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LIFE-HISTORY VARIATION WITHIN A POPULATION OF THE  
COLONIAL ASCIDIAN *BOTRYLLUS SCHLOSSERI*.

I. THE GENETIC AND ENVIRONMENTAL  
CONTROL OF SEASONAL VARIATION

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*Abstract.*—Many empirical analyses of life-history tactics are based on the assumption that demographic variation ought to be greatest among populations or species living in different environments. However, in a single population of the sessile colonial sea squirt *Botryllus schlosseri*, there are two discrete life-history morphs. Semelparous colonies are characterized by a) death immediately following the production of a single clutch, b) early age at first reproduction, c) rapid growth to first reproduction, and d) high reproductive effort. In contrast, iteroparous colonies a) produce at least three clutches before dying, b) postpone sexual reproduction until they are nearly twice the age of semelparous colonies, c) grow at about half the rate of semelparous colonies, and d) invest roughly 75% less in reproductive effort than semelparous colonies. Semelparous colonies numerically dominate the population through midsummer; later in the summer, iteroparous colonies are most numerous. Field and laboratory common-garden experiments, along with breeding studies, indicate that the demographic differences between the morphs are genetically determined. Consequently, the seasonal switch from dominance by semelparous colonies to dominance by iteroparous colonies may be an evolved response to a seasonally changing environment. On theoretical grounds, temporal variation in selection is thought to play a relatively unimportant role in maintaining genetic polymorphism; nonetheless, the seasonally recurrent life-history polymorphism shown in this study indicates that temporal variation in selection can lead to the maintenance of genetic polymorphism for traits strongly affecting fitness.

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Most field tests of life-history theory involve comparisons between populations (or higher taxa) living in environments that presumably select for divergent demographic responses (reviewed in Stearns [1976, 1977, 1980]). In practice, demographic variation within populations is obscured by the use of population-based parameters, such as age-specific birth and death probabilities or the intrinsic rate of increase, to characterize life-history tactics of populations (Berry, 1979; Law, 1979). The theoretical justification for disregarding individual life history is based implicitly on the assumption that directional or stabilizing selection on fitness traits ought to produce a solution that maximizes fitness subject to the ecological and genetic constraints at hand (Lande, 1976, 1982; Istock, 1978, 1982; Soulé, 1982). Such selection leads to the erosion of additive genetic variation within populations and to the prediction that most genetically based life-history variation will be found among higher taxa living in different environments (Bell, 1980; Stearns, 1980; Hegmann and Dingle, 1982; Brown,

1983; but see Istock [1978, 1981] and Berry [1979]).

Despite this prediction, there are numerous studies showing that life-history traits can vary dramatically among members of a population. For example, heritable intrapopulation life-history variation has been reported in insects (Buzzati-Traverso, 1955; Dingle et al., 1977; Istock, 1981, 1982; Rose and Charlesworth, 1981a, 1981b; Hegmann and Dingle, 1982; Rose, 1984), copepods (McLaren, 1976; McLaren and Corkett, 1978; Hart and McLaren, 1978), amphipods (Doyle and Hunte, 1981), cladocerans (Loaring and Hebert, 1981; Lynch, 1983; Pace et al., 1984), rotifers (Snell and King, 1977), bryozoans (Hughes and Hughes, 1986), fish (Reznick, 1982, 1983; Stearns, 1983), rodents (Krohne, 1981), birds (Perrins and Jones, 1974; Cooke and Findlay, 1982), and numerous plants (Myers and Garber, 1942; Jain and Marshall 1967; Kannenberg and Allard, 1967; Allard and Adams, 1969; Chestnutt and Lowe, 1970; Solbrig and Simpson, 1974; Law et al., 1977; Turkington and Harper, 1979; Burdon and

Harper, 1980; Brand, 1981; Grace and Wetzel, 1982).

Documentation of intrapopulation variation and identification of the evolutionary significance of such variation are often hampered by a number of empirical complications. These range from the difficulty of following mobile individuals through their life cycles (rather than averaging performances of all individuals) to the separation of environmental from genetic sources of life-history variation (Berven et al., 1977; Stearns, 1983; Browne et al., 1983; Fletcher, 1984). Furthermore, the mere existence of heritable demographic variation does not reveal the mechanism by which the variation is maintained. Mendelian and quantitative-genetic models suggest that spatially varying selection pressures play a more important role than temporal variation (reviewed in Grant and Price [1981] and Hedrick [1986]). Nonetheless, the models of Hoekstra (1978) and Chesson (1985) suggest that seasonal variation, especially when combined with spatial variation, can maintain genetic polymorphism. Indeed, several recent empirical studies on parthenogenetic cladocerans suggest that seasonally varying selection can make a substantial contribution to the maintenance of genetic diversity (Lynch, 1983; Pace et al., 1984; Carvalho, 1987; Carvalho and Crisp, 1987).

The ecological and developmental attributes of sedentary clonal organisms, such as benthic colonial invertebrates and numerous plants, circumvent many of the demographic and evolutionary uncertainties posed by asexual mobile organisms. Sessile organisms can be followed individually from birth to death both in the field and lab; thus, intrapopulation variation for age-specific traits is readily quantified. Clonal replication of genotypes permits precise estimation of environmental contributions to phenotypic variation in a variety of conditions, as well as the determination of within-genotype values for probabilistic traits (e.g.,  $l_x$  and  $m_x$ ). Perhaps most importantly, the performance of a genotype (or genotypes) can be analyzed in an array of selective regimes (e.g., Solbrig and Simpson, 1974; Service and Lenski, 1982).

For these reasons, I studied life-history variation among individuals in a popula-

tion of the sessile colonial ascidian *Botryllus schlosseri*. In this paper, I document 1) the existence of two discrete life-history morphs, 2) seasonal variation in the abundance of the morphs, and 3) reproductive and survivorship differences between morphs. I also report the results of laboratory and field experiments, as well as a breeding study, designed to reveal the extent to which life-history variation is phenotypically plastic and whether the demographic differences between the morphs have a genetic basis.

#### MATERIALS AND METHODS

##### *Natural History of Botryllus schlosseri*

*Botryllus schlosseri* (Pallas) Savigny is a sessile colonial ascidian (Order Pleurogona: Suborder Stolidobranchia: Family Styliidae). The genus is globally distributed, but *B. schlosseri* is limited to the temperate waters of the Atlantic and the eastern Pacific (possibly) oceans and the Mediterranean, Adriatic, Black, and Baltic seas (Van Name, 1945; Berrill, 1950). Colonies of *Botryllus* are founded by sexually produced tadpole larvae, which rapidly settle onto hard surfaces (Grave and Woodbridge, 1924; Grosberg and Quinn, 1986; Grosberg, 1987). Metamorphosis of a larva into the first zooid of a colony (the oozoid) follows shortly after settlement.

Colonies grow by asexual multiplication which produces a colony composed of morphologically identical modular units termed blastozooids. All of the zooids in a colony usually remain physiologically connected by a blood-vascular system. In contrast to many other colonial ascidians, especially members of the Family Didemnidae (Bak et al., 1981; Ryland et al., 1984), colonies of *Botryllus schlosseri* rarely propagate clonally (only two colonies of more than 3,000 that I observed from recruitment to death in this study ever fragmented).

After larval settlement and metamorphosis, the oozoid produces a set of asexual buds that grow and differentiate synchronously; after approximately six days, the buds differentiate into functional blastozooids (Berrill, 1941; Izzard, 1973). This budding process is termed blastogenesis. As these buds asexually mature, the oozoid is resorbed, and the new blastozooids open

their siphons and begin to feed. In their turn, these blastozooids bud off still more blastozooids (=zooids).

Blastogenesis occurs synchronously among all zooids in a colony (Milkman, 1967; Sabbadin, 1971). Thus, a colony is composed at any given time of blastozooids at three discrete stages of development: 1) adult feeding zooids, 2) the buds on the adult zooids (=primary buds), and 3) the buds on the primary buds (=secondary buds). Every 5–7 days, all of the adult zooids synchronously regress and are resorbed by the colony. At the same time, all of the primary buds open their siphons and begin to feed and replace the former "generation" of adults. Also at this time, the secondary buds become primary buds, new secondary buds appear on the primary buds, and an asexual cycle is completed. The duration of an asexual cycle is inversely correlated to water temperature (Sabbadin, 1955, 1958), and varies only a few hours among colonies grown at the same temperature (Grosberg, 1982).

After 5–10 asexual cycles, mature ovaries and testes (one pair each) appear in the blastozooids (Milkman, 1967). The sexual reproductive cycle is synchronized with the asexual cycle. Once a colony reaches sexual maturity, as each new generation of blastozooids opens its siphons and begins to feed, ovulation occurs. The ova are rapidly fertilized, presumably by sperm brought in with the incurrent flow of water. Because the testes in a zooid ripen after the ova (Milkman, 1967), self-fertilization is probably rare in nature.

Fertilized ova remain in the parental zooid, and embryogenesis is completed just before regression of the parental zooids. The tadpole larvae then swim out of the exhalant siphons of the colony and begin their brief planktonic lives. Because of the synchrony of the asexual and sexual cycles, all sibling larvae are released as a temporally discrete clutch.

#### *Study Site*

All of the field studies described here took place in the Eel Pond at Woods Hole, Massachusetts. The Eel Pond is a typical Cape Cod tidal pond, with a single narrow connection to the sea and several small fresh-

water inputs. The surface area of the Eel Pond is about 1 ha, and its maximum depth at high water is about 5.0 m. Over the two-year period of this study, temperature 1 m below the surface ranged from a winter low of  $-2.5^{\circ}\text{C}$  up to a summer high of  $25.4^{\circ}\text{C}$ . The surface salinity ranged from 13.0 parts per thousand (immediately after summer rains) to 34.5 parts per thousand (during the winter). In the Eel Pond, settlement of *Botryllus schlosseri* larvae begins in early June and declines dramatically after the end of September (Grosberg, 1982).

#### *Field Censusing Techniques*

I examined individual life histories, from settlement to death, by mapping colonies of *Botryllus schlosseri* that recruited onto two sets of five identical glass plates, each measuring 14 cm  $\times$  20 cm (2.25 mm thick). The plates were held in plastic racks suspended horizontally 1 m below the Marine Biological Laboratory's floating supply dock. One set of plates was positioned on 26 May 1979, the other on 26 May 1980. There was little larval recruitment to the upward-facing surfaces of the plates, and survival of these recruits was low (probably due to smothering by sediment). Therefore, only colonies that settled on the downward-facing surfaces of the plate were censused. Colonies that grew onto a 1-cm-wide border on all edges of the plates were not considered in the analyses, as these colonies occasionally grew onto the upward-facing surface of the plates. At every census, I numbered and mapped all newly recruited *B. schlosseri* colonies, using a dissecting microscope and camera lucida drawings. Color photographs were also taken to confirm the mapping data.

In addition to *Botryllus*, many other species recruited onto the plates, and I made every effort not to disturb these colonists. Inevitably, some organisms must have been injured and lost during the sampling process. I did not, however, control for the potential effects of repeated sampling on species distribution and abundance (Schoener and Greene, 1981).

The sampling intervals varied according to the duration of an asexual cycle at ambient water temperature (see next section). At each sampling interval, the five glass

plates were removed from the submerged racks, and each plate was placed vertically in a plastic rack held in a 20-liter bucket of seawater at ambient temperature. The plates were then taken to the lab and immediately put into an aquarium with running seawater (at or near ambient Eel Pond temperature). During censusing, the plates were transferred to a plastic dish fitted with a stand-pipe system, so that fresh seawater continually flowed over the plates. None of the plates ever remained out of the Eel Pond for more than 24 hours.

#### *Calculation of Life-History Parameters*

I gathered the following life-history data from every colony at each census: 1) total number of adult zooids, 2) total number of primary asexual buds borne on the adult zooids, 3) total number of embryos contained in all adult zooids and total number of ova in all primary buds, and 4) the asexual stage of each colony, according to the scheme of Izzard (1973).

I recorded water temperature at the study site at every census. Because all zooids in a colony are developmentally synchronized and the relationship between developmental staging and temperature is known across a range of temperatures (Sabbadin, 1958; Grosberg, 1982), I could determine when the previous change of generation had occurred and predict when the next change would be. Similarly, I inferred the recruitment date of a colony from the developmental stage of its first asexual buds.

Measurement of these static life-history traits, when summed over all asexual cycles, yields a temporally complete description of a colony's life history. Therefore, I censused at intervals just shorter than the duration of an asexual cycle. During the summer, when water temperatures were high and asexual generation times short, I censused the glass plates every five days. During the winter, censusing intervals were increased to as long as 14 days.

If a colony died between census dates, its exact date of death could not be known. I assumed that colonies missing from a given census had died at the end of the asexual generation attained in the previous census. Also, if a newly settled colony died before its first potential census (usually within five

days of settlement), it could not be recorded. Early postsettlement mortality is thus underestimated by this sampling regime. Field data (Grosberg, 1981, 1982) suggest that mortality of *B. schlosseri* does not exceed 8% of a cohort between settlement and the first asexual change of generations several days after settlement.

*Growth Rates.*—There are two components to growth rate in *Botryllus*: 1) the number of buds per zooid in each asexual cycle and 2) the duration of an asexual cycle. The duration of an asexual cycle varies only a few hours among colonies growing at a given temperature but is inversely related to temperature. In the field, therefore, daily growth rates vary according to temperature and can only be used to compare colonies that are growing at the same temperatures. This temperature effect confounds comparisons between colonies growing at different seasons. Nonetheless, because all zooids in a colony are developmentally synchronized asexually and sexually, it is possible to standardize all rate measurements according to asexual cycles rather than solar time.

My growth-rate data (Grosberg, 1982; herein) and those of Morgan (1977), Yamaguchi (1975), and Brunetti (1974) suggest that growth rates (in terms of changes in number of zooids per unit time) of individual botryllid ascidian colonies are constant and exponential until the onset of sexual maturity. Therefore, in the case of *B. schlosseri*, the average number of buds per zooid in each asexual cycle prior to sexual maturity should provide a reliable means to compare growth rates of colonies growing at different temperatures. I calculated pre-reproductive growth rates ( $g$ ) as

$$g = \frac{\log(z_{n-1})}{\log(n-1)}$$

where  $z_n$  = number of zooids in a colony at asexual cycle  $n$  and  $n$  = cumulative number of asexual cycles at sexual maturity. The value  $g$  is an estimate of the mean number of buds per zooid in each asexual cycle averaged over the prereproductive life of a colony. (In figures and tables, growth-rate data are presented as buds per zooid.) Because these data are standardized for asexual cycles

rather than solar time, the effect of temperature on growth rate is removed.

*Age at First Reproduction.*—When comparing age at first reproduction (or longevity) among colonies growing at different temperatures, the number of asexual cycles, rather than solar time, must again be used to avoid the confounding effects of temperature. Thus, I calculated age at first reproduction for each colony by counting the number of asexual cycles between metamorphosis and the first release of larvae.

*Number of Clutches.*—Each synchronous release of larvae constitutes a clutch, and the total number of releases over the lifetime of a colony yields clutch number.

*Reproductive Effort.*—The number of ova within a primary bud or the number of larvae within an adult zooid can be counted directly with a dissecting microscope without disrupting a colony; thus, the number of ova per primary bud or the number of embryos per zooid can easily be quantified on a per clutch basis. I removed the confounding effect of colony size on clutch size simply by counting the total number of embryos that composed a clutch and dividing this value by the number of zooids that held the embryos. This yields the number of embryos per zooid in each clutch. For colonies that produced more than one clutch, I estimated reproductive effort by dividing the sum of the number of embryos in each clutch by the sum of the number of zooids in each clutch over the reproductive span of the colony.

#### *Genetic and Environmental Control of Life-History Variation*

The field data taken in 1979 suggested that there was considerable life-history variation in the Eel Pond population of *B. schlosseri*. To determine how environmental variation affected the expression of life-history variation and whether this variation had a genetic component, I initiated three types of experimental study.

*Laboratory Study.*—To examine the phenotypic response of individual genotypes to a controlled array of environmental conditions, I varied feeding level and temperature in a factorially designed laboratory experiment. On 24 July 1980, I collected ten newly recruited (within the previous five

days) colonies of *B. schlosseri* from the side of the Marine Biological Laboratory (MBL) supply dock. I consider these colonies to be separate genotypes, because each colony was founded by a sexually produced larva. I chose five rapidly growing colonies (with more than 4.0 buds per zooid) and five slowly growing colonies (with fewer than 2.5 buds per zooid) to represent the two life-history morphs identified in the field censuses. I allowed these colonies to continue growing in running seawater until they reached a size of at least 50 zooids. From each of these 10 colonies, I isolated single zooids, which served as clonal replicates. I attached each of these zooids individually to a 10 cm × 10 cm glass plate (methods given in Grosberg [1982]). The glass plates were held vertically, 2 cm apart, in acrylic plastic racks. The racks were placed in glass aquaria holding 60 liters of filtered seawater (1  $\mu$ m). Every other day, the water in the aquaria was replaced with previously unused, acclimated filtered seawater. All experiments were conducted using the same lot of seawater, and all colonies were reared on a 12L:12D photoperiod cycle.

There were three feeding and three temperature treatments; thus, there were nine treatments in all. The three culture temperatures were 15°C, 20°C, and 25°C. This temperature range encompasses the in situ temperature range during the reproductive season of *B. schlosseri*. Colonies were fed a commercially prepared diet that consists primarily of a colloidal suspension of yeast particles (Marine Invertebrate Diet, Aquarium Products, Inc., Houston, TX). Because the colonies were cultured in a fixed volume of seawater, I manipulated feeding level by providing a prescribed amount of food per zooid in each aquarium every other day. As I censused the colonies, I calculated the total number of zooids in each aquarium. In the low feeding level treatment (1 $\times$ ), I added 0.1 ml of Marine Invertebrate Diet per 1,000 zooids to each aquarium; in the medium-level treatment (2 $\times$ ), I added 0.2 ml of food per 1,000 zooids; and in the high level treatment (3 $\times$ ), I added 0.3 ml of food per 1,000 zooids.

Five single-zooid clonal replicates from each of the 10 original colonies were reared in all nine temperature and feeding com-

binations. Of the 450 colonies (9 treatments by 10 genotypes by 5 clonal replicates) used in this experiment, eight died before reaching sexual maturity. Extra clonal replicates of each colony in each treatment were maintained, and data from these replicates were used to replace data lost from colonies dying before they sexually reproduced.

All 50 colonies (five replicates of the ten genotypes) in a given temperature and food treatment were reared in the same 60-liter aquarium. The three food-treatment aquaria (i.e., 1×, 2×, and 3×) at a given temperature were placed in the same environmentally controlled incubator; the three incubators were held at 15°C, 20°C, and 25°C.

I started the experiment on 12 September 1980, and all colonies were censused every fourth day thereafter until their deaths. The data were analyzed using a partially nested mixed-model ANOVA (SAS Institute, 1985), with the five colonies derived from both the fast- and slow-growing types nested within life-history morph. The life-history-morph effect was treated as a fixed effect and tested using the genotype within life-history-morph mean square as the error term. Temperature and feeding level were also considered to be fixed effects in the ANOVA model. Genotype nested within life-history morph was considered as a random effect, as were all interaction terms containing this effect. The residuals were not distributed normally (Kolmogorov-Smirnov *D* statistic; SAS Institute, 1985); however, a logarithmic transformation of each of the dependent variables normalized the residuals. All estimates are reported in the original units of measurement.

*Field Study.*—At any given time from the early summer through late autumn, there were at least 15 species of sedentary encrusting and arborescent animals inhabiting the plates used in the field censuses (Grosberg, 1981, unpubl.). To remove the confounding effects of this potential source of life-history variation, I recorded patterns of life-history variation within and among temporally discrete cohorts of *B. schlosseri* grown in isolation.

Beginning on 15 June 1980, every 15 or 16 days, I suspended a set of ten identical glass plates (20 cm × 20 cm) under the MBL

supply dock using the racks described above. One day after placement, I recovered the plates and used a razor blade to remove all organisms that had colonized the plates, except for the single *B. schlosseri* colony located closest to the center of each plate. Subsequently, every second day, I removed all other organisms that colonized the plates and monitored the life-history traits of the single *B. schlosseri* on the plate. I recorded the life history of eight cohorts, each composed of 10 colonies growing singly on identical plates, until all members of a given cohort had died.

*Breeding Study.*—To determine whether naturally occurring variation in reproductive effort was genetically based, I mated each of the ten colonies used for the laboratory study in a complete set of diallel crosses (sensu Falconer, 1981). Because colonies are hermaphroditic, each colony was used reciprocally as a male and female in all possible combinations; thus, there were 100 crosses in all. I mated the colonies using the *in vitro* methods described in Grosberg (1987). Ten progeny from each cross were reared individually on 10 cm × 10 cm glass plates. The parental colonies and their progeny were grown at 20°C and fed at the 2× level.

The data on *F*<sub>1</sub> reproductive effort were analyzed using a partially nested, mixed-model ANOVA. The main effects were 1) paternal life-history morph, 2) maternal life-history morph, 3) paternal genotype nested within life-history morph, and 4) maternal genotype nested within life-history morph. The first two independent variables were considered as fixed effects, whereas the second two variables were treated as random effects.

## RESULTS

### *Seasonal Patterns of Life-History Variation in the Field*

From June 1979 through June 1981, 3,393 *B. schlosseri* colonies settled onto the two sets of five plates beneath the MBL supply dock and survived to reproduce sexually at least once. Data on reproduction and growth are presented only for these survivors (i.e., those settlers that survived until I actually censused them); however, survivorship data

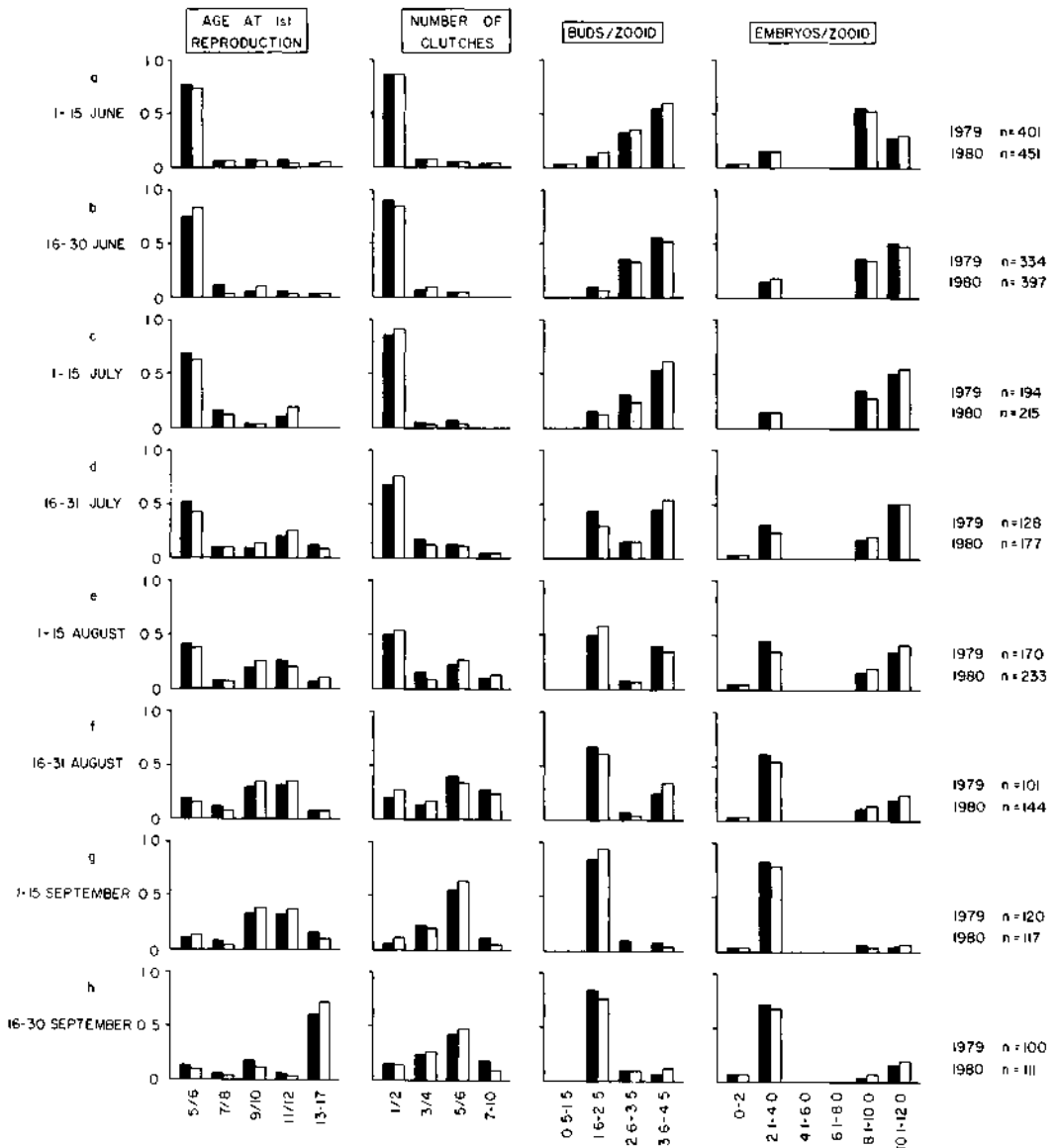


FIG. 1. Frequency distributions of four life-history traits: 1) age at first reproduction (asexual cycles), 2) number of clutches, 3) number of buds per zooid per asexual cycle (growth rate), and 4) number of embryos per zooid per clutch (reproductive effort). The distributions are based on colonies that recruited in the field during the intervals shown in a-h. Solid bars represent data from 1979 cohorts; open bars represent data from 1980 cohorts.

are reported for all recruits, regardless of whether they became sexually mature.

To document seasonal patterns of life-history variation, I divided the recruitment season into eight approximately two-week intervals from 1 June to 30 September and sorted colonies into cohorts according to when they recruited. Few colonies of *B.*

*schlosseri* recruited before or after these dates. Figure 1 shows frequency histograms for 1) age at first reproduction, 2) number of clutches, 3) mean number of embryos per zooid, and 4) number of buds per zooid (during the prereproductive period) for colonies that recruited during both years of this study.



*Age at First Reproduction.*—Over all cohorts, colonies reproduced either at asexual cycles 5 and 6, or at cycle 9 and thereafter; few colonies reproduced at intermediate ages (i.e., cycles 7 and 8). There was a seasonal pattern in the timing of first reproduction during both years of the study. Colonies appearing early in the summer generally reproduced at the fifth or sixth asexual cycle (Fig. 1a–d). By midsummer, about half of the newly recruiting colonies reproduced at the 5th or 6th cycle, but nearly 50% postponed reproduction until the ninth cycle and beyond (Fig. 1e,f). By the end of the settlement season, the majority of new colonies delayed reproduction until the ninth asexual cycle and later. Virtually all members of the last cohort failed to reproduce sexually until the following spring. Yet, even among these late recruits, the distribution of ages at first reproduction, although shifted somewhat later than for earlier recruits, remained weakly bimodal (Fig. 1h).

*Number of Clutches.*—Over the course of the summers, there were two types of reproductive pattern in terms of total number of clutches. Among early-summer cohorts, most colonies produced one clutch (Fig. 1a–d). In fact, 95% of colonies in the 1–2-clutch category reproduced once, then died. By midsummer, about 50% of recruiting colonies released a single clutch, and about 50% released four or more clutches (Fig. 1e,f). By the end of the summer, nearly all recruiting colonies produced at least four or five clutches before their deaths (Fig. 1g,h). Few colonies produced only three or four clutches.

*Growth Rate.*—Throughout the recruitment season, relatively few colonies had intermediate growth rates (i.e., 2.6–3.5 buds per zooid). During the first eight weeks of summer, more than 80% of colonies grew, on average, at a rate greater than 2.5 buds per zooid (per asexual cycle) during prereproductive growth; 50% of recruiting colonies produced at least 3.6 buds per zooid (Fig. 1a–d). In contrast, by midsummer, about half the recruiting colonies produced 2.5 bud per zooid or fewer. By the end of the summer, over 80% of recruiting colonies grew relatively slowly, producing 2.5 buds per zooid or fewer. Among overwintering colonies, growth rates decreased for all col-

onies when compared to earlier intervals. Nevertheless, the bimodal phenotypic distribution remained (Fig. 1g).

*Reproductive Effort.*—The mean clutch size of colonies that settled during June and July consistently exceeded eight embryos per zooid (Fig. 1a–d). This pattern predominated until August, when recruiting colonies having about 50% the reproductive effort of earlier cohorts came to dominate the population (Fig. 1e,f). By the end of the settlement season, nearly all recruiting colonies had relatively low reproductive effort (i.e., 4 embryos per zooid or fewer; Fig. 1g,h).

*Survival to First Reproduction.*—With the exception of overwintering colonies, the proportion of colonies in a cohort surviving from recruitment (usually within five days of settlement) to sexual maturity (the first release of larvae) ranged from a low of 7.7% for the 16–31 July 1979 interval to a high of 21.8% during the 1–15 June 1979 interval. Most of the colonies recruited at the end of the settlement season (after 15 September) did not reproduce sexually until the following spring. Overwintering survivorship of these colonies exceeded 90% in both 1979 and 1980.

*Annual Variation.*—To determine whether comparable sampling intervals in 1979 and 1980 had similar frequency distributions of the four life-history traits (excluding survival to first reproduction), I compared frequency distributions in 1979 and 1980 for each trait at each time interval using a chi-square test of independence. I pooled categories when necessary to avoid cell sizes that were less than 5. In three of 32 (eight cohorts  $\times$  four traits) annual comparisons, there were small but significant differences between years (i.e., age at first reproduction of the 16 June cohorts [ $X^2 = 33.043$ ,  $d.f. = 4$ ,  $P < 0.001$ ], growth rate of the 16–31 August [ $X^2 = 7.225$ ,  $d.f. = 2$ ,  $P = 0.03$ ] and 1–15 September cohorts [ $X^2 = 5.189$ ,  $d.f. = 1$ ,  $P = 0.02$ ]). In general, however, the frequency distributions were quite similar between years.

*Correlations Among Life History Traits.*—The histograms shown in Figure 1 suggest possible correlations among particular life-history traits. The Pearson product-moment correlations (based on log-transformed data) among age at first reproduc-

TABLE 1. Pearson product-moment correlations among age at first reproduction, number of clutches, growth rate, and reproductive effort, based on colonies in the field. All correlations are significant at  $P < 0.001$ .

Character	Character		
	Number of clutches	Growth rate	Reproductive effort
Age at first reproduction	0.664	-0.749	-0.523
Number of clutches	—	-0.603	-0.650
Growth rate	—	—	0.603

tion, clutch number, growth rate, and reproductive effort are reported in Table 1. The correlations show that 1) age at first reproduction is positively associated with the number of clutches but negatively correlated with both growth rate and reproductive effort, 2) number of clutches is negatively correlated with growth rate and reproductive effort, and 3) growth rate is positively related to reproductive effort.

The bivariate plots shown in Figure 2 are syntheses of the histograms and the correlations. The presence of two distinct groups of observations in each plot corroborates the rarity of intermediate phenotypes for the entire suite of four life-history traits. The strong correlations between life-history traits and the bimodal distributions of each of these traits show that there are two discrete life-history phenotypes among *Botryllus schlosseri* colonies in the Eel Pond. Most colonies settling early in the summer 1) reproduce sexually at the fifth or sixth asexual cycle, 2) produce a single clutch, 3) grow rapidly (at rates approaching 4–5 buds per zooid), and 4) have a high reproductive effort (10–12 embryos per zooid in each clutch). I term colonies possessing this suite of life-history characters "semelparous" morphs. In contrast, after mid-August, most recruiting colonies 1) postpone reproduction until the ninth or tenth asexual cycle, 2) produce three or more clutches, 3) grow relatively slowly (at rates between 1.5 and 2.5 buds per zooid), and 4) have a low re-

TABLE 2. Life table on the cohort of iteroparous colonies recruited in the field during 1–15 September 1979. Iteroparous colonies do not, in general, reproduce sexually before the ninth asexual cycle. Hence, survivorship data prior to the ninth asexual cycle are omitted. Estimates of survivorship do not include planktonic mortality of larvae. Decreasing age-specific fecundity results from decreasing colony size with age and not from decreasing reproductive effort.

Age (x) (number of asexual cycles)	Survivorship ( $l_x$ ) (proportion of cohort)	Fecundity ( $m_x$ ) (mean clutch size)
9	0.207	1,596
10	0.201	1,932
11	0.186	2,318
12	0.173	1,957
13	0.110	1,843
14	0.053	1,639
15	0.021	1,704

productive effort (between two and four embryos per zooid). I term these colonies "iteroparous" morphs.

*Intrinsic Rates of Increase.*—The calculation of maximum intrinsic rate of increase ( $r_{max}$ ) from cross-sectional population data requires the assumption of a stable age-distribution. This is clearly not the case in the Eel Pond population of *B. schlosseri*. However, because I monitored individual life histories, I could construct the life table of a cohort of recruits without assuming a stable age-distribution. I calculated  $r_{max}$  for semelparous colonies using the cohort recruited during 15–30 June 1979, when the survivorship of recruits to first reproduction was greatest. Similarly, I calculated  $r_{max}$  for iteroparous colonies during 1–15 September 1979, when survivorship to first reproduction was highest. For both semelparous and iteroparous colonies, survivorship estimates are inflated because a) I could not estimate larval mortality in the plankton and b) I chose periods of maximum survivorship to construct the life tables. There is no a priori reason to assume that rates of larval mortality differ between semelparous and iteroparous morphs; nonetheless, these estimates of  $r_{max}$  for *B. schlosseri* cannot be compared to other taxa.

→

FIG. 2. Bivariate plots based on field data showing the relationships among 1) age at first reproduction, 2) number of clutches, 3) number of buds per zooid per asexual cycle (growth rate), and 4) number of embryos per zooid per clutch. Numbers in parentheses represent overstrikes. The plotted data represent a random subsample of 200 of the 3,393 colonies that recruited to the panels during this study.

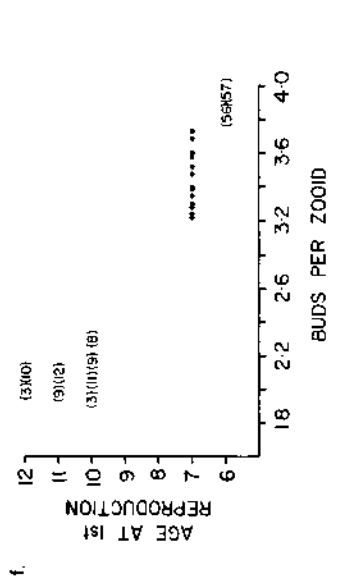
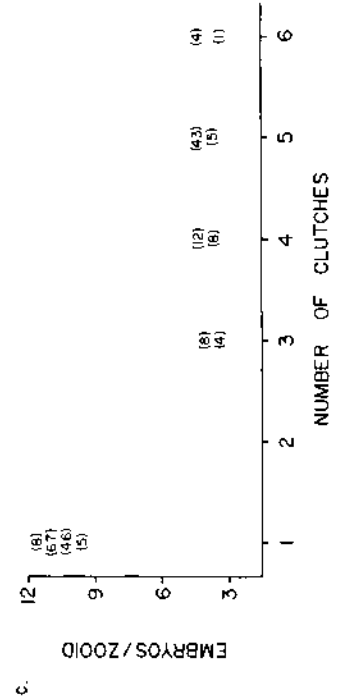
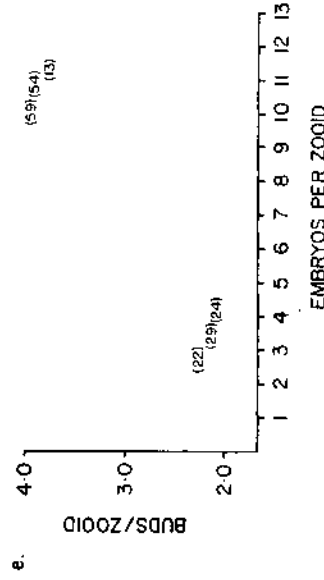
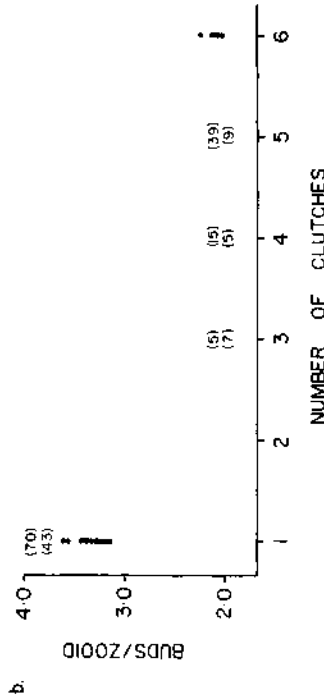
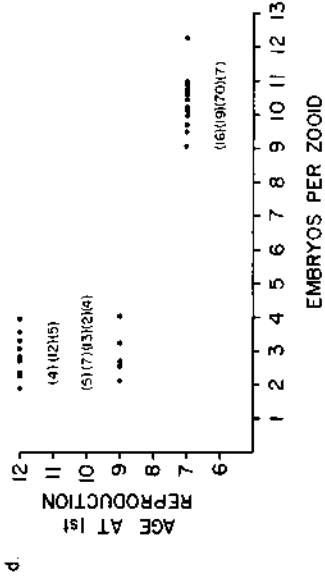
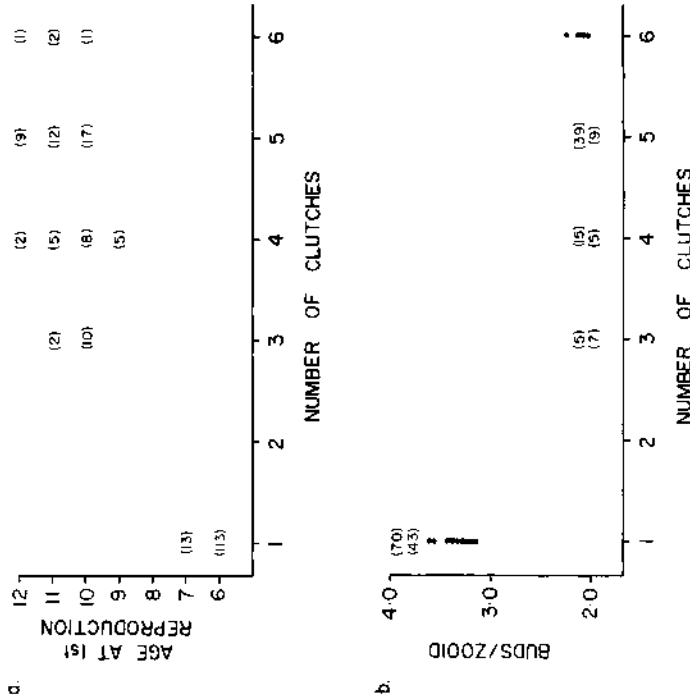


TABLE 3. The means of five life-history traits for each temperature and life-history morph in the laboratory study. Key to life-history traits: 1) age at first reproduction (number of asexual cycles), 2) size at first reproduction (number of zooids), 3) number of clutches, 4) growth rate (buds per zooid per asexual cycle), and 5) reproductive effort (embryos per zooid per clutch).

Life-history morph	Temperature (°C)	Life-history trait				
		1	2	3	4	5
Semelparous	15	7.57	224.65	1	3.12	10.06
Semelparous	20	7.56	227.68	1	3.11	9.88
Semelparous	25	7.60	224.12	1	3.10	10.04
Iteroparous	15	12.81	672.53	4.66	1.86	2.85
Iteroparous	20	12.74	658.80	4.56	1.86	2.91
Iteroparous	25	12.85	646.68	4.62	1.84	2.95

To calculate  $r_{\max}$  for semelparous colonies, I first estimated the mean age at first reproduction to be 6.28 asexual cycles (SD = 0.57 cycles). During 1–15 June, the survivorship from recruitment to first reproduction was 0.218. The mean fecundity of the survivors was 2,267 embryos (SD = 298 embryos). Substitution of these values into the Euler-Lotka equation (Mertz, 1970) yields  $r_{\max} = 0.99$ . I calculated  $r_{\max}$  for iteroparous colonies based on the life table shown in Table 2. Based on the method of Birch (1948) for solving the Euler-Lotka equation, the best iterative solution for  $r_{\max}$  is 0.72.

#### *Genetic and Environmental Control of Life-History Variation*

*Laboratory Study.*—The mean values of the five life-history traits for the two life-history morphs are shown classified according to temperature in Table 3 and classified according to feeding level in Table 4. The results of the analyses of variance are shown in Table 5. There were no significant differences among genotypes within life-history morphs. In contrast, there was always

a highly significant effect of life-history morph on all five of the dependent variables. Indeed, estimation of the magnitude of the life-history-morph effect (Winer, 1971 p. 429) shows that this factor accounts for 71–95% of the total variance of all life-history traits (Table 5).

Temperature did not significantly affect age at first reproduction (in asexual cycles), growth rate, or lifetime number of clutches (Tables 3, 5). Temperature had a small ( $< 1\%$  of the total variance) but nonetheless significant effect on size at first reproduction. In the case of reproductive effort, there is a minor effect ( $< 1\%$  of the total variance) of the interaction between temperature and feeding level.

Feeding level significantly affected all five life-history traits but never accounted for more than 20% of the variance (Table 5). The middle and upper feeding levels (2 $\times$  and 3 $\times$ ) had similar effects on the dependent variables (Table 4). The effects of feeding level, however, were always confounded by significant interactions with life-history morph (Table 5). The low feeding level (1 $\times$ ) was associated with nearly a 40% delay in

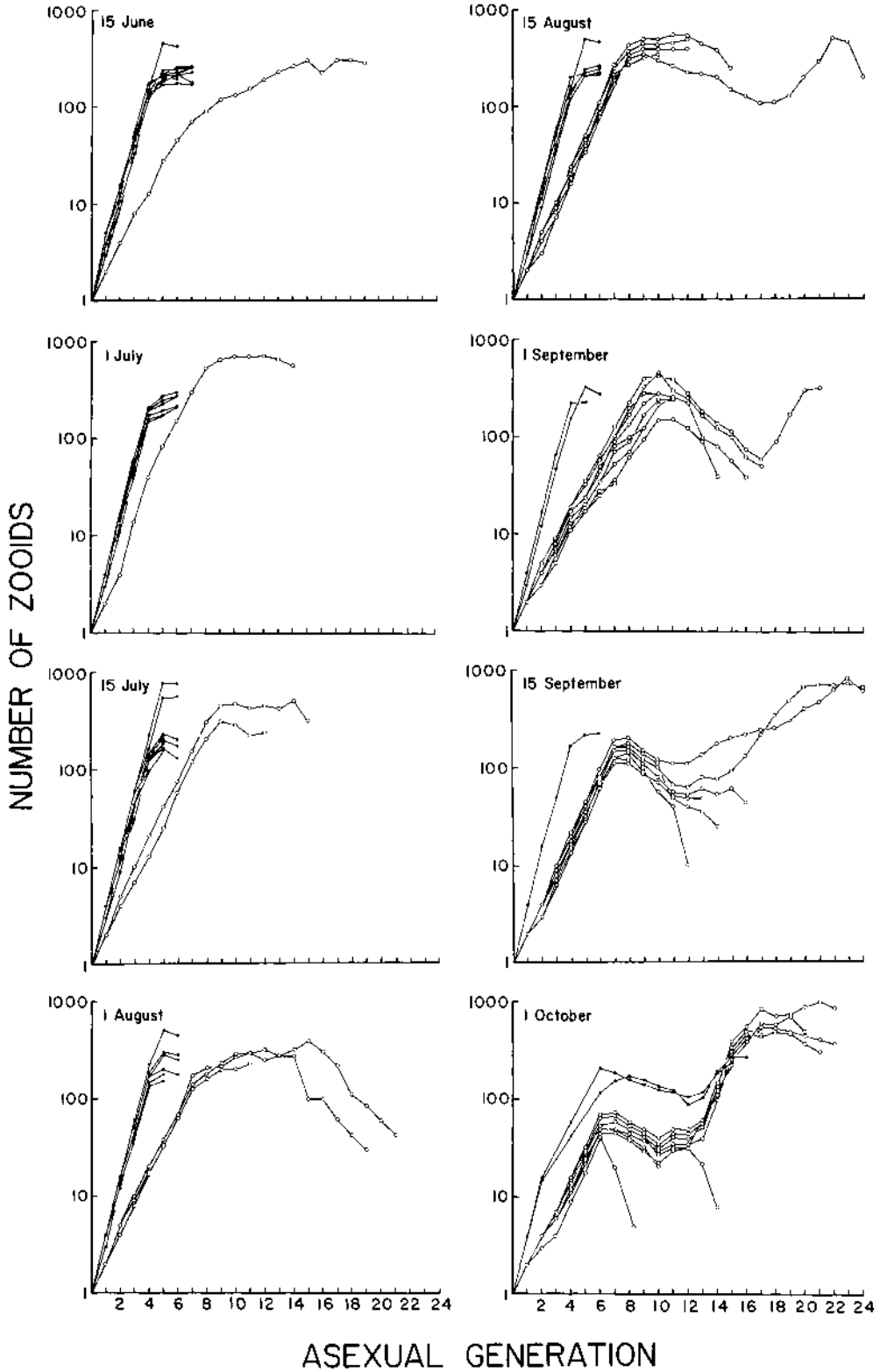
TABLE 4. The means of five life-history traits for each feeding level and life-history morph in the laboratory study. Key to life-history traits: 1) age at first reproduction (number of asexual cycles), 2) size at first reproduction (number of zooids), 3) number of clutches, 4) growth rate (buds per zooid per asexual cycle), and 5) reproductive effort (embryos per zooid per clutch).

Life-history morph	Feeding level	Life-history trait				
		1	2	3	4	5
Semelparous	1 $\times$	10.26	237.88	1	1.99	10.02
Semelparous	2 $\times$	6.26	217.61	1	3.64	9.99
Semelparous	3 $\times$	6.20	220.96	1	3.70	9.97
Iteroparous	1 $\times$	15.45	654.22	4.12	1.62	2.11
Iteroparous	2 $\times$	11.37	659.69	4.84	1.99	3.24
Iteroparous	3 $\times$	11.58	664.17	4.89	1.97	3.37

TABLE 5. Analyses of variance on the effects of temperature, feeding level, colony life-history morph, and genotype on age and size at first reproduction, number of clutches, size at first reproduction, growth rate, and reproductive effort in the laboratory study. Percentages of total variance, calculated by the method of Winer (1971), are given in parentheses. The *F* ratios for all effects were constructed using for the denominator the mean-square term lacking only that effect as a variance component, e.g., the life-history-morph effect was tested using the genotype(life-history-morph) effect as the denominator. All terms containing the genotype effect were treated as random effects.

Source of variation	d.f.	Character									
		Age at first reproduction		Size at first reproduction		Number of clutches		Growth rate		Reproductive effort	
		MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>	MS	<i>P</i>
Temperature	2	2.27 × 10 <sup>-4</sup>	ns	3.25 × 10 <sup>-3</sup>	*	5.64 × 10 <sup>-3</sup>	ns	2.36 × 10 <sup>-4</sup>	ns	2.04 × 10 <sup>-3</sup>	ns
Feeding level	2	1.50 (19.2)	***	1.25 × 10 <sup>-2</sup>	***	4.05 × 10 <sup>-2</sup>	***	1.52 (18.8)	***	4.69 × 10 <sup>-1</sup>	***
Life-history morph	1	6.28 (75.8)	***	24.38 (95.1)	***	22.18 (93.8)	***	4.81 (71.0)	***	33.53 (92.4)	***
Genotype(life-history morph)	8	1.92 × 10 <sup>-4</sup>	ns	7.20 × 10 <sup>-4</sup>	ns	9.20 × 10 <sup>-4</sup>	ns	2.26 × 10 <sup>-4</sup>	ns	7.77 × 10 <sup>-4</sup>	ns
Temperature × feeding level	4	5.57 × 10 <sup>-4</sup>	ns	1.42 × 10 <sup>-3</sup>	ns	6.40 × 10 <sup>-4</sup>	ns	4.05 × 10 <sup>-4</sup>	ns	3.23 × 10 <sup>-4</sup>	ns
Temperature × life history	2	1.25 × 10 <sup>-4</sup>	ns	2.97 × 10 <sup>-3</sup>	*	5.64 × 10 <sup>-4</sup>	ns	1.10 × 10 <sup>-5</sup>	ns	2.30 × 10 <sup>-3</sup>	ns
Feeding level × life history	2	9.89 × 10 <sup>-2</sup>	***	1.90 × 10 <sup>-2</sup>	***	4.04 × 10 <sup>-2</sup>	***	3.97 × 10 <sup>-1</sup>	***	4.89 × 10 <sup>-1</sup>	***
Temperature × genotype	16	3.45 × 10 <sup>-4</sup>	ns	6.27 × 10 <sup>-4</sup>	ns	1.13 × 10 <sup>-3</sup>	ns	4.77 × 10 <sup>-4</sup>	ns	1.77 × 10 <sup>-3</sup>	***
Feeding level × genotype	16	3.62 × 10 <sup>-4</sup>	ns	4.70 × 10 <sup>-4</sup>	ns	1.26 × 10 <sup>-3</sup>	ns	5.41 × 10 <sup>-4</sup>	ns	1.02 × 10 <sup>-3</sup>	ns
Temperature × feeding level × genotype	32	2.52 × 10 <sup>-4</sup>	ns	6.93 × 10 <sup>-4</sup>	ns	1.82 × 10 <sup>-3</sup>	ns	3.84 × 10 <sup>-4</sup>	ns	5.71 × 10 <sup>-4</sup>	ns
Temperature × feeding level × life history	4	1.30 × 10 <sup>-3</sup>	ns	4.70 × 10 <sup>-4</sup>	ns	6.40 × 10 <sup>-4</sup>	ns	6.50 × 10 <sup>-4</sup>	ns	2.60 × 10 <sup>-3</sup>	**
Residual	360	5.52 × 10 <sup>-4</sup>	ns	8.52 × 10 <sup>-4</sup>	ns	1.66 × 10 <sup>-3</sup>	ns	8.64 × 10 <sup>-4</sup>	ns	6.35 × 10 <sup>-4</sup>	ns

\* *P* < 0.05; \*\* *P* < 0.01; \*\*\* *P* < 0.001.



sexual maturity among semelparous colonies and a 26% delay for iteroparous colonies (Table 4). There was a minor increase (~8%) in size at first reproduction for semelparous colonies at low feeding levels, whereas size at first reproduction decreased slightly among iteroparous colonies. At the lowest feeding level (1×), both iteroparous and semelparous colonies had lower growth rates; however, the effect of starvation on growth rate was greater for semelparous (~45% decrease) compared to iteroparous (~18% decrease) colonies. Although there was no obvious effect of feeding level on reproductive effort among semelparous colonies, iteroparous colonies suffered at least a 45% decline in reproductive effort at the lowest feeding level compared to higher feeding levels. This effect of feeding level on reproductive effort of iteroparous colonies was slightly influenced by temperature (Table 5: temperature × feeding level × life-history morph interaction). Finally, semelparous colonies always produced a single clutch, whatever the feeding level; in contrast, the number of clutches produced by iteroparous colonies at the lowest feeding level decreased some 15%.

In general, both life-history morphs showed some measure of phenotypic plasticity in response to environmental variation. However, the significant interaction between feeding level and life-history morph indicates that the morphs responded differently to changes in feeding level. For semelparous morphs, reproductive effort, size at first reproduction, and clutch number appear to be relatively fixed characters; the starvation-mediated decline in growth rate translates into delayed reproduction but not lowered reproductive effort or total reproductive output. Iteroparous colonies also fix size at first reproduction in the lab and suffer decreased growth rates at low feeding levels; in contrast to semelparous colonies, reproductive effort declines significantly when colonies are starved. Despite the plastic re-

sponses of both life-history morphs to variation in temperature and feeding regime, the phenotypes of the two morphs, once determined, remained distinct across all treatments.

*Field Study.*—Because of the bimodal distribution of life-history phenotypes indicated in Figures 1 and 2, it is potentially misleading to represent the demographic structure of a cohort simply with parametric summary statistics. Rather than presenting data on the complete life history of each recruit, I show only the growth trajectories of all colonies in each cohort (Fig. 3). As growth rate is significantly phenotypically correlated to reproductive effort, number of clutches, and age at first reproduction, these trajectories provide a reasonably complete portrait of the life histories of each recruit.

Two patterns emerge from these data. First, in every cohort there were two classes of growth trajectories: slow-growing morphs grew exponentially at a rate of 1.6–2.5 buds per zooid until the asexual cycle preceding sexual maturity. In general, exponential growth terminated, and sexual maturity commenced, sometime near the tenth asexual cycle (at the point of inflection of the curves). Most such colonies maintained a fairly constant size or shrank slightly once reproduction began. Rapidly growing colonies also grew exponentially until the asexual cycle preceding sexual maturity. In comparison to the slow-growing colonies, these colonies grew twice as fast (3.6–4.5 buds per zooid), ceased growing at the fifth or sixth asexual cycle, produced a single, large clutch, then all promptly died. Of the last cohort of colonies (1 October), 80% of the colonies survived the winter, but none managed to reproduce before the onset of winter. Such high overwintering survival agrees with that found on the unmanipulated panels. The following spring, all of the colonies that had survived the winter reproduced sexually, but the colonies that grew initially as semelparous colonies in the previous fall reproduced

←

FIG. 3. The growth trajectories of eight cohorts (each composed of 10 colonies) initiated fortnightly in the field common-garden experiment. The solid circles show trajectories for semelparous colonies; the open circles show trajectories for iteroparous colonies. The end of each trajectory represents the death of the colony. The ordinate is on a logarithmic scale.

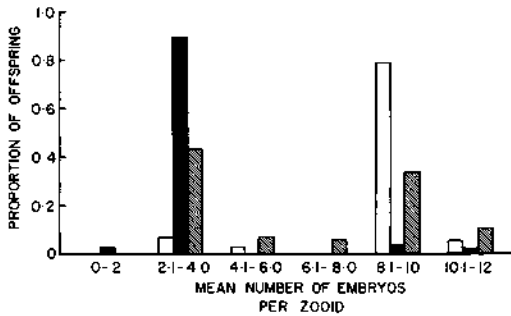


FIG. 4. Phenotypic frequencies of  $F_1$  reproductive effort according to parental life-history morph. Open bars show data for  $F_1$ 's from crosses between semelparous parents; solid bars show data from crosses between iteroparous parents; hatched bars show data from semelparous  $\times$  iteroparous crosses ( $N = 100$  crosses).

about four weeks before iteroparous colonies.

Second, in parallel with the field data, both life-history morphs recruited to the panels in every cohort, and there was a seasonal shift from initial numerical dominance of the cohorts by semelparous colonies to dominance by iteroparous colonies (Fig. 3).

*Breeding Study.*—Figure 4 shows the phenotypic distributions of reproductive effort of  $F_1$  progeny according to the life-history phenotypes of their parents. Crosses involving semelparous parental genotypes with high reproductive effort yielded progeny with similar phenotypes. Likewise, most progeny from crosses between iteroparous parents had patterns of reproductive effort that are typical of iteroparous colonies. Crosses between semelparous and iteroparous parents produced roughly equal fractions of  $F_1$ 's with high and low reproductive effort; intermediate phenotypes were rare. Within  $F_1$  sibships of crosses between semelparous and iteroparous parents, the relative frequencies of semelparous and iteroparous progeny did not deviate significantly from 1:1 ( $\chi^2 = 2.45$ ,  $d.f. = 2$ ,  $P > 0.4$ ). The patterns of inheritance of other life-history traits, including growth rate, age at first reproduction, and number of clutches, are very similar to that reported here for reproductive effort (Grosberg, 1982).

An ANOVA of these data (Table 6) shows that paternal and maternal life-history type make highly significant contributions to  $F_1$

phenotypic variance. Likewise, paternal and maternal genotypes nested within life-history type also account for significant amounts of  $F_1$  variance. This latter result indicates that there is some variation among genotypes of a specific life-history type in their contributions to  $F_1$  phenotype. The nearly equal proportions of variance explained by maternal and paternal effects, as well as the absence of any significant interaction terms, suggest that the effects of gender on  $F_1$  phenotype are minimal.

Individually, the significant terms in this ANOVA explain a relatively small fraction of the total variance; even taken together, these terms explain less than 40% of the total  $F_1$  phenotypic variance. This can be understood in terms of the phenotypic distributions shown in Figure 4: crosses between semelparous and iteroparous morphs result in roughly equal fractions of semelparous and iteroparous progeny, thereby minimizing the apparent correlation between parental phenotype and  $F_1$  phenotype in the ANOVA.

## DISCUSSION

In this two-year study of life-history variation within a population of the colonial ascidian *Botryllus schlosseri*, I found that there was substantial phenotypic variation in four life-history traits, and that this variation was bimodally distributed under field and controlled laboratory conditions. In combination with the strong correlations among traits, this bimodal pattern indicates that two discrete life-history morphs settled onto plates in the field. The semelparous morph is characterized by a) an early age at first reproduction, b) rapid growth to first reproduction, c) high reproductive effort, and d) death immediately following the production of a single clutch. In contrast, the iteroparous morph a) postpones sexual reproduction until it is nearly twice the age (and three times the size) of semelparous colonies, b) grows at about half the rate of prereproductive semelparous colonies, c) invests roughly 75% less than semelparous colonies in reproductive effort, and d) produces at least three clutches before dying.

The field data, by themselves, do not reveal whether the discrete life-history poly-



TABLE 6. Analysis of variance on the effects of maternal and paternal life-history morph and genotype (life history) on the reproductive effort of their  $F_1$  progeny. The variance components of the mean squares were calculated assuming that the genotype effect was random. The  $F$  ratios for all effects were calculated using as the denominator the mean square term lacking that effect as a variance component. The percentages of total variance were calculated by the method of Winer (1971).

Source of variation	<i>d.f.</i>	MS	<i>F</i>	<i>P</i>	% Variance
Maternal life-history morph	1	2,367.03	76.80	<0.001	8.7
Paternal life-history morph	1	2,430.91	88.24	<0.001	10.0
Maternal genotype(life history)	8	30.82	7.88	<0.005	6.3
Paternal genotype(life history)	8	27.55	9.04	<0.005	7.4
Maternal × paternal life-history morph	1	4.38	1.48	ns	
Maternal × paternal genotype(life-history morph)	64	2.96	0.21	ns	
Paternal life history × maternal genotype(life-history morph)	8	3.91	1.32	ns	
Maternal life history × paternal genotype(life-history morph)	8	3.05	1.03	ns	
Residual	900	13.98			

morphism is genetically controlled and, hence, potentially maintained by selection. Such discontinuous phenotypic polymorphism could just as well arise from maternal effects or via environmentally induced developmental switches (Harper, 1977; Berven et al., 1979; Walker, 1980; Smith-Gill, 1983; Harvell, 1984; Lively, 1986). The factorial laboratory study examined whether a given genotype, initiated from a single zooid, could switch from one life-history morph to the other: across a range of environments, semelparous phenotypes remained distinct from iteroparous phenotypes for all of the demographic traits measured. Although the environment was certainly changing in the Eel Pond during the field common-garden experiment, all members of a given cohort experienced similar environmental changes. The simultaneous presence of semelparous and iteroparous recruits in all cohorts throughout the summer, despite the seasonally changing relative frequencies of the morphs, suggests that life-history phenotype is determined prior to larval settlement. The results of the breeding study, in which paternal and maternal life-history type and genotype make significant and similar contributions to  $F_1$  phenotype, indicate that life-history phenotypes are largely determined genetically in *Botryllus schlosseri*. Nevertheless, the results cannot exclude the possibility that there is genetic variation for response to some environmental cue that triggers the production of one life-history morph or the other.

Discrete genetically determined pheno-

types are known for morphological and biochemical characters in herbaceous plants (Harper, 1977 Ch. 24), the wing polymorphisms of some insects (reviewed in Harrison [1980]), morphological traits as in homoeotic mutants (reviewed in Raff and Kaufman [1983]), and susceptibility to pathogens (reviewed in Bodmer and Bodmer [1978]). However, in most taxa, demographic variation is continuously distributed and is usually inherited as a quantitative, rather than as a simple Mendelian, character set (Stearns, 1980; Falconer, 1981; but see Pianka [1974]). The bimodal distribution of life-history phenotypes in the Eel Pond population of *B. schlosseri*, along with the results of the mating study, suggests that life-history variation could be controlled largely by a single Mendelian locus or a group of closely linked loci. However, in the absence of backcrossing data, this hypothesis lacks strong support.

The large difference in  $r_{max}$  between the two *B. schlosseri* life-history morphs poses a demographic and evolutionary enigma: how do the two morphs coexist? Semelparous morphs ( $r_{max} = 0.99$ ) potentially have a large reproductive advantage over iteroparous colonies ( $r_{max} = 0.72$ ). If these values of  $r_{max}$  accurately reflect the demographic potential of the two life-history morphs, then the semelparous morph should quickly come to dominate the Eel Pond population. Yet, the field data show a recurrent life-history polymorphism: early in the summer, semelparous recruits dominate the population of new *B. schlosseri* colonists on the settle-

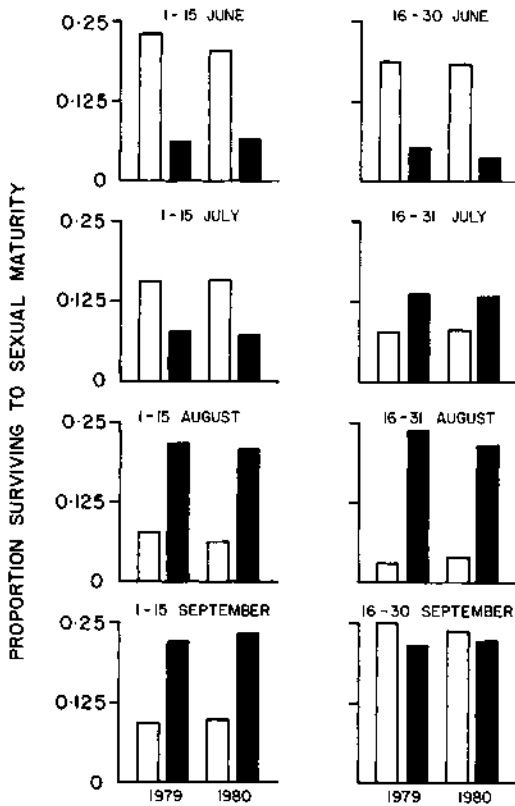


FIG. 5. The proportion of a cohort of field colonies that survives from settlement to sexual maturity. The data are taken from the same colonies used to construct Figure 1 (which contains sample sizes of surviving colonies for each cohort). Open bars show cohort-specific survivorships of semelparous colonies; solid bars show cohort-specific survivorships of iteroparous colonies. Prereproductive colonies were categorized demographically according to their growth rates: colonies producing 3.6 buds per zooid or more were classified as semelparous; colonies producing 2.5 buds per zooid or fewer were classified as iteroparous.

ment plates. This pattern is consistent with the observation cited previously that overwintering semelparous colonies reproduce in the spring approximately four weeks before overwintering iteroparous colonies. Later in the summer, especially after the end of July, iteroparous colonies come to dominate the newly recruited population.

This seasonal change in recruitment frequencies suggests that the abundance of semelparous larvae decreases relative to iteroparous larvae after midsummer. In turn, changes in larval availability could have two demographic causes. First, the survivorship of newly settled semelparous colonies may

decrease after midsummer, whereas that of juvenile iteroparous colonies increases. This is certainly an important factor, as shown by the seasonal morph-specific changes in survival to first reproduction (Fig. 5). Second, because reproductive effort is tightly correlated to reproductive output for semelparous colonies (as they produce a single clutch at a relatively invariant size), declining reproductive effort of semelparous colonies could account for decreased numbers of semelparous recruits. To distinguish between changes in morph-specific survivorship and changes in fecundity as causes of the shift in relative recruitment frequencies, I plotted reproductive effort of semelparous and iteroparous colonies according to season. Figure 6 indicates that there is no apparent relationship between reproductive effort and season for either life-history morph (for both morphs,  $r < 0.1$ ,  $P > 0.9$  [Pearson product-moment correlation]). Thus, the initial early-summer abundance of semelparous recruits is probably a consequence of overwintering semelparous colonies initiating sexual reproduction several weeks before overwintering iteroparous colonies. The subsequent decline in semelparous recruitment rate relative to iteroparous colonies results from both the initiation of reproduction by overwintering iteroparous colonies and the increasing mortality rate of semelparous colonies.

The genetic control of life-history polymorphism in *B. schlosseri* implies that the repeated, single shift in frequencies of the two morphs is underlain by temporal variation in selection. A similar pattern of seasonal succession of demographically distinct clones is known from the cladocerans *Daphnia pulex* (Lynch, 1983), *D. parvula* (Pace et al., 1984), and *D. magna* (Carvalho, 1987; Carvalho and Crisp, 1987); in these examples, genotype-specific fitnesses appear to depend upon abundance of particular predators or temperature changes. Snell (1979) suggested that interclonal competition for food mediates seasonal cycles of clonal succession in the rotifer *Asplanchna brightwelli*. In the Eel Pond population of *B. schlosseri*, the increase in mortality of semelparous colonies occurs considerably before recruitment of iteroparous colonies increases; thus, direct com-

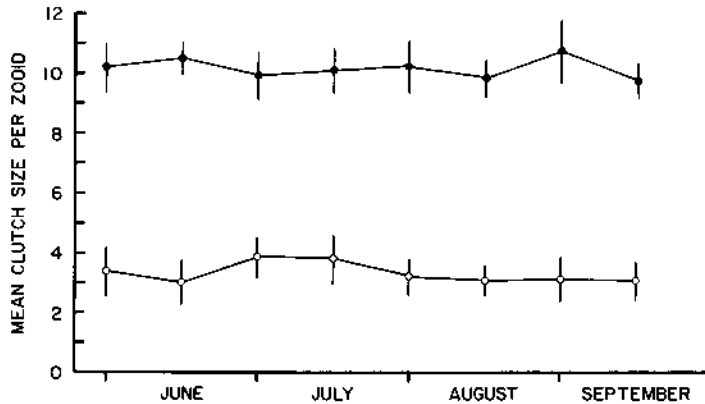


FIG. 6. The reproductive effort of semelparous (solid circles) and iteroparous (open circles) colonies according to season. The data are based on the field cohorts used to construct Figure 1. Error bars show standard errors.

petitive interactions between the two life-history morphs are unlikely to cause the shift in morph frequencies. Other data indicate that the seasonal increase in semelparous colony mortality is mediated ecologically by increasing densities of another colonial ascidian, *Botrylloides leachi* (Grosberg, 1982). *Botrylloides* is competitively dominant to semelparous *Botryllus schlosseri*, but iteroparous *B. schlosseri* are rarely overgrown by *Botrylloides*. As *Botrylloides* density increases, so too does the mortality rate of semelparous colonies.

The power of temporal variation in selection to maintain polymorphism depends upon a balance between the relative number of generations over which a particular selective regime persists and the selective differentials among the regimes (Haldane and Jayakar, 1963; Gillespie, 1974; Felsenstein, 1976; Slatkin and Lande, 1976; Schaffer and Rosensweig, 1977; Maynard Smith, 1979; Grant and Price, 1981; Hedrick, 1986). If genotype-specific fitness differs greatly (i.e., by more than 10–20%) between regimes, then temporal variation could maintain polymorphism at evolutionary equilibrium (Hedrick, 1983). With less intense selection in seasonal environments, the approach to evolutionary equilibrium may be on the order of hundreds or thousands of generations, especially if environments alternate predictably between generations (Hedrick, 1983).

The dramatic morph-specific seasonal change in mortality schedules suggests that

selection differentials are large in the Eel Pond population of *Botryllus schlosseri*. At evolutionary equilibrium, coexistence of the two morphs would require that the seasonal, morph-specific fitness advantages balance out (Lloyd, 1977). However, successional data taken over the short interval of this study cannot be used to determine whether a population is in ecological and evolutionary equilibrium. Indeed, with the onset of winter, recruitment of *Botryllus schlosseri* and *Botrylloides leachi* stops (Grave, 1933; Grosberg, 1982), and surviving colonies shrink. This annual interruption in recruitment and the subsequent decline in the intensity of spatial competition could prevent the *B. schlosseri* population from reaching ecological and, consequently, evolutionary equilibrium. Under these conditions, seasonal variation in selection could dramatically slow the loss of genetically based life-history variation from a population.

As this study has shown, seasonal variation in the life-history traits of a population may actually represent persistent genetic variation due to temporally varying selection, and not necessarily phenotypic plasticity. Before the theoretical and empirical significance of seasonal variation in selection can be weighed against the view that selection should purge rather than maintain variation, much remains to be known about the genetic basis of life-history variation, the relative fitnesses of life-history variants in field populations, and the temporal dynamics of selection.

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