Demographic Consequences of Larval Development Mode: Planktotrophy vs. Lecithotrophy in Streblospio Benedicti
Author(s): Lisa A. Levin, Hal Caswell, Kathy D. DePatra, Elizabeth L. Creed
Source: *Ecology*, Vol. 68, No. 6 (Dec., 1987), pp. 1877-1886
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1939879

Ecology, 68(6), 1987, pp. 1877–1886

DEMOGRAPHIC CONSEQUENCES OF LARVAL DEVELOPMENT MODE: PLANKTOTROPHY VS. LECITHOTROPHY IN *STREBLOSPIO BENEDICTI*[1]

LISA A. LEVIN
Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, North Carolina 27695-8208 USA

HAL CASWELL
Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543 USA

AND

KATHY D. DEPATRA AND ELIZABETH L. CREED
Department of Marine, Earth, and Atmospheric Sciences, North Carolina State University, Raleigh, North Carolina 27695-8208 USA

Abstract. This paper examines the demographic consequences of planktotrophic and lecithotrophic development in an estuarine polychaete. Two strains of *Streblospio benedicti* (Spionidae) were reared in the laboratory from birth through death at 20°C and salinity 34‰. Survivorship and reproductive data were collected weekly and were used to construct life tables and population projection matrices for each development mode. Planktotrophic females reproduced earlier, and had higher fecundity and a shorter generation time than lecithotrophic females, but also exhibited higher mortality early in life. Despite the apparently opportunistic nature of the planktotrophic life history traits, the finite rate of increase (λ) in the lecithotrophic strain (1.319 wk^{-1}) exceeded that of the planktotrophic strain (1.205 wk^{-1}). Net reproductive rate (R_0) was also higher for the lecithotrophs (93.4) than for the planktotrophs (17.6). Peak reproductive values were attained earlier in planktotrophs than in lecithotrophs. Sensitivity analyses indicate that λ is most sensitive to changes in larval and juvenile survivorship, and that the differences in λ were almost completely determined by life table differences during the first 15 wk of life. The potential population growth rates obtained in this study agree well with those estimated for other opportunistic polychaete species such as *Capitella* sp. I and *Polydora ligni*. Under uniform conditions the two strains of *S. benedicti* achieved similar growth rates with very different life history traits. We hypothesize that each combination of traits may be adaptive under different circumstances in the field.

Key words: demography; larval development; larval trophic mode; lecithotrophy; Leslie matrices; life history; life table; planktotrophy; poecilogony; polychaete; Streblospio benedicti.

INTRODUCTION

Benthic marine invertebrates exhibit a variety of developmental patterns. Among those possessing planktonic larvae, there is an important dichotomy between planktotrophy, in which larvae derive nutrition by feeding, and lecithotrophy, in which larvae develop from yolk supplies in the ovum and do not feed. Though some lecithotrophic larvae may be capable of facultative planktotrophy (e.g., Kempf and Hadfield 1985, Emlet 1986), most workers assume that species are limited to one mode of development or the other by the available yolk (e.g., Thorson 1950, Vance 1973*a*) and the presence or absence of feeding organs and a complete gut (Strathmann 1978). Planktotrophic development usually involves production of large numbers of small ova, and lecithotrophic development involves small numbers of large ova. Planktotrophic larvae typically have a longer planktonic phase than lecithotrophic larvae, as they must feed in the water column to attain the size and maturity necessary for settlement and metamorphosis. Thus, planktotrophic larvae are generally believed to possess greater powers of dispersal.

Thorson (1946, 1950) was the first to synthesize patterns of planktotrophy and lecithotrophy in the world's oceans and attempted to interpret their importance for the distribution and demography of marine benthic species. Since Thorson's time attention has focused on many aspects of this developmental dichotomy: mechanisms responsible for its maintenance (Vance 1973*a*, *b*, Christiansen and Fenchel 1979, Ayal and Safriel 1982) and breakdown (Pechenik 1979, Caswell 1981), energy costs (Hines 1979, Lassen 1979, Todd 1979, Hughes and Roberts 1980, Hart and Begon 1982), relation to body size, egg size, and fecundity (Thiel 1975, Strathmann and Strathmann 1982, Kabat 1985), de-

---

[1] Manuscript received 1 August 1986; revised 21 January 1987; accepted 10 February 1987.

mographic consequences (Scheltema 1971, Strathmann 1974, 1980, 1982, Vance 1980, Strathmann et al. 1981, Levin 1984*a,* Chernoff 1985, Perron, 1986), genetic consequences (Burton 1983, Burton and Swisher 1984), and evolutionary implications (reviewed in Jablonski and Lutz 1983). All of these problems require an understanding of how life history differences associated with larval development are translated into differences in population dynamics and fitness.

This paper focuses on that translation. We attempt to quantify the demographic consequences of the fecundity and survival differences between planktotrophic and lecithotrophic forms. Because life table data are difficult to acquire for marine invertebrate species, there have been relatively few attempts to examine this aspect of developmental mode, and most are based on comparisons between related or ecologically similar species. Perron (1986), for example, compared planktotrophic and lecithotrophic life tables for several species of the predatory gastropod *Conus.* He observed contrasting patterns of reproductive effort, iteroparity, fecundity, and reproductive timing, which differed from the classic predictions of *r* and *K* theory. Species that exhibit both planktotrophic and lecithotrophic development are relatively rare (examples are found in Eyster 1979, West et al. 1984, Levin 1984*b*), but offer the least complicated systems for evaluating the influence of larval development mode on population-level processes.

The occurrence of multiple development modes (poecilogony) in *Streblospio benedicti* (Webster) is described in Levin (1984*b*). In both planktotrophic and lecithotrophic forms of reproduction larvae are brooded in paired dorsal brood pouches and females are iteroparous. Mature planktotrophic ova are ≈70 μm in diameter and mature lecithotrophic ova are 100 μm or larger (Eckelbarger 1986). Planktotrophic larvae are released from brood pouches at the 3 to 5 setiger stage in batches of 100 to 400 larvae, and they feed in the plankton for ≈10–21 d (but up to 45 d) before settlement. Lecithotrophic larvae are released at the 8 to 10 setiger stage in broods of <70. They are capable of immediate settlement but may remain planktonic for <7 d without feeding. *S. benedicti* exhibits both planktotrophic and lecithotrophic development in Bogue Sound, North Carolina (Levin and Creed 1986). Laboratory studies involving environmental manipulations (Levin and Creed 1986) and genetic crosses (L. A. Levin and E. L. Creed, *personal observation*) indicate that larval trophic mode is under genetic control, and that individual females cannot switch development mode. Both developmental types are reproductively compatible in the laboratory. Approximately 10–20% of the individuals collected in Bogue Sound appeared to be trophic hybrids (L. A. Levin and E. L. Creed, *personal observation*). Hybrid larvae exhibit facultative planktotrophy and have planktonic periods and yolk supply intermediate between the two pure forms (L. A. Levin and E. L. Creed, *personal observation*). We presently view larval trophic mode in *S. benedicti* as a polymorphism.

In this paper we compare laboratory life tables for strains of the spionid polychaete *S. benedicti* with planktotrophic and lecithotrophic development. Matrix population models ("Leslie matrices") are used to evaluate population growth rates, stable age distributions, reproductive values, and the sensitivities of population growth rate to changes in the life history parameters. Our objective is to identify the demographic consequences of the two development modes under common physiological, environmental, and historical influences. Results reflect laboratory conditions in which food was abundant and predation pressure was absent.

METHODS

Laboratory studies

Individuals used in this study were the offspring of females taken from laboratory cultures that had produced pure planktotrophic or lecithotrophic larvae for the previous 6–10 mo. These laboratory cultures were initiated with females collected at Tar Landing Bay in Bogue Sound, North Carolina (32°42′ N, 76°42′ W). The individuals for which we collected life history data were one or two generations removed from the field.

Sibling larvae were reared together in covered crystallizing dishes (90 mm diameter × 50 mm depth) at 20°C and salinity 34‰. They were fed a mixed assemblage of dinoflagellates and blue-green algae in excess amounts. Soon after release, larvae were provided with a thin layer (3 mm) of defaunated sediment from the Tar Landing salt marsh. The sediment had been sieved through a 500-μm mesh, frozen for several weeks, thawed, and reconstituted with 0.1 μm filtered seawater. Cultures were checked every 1–2 d and date of settlement, determined by appearance of tubes in the sediment, was noted. When recruits were 3–4 wk old, one recruit from each of 35 planktotrophic and 37 lecithotrophic broods was transferred to a covered Petri dish (60 mm diameter × 20 mm depth). Dishes contained 75 mL of seawater with 34‰ salinity and 25 mL of defaunated marsh sediment. Individuals were reared at 20° in continual darkness. Seawater and sediment were changed once a week by sieving dish contents through a 125-μm screen and adding fresh water and sediment. When female recruits were old enough to sex, each was paired with one male (of the same developmental type) from the original Tar Landing cultures. If the male died before the female, another male was added to her dish.

Individuals were monitored at weekly intervals from age 4 or 5 wk through death. Body length (mm), and number of setigers were recorded for all individuals. Females were measured for position of the first gametogenic setiger, the number of ova per ovary, the number and position of paired brood pouches, the number of larvae brooded per brood pouch, and total brood size. All measurements were made on individuals relaxed with 10% $MgCl_2$ using a dissecting microscope and ocular micrometer. Two-way analysis of variance and a posteriori LSD tests were performed to examine independent effects of development mode and brood number (sequence in production) on adult body size and reproductive traits. The number of broods produced by each female ranged from 0 to 14 among planktotrophs and from 0 to 12 among lecithotrophs. None of the traits examined exhibited significant interaction between development mode and brood sequence. Analyses were carried out using SAS software (Ray 1982).

Life table construction

Larval survivorship from release to settlement was determined in a separate study (L. A. Levin and E. L. Creed, *personal observation*) in which 200 planktotrophic larvae (four separate broods) and 104 lecithotrophic larvae (three separate broods) from the Tar Landing cultures were reared individually in test tubes containing water and marsh sediment. Larvae were monitored three times each week for settlement.

To measure postsettlement survival, newly settled individuals were reared in batch culture with siblings sharing the same dish, until they became large enough to handle (≈4 wk after settlement). At this point, 35 planktotrophs (21 females, 14 males) and 37 lecithotrophs (15 females, 22 males) were monitored individually. Because no significant differences were observed between male and female survivorship (two-sample Kolmogorov-Smirnov tests, $P \gg .10$), the sexes were pooled in calculating life tables.

Together, these two studies provide estimates of survival from release to settlement and from 4 wk postsettlement to death. Because no measurements were available for the first 4 wk after settlement, weekly survival probability during this period was set equal to the average for the following 4 wk (0.65 for planktotrophs and 0.89 for lecithotrophs). This assumption may slightly overestimate actual values and lead to elevated growth rate calculations.

Fecundity schedules (m_x) for the two strains were derived directly from the number of offspring released weekly by each female (reared from settlement). Several females did not produce any young but were included in the life table calculations. The failure to reproduce may have been due to mate infertility.

Demographic analysis

Leslie matrices, for time and age intervals of 1 wk, were calculated from the life tables using the standard methods of Keyfitz (1968:26–30). The survival probabilities P_i appearing on the subdiagonal were calculated as

$$P_i = \frac{l_{i+1} + l_i}{l_i + l_{i-1}} \tag{1}$$

and the age-specific fecundities F_i in the first row as

$$F_i = (l_0 l_1)^{1/2}\left(\frac{m_i + P_i m_{i+1}}{2}\right). \tag{2}$$

The $(l_0 l_1)^{1/2}$ term is a geometric mean approximation to the probability that a newborn individual survives to age ½; it is more accurate for organisms with high neonatal mortality than the arithmetic mean used by Keyfitz (1968) for human populations.

The finite population growth rate λ was obtained as the dominant eigenvalue of the projection matrix; the stable age distribution is given by the corresponding right eigenvector $\boldsymbol{w}$ and the reproductive value distribution by the corresponding left eigenvector $\boldsymbol{v}$. The eigenvalues and eigenvectors were calculated in double precision using IMSL (International Mathematical and Statistical Library) routines. The sensitivity of λ to changes in the entries of the projection matrix was calculated following Caswell (1978, 1985):

$$\frac{\partial\lambda}{\partial P_i} = \frac{w_i v_{i+1}}{\langle \boldsymbol{w}, \boldsymbol{v}\rangle} \tag{3}$$

$$\frac{\partial\lambda}{\partial F_i} = \frac{v_1 w_i}{\langle \boldsymbol{w}, \boldsymbol{v}\rangle}, \tag{4}$$

where $\langle \boldsymbol{w}, \boldsymbol{v}\rangle$ denotes the scalar product.

RESULTS

Female reproductive traits

Planktotrophic and lecithotrophic females of reproductive age did not differ in size, as measured by length or segment number, though many reproductive traits did vary (Table 1). Older females had a tendency to autotomize posterior segments, leading to slight decreases in segment number and length in both strains. As found in previous studies (Levin 1984*b*, Levin and Creed 1986), planktotrophic females experienced gametogenesis in more anterior segments, had smaller ova and generated more ova per ovary (at one time) than lecithotrophic females. Although the number of brood pouches generally did not differ, more planktotrophic larvae were brooded in each pouch and total brood size was larger among planktotrophs than lecithotrophs. These differences were consistent throughout reproductive life (Table 1).

Reproduction began 4 wk earlier in planktotrophic females than in females with lecithotrophic development (Table 1). No differences were observed in the size of females (length or segment number) at first reproduction; planktotrophic females attained this size through more rapid growth. The interval between broods was ≈7 d for planktotrophic broods and 12–14 d for lecithotrophic broods, though some females occasionally exhibited greater gaps between broods. Although the interbrood interval for lecithotrophs was roughly twice that of planktotrophs, the total number of broods produced per lifetime was, on average, the same for planktotrophic females ($\bar{X} = 6.2$) and leci-

TABLE 1. Mean values for reproductive traits of female *Streblospio benedicti* reared in the laboratory at 20°C, salinity 34‰. P = planktotrophs; L = lecithotrophs.

	First brood		Middle brood		Last brood		All broods		Two-way ANOVA	
									Trophic mode ($F_{1,155}$)	Brood sequence ($F_{13,155}$)
	P	L	P	L	P	L	P	L		
Age (wk)	9.6	13.4	15.1	19.1	18.8	25.6	16.8	19.9	6.24 (P = .014)	10.36****
Length (mm)	10.1	9.5	9.4	10.5	9.9	8.7	9.8	9.8	NS	NS
Segment number	51.7	52.1	50.4	55.4	49.4	48.3	50.9	53.2	NS	NS
First gametogenic setiger	9.9	12.4	10.6	11.8	10.9	12.5	10.5	12.3	20.31****	NS
Ovum diameter (μm)	49.3	95.5	55.7	87.3	51.4	80.0	53.5	91.8	46.01****	NS
No. of ova/ovary	6.9	3.6	8.5	4.0	9.7	4.6	8.7	4.2	82.66****	1.96 (P = .029)
No. of brood pouches	14.3	13.5	12.6	15.5	13.8	14.2	13.7	14.5	NS	NS
No. of larvae/brood pouch	9.1	3.0	10.4	2.7	7.2	2.5	9.2	2.2	116.46****	NS
No. larvae/brood	220.1	51.5	254.2	54.6	171.1	37.7	213.6	56.1	45.40****	NS

**** $P \leq .0001$.

thotrophic females ($\bar{X}$ = 6.0). The total number of planktotrophic offspring produced by each female averaged 886, almost four times higher than the per capita number of lecithotrophic offspring. The average duration of reproductive activity (time between production of first and last broods) was 3 wk longer among lecithotrophic females. Thus females producing their last lecithotrophic brood were significantly older than their planktotrophic counterparts (Table 1). Life expectancy at 4 wk of age was much greater for lecithotrophic (15.08 wk) than for planktotrophic (4.80 wk) females.

Life tables

The life tables and Leslie matrix elements are given in the Appendix. Mortality rates differed during the first 7 wk of life but were similar beyond that age (Fig. 1). The larval period in lecithotrophs was ≈1 wk, and survivorship to settlement was 0.707. The planktotrophic larval phase lasted ≈2 wk, and survivorship to settlement was 0.170. The average weekly survival probability for planktotrophic larvae was thus 0.412, slightly over half that of lecithotrophic larvae.

Comparisons of age-specific fecundity (m_x) schedules indicate earlier and substantially greater reproductive output by planktotrophic females (Fig. 2). Both curves display an unusual polymodality. In planktotrophs birth rates reach a minor peak at 9–10 wk, decline, and then ascend to a much higher second peak, which occurs at 21–22 wk. In lecithotrophs fecundity maxima occur at 7, 13–14, and 23–26 wk. Both developmental strains exhibit a rapid drop in birth rate following the final maximum (Fig. 2).

Net reproductive rate, R_0 ($= \sum l_x m_x$) was 17.60 for the planktotrophic strain and 93.36 for the lecithotrophic strain. Generation times ($\ln R_0)/r$, were 15.4 and 16.4 wk for the two groups, respectively (Table 2).

The finite population growth rates for the two populations were λ = 1.205 ($r = \ln \lambda = 0.186$) for planktotrophs and λ = 1.319 (r = 0.277) for lecithotrophs (Table 2). Age-specific reproductive values (v_x) were very different in females with planktotrophic and lecithotrophic development, but patterns of change with age were similar. Both strains exhibited an early climb, a leveling off, and a late maximum (Fig. 3). However, peak reproductive values were reached earlier (at 20–21 wk) in planktotrophs than in lecithotrophs (24–25 wk).

The predicted stable age distributions of the two forms are both dominated by young individuals (Fig. 4), but this effect is more extreme among planktotrophs than lecithotrophs. Less than 1% of the stable planktotrophic and lecithotrophic population would be above mean reproductive age.

Sensitivity analysis

The rate of increase λ, the stable age distribution $\boldsymbol{w}$, and the reproductive value distribution $\boldsymbol{v}$ are integrative measures; their values depend on the entire age-

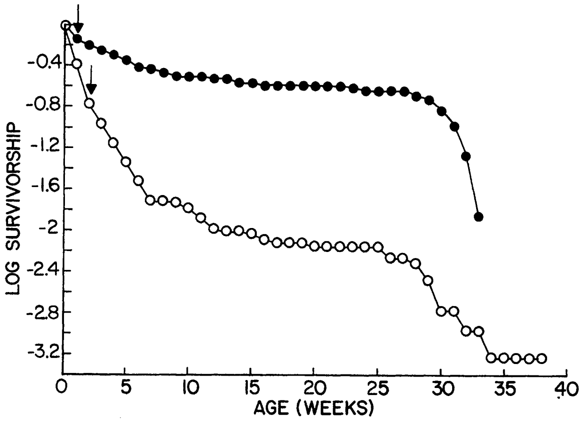

FIG. 1. Survivorship of *Streblospio benedicti* with planktotrophic and lecithotrophic development, reared in the laboratory at 20°C and salinity 34‰. (○) planktotrophic strain; (●) lecithotrophic strain. Age 0 corresponds to the time of release of larvae from the mother. ↓ Indicates the time of settlement.

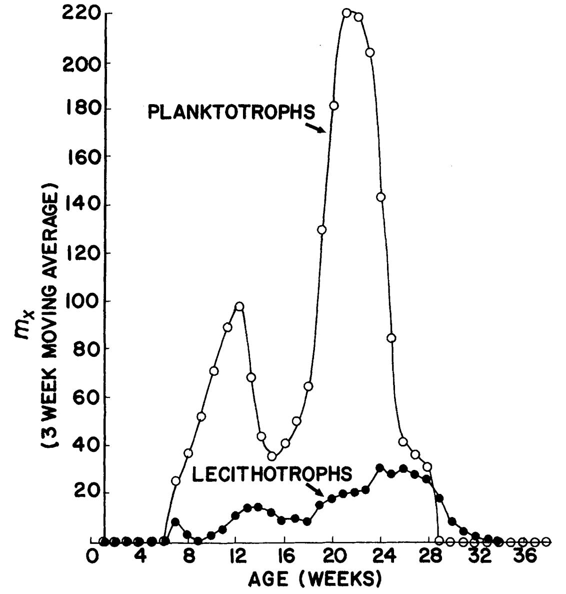

FIG. 2. Age-specific fecundity (m_x) of *Streblospio benedicti* with planktotrophic and lecithotrophic development, reared in the laboratory at 20°C and salinity 34‰.

specific survivorship and maternity functions. Using sensitivity analysis, it is possible to investigate the way in which these indices, particularly λ, depend on the specific fecundities and survival probabilities.

The sensitivities of λ to changes in age-specific fecundity and survival span seven orders of magnitude (Fig. 5). Larval and juvenile survivorship are by far the most important parameters in both strains. In both strains, λ is far more sensitive to survival probability than to fecundity over most of the life-span. The sensitivities to survival changes are similar for the two strains, while lecithotrophs are about an order of magnitude more sensitive to fecundity changes than are planktotrophs.

Models for the evolution of larval life histories (e.g., Vance 1973*a, b,* Christiansen and Fenchel 1979, Caswell 1981) assume that some of the differences between the two development modes compensate for others. Increased reproductive output is supposed, for example, to compensate for reduced egg size and larval survival. In an evolutionary context, all such trade-offs must be expressed in terms of fitness, usually measured by λ. The life table differences alone provide no insight into this problem. Huge differences in survival or fecundity at ages when λ is very insensitive to those differences may make no contribution to differences in λ; much smaller life table differences at ages when λ is very sensitive may make much larger contributions. By combining the observed life table differences with the sensitivity analysis, we can quantify the contributions of the demographic differences between strains to overall fitness (H. Caswell and A. Olson, *personal observation*).

Our data provide us with two Leslie matrices, A_1 for lecithotrophs and A_2 for planktotrophs, with respective growth rates λ_1 and λ_2. To the first order, the difference in growth rate $\Delta\lambda = \lambda_1 - \lambda_2$ can be written

$$\Delta\lambda \approx \sum_i \sum_j \Delta a_{ij} \frac{\partial \lambda}{\partial a_{ij}}, \qquad (5)$$

where Δa_{ij} is the difference between the (i, j) entries of A_1 and A_2 and the partial derivative is evaluated (using Eqs. 3 and 4) at the average of A_1 and A_2.

Each term in the summation represents the contribution of the demographic difference Δa_{ij} to the fitness difference $\Delta\lambda$ between the two strains. Fig. 6 plots these contributions for the age-specific survival probability and fecundity differences. Life table differences occurring after 15 wk of age, including an enormous planktotrophic fecundity advantage between 18 and 25 wk of age (Fig. 2), make little or no contribution to the difference in growth rate. The demographically important differences between the two life histories are

TABLE 2. Summary of demographic analyses for polychaetes. P = planktotrophic; L = lecithotrophic.

Species	Larval trophic mode	Culture conditions		λ*	r*	Generation time, T (wk)	R_0 ($\sum l_x m_x$)
		Temp. (°C)	Salinity (‰)				
Streblospio benedicti†	P	20°	34	1.205	0.186	15.4	17.6
	L	20°	34	1.319	0.277	16.4	93.4
Capitella capitata‡	L	18°	30	1.298	0.261	13.8	36.7
	L	15°	25	1.214	0.194	19.2	41.75
Polydora ligni§		Field (Connecticut)					
	P	Spring		1.381	0.276	8.2	9.52
	P	Early Summer		1.221	0.200	7.5	4.46
Ophryotrocha diadema‖	L		34	2.392–2.469	0.872–0.904	5.8–6.6	160.4–341.1

* Calculated for 1-wk age intervals.
† This study.
‡ From Redman 1984.
§ From Zajac 1985.
‖ From Åkesson 1982.

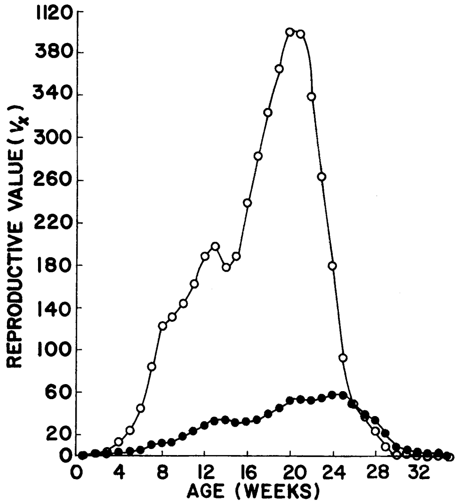

FIG. 3. Age-specific reproductive value (v_x) of *Streblospio benedicti* with planktotrophic and lecithotrophic development, reared in the laboratory at 20°C and salinity 34‰. $v(1) = 1$. (○) planktotrophic strain; (●) lecithotrophic strain.

the lecithotrophic survival advantage during the first 6 wk of life and the planktotrophic fecundity advantage during weeks 7–14. Under the experimental conditions, the contribution of the lecithotrophic survival advantage exceeds that of the planktotrophic fecundity advantage, and the lecithotrophic growth rate is correspondingly higher. As with all other results of laboratory life table studies, this difference may not be preserved under different experimental conditions or in the field.

DISCUSSION

Planktotrophic and lecithotrophic strains of *S. benedicti* differ in a number of life history parameters. The earlier age at first reproduction (Table 1), shorter generation time (Table 2), and higher fecundities (Fig. 2) of individuals with planktotrophic development, are usually thought to be associated with an opportunistic lifestyle. It is surprising to find that despite these differences, the lecithotrophic life table generates a higher net reproductive rate and intrinsic rate of increase (Table 2) under density-independent laboratory conditions. Thus in *S. benedicti,* as in many other invertebrates, reproductive patterns do not align clearly with the expectations derived from early life history theory (see Grahame and Branch 1985). Studies of *Littorina rudis* (Hart and Begon 1982), *Conus* spp. (Perron 1986), and *Ophyrotrocha diadema* (Åkesson 1982) all document life history patterns that conflict with *r* and *K* classifications.

Some similarities between the two strains of *S. benedicti* deserve mention. Larval development times are similar, despite different egg sizes. Lecithotrophic larvae are brooded for ≈2 wk and remain planktonic for ≈1 wk following release. Planktotrophic larvae are brooded for only 1 wk and spend 2 wk feeding in the plankton. In this case development time is not linked to ovum volume. Vance (1973*a, b*) assumed an inverse relationship between ovum volume and development time in his model of selection on larval development. Underwood (1974) pointed out that this assumption was incorrect for prosobranch gastropods and suggested that the absence of correlation between developmental period and egg size was a general phenomenon.

Both planktotrophic and lecithotrophic strains of *S. benedicti* are iteroparous, producing a similar number of broods, despite a twofold difference in the interval between successive broods. Levin and Creed (1986) demonstrated that the volume of oogenic material invested in planktotrophic and lecithotrophic broods is similar. Reproductive effort is probably identical in the two strains, only the packaging of oogenic material differs. *S. benedicti* may provide a single-species example of the situations modeled by Christiansen and Fenchel (1979) in which, given constant reproductive effort, two different egg sizes can be evolutionarily stable. An example of this trade-off, expressed interspecifically, is given by Van Dolah and Bird (1980). They found that gammarid amphipod species living as epifauna produced clutches containing more and smaller eggs than found in clutches of infaunal gammarid species, but that clutch volume did not differ between the two types.

Our estimates of finite and intrinsic rates of increase for *S. benedicti* are similar to those reported for two other opportunistic polychaetes (Table 2). Redman (1984) gives almost identical values for λ and generation time of *Capitella* sp. I reared in the laboratory under similar temperature, salinity, and food conditions. Zajac (1985) estimated λ for different cohorts of *Polydora ligni* in the field. The spring cohorts of *P. ligni* exhibited a λ of 1.38, similar to lecithotrophic *S. benedicti.* However, these cohorts had a shorter generation time (T) and lower net replacement rate (R_0) than either

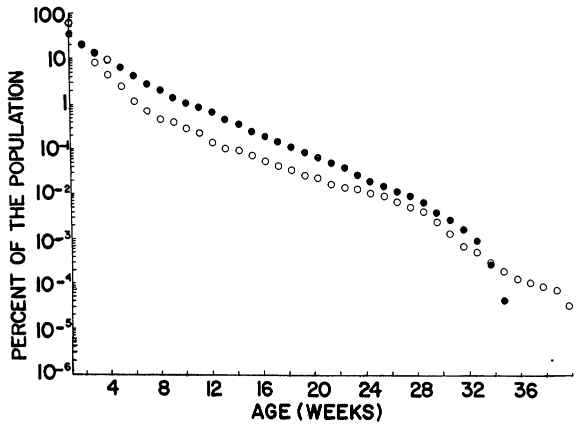

FIG. 4. Predicted stable age distribution (w) of *S. benedicti* under laboratory conditions at 20°C and salinity 34‰. (○) planktotrophic strain; $\lambda = 1.2049$; (●) lecithotrophic strain; $\lambda = 1.3195$.

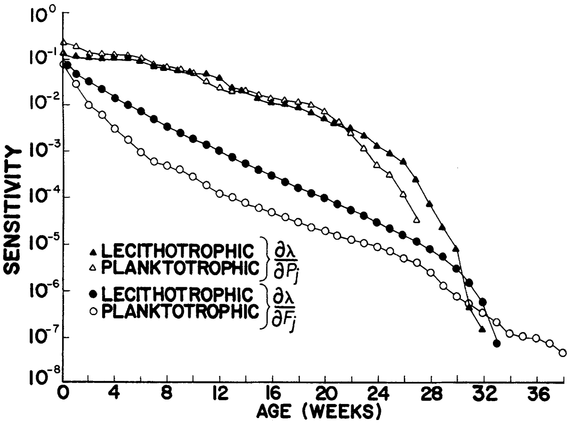

FIG. 5. Sensitivity of the finite rate of increase, λ, to changes in age-specific fecundity (F_j) and survivorship (P_j). Matrices were derived from survivorship and fecundity schedules of *Streblospio benedicti* reared at 20°C and salinity 34‰. Sensitivities are based on the formulations by Caswell (1978).

strain of *S. benedicti.* The early summer cohort of *P. ligni* had λ= 1.22, similar to planktotrophic *S. benedicti,* but even lower values of T and R_0 than the spring cohort. Both *Capitella* and *Polydora* frequently co-occur with *S. benedicti.* All three species are of similar size (10–20 mm) and seem to colonize similar types of disturbed settings (Grassle and Grassle 1974, McCall 1975, Pearson and Rosenberg 1978, Levin 1984*a*). Åkesson (1982) reported that in the laboratory a small (4 mm) dorvilleid polychaete *Ophryotrocha diadema* had generation times ½ to ⅓ those of *S. benedicti* and *Capitella* sp. I, and exhibited finite and intrinsic rates of increase 2 and 4 times (respectively) as high as the other polychaete species. Of the four studies, only Åkesson's involved a nonnatural source of food, spinach.

The population growth rates achieved by planktotrophic and lecithotrophic strains of *S. benedicti* in the laboratory, though similar, are unlikely to explain coexistence of these forms in the field. Under density-independent conditions in the laboratory lecithotrophs have a fitness advantage of almost 10%/wk. If this advantage were maintained, the field planktotrophs would quickly disappear. A number of factors may maintain the observed developmental polymorphism in *S. benedicti*: hybrids may experience superior fitness, environmental variations in time may favor one strain, then another, fine-scale spatial heterogeneity could permit persistence of different forms in different places, or dispersal ability and competitive ability may interact in a compensatory fashion. Several of these possibilities are presently under investigation in Bogue Sound.

Despite the similarities in population growth rates reported for field and laboratory populations of polychaetes (Table 2), the values presented here for *S. benedicti* are almost certainly higher than those achieved in the field. Additional mortality sources, such as loss of larvae, postlarvae, and adults by advection, predation, disease, or starvation, will certainly reduce survivorship in the field. The brood sizes measured in the laboratory (Table 1) were also generally higher than those observed in the field for both planktotrophic and lecithotrophic strains (Levin and Creed 1986). One possible explanation is that animals reared in the laboratory are submerged and can feed 24 hr a day, while those dwelling in intertidal zones cannot feed during low water.

Laboratory studies of the type described here are best used to explore the influence of development mode on population parameters that determine growth potential. The (usually) longer planktonic period experienced by planktotrophic larvae suggests that planktotrophy confers better powers of dispersal, and thus a more opportunistic lifestyle, than does lecithotrophy. However, the life table approach indicates that comparable or higher population growth rates can be achieved through lecithotrophy (Table 2). The best dispersers are not necessarily the most effective colonizers, nor are they necessarily capable of the most rapid population increases. Infaunal species that exhibit rapid population explosions following local disturbances typically have lecithotrophic development and brooded

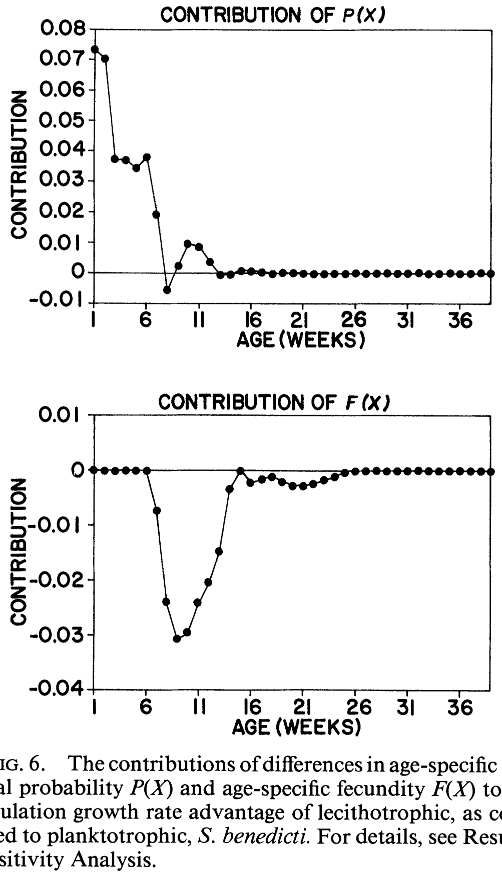

FIG. 6. The contributions of differences in age-specific survival probability $P(X)$ and age-specific fecundity $F(X)$ to the population growth rate advantage of lecithotrophic, as compared to planktotrophic, *S. benedicti.* For details, see Results: Sensitivity Analysis.

larvae (Grassle and Grassle 1974, Levin 1984*a*). These larvae disperse locally, experience high survivorship, and mature rapidly after settlement.

The work presented here is only a first step in understanding the demographic implications of planktotrophy and lecithotrophy. In the present study we have observed that within a single species, under identical laboratory conditions, very different combinations of life history traits can confer a similar capacity for population growth. Both planktotrophic and lecithotrophic modes of development exhibit high population growth rates, the former through a fecundity advantage, the latter through a survivorship advantage early in life. It remains to be seen whether the relationships identified in the laboratory, between development mode and life history parameters, can be extended to the field. Previous studies (Levin and Creed 1986) have demonstrated that both strains exhibit similar responses to variations in temperature and food supply, but many other factors may vary in field settings. Dispersal characteristics were not considered in this study, but undoubtedly play a key role in defining the success of each reproductive strain in the field. An understanding of the adaptive value of different development modes at the population level must therefore focus on the mechanisms by which growth is achieved and the conditions under which particular traits are most successful.

Acknowledgments

Discussions with K. Pollock, D. Crouse, A. Olson, and D. W. Smith contributed to the development of this work. We thank W. Sousa, R. Vance, B. Åkesson, and an anonymous reviewer for suggestions that improved the paper. Access to seawater facilities was provided by C. H. Peterson and the University of North Carolina at Chapel Hill, Institute of Marine Sciences. Drafting was done by P. Bowers and programming by D. W. Smith. The research was supported by NSF Grants OCE 84-00123 and OCE 86-00539 to L. A. Levin and by NSF Grant BSR 82-14583 and NOAA Grant NA83AA-D-00058 to H. Caswell. Woods Hole Oceanographic Institution Contribution 6273.

Literature Cited

Åkesson, B. 1982. A life table study on three genetic strains of *Ophryotrocha diadema* (Polychaeta, Dorvilleidae). International Journal of Invertebrate Reproduction **5**:59–69.

Ayal, U., and U. N. Safriel. 1982. *r* curves and the cost of the planktonic stage. American Naturalist **119**:391–401.

Burton, R. S. 1983. Protein polymorphisms and genetic differentiation of marine invertebrate populations. Marine Biology Letters **4**:193–206.

Burton, R. S., and S. G. Swisher. 1984. Population structure of the intertidal copepod *Tigriopus californicus* as revealed by field manipulation of allele frequencies. Oecologia (Berlin) **65**:108–111.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theoretical Population Biology **14**:215–230.

———. 1981. The evolution of "mixed" life histories in marine invertebrates and elsewhere. American Naturalist **117**:529–536.

———. 1985. The evolutionary demography of clonal reproduction. Pages 187–224 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.

Chernoff, H. 1985. The distribution and abundance of epifauna on the seagrass *Thalassia testudinum* Konig. Thesis. Florida State University, Tallahassee, Florida, USA.

Christiansen, F. B., and T. M. Fenchel. 1979. Evolution of marine invertebrate reproductive patterns. Theoretical Population Biology **16**:267–282.

Eckelbarger, K. J. 1986. Vitellogenic mechanisms and the allocation of energy to offspring in polychaetes. Bulletin of Marine Science **39**:426–443.

Emlet, R. B. 1986. Facultative planktotrophy in the tropical echinoid *Clypeaster rosaceaus* (Linnaeus) and a comparison with obligate planktotrophy in *Clypeaster subdepressus* (Gray) (Clypeasteroida:Echinoidea). Journal of Experimental Marine Biology and Ecology **95**:183–202.

Eyster, L. S. 1979. Reproduction and developmental variability in the opisthobranch *Tenellia pallida*. Marine Biology **51**:133–140.

Grahame, J., and G. M. Branch. 1985. Reproductive patterns of marine invertebrates. Oceanography and Marine Biology: an Annual Review **23**:373–398.

Grassle, J. F., and J. P. Grassle. 1974. Opportunistic life histories and genetic systems in marine benthic polychaetes. Journal of Marine Research **32**:253–284.

Hart, A., and M. Begon. 1982. The status of general reproductive-strategy theories, illustrated in winkles. Oecologia (Berlin) **52**:37–42.

Hines, A. H. 1979. The comparative reproductive ecology of three species of intertidal barnacles. Pages 213–234 *in* S. E. Stancyk, editor. Reproductive ecology of marine invertebrates. University of South Carolina Press, Columbia, South Carolina, USA.

Hughes, R. N., and D. J. Roberts. 1980. Reproductive effort of winkles (*Littorina* spp.) with contrasted methods of reproduction. Oecologia (Berlin) **47**:130–136.

Jablonski, D. J., and R. A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. Biological Reviews of the Cambridge Philosophical Society **58**:21–89.

Kabat, A. R. 1985. The allometry of brooding in *Transenella tantilla* (Gould) (Mollusca:Bivalvia). Journal of Experimental Marine Biology and Ecology **91**:271–279.

Kempf, S. C., and M. G. Hadfield. 1985. Planktotrophy by the lecithotrophic larvae of a nudibranch, *Phestilla sibogae* (Gastropoda). Biological Bulletin (Woods Hole) **169**:119–129.

Keyfitz, N. 1968. Introduction to the mathematics of populations. Addison-Wesley, Reading, Massachusetts, USA.

Lassen, H. H. 1979. Reproductive effort in Danish mudsnails. Oecologia (Berlin) **40**:365–369.

Levin, L. A. 1984*a*. Life history and dispersal patterns in a dense infaunal polychaete assemblage: community structure and response to disturbance. Ecology **65**:1185–1200.

———. 1984*b*. Multiple patterns of development in *Streblospio benedicti* Webster (Spionidae) from three coasts of North America. Biological Bulletin (Woods Hole) **166**:494–508.

Levin, L. A., and E. L. Creed. 1986. Effect of temperature and food availability on reproductive responses of *Streblospio benedicti* (Polychaeta: Spionidae) with planktotrophic or lecithotrophic development. Marine Biology **92**:103–113.

McCall, P. L. 1975. Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. Journal of Marine Research **35**:221–266.

Pearson, T. H., and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanography and Marine Biology Annual Reviews **16**:229–311.

Pechenik, J. A. 1979. Role of encapsulation in invertebrate life histories. American Naturalist **114**:859–870.

Perron, F. E. 1986. Life history consequences of differences in developmental mode among gastropods in the genus *Conus*. Bulletin of Marine Science **39**:485–497.

Ray, A. A. 1982. SAS user's guide: statistics. SAS Institute, Cary, North Carolina, USA.

Redman, C. M. 1984. Effect of temperature and salinity on the life history of *Capitella capitata* (Type I). Dissertation. City University of New York, New York, New York, USA.

Scheltema, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. Biological Bulletin (Woods Hole) **140**:284–322.

Strathmann, R. R. 1974. The spread of sibling larvae of sedentary marine invertebrates. American Naturalist **108**: 29–44.

———. 1978. The evolution and loss of feeding larval stages of marine invertebrates. Evolution **32**:894–906.

———. 1980. Why does a larva swim so long? Paleobiology **6**:373–376.

———. 1982. Selection for retention or export of larvae in estuaries. Pages 521–536 *in* V. S. Kennedy, editor. Estuarine comparisons. Academic Press, New York, New York, USA.

Strathmann, R. R., E. S. Branscomb, and K. Vedder. 1981. Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. Oecologia (Berlin) **48**: 13–18.

Strathmann, R. R., and M. F. Strathmann. 1982. The relationship between adult size and brooding in marine invertebrates. American Naturalist **119**:91–101.

Thiel, H. 1975. The size structure of deep-sea benthos. Internationale Revue der gesamten Hydrobiologie **60**:575–606.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. Meddelelser fra Kommissionen for Havundersoegelser Serie Plankton **4**(1): 1–523.

———. 1950. Reproduction and larval ecology of marine bottom invertebrates. Biological Reviews of the Cambridge Philosophical Society **25**:1–45.

Todd, C. D. 1979. Reproductive energetics of two species of dorid nudibranchs with planktotrophic and lecithotrophic larval strategies. Marine Biology **53**:57–68.

Underwood, A. J. 1974. On models for reproductive strategy in marine benthic invertebrates. American Naturalist **108**:874–878.

Vance, R. R. 1973*a*. On reproductive strategies in marine benthic invertebrates. American Naturalist **107**:339–352.

———. 1973*b*. More on reproductive strategies in marine benthic invertebrates. American Naturalist **107**:353–361.

———. 1980. The effect of dispersal on population size in a temporally varying environment. Theoretical Population Biology **18**:343–362.

Van Dolah, R. F., and E. R. Bird. 1980. A comparison of reproductive patterns in epifaunal and infaunal Gammaridean amphipods. Estuarine and Coastal Marine Science **11**:593–604.

West, H. H., J. F. Harrigan, and S. K. Pierce. 1984. Hybridization of two populations of a marine opisthobranch with different developmental patterns. Veliger **26**:199–206.

Zajac, R. N. 1985. Population dynamics and life history variation in *Polydora ligni* (Annelida:Polychaeta). Dissertation. University of Connecticut, Storrs, Connecticut, USA.

APPENDIX

Life table values and population projection matrix elements for *S. benedicti* reared at 20°C, salinity level of 34‰.

Age	Planktotrophic development				Lecithotrophic development			
(wk)	l_x	m_x	P_i	F_i	l_x	m_x	P_i	F_i
0	1.000	...	0.412	0.000	1.00	...	0.784	0.000
1	0.4123	0	0.482	0.000	0.707	0	0.894	0.000
2	0.1700	0	0.650	0.000	0.632	0	0.894	0.000
3	0.1105	0	0.650	0.000	0.565	0	0.894	0.000
4	0.0718	0	0.650	0.000	0.505	0	0.873	0.000
5	0.0467	0	0.649	0.000	0.452	0	0.901	0.000
6	0.0303	0	0.788	6.383	0.383	0	0.945	3.434
7	0.0197	25.23	0.985	18.413	0.369	8.64	0.924	3.632
8	0.0197	32.62	0.925	26.538	0.342	0	0.959	0.375
9	0.0191	54.08	0.844	36.428	0.315	0.93	1.000	1.080
10	0.0168	70.36	0.795	45.418	0.315	1.64	0.978	4.036
11	0.0135	89.40	0.859	58.291	0.315	8.14	0.977	6.475
12	0.0106	107.30	0.976	65.096	0.301	7.43	0.953	11.141
13	0.0101	97.82	0.970	31.405	0.301	20.00	0.951	14.715
14	0.0101	0.00	0.913	10.157	0.273	15.77	0.976	10.118
15	0.0095	34.64	0.905	31.623	0.273	8.50	0.976	9.008
16	0.0084	70.56	0.963	29.078	0.260	13.25	1.000	8.627
17	0.0078	20.78	1.000	26.436	0.260	7.27	1.000	7.298
18	0.0078	61.56	0.962	54.441	0.260	10.09	1.000	7.378
19	0.0078	112.33	0.960	102.431	0.260	7.46	1.000	15.366
20	0.0072	215.33	1.000	138.801	0.260	29.09	1.000	20.142
21	0.0072	217.00	1.000	144.117	0.260	18.82	0.973	14.941
22	0.0072	231.89	1.000	141.690	0.260	17.18	0.945	18.450
23	0.0072	209.44	1.000	122.392	0.246	28.27	0.971	21.312
24	0.0072	171.78	0.889	69.294	0.232	23.10	1.000	27.415
25	0.0072	49.56	0.875	25.791	0.232	42.11	1.000	25.692
26	0.0056	35.17	0.946	24.002	0.232	19.00	0.942	19.736
27	0.0056	41.83	0.792	21.724	0.232	29.67	0.906	26.273
28	0.0050	32.60	0.607	10.466	0.205	36.22	0.861	20.375
29	0.0034	0	0.667	0.000	0.191	14.22	0.760	7.457
30	0.0017	0	0.824	0.000	0.150	4.63	0.633	3.988
31	0.0017	0	0.786	0.000	0.109	7.67	0.421	3.331
32	0.0011	0	0.773	0.000	0.055	0.60	0.203	0.338
33	0.0011	0	0.706	0.000	0.014	1.00		0.428
34	0.0006	0	1.000	0.000	0	1.00		
35	0.0006	0	1.000	0.000	0	0		
36	0.0006	0	1.000	0.000	0	0		
37	0.0006	0	0.500	0.000	0	0		
38	0.0006	0		0.000	0	0		