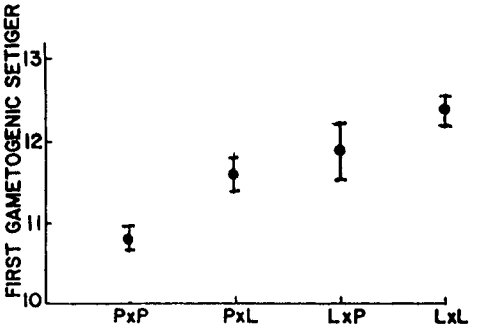
Significant nuclear additive variance was detected for a number of female traits at first reproduction, including body length, positions of the first gametogenic setiger and the first brood pouch, egg diameter, and three measures of fecundity. Only setiger number and number of paired brood pouches did not exhibit significant nuclear additive variance (Table 2). Where significant nuclear additive variance components were detected, they accounted for relatively large fractions of total phenotypic variance, indicating high heritability: 86% for length, 94% and 88% for positions of the first gametogenic setiger and first brood pouch, respectively, 75% for ovum diameter, and 90%, 93%, and 91% for the three fecundity measures: numbers of ova per ovary, larvae per brood pouch, and larvae per brood, respectively. The jackknife estimates for nuclear additive contribution to total variation ($4\sigma^2_n/V_y$) were significant and high (0.70 to 0.93) for all traits (Table 2). Nuclear interaction variance was significant for the number of ova produced per ovary (Table 2), where it accounted for 6.2% of the phenotypic variance. No significant paternal or maternal variance components were detected for female reproductive traits, indicating no extranuclear contributions from the mother or father.

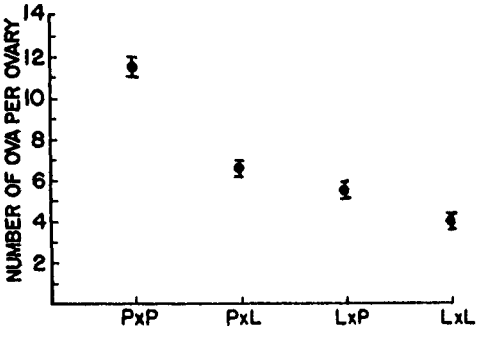
Several of the adult female reproductive traits examined exhibited strong nuclear additive correlations with one another (Table 3). Nuclear additive correlations were positive and near 1.00 among the three fecundity measures (Table 3). Nuclear additive correlations were negative and relatively high ($r_n < -0.98$) between the three mea-

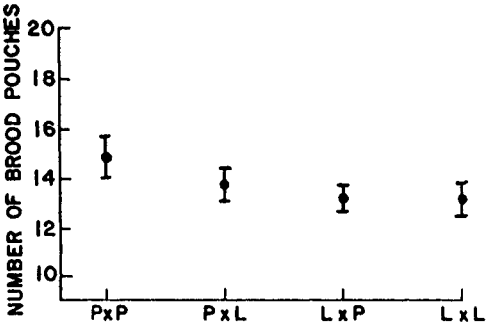

ADULT LENGTH (mm)
13
12
11
10
9
8
7
6
PxP
PxL
LxP
LxL

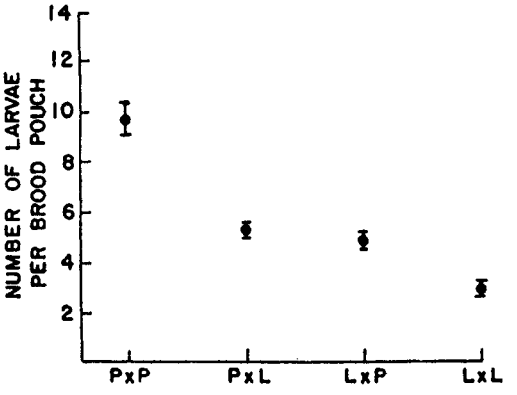

ADULT SETIGER NUMBER
65
60
55
50
45
40
PxP
PxL
LxP
LxL


OVUM DIAMETER (μm)
140
120
100
80
60
40
20
PxP
PxL
LxP
LxL


FIRST GAMETOGENIC SETIGER
13
12
11
10
PxP
PxL
LxP
LxL


NUMBER OF OVA PER OVARY
14
12
10
8
6
4
2
PxP
PxL
LxP
LxL


NUMBER OF BROOD POUCHES
20
18
16
14
12
10
PxP
PxL
LxP
LxL


NUMBER OF LARVAE PER BROOD POUCH
14
12
10
8
6
4
2
PxP
PxL
LxP
LxL

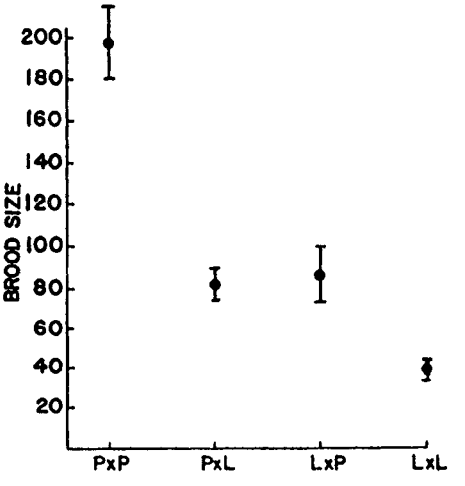

BROOD SIZE
200
180
160
140
120
100
80
60
40
20
PxP
PxL
LxP
LxL

TABLE 2. Estimates of variance components for female *S. benedicti* traits at first reproduction.

	Nuclear additive variance $\sigma^2_n \pm$ SE	Nuclear interaction variance $\sigma^2_i \pm$ SE	$4\sigma^2_n/V_y \pm$ SE
Length	359.79 ± 268.15†	(−136.32 ± 75.49)	0.86 ± 0.15**
Setiger no.	(6.17 ± 6.32)	(0 ± 0)	0.77 ± 0.19**
Position of 1st gametogenic setiger	0.25 ± 0.09**	(−0.04 ± 0.04)	0.94 ± 0.05**
Ovum diameter	67.37 ± 34.08†	(−3.71 ± 2.53)	0.75 ± 0.15**
No. of ova/ovary	6.53 ± 1.21**	1.82 ± 1.24†	0.90 ± 0.04**
Position of 1st brood pouch	0.28 ± 0.14*	(−0.02 ± 0.02)	0.88 ± 0.06**
No. of paired brood pouches	(0.38 ± 0.65)	(−0.08 ± 0.08)	0.67 ± 0.47†
No. of larvae/brood pouch	5.25 ± 1.14**	(0.74 ± 0.71)	0.93 ± 0.03**
No. of larvae/brood	2,874.44 ± 626.42**	(586.85 ± 593.98)	0.91 ± 0.03**

† $P < 0.10$.
* $P < 0.05$.
** $P < 0.01$.
( ) Not significant.

sures of fecundity and position of the first gametogenic setiger. Nuclear additive effects of body length were positively correlated with those of the three fecundity measures (r_n = 0.95–0.96), whereas nuclear additive effects of ovum diameter were negatively correlated with fecundity (−0.94) (Table 3).

Phenotypic correlations between adult female traits were always lower and in the same direction as nuclear additive correlations (Table 3). Positive phenotypic correlations were documented among the three fecundity measures, and between position of the first brood pouch and brood size. Negative phenotypic correlations were observed between positions of the first gametogenic setiger and first brood pouch, and between position of the first gametogenic setiger and each of the fecundity measures (Table 3).

Larval Characters

Of the seven larval traits examined, only the presence of swimming setae and the median planktonic period exhibited significant nuclear additive variance (Table 4). Nuclear additive variance accounted for 93.9% and nuclear interaction variance accounted for 1.3% of the total variance in swimming setae. Swimming setae were present in the majority of broods produced by PP mothers or fathers, and less frequently in other crosses (Fig. 2).Nuclear additive variance accounted for 98.4% of the total variance in median planktonic period (Table 4). The longest planktonic periods were generally exhibited by larvae with PP mothers and fathers; however, the range of values observed for minimum, median, and maximum planktonic period was similar, approximately eight days (Fig. 3), suggesting that these measures are not separate traits.

Larval size varied as a function of larval stage and was generally greater (at a given stage) for larvae released by LL or LP mothers (Fig. 4), but no significant genetic variance components were detected. The occurrence of larval feeding was greatest among broods produced by PP and PL mothers (Fig. 2b), but also did not exhibit significant genetic variance components.

The nonsignificance of many of the nuclear additive variance estimates for larval traits in Table 4 do not mean there is no additive variance component for these traits, only that they were not detected by our experiment. The jackknife estimates for the proportion of nuclear additive variance to the total variance were significant for all larval traits except survivorship (Table 4), indicating the possibility that some additive variance might be detected by a larger experiment.

Larval survivorship to settlement varied

←

FIG. 1. Mean values (± SE) for traits of female *Streblospio benedicti* at first reproduction. Females were produced in a series of 2 × 2 reciprocal crosses and mated as maternal lines in a series of 4 × 4 crosses (see Table 1) using planktotrophic (P) and lecithotrophic (L) lines. The maternal parent is listed first, the paternal is listed second.

TABLE 3. Estimates of nuclear additive correlations of (r_n) and phenotypic correlations (r_y) among adult *S. benedicti* traits at first reproduction. Correlations are given only for trait combinations having significant [$\alpha = 0.10$] covariance. Values are ± SE.

		Length at 1st reproduction	Setiger number	Position of 1st gametogenic setiger	Ovum diameter	No. ova/ovary	Position of 1st brood pouch	No. of paired brood pouches	No. of larvae/brood pouch
1. Length at 1st reproduction	r_n								
	r_y								
2. Setiger no.	r_n	NA							
	r_y	NA							
3. Position of 1st gametogenic setiger	r_n	(−0.93 ± 0.61)	(−0.91 ± 0.91)						
	r_y	(−0.84 ± 0.81)	(−0.80 ± 1.38)						
4. Ovum diameter	r_n	(−0.86 ± 1.01)	(−0.82 ± 1.30)	(0.91 ± 0.53)					
	r_y	(−0.65 ± 2.32)	NA	(0.77 ± 1.08)					
5. No. ova/ovary	r_n	0.95 ± 0.48†	(0.92 ± 1.37)	−0.99 ± 0.34*	(−0.95 ± 0.59)				
	r_y	(0.86 ± 0.95)	(0.80 ± 1.42)	−0.92 ± 0.42*	(−0.86 ± 0.84)				
6. Position of 1st brood pouch	r_n	(0.99 ± 1.12)	NA	(−0.99 ± 1.08)	(−0.92 ± 1.55)	(1.03 ± 1.45)			
	r_y	(0.95 ± 0.55)	NA	−0.87 ± 0.39*	(−0.77 ± 1.32)	(0.88 ± 0.57)			
7. No. of paired brood pouches	r_n	NA	NA	NA	NA	NA	NA		
	r_y	NA	NA	NA	NA	NA	NA		
8. No. of larvae/brood pouch	r_n	0.95 ± 0.48†	(0.92 ± 1.09)	−0.99 ± 0.17**	−0.94 ± 0.41*	1.00 ± 0.05**	(1.01 ± 1.17)	NA	
	r_y	(0.86 ± 1.04)	(0.80 ± 1.48)	−0.93 ± 0.45†	(−0.84 ± 0.97)	1.00 ± 0.02**	(0.89 ± 0.58)	NA	
9. No. of larvae/brood	r_n	0.96 ± 0.40*	(0.92 ± 1.18)	−0.98 ± 0.28**	(−0.94 ± 0.56)	1.00 ± 0.04**	(1.03 ± 1.21)	NA	1.00 ± 0.03**
	r_y	(0.89 ± 0.93)	(0.83 ± 1.42)	−0.91 ± 0.54†	(−0.82 ± 1.10)	0.99 ± 0.06**	0.90 ± 0.49†	NA	0.99 ± 0.04**

† $P < 0.10$.
* $P < 0.05$.
** $P < 0.01$.
( ) Correlations were not significant, but covariances were [$\alpha = 0.10$].
NA Covariances were not significant [$\alpha = 0.10$].

TABLE 4. Estimates of variance components for *S. benedicti* larval traits.§

	Nuclear additive variance $\sigma^2_n \pm$ SE	Nuclear interaction variance $\sigma^2_t \pm$ SE	Maternal variance $\sigma^2_m \pm$ SE	$4\sigma^2_n/V_y \pm$ SE
Larval length	(58.69 ± 884.64)	(−37.82 ± 1,516.26)	(514.96 ± 717.58)	0.61 ± 0.45†
Presence of swimming setae	0.12 ± 0.04**	0.02 ± 0.01*	(0 ± 0)	0.94 ± 0.02**
Feeding	(−0.03 ± 0.07)	(−0.28 ± 0.25)	(−0.09 ± 0.04)	1.061 ± 0.76†
Minimum planktonic period	(0.85 ± 1.48)	(−0.26 ± 0.26)	(0.75 ± 3.04)	0.58 ± 0.23*
Median planktonic period	6.69 ± 2.22**	(0 ± 0)	(−3.36 ± 2.21)	0.98 ± 0.05**
Maximum planktonic period	(2.18 ± 6.50)	(−2.65 ± 2.65)	(0 ± 0)	0.97 ± 0.35**
Larval survivorship	(−159.97 ± 98.62)	408.86 ± 252.39†	129.79 ± 79.80†	(−1.13 ± 0.69)

§ The jackknife method produces variance estimates of 0 if all estimates are negative or 0. When some estimates are positive and some are negative, then negative variance estimates can result.
† $P < 0.10$.
* $P < 0.05$.
** $P < 0.01$.
( ) Not significant.

by a factor of 10 among genotypes (Fig. 5). Larval survivorship did not exhibit significant nuclear additive variance, but nuclear interaction variance accounted for 64.3%, and nuclear maternal variance accounted for 20.4% of the total variance. Three of the four maternal lines (all except the LP line) produced larvae with higher survivorship when mated to males from the same line, than in any other combination (Fig. 5). Larvae resulting from LP × LP crosses were an exception; they were often released prematurely and survivorship was very low (Fig. 5).

There were only a few significant nuclear additive correlations among larval traits (Table 5). The presence of swimming setae exhibited positive nuclear additive variance correlations with minimum and median planktonic period. Nuclear additive effects of larval survivorship and median and maximum planktonic periods were negatively correlated.

Positive phenotypic correlations were observed between the presence of swimming setae and median planktonic period and between minimum and median planktonic period, though this latter observation might be expected for mathematical reasons. Negative phenotypic correlations were observed between larval survivorship and planktonic period (Table 5).

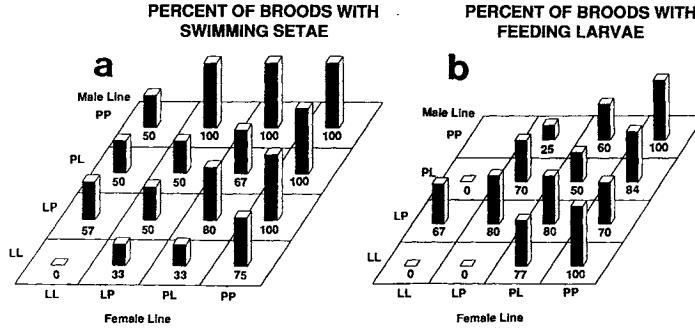


FIG. 2. Percent of *S. benedicti* broods produced in a series of 4 × 4 reciprocal crosses (see Table 1) that have a) larvae with swimming setae present, and b) feeding larvae. Lines are PP, PL, LP, and LL. (P)—Planktotropic; (L)—Lecithotrophic.

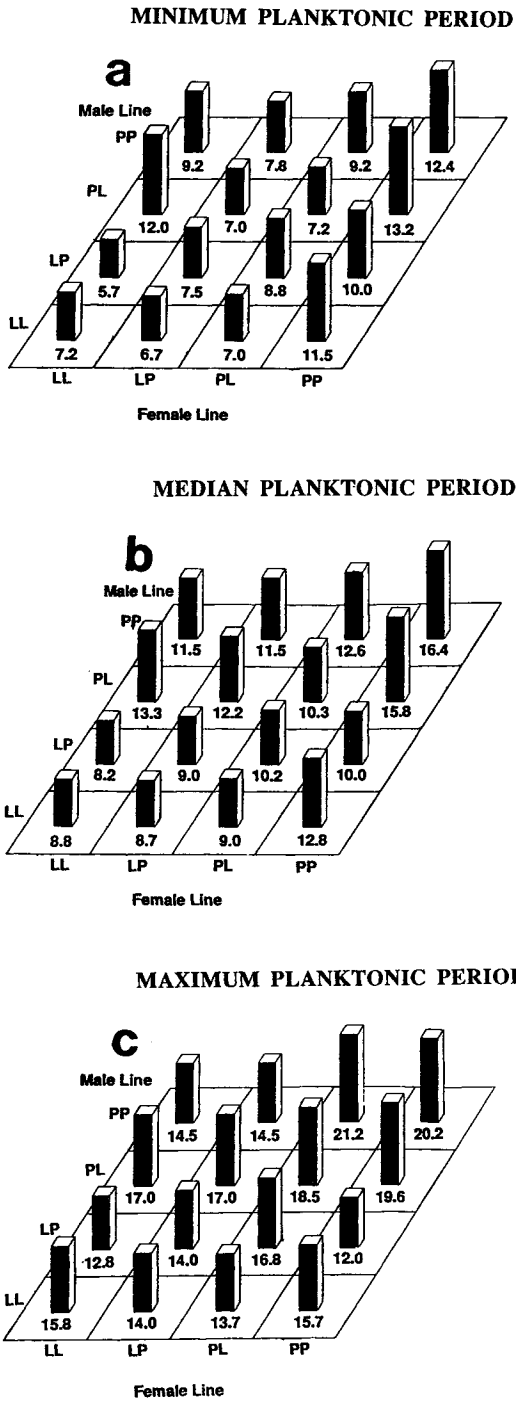


FIG. 3.—Planktonic period for *S. benedicti* larvae produced in a series of 4 × 4 reciprocal crosses (see Table 1). The 4 lines are PP, PL, LP, and LL. (P)—Planktotrophic; (L)—Lecithotrophic. Larvae were reared individually in 5 ml test tubes at 20°C, 34‰ salinity, 12 hr light/12 hr dark, and fed a mixed culture of dinoflagellates and blue-green algae. Time given is the number of days spent in the plankton from release to settlement. a. Minimum planktonic period. Mean values are given for the first larva to settle in each brood. b. Median planktonic period. Mean values are given for the number of days following release when 50% of the larvae that settled from each brood had done so. c. Maximum planktonic period. Mean values are given for the last larva to settle in each brood.

Correlations of Adult and Larval Traits

Because adult reproductive traits were measured on parents, and larval traits were measured on their offspring, only simple, product-moment correlations were evaluated (Table 6). These were generally lower in magnitude than the genetic correlations. The strongest correlations ($r_y > 0.70$) were observed between larval length and adult female reproductive characters (Table 6). Body size at first reproduction was negatively correlated with the offspring's larval length and survivorship, and positively correlated with the presence of swimming setae and with minimum planktonic period. Ovum diameter was positively correlated with the offspring's larval length and survivorship, but negatively correlated with the larval feeding ability, the presence of swimming setae, and with planktonic period. The three fecundity measures were correlated with the same larval traits as egg diameter, but in an opposite direction (Table 6). Position of the first gametogenic setiger was positively correlated with larval length and larval survivorship and negatively correlated with larval feeding ability, swimming setae, and planktonic period. Position of the first brood pouch exhibited many of the same correlations, but in opposite directions (Table 6).

DISCUSSION

Genetic Variation

Additive variation was detected for the majority of adult female reproductive characters, and several of the larval traits examined in *S. benedicti* (Table 7), indicating these traits are heritable. Heritability is important in understanding patterns of invertebrate development because it determines population responses to selection. The small sample sizes used in our study would gen-

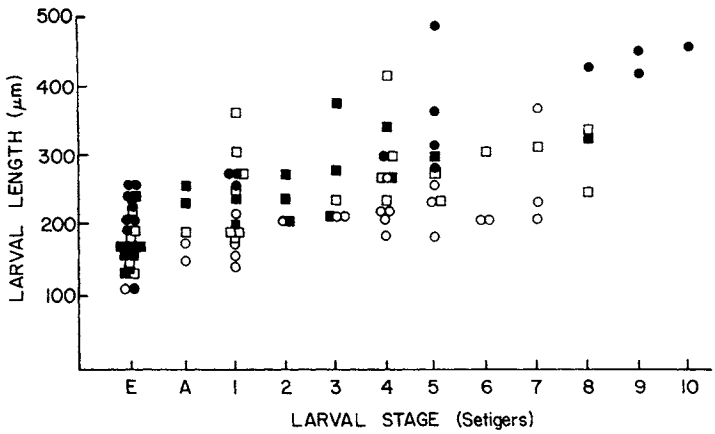


FIG. 4. Length of *Streblospio benedicti* larvae (at release) as a function of development stage. Larvae were produced in a series of 4 × 4 reciprocal crosses involving PP, PL, LP, and LL lines. Overall regression line y = 185.1 + 18.7x, $R^2 = 0.46$; (P)—Planktotrophic; (L)—Lecithotrophic; ○—produced by PP maternal line; ●—produced by LL maternal line; □—produced by PL maternal line; ■—produced by LP maternal line.

erally allow detection of only large additive variances, yet such large variances were observed for many traits (Tables 2, 4). The importance of additive variance relative to other sources of variation (i.e., heritability) is thought to be greater for morphological or behavioral traits than for life-history characters (Falconer, 1981; Mousseau and Roff, 1987; Roff and Mousseau, 1987). This is because natural selection is expected to eliminate heritable variation most rapidly in traits tied directly to fitness. However, our observations add to a growing number of studies in which high heritability of life-history traits is documented for natural populations (Dingle and Hegmann, 1982; Istock, 1983; Mousseau and Roff, 1987; McLaren and Corkett, 1978).

Mechanisms maintaining high levels of additive variance include heterozygote advantage (Falconer, 1981), mutation-selection balance (Lande, 1977), antagonistic pleiotropy (Rose, 1982) and variable selection in time and space combined with migration (Felsenstein, 1976). Unusually high heritability of body size in a marine copepod was attributed to assortative mating and the possible existence of cryptic species (McLaren and Corkett, 1978). No assortative mating occurs among *S. benedicti* in the laboratory (Levin, unpubl. data), but the geographic distribution of development modes suggests allopatric divergence may have occurred in North America. Pacific coast populations exhibit only lecithotrophy and planktotrophy dominates on the Atlantic coast. However, lecithotrophic development cooccurs with planktotrophic development in at least five populations on the Atlantic Coast as well (Levin, 1984*b*, unpubl. data). A likely scenario is that planktotrophy and lecithotrophy evolved allopatrically and cooccurrence is a relatively recent event, possibly related to human activities (Carlton, 1985). Under such circumstances the observed high additive variation could be in transition, destined ultimately to be reduced by selection.

LARVAL SURVIVORSHIP

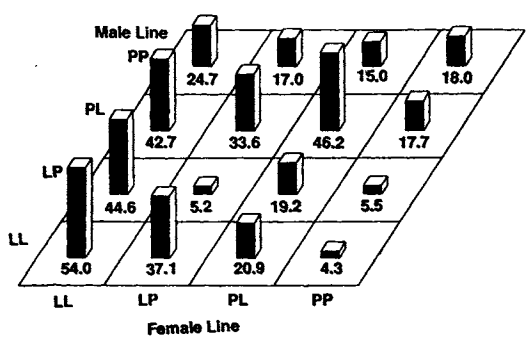


FIG. 5. Larval survivorship from release to settlement of *S. benedicti* larvae produced in a series of 4 × 4 reciprocal crosses (see Table 1). Larvae were reared as described in Figure 3. The 4 lines were PP, PL, LP, and LL. (P)—Planktotrophic; (L)—Lecithotrophic.

TABLE 5. Estimates of nuclear additive correlations (r_n) and phenotypic correlations (r_y) for *S. benedicti* larval traits. Data are presented only for trait combinations having significant [$\alpha = 0.10$] covariances. Values are ± SE.

		Larval length	Presence of swimming setae	Feeding ability	Minimum planktonic period	Median planktonic period	Maximum planktonic period
1. Larval length							
2. Presence of swimming setae	r_n	NA					
	r_y	NA					
3. Feeding ability	r_n	NA	NA				
	r_y	NA	NA				
4. Minimum planktonic period	r_n	NA	1.02 ± 0.26**	NA			
	r_y	NA	NA	NA			
5. Median planktonic period	r_n	NA	0.90 ± 0.11**	NA	NA		
	r_y	NA	0.89 ± 0.04**	NA	0.96 ± 0.15**		
6. Maximum planktonic period	r_n	NA	NA	NA	NA	NA	
	r_y	NA	NA	NA	NA	NA	
7. Larval survivorship	r_n	NA	NA	NA	NA	$\ll -1.00 \pm \ll -1.00$**	$\ll -1.00 \pm \ll 1.00$**
	r_y	NA	NA	NA	NA	-1.00 ± 0.17**	NA

† $P < 0.10$.
* $P < 0.05$.
** $P < 0.01$.
NA indicates that covariances were not significant ($\alpha = 0.10$).

An alternative (or additional) explanation for the observed high additive variance may lie with the fact that North Carolina *S. benedicti* populations have four cohorts per year with partially overlapping generations. Animals reared in the laboratory exhibit life cycles and demography resembling the fall, overwintering cohort (Levin and Huggett, 1990). Because this study examined only traits at first reproduction and only for one cohort type under laboratory conditions at one time, we may have underestimated the phenotypic variation expressed in nature, and hence overestimated the realized heritabilities.

Larval success is often considered to be tied to stochastic events in the water column or on the bottom (e.g., Thorson, 1950; Butman, 1987; Roughgarden et al., 1988). The extent to which heritable intraspecific variation in larval development time, behavior in the water column, and settlement success can affect recruitment and subsequent fitness is unknown. In this context, our findings of nuclear additive variance in larval planktonic period suggest that genetic factors can influence the fate of larvae as well.

The duration of the larval planktonic period is of interest because it directly affects dispersal and gene flow between populations. Laboratory estimates of sources of variation in planktonic period clearly cannot accurately incorporate many of the important variables encountered in the field (e.g., food availability, temperature fluctuations, predation); however, they can hint at the existence of genetic effects that set environment-specific limits on pre- and post-competent development periods, and may govern behaviors that modify planktonic period. Genetically based variations, such as the four- to eight-day differences observed for *S. benedicti* planktonic periods (Fig. 3), could substantially alter gene flow between estuarine populations.

There are no previous reports of genetic variation in planktonic period of marine invertebrate larvae. However, heritabilities reported for larval-development rate in insects (Istock, 1983) and duration of the free-swimming larval stage in anuran tadpoles (Travis, 1980; Travis et al., 1987) were nowhere near the 98% additive contribution to total variation in median planktonic pe-

TABLE 6. Simple correlation coefficients for *S. benedicti* adult and larval traits.

	Larval length	Presence of swimming setae	Minimum planktonic period	Median planktonic period	Maximum planktonic period	Larval survivorship	Larval feeding
Length at 1st reproduction	−0.71**	0.57*	0.49†	(0.40)	(−0.01)	−0.69**	(0.38)
Setiger no. at 1st reproduction	−0.60*	0.50†	(0.37)	(0.21)	(−0.07)	−0.64**	(0.35)
Position of 1st gametogenic setiger	0.68*	−0.53*	−0.59*	−0.53*	(−0.27)	0.63*	−0.64**
Ovum diameter	0.70**	−0.45†	−0.57*	−0.48†	(−0.36)	0.53*	−0.46†
No. ova/ovary	−0.82**	0.64**	0.68**	0.59*	(0.34)	−0.61*	0.62†
Position of 1st brood pouch	−0.79**	0.57*	(0.40)	(0.32)	(−0.05)	−0.83**	(0.43)
No. of paired brood pouches	−0.47†	0.57*	(0.40)	(0.22)	(0.06)	−0.57*	0.45†
No. of larvae/brood pouch	−0.78**	0.61*	0.67**	0.59*	(0.32)	−0.66**	0.68**
No. of larvae/brood	−0.76**	0.58*	0.64**	0.54*	(0.23)	−0.70**	0.63*

† $P < 0.10$.
* $P < 0.05$.
** $P < 0.01$.
( ) Not significant.

riod in *S. benedicti* (Table 4). Our estimates of additive variation, for this and other traits, may be inflated if interbreeding between the planktotrophic and lecithotrophic morphs is not completely random.

In the case of larval planktonic period, maternal genetic contribution in terms of yolk or egg size was not the overriding influence we had expected. The absence of maternal variance components and the presence of large nuclear additive variance components (Tables 4, 7) indicate equal maternal and paternal contribution. Paternal contribution to planktonic period is evident in Figure 3; larvae with PP or PL fathers averaged 13 days in the plankton, whereas larvae with LP or LL fathers averaged 9.4–9.8 days. However, we did observe a negative correlation between maternal egg size and both minimum and median planktonic period (Table 6). Though it was not examined explicitly in our study, there seems to be no effect of egg size or planktonic period on size of larvae at settlement (Levin, unpubl. data).

Significant additive effects have been reported for larval survivorship of marine invertebrates (Mallet and Haley, 1984; Lannan, 1972; Newkirk et al., 1977; Losee, 1978). Several studies of marine species, including ours (Table 4), report no additive genetic variance but significant nonadditive effects in larval survivorship (McLaren, 1976; McLaren and Corkett, 1978; Mallet and Haley, 1984). Mallet and Haley (1984) observed reduced larval survivorship for

TABLE 7. Summary of variance components detected in *S. benedicti* life-history traits. Significance level is $P < 0.05$ unless otherwise noted.

Nuclear additive variance	Nuclear interaction variance	Maternal variance
Female body length†	Number of ova/ovary†	Larval survivorship†
Egg diameter	Presence of larval swim setae	
Fecundity	Larval survivorship†	
No. ova/ovary		
No. larvae/brood pouch		
No. larvae/brood		
Position of reproductive structures		
1st gametogenic setiger		
1st brood pouch		
Presence of larval swimming setae		
Median larval planktonic period		

† $P < 0.10$.

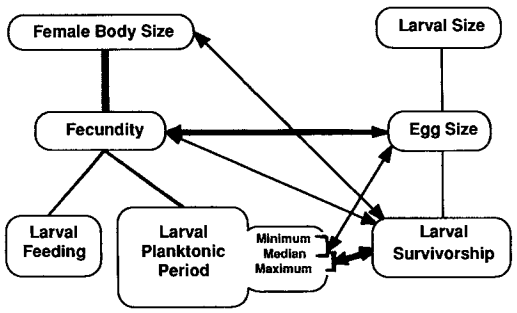


FIG. 6. Schematic representation of the correlation structure of major *S. benedicti* life-history traits associated with planktotrophic and lecithotrophic development. Double arrows indicate negative correlations; straight lines indicate positive correlations. Heavy lines indicate genetic (additive) correlations; thin lines indicate product-moment correlations.

offspring of between-population crosses of the oyster *C. virginica* and reported significant specific combining ability (interaction effects) and maternal effects in survivorship. These are essentially the same components found to account for 85% of the total variance in larval survivorship of *S. benedicti* (Tables 4, 7). These observations support results of other empirical studies and theoretical predictions indicating that interaction (often dominance) variance increases with the strength of a trait's connection to fitness (Hilbish and Koehn, 1985; Travis et al., 1987). Of all the traits examined in this study, larval survivorship is most directly tied to fitness. Large nonadditive variance might be expected if both planktotrophic and lecithotrophic life histories have experienced selection to maximize larval survivorship, while employing different clusters of character states to achieve this.

Though the occurrence of larval feeding was not shown to be heritable in this study, parents or grandparents that were planktotrophic as larvae appeared to contribute at least facultative feeding potential to their descendents (Fig. 2b). Facultative planktotrophy has been reported for several species of marine invertebrate larvae (Kempf and Hadfield, 1985; Emlet, 1986; Kempf and Todd, 1989) and anuran tadpoles (Novak and Robinson, 1975; Crump, 1989), and may reflect evolutionary stages in transition between obligate feeding and nonfeeding modes of development (Kempf and Todd, 1989). In *S. benedicti,* additive variance present in the occurrence of larval feeding might have gone undetected due to methodological problems. We did not evaluate the proportion of feeding larvae in each brood, differentiate between facultative and obligatory planktotrophy, or distinguish between ingestion and digestion. In retrospect, it is likely that many of the larvae produced in hybrid combinations were able to feed, but might not have been required to do so for successful settlement. Both these experimental biases could have confounded our genetic interpretations.

Correlation Structure of Life-History Traits

The correlation structure of life-history traits provides information about recent past and present constraints on trait evolution (Stearns, 1989*a*). Correlations in *S. benedicti,* among body size, egg size, fecundity, larval size at release, planktonic period and survivorship (Fig. 6), form the crux of the development-mode trait cluster and may result from either linkage or pleiotropy. Our intragenerational comparisons indicate clear tradeoffs between egg size and at least one measure of fecundity (Table 3) and between planktonic period and larval survivorship (Table 5). These results suggest that enhanced dispersal resulting from extended planktonic periods will take place at the expense of larval survivorship for genetic as well as expected environmental reasons. Though our experimental design did not allow us to examine the intergenerational genetic correlations between adult and larval traits, we propose that the strong negative product-moment correlations between egg size and minimum or median planktonic period (Table 6, Fig. 6) may have a genetic basis as well.

In *S. benedicti,* female body size exhibits genetic correlations that imitate interspecific evolutionary trends observed among marine invertebrates. Larger-bodied benthic species generally exhibit high fecundities and produce planktotrophic larvae with poor survivorship, whereas smaller species usually brood low numbers of lecithotrophic larvae that have relatively high survivorship (Strathmann and Strathmann, 1982; Strathmann, 1990). *S. benedicti* length at first reproduction exhibited positive ge-

netic correlations with fecundity (larger females produce more eggs) and negative product-moment correlations with larval survivorship (Fig. 6).

Evolution of Planktotrophy and Lecithotrophy

The clusters of reproductive and development traits associated with planktotrophy and lecithotrophy in *S. benedicti* appear to be highly adaptive. In planktotrophic forms large female body size permits increased numbers of brooded offspring (Strathmann and Strathmann, 1982) necessary to offset diminished larval survivorship. Swimming setae, which serve primarily as protection from predators (Levin, unpubl. data), and larval feeding both improve survivorship during lengthy planktonic periods. Lecithotrophic forms generally exhibit opposite patterns; larvae are adapted to lesser time in the plankton and to regimes conferring high offspring survivorship.

The pervasiveness of planktotrophic and lecithotrophic trait complexes among benthic invertebrates has been explained by several models that show there are only two evolutionarily stable egg sizes or development states (Vance, 1973*a*, 1973*b*; Christiansen and Fenchel, 1979). These models assume tradeoffs between egg size and fecundity, and between fecundity and survivorship, formulated in terms of reproductive effort. Here we have documented a genetic basis for such tradeoffs, thereby reinforcing the model assumptions.

True cases of poecilogony may be as rare as they are (Hoagland and Robertson, 1988; Bouchet, 1989) because of the constraints imposed by the genetic structure of the life-history traits involved (Fig. 6). Intermediate fecundities or egg sizes may be associated with planktonic periods that are too long or larval survivorship that is too low to promote sufficient individual success within a population (relative to higher or lower fecundities or egg sizes). Additional constraints that interface with the genetic systems include those imposed by morphology, allometry, time, energy (food availability), and systematics (evolutionary history). For example, given unlimited energy, the worms have only limited physical space to brood larvae and limited time to produce young, constraining the total number of offspring produced. Such constraints diminish on an interspecific level, as contrasting development modes are observed frequently among congeners in many invertebrate groups (Grahame and Branch, 1985).

Our two strains of *S. benedicti* exhibit distinct trait complexes. The majority of the life-history characters involved exhibit substantial additive variance (Table 7) and this variance is highly correlated among many traits (Fig. 6). Thus, variation in the traits associated with planktotrophy and lecithotrophy has a clear genetic basis. If the observed correlation structure persists in nature, we suggest it is unlikely that these traits evolve independently. Additional estimates of genetic variation and correlation structure, and particularly of gene-environment interactions, focusing on both within- and between-development-mode variation in poecilogonous species, should provide further insight into the rarity of poecilogony and the evolution of invertebrate life histories.

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