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## THE TIMING OF SEXUAL MATURITY IN CLONAL ANIMALS<sup>1,2</sup>

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**Abstract.** The indeterminate growth potential of many clonal organisms sets them apart from solitary organisms on two demographic counts: (1) fecundity may increase indeterminately and (2) the age-specific probability of genet mortality may decline exponentially with size. In contrast to most solitary organisms, the fecundity benefits of postponing sexual reproduction are not necessarily offset by a rapidly increasing risk of mortality among clonal organisms with indeterminate growth. We examined patterns and causes of variation in the timing of sexual maturity in clonal organisms through experimental manipulations of two phylogenetically distinct, sessile, colonial marine invertebrates. In the bryozoan *Membranipora membranacea*, both crowding by conspecifics and simulated grazing triggered the onset of sexual maturity. Within a population of the colonial ascidian *Botryllus schlosseri*, there are two genetically determined life history morphs. The semelparous morph grows determinately and reproduces at a fixed size. The iteroparous morph can grow indeterminately and reproduces when extrinsic factors (e.g., substratum limitation) intervene.

Analysis of the literature on other sessile, clonal taxa suggests that reproduction is timed differently for annual, indeterminately growing, and perennial, determinately growing, taxa. Many annual clonal species show extreme flexibility in size of first reproduction and reproduce over a wide range of sizes depending on extrinsic factors. Many long-lived clonal species delay reproduction throughout unfavorable conditions until attaining some minimum size. Beyond this size, a combination of age and extrinsic factors appears to modify the actual size at first reproduction.

**Key words:** *Ascidia*; *Bryozoa*; clonal organisms; conditional strategies; evolution of life histories; timing of reproduction.

### INTRODUCTION

Since Cole (1954) first recognized that small changes in the timing of first reproduction can have large effects on the intrinsic rate of increase, prediction of the optimal age of sexual maturity has been a major focus of life history theory (Lewontin 1965, Gadgil and Bossert 1970, Charlesworth 1980, Goodman 1982). The development of this body of theory, and empirical tests of theory, traditionally focus on asexual, or unitary, organisms in which the physiological and genetic individual are necessarily one. Theoretically, reproduction should begin when there is a balance among the advantages of short generation time, the fecundity benefits of postponing reproduction, and the increasing risk of mortality through time (Schaffer and Gadgil 1975). In turn, the timing of this balance depends specifically on the trade-offs among growth, survival, and reproduction, as well as the demographic status of a

population (Mertz 1970, Stearns 1976, Caswell and Hastings 1980).

The process of growth, and consequently the demography, of clonal organisms differs from asexual organisms. Growth in clonal organisms is not limited to the increase in size of a single somatic unit. Rather, clonal organisms grow primarily by the iteration of units variously termed modules, zooids, polyps, or ramets (Harper 1977, Coates and Jackson 1985), each potentially capable of independent asexual proliferation as well as sexual reproduction. The units may be physically separate and autonomous, as are the clones that compose a rotifer genet (sensu Harper 1977). Alternatively, the clonally produced units may be physically connected and physiologically integrated, as are the zooids of bryozoan and ascidian colonies.

Regardless of the degree of clonal integration, the potential for developmental and reproductive independence among ramets carries two crucial demographic consequences that make prediction of the onset of first reproduction a more complex affair than in asexual organisms. First, if clonal units die independently of one another, then as the number of clonal

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units in a genet increases, the probability of genet mortality will decrease exponentially (Cook 1979, Highsmith 1982, Jackson 1985). Indeed, as clones become very large, their mortality rates may become infinitesimally small (Hughes and Jackson 1985, Jackson 1985). Second, the modular construction of clonal organisms allows the genet (though not necessarily modules; see Sebens 1979, 1982) to escape the intrinsic physiological and biomechanical scaling constraints that ultimately limit the size of a clonal organism (Jackson 1979, Sebens 1982, Coates and Jackson 1985, Hughes and Cancino 1985, Hughes and Hughes 1986). Consequently, to the extent that fecundity is proportional to genet size (Thorpe 1979), reproductive output of clonal organisms is not necessarily intrinsically limited (Hayward and Ryland 1975, Hughes and Jackson 1980, Ryland 1981, Harvell and Greene 1984, Coates and Jackson 1985, Hughes and Cancino 1985, Jackson 1985).

Although size, fecundity, and survival rate can theoretically increase indefinitely in clonal organisms, genet expansion will eventually be limited by extrinsic factors such as availability of food or living space. However, because reproductive potential can increase until growth is checked by such extrinsic factors, several authors have suggested that clonal organisms with indeterminate growth should postpone sexual reproduction until the potential for clonal proliferation or growth of the genet actually becomes limiting (Abrahamson 1975, Williams 1975, Bell 1982, Hughes and Cancino 1985). Despite the intuitive appeal of this hypothesis, it has never been tested for short-lived organisms that cannot delay reproduction until the eventual return of favorable conditions. In this paper, we experimentally examine whether age and size at first reproduction are intrinsically fixed, or if these life history traits are sensitive to extrinsic factors that ultimately limit further growth. The study focuses on two phylogenetically distinct species of colonial marine invertebrate, the bryozoan *Membranipora membranacea* and the compound ascidian *Botryllus schlosseri*. With field and laboratory experiments, we show that the onset of sexual maturity is closely associated with extrinsic limitations to further growth that are imposed by intraspecific competition for space and predation, rather than being set according to age or size.

#### NATURAL HISTORY

##### *Membranipora membranacea*

*Membranipora membranacea* is a circumglobally abundant cheilostome bryozoan that is epiphytic on laminarian kelps (Osburn 1950). In the San Juan Archipelago, Washington, the planktonic larvae of *Membranipora* first recruit onto the kelps during May. Recruitment continues until September, when the adult colonies die (Harvell 1985). As the sessile colonies peripherally grow, they eventually contact one another, and growth ceases (Harvell 1985). Although growth

may be redirected toward unobstructed regions of the colonial margin, once a colony is completely surrounded by conspecifics further growth becomes impossible. The size at which asexual growth becomes limited varies both seasonally, according to changes in settlement density, and spatially: some larvae may recruit to kelp blades with high colony densities, whereas other larvae may have few neighbors. Similarly, the intensity of nudibranch predation on *Membranipora* varies seasonally and spatially (Yoshioka 1982a, Harvell 1985).

Like some other cheilostome bryozoans, *Membranipora* is a protandrous hermaphrodite. Individual colonies ontogenetically progress from a prereproductive stage through a male stage to a transitional state, when both sperm and oocytes are produced. Finally, the colony may reach a fully female stage, when only oocytes are produced. This sequence of reproductive stages appears developmentally set; however, the time spent in any one stage is variable and not well correlated with colony size (Harvell 1985).

Mature oocytes are fertilized internally (in a vestibule located between the feeding tentacles) by sperm thought to be derived from neighboring colonies (Silen 1966, Schopf 1974). Unlike most bryozoans, which brood their offspring, colonies of *Membranipora* release fertilized eggs, which develop in the plankton into ciliated feeding larvae (Atkins 1955, Yoshioka 1982b). After several weeks, the larvae settle and metamorphose to initiate new colonies. Colonies grow by asexual budding whereby the initial feeding zooid (the ancestrula) produces more zooids, which, in turn, peripherally bud still more zooids. The resulting clone of zooids remains physically, and physiologically, connected throughout the life cycle; colony fragmentation is unusual (Harvell 1985). Because growth may continue to increase throughout a colony's lifetime, we consider growth to be indeterminate (*sensu* Comfort 1979, Sebens 1982, Kirkpatrick 1984). Nonetheless, on the rare occasion when growth is unimpeded, *Membranipora* colonies will eventually stop growing at a large size (usually > 100 mm in diameter) and become sexually mature (Harvell 1985).

*Membranipora* colonies were collected from blades of the kelp *Laminaria groenlandica* at two subtidal locations near Friday Harbor Laboratories (FHL), San Juan Island, Washington, USA. At both the Shady Cove and FHL breakwater sites, *L. groenlandica* encrusted with *Membranipora* is abundant throughout the summer. Similarly, *Membranipora* colonies are abundant at both sites and occupy up to 80% of the surface area of the large blades of kelp (many blades exceed 3 m in length). Even though some free space persists throughout the growing season, by July colony densities are so high that space generally remains unavailable to the sessile, resident colonies. However, on some blades initially lightly colonized, or at some uncolonized sites on densely populated blades, larvae continue to settle, and resident colonies may continue

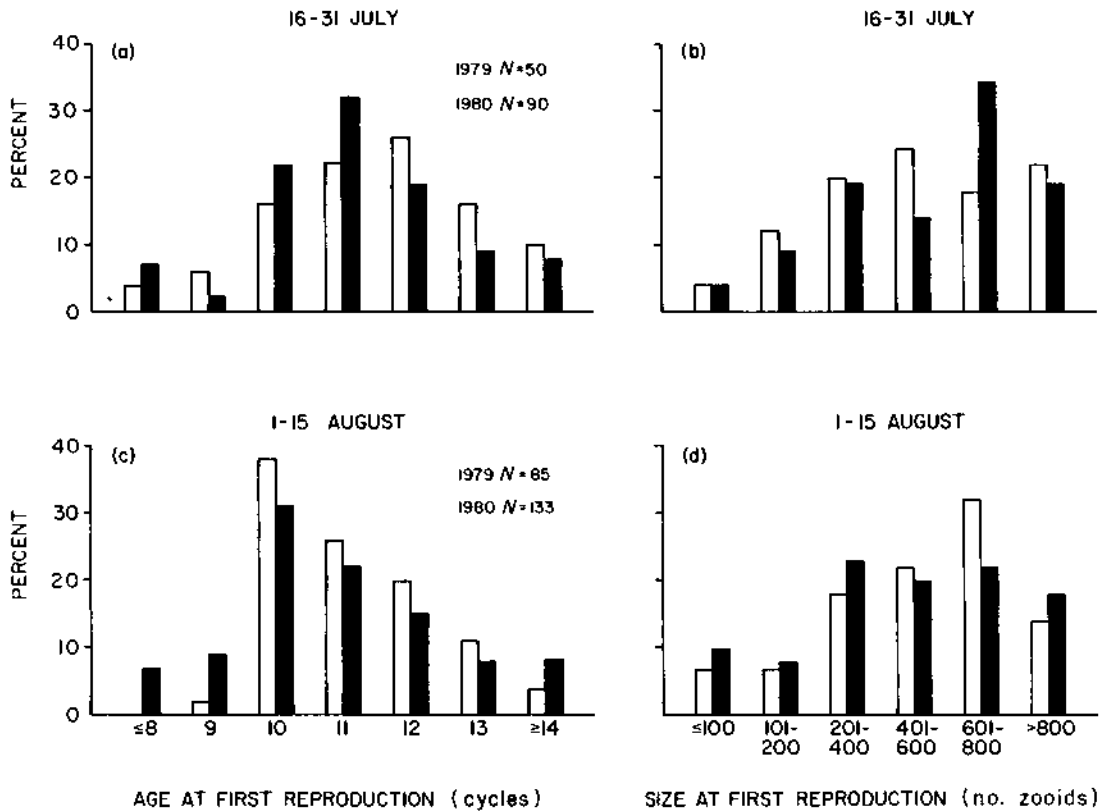


FIG. 1. Frequency distributions for age (in asexual cycles; see Natural History: *Botryllus schlosseri* for explanation) and size at first reproduction (in number of zooids) for two field cohorts of iteroparous *Botryllus schlosseri*. (a, c) Age at first reproduction for colonies recruiting during the indicated interval; (b, d) size at first reproduction for colonies recruiting during the indicated interval. Open bars show data from 1979 cohorts; solid bars show data from comparable cohorts in 1980.

to grow beyond July through the end of the summer. Where unimpeded, colonies may double beyond their July sizes (Harvell 1985).

#### *Botryllus schlosseri*

The colonial ascidian *Botryllus schlosseri* is a common member of epibenthic species assemblages in temperate waters of the northeastern and northwestern Atlantic, as well as the Mediterranean (Berrill 1950). Within the *B. schlosseri* population in the Eel Pond at Woods Hole, Massachusetts, USA, there are two phenotypically discrete and genetically determined life history morphs (Grosberg 1982, 1988). The semelparous morph grows rapidly, reproduces once, then dies. There is little variation in size at first reproduction, and because colonies die soon after reproducing at an invariant size, semelparous colonies are determinate growers. The other life history morph is iteroparous: iteroparous colonies grow at about half the age of semelparous colonies, produce numerous clutches, and may survive for well over a year. For iteroparous colonies growing in the field, age and size at first reproduction vary considerably, even among members of single cohorts (Fig. 1a-d; Grosberg 1988). The causes underlying this variation have heretofore been unclear. As

with *Membranipora*, the colony size of iteroparous colonies is proximally limited by the intensity of intraspecific competition for space: iteroparous colonies stop growing when surrounded by conspecifics (Brunetti 1974, Grosberg 1982). Similarly, when semelparous colonies contact conspecifics, lateral growth ceases; however, colony size usually continues to increase, with the colony throwing itself into convolutions, until sexual maturity is reached at  $\approx 200$  zooids. In the Eel Pond, by mid-July, there is virtually no open space on hard substrata, and *B. schlosseri* coverage reaches 50–100% (Grave 1933, Grosberg 1982).

The life cycle of *Botryllus* is complex, even by the standards of other clonal organisms, because of its cyclical growth. As with *Membranipora*, the sessile phase of the life cycle begins when a planktonic tadpole larva settles onto a hard surface and metamorphoses into the initial feeding zooid (the oozoid). This founder zooid then asexually produces a set of buds, which, after 6 d at 20°C, synchronously mature into feeding, adult zooids (Milkman 1967, Sabbadin 1970, Grosberg 1982). At the time these buds become functional, the oozoid is resorbed by the colony. The now functional adult zooids then produce buds, and in their turn, all of the buds in a colony simultaneously become adults

while the previous "cohort" of zooids is resorbed by the colony. This process of synchronous budding, resorption of adult zooids, and maturation of the buds into adults is termed an asexual cycle.

Repetition of the asexual cycle produces a colony of morphologically and genetically identical zooids that are physiologically united and developmentally synchronized. In contrast to the life histories of numerous other colonial marine invertebrates where fragmentation of colonies may be common (reviewed by Highsmith 1982, Hughes and Jackson 1985), asexual fission occurs in <1% of *B. schlosseri* colonies (Grosberg 1988).

Not only is the asexual cycle synchronized among zooids, but so is the sexual cycle. Furthermore, the sexual cycle is locked in phase to the asexual cycle such that ova are synchronously ovulated as each "cohort" of buds attains functional maturity. The testicular cycle also is synchronized among zooids; however, the male aspect of the sexual cycle is offset from the female aspect such that the testes do not begin to release sperm until the midpoint of the asexual cycle (Milkman 1967). The embryos are brooded until they are mature larvae. These larvae are then synchronously released from their parental colonies just before the adult zooids containing the larvae are resorbed. Thus, clutches are temporally discrete. The first sign of sexual maturity in a colony is the appearance of small testes in the zooids. Ovaries mature an asexual cycle, or so, after the testes first appear (Sabbadin 1970).

#### MATERIALS AND METHODS

##### *Membranipora membranacea*

*Colony size, crowding, and reproductive state.*—To assess the relationships among colony size, crowding, and reproductive condition, we first assigned the nearly circular colonies to one of four discrete size classes (measured as colony diameter): 3–6, 15–18, 27–30, and 36–47 mm. Because colonies vary widely in size and are sessile, population density per se is a poor indicator of crowding. For example, even at quite high densities (>15 colonies/100 cm<sup>2</sup>) small colonies can grow unimpeded, or a large colony may find itself without neighbors. In contrast, at low densities (<3 colonies/100 cm<sup>2</sup>) large colonies may be unable to grow on any side, or small colonies may be confined by locally abundant neighbors. We consequently classified colonies as crowded only if a given colony touched one or more conspecifics such that it was peripherally surrounded and no further growth was possible. Finally, we considered a colony to be sexually mature if oocytes were visible through the frontal membrane with a dissecting microscope.

We sampled colonies taken from *Laminaria* blades at the FHL breakwater ( $N = 6$  blades) and Shady Cove ( $N = 9$  blades). Colonies were selected by size category, and thus sampling was independent of reproductive condition. Usually we sampled all colonies of a given

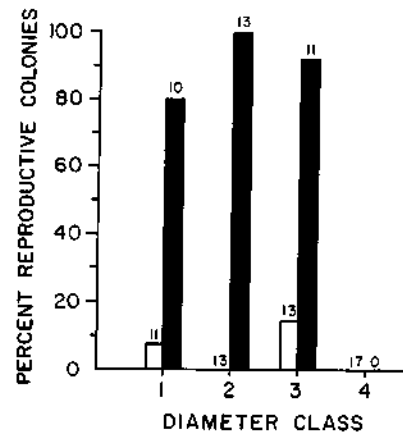


FIG. 2. The percentage of reproductive *Membranipora membranacea* colonies according to diameter class (1 = 3–6 mm; 2 = 15–18 mm; 3 = 27–30 mm; 4 = 36–47 mm) and crowding. Solid bars are data for crowded colonies; open bars are data for uncrowded colonies. Total sample sizes for crowded and uncrowded colonies are shown above the bars for each size class.

size class and crowding category from a blade. For the larger size classes, at least one colony from each size class was sampled on each blade. For the more numerous smallest size class, we haphazardly sampled colonies from only five blades at each site. These represent a truly haphazard assemblage because we could not determine reproductive condition until we placed colonies under a microscope. We assessed the reproductive condition of these colonies according to their size classification and whether they were crowded or not. Sample sizes for each category are given in Fig. 2.

*Reproductive state and predation.*—Our unpublished field observations suggested that even uncrowded colonies would reproduce at a small size if injury by predators slowed or stopped growth. To test the hypothesis that injury accelerates the onset of sexual maturity, we simulated the damage inflicted by nudibranch predators by removing with a razor blade 1–2 mm (about 1 zooid length) of living tissue from the entire perimeter of 23 colonies that had recruited to five acrylic plates. "Grazing" the edge simulates damage caused by *Doridella steinbergae*, a small and locally abundant nudibranch that preferentially attacks colony edges (Harvell 1985). All colonies were completely nonreproductive (i.e., they contained no mature male gametes) at the start of the experiment. Thirteen colonies were left untrimmed as controls. The size range of the manipulated colonies encompassed that of all the colonies on the plates. Colony areas were measured at the start of the experiment after the trimming and again 10 d after the simulated grazing. We determined the reproductive state of all colonies during the second observation.

*Reversibility of allocation to sexual reproduction.*—To determine if crowding-induced allocation to sexual reproduction is irreversible and prevents colonies from

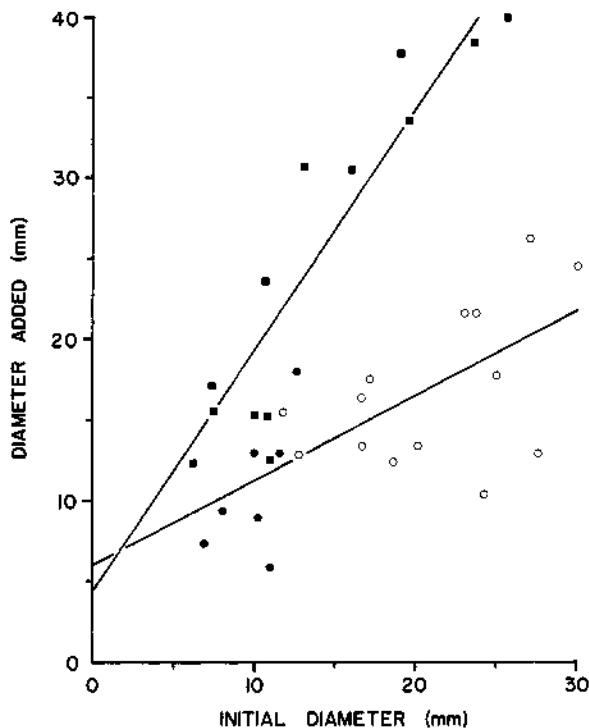


FIG. 3. Plot of diameter added to colonies (after 10 d) vs. their initial size before any manipulation for control (unmanipulated) and trimmed colonies of *Membranipora membranacea*. Circles represent data for trimmed colonies: ○ reproductive colonies; ● nonreproductive colonies. ■ unmanipulated, control colonies; no control colonies became reproductive over the 10 d of observation. Lines are least-squares regressions.

growing even if conditions change again, we removed all conspecific colonies from the margins of nine crowded colonies growing on laminarian blades. We monitored these nine colonies on alternate days for signs of regrowth.

#### *Botryllus schlosseri*

*Substratum size and the onset of sexual maturity.*— Because substratum availability is known to limit colony size in *Botryllus* and many other colonial ascidians (Brunetti 1974, Yamaguchi 1975, Russ 1980, 1982, Grosberg 1982), we examined the effects of different substratum sizes on two demographic parameters: (1) age at first reproduction and (2) size at first reproduction. We chose colonies of three semelparous and three iteroparous genotypes derived from laboratory stocks of *B. schlosseri*. We cultured individual colonies on square glass plates, 2.5 mm thick, of four sizes: 4, 9, 25, and 64 cm<sup>2</sup>. The edges of the glass plates were wrapped with a 1 cm high wall of 0.2 mm thick stainless steel such that colony growth was restricted to one surface of the glass plate. We replicated all substratum size treatments by using three clonal replicates of each of three strains of each life history morph. We attached

these clonal replicates (using the methods of Grosberg 1982), each composed of three zooids, onto the centers of the glass plates.

The glass plates carrying the colonies were held vertically, 2 cm apart, in acrylic plastic racks. Each rack held the set of 18 plates composing each substratum size treatment (i.e., two life history morphs, with three replicates of three genotypes of each morph). The four racks were placed in the same 100-L aquarium, filled with 1.0- $\mu$ m filtered seawater. The water was changed every other day. The colonies were reared at 20°C, on a 12 h:12 h light:dark cycle, with constant gentle aeration, and fed a daily ration of 0.2 mL Marine Invertebrate Diet (Aquarium Products, Incorporated, Houston, Texas, USA) per 1000 zooids in the aquarium.

As testes can be resorbed without the release of sperm (Milkman 1967), whereas ova are not resorbed once ovulated, we used the first ovulation following the initiation of a colony (either by larval settlement or clonal propagation from single zooid isolates) to mark the onset of sexual reproductive maturity. Values for age at first reproduction are reported in units of asexual cycles rather than solar time, because (1) temperature substantially influences the duration of an asexual cycle, but has little direct effect on the number of prereproductive asexual cycles (Grosberg 1982, 1988) and (2) the sexual and asexual cycles are developmentally synchronized in *Botryllus schlosseri* (Milkman 1967). Under the uniform temperature conditions in the laboratory experiments, it makes little difference whether age at first reproduction is calculated in units of solar time or asexual cycles. However, under field conditions, the effect of changing temperature on the duration of an asexual cycle (and the onset of sexual maturity) makes it difficult to compare ages at first reproduction unless values are standardized in units of asexual cycles.

We allowed the colonies to grow until they produced a clutch of ova. At this time, we recorded colony size (as number of zooids), age (as number of asexual cycles), and reproductive effort (as the total number of ova in a colony divided by the total number of zooids at first ovulation).

## RESULTS

### *Membranipora membranacea*

Crowded *Membranipora* colonies reproduced regardless of their size, whereas uncrowded colonies did not (Fig. 2). We were unable to find large colonies that were crowded; however, among members of the three smallest size classes, a log-linear analysis of independence (Sokal and Rohlf 1981) shows no three-way interaction among crowding, colony size, and reproductive state ( $G = 5.27$ ,  $df = 2$ ,  $P > .05$ ). This implies that for these three size classes, the effects of crowding on reproductive state did not vary with colony size. The two-way interaction between crowding and reproductive state was significant ( $G = 61.99$ ,  $df = 3$ ,  $P <$

.001). Indeed, for the three smallest size classes, reproductive state strongly depended on whether a colony was crowded or not ( $G$  test: 3–6 mm,  $G = 8.67$ ,  $df = 2$ ,  $P < .001$ ; 15–18 mm,  $G = 26.22$ ,  $df = 2$ ,  $P < .001$ ; 27–30 mm,  $G = 11.78$ ,  $df = 2$ ,  $P < .001$ ).

In the grazing simulation experiment, all but the smallest trimmed colonies contained oocytes after 10 d, whereas none of the control colonies were sexually mature (Fig. 3). Linear regressions of the size-specific growth rates show that control colonies grew significantly over the 10-d period ( $y = 1.52x + 3.74$ ,  $r^2 = 0.85$ ,  $P < .001$ ), whereas manipulated colonies did not grow appreciably ( $y = 0.52x + 5.89$ ,  $r^2 = 0.45$ ,  $P > .1$ ). To simplify comparison between the areas measured in this experiment and the diameters measured in the field census of reproductive condition, we converted the areas to diameter equivalents. We assumed the colonies to be circular and transformed the areas as follows to determine diameter equivalents:  $2(\sqrt{\text{area} \div \pi})$ . This transformation in no way affected the relative value of the measurements ( $r^2$  values were unchanged).

Where intraspecific competitors were experimentally removed, crowded colonies eventually resumed somatic growth. Nine days after the removal of competitors, two of nine colonies had produced new peripheral growth. Three days later, a total of five colonies had reinitiated somatic growth. After 13 d, all nine colonies were adding new tissue at the margin. This indicates that the allocation from growth to reproduction triggered by crowding does not prevent a colony from resuming growth if conditions change.

#### *Botryllus schlosseri*

The influence of substratum size on age at first reproduction in *Botryllus schlosseri* differed markedly between semelparous and iteroparous life history morphs. Therefore, we analyzed the two morphs separately.

A fixed-effects ANOVA on semelparous colonies shows that substratum size affected neither age at first reproduction ( $F_{3,24} = 0.12$ ,  $P = .94$ ), nor reproductive effort ( $F_{3,24} = 0.62$ ,  $P = .59$ ). There was a significant effect of substratum size on colony size at first reproduction ( $F_{3,24} = 21.70$ ,  $P < .001$ ): individuals grown

TABLE 2. Ages and sizes at first reproduction for iteroparous *Botryllus schlosseri* colonies grown on different substratum sizes. Sample size for all treatments is 9. Results of analyses of variance are described in Results: *Botryllus schlosseri*.

Substratum size (cm <sup>2</sup> )	Age (no. asexual generations)		Grouping*	Size (no. zooids)		Grouping*
	$\bar{X}$	SD		$\bar{X}$	SD	
4	8.67	0.71	A	56.00	4.24	A
9	9.11	0.78	A	118.67	5.89	B
25	10.11	0.60	B	350.11	20.90	C
64	11.00	0.72	C	642.44	19.14	D

\* Means within different letters are significantly different at  $P < .05$  (Student-Newman-Keuls multiple comparisons test for differences among means).

on larger substrata generally attained sexual maturity at slightly larger sizes than those grown on smaller substrata (Table 1). The magnitude of this effect was small, and semelparous colonies became reproductive when they reached sizes of  $\approx 200$  zooids. Indeed, semelparous colonies grown on 4- and 9-cm<sup>2</sup> substrata covered the surface at  $\approx 50$  and 100 zooids, respectively, but continued to grow vertically by folding of the colony surface. There were no significant effects due to genotypes or interactions.

In contrast to the negligible effect of substratum size on age at first reproduction in semelparous colonies, iteroparous colonies consistently began reproduction at a significantly smaller size on smaller substrata ( $F_{3,24} = 3200$ ,  $P < .001$ ; Table 2). The magnitude of this effect among iteroparous colonies was much greater than for semelparous colonies (Table 2). Similarly, the magnitude of the response of size at first reproduction to increasing substratum size was much greater for iteroparous than for semelparous communities. In fact, size at sexual maturity for iteroparous colonies increased in roughly direct proportion to substratum size, except on the largest plates, where sexual maturity always occurred before colonies had completely covered the surface.

#### DISCUSSION

Conditional reproductive strategies based on extrinsic cues are thought to evolve rarely because (1) most cues predictive of future conditions are risky (Lloyd 1984) and (2) conditional responses carry a fitness cost proportional to the likelihood of irreversibly initiating reproduction when conditions actually favor postponing reproduction (Bradshaw 1965, Maynard Smith 1982, Lively 1986). Because of these risks, natural selection should favor the evolution of conditional reproductive strategies primarily in groups such as clonal organisms in which (1) the size-dependent fecundity benefits of postponing reproduction can increase without intrinsic limit and (2) the cumulative risk of reproductive failure through genet mortality increases very slowly with genet size. Our studies show that in

TABLE 1. Sizes at first reproduction for semelparous *Botryllus schlosseri* colonies grown on different substratum sizes. Results of analyses of variances are described in Results: *Botryllus schlosseri*.

Substratum size (cm <sup>2</sup> )	N	Size (no. zooids)		Grouping*
		$\bar{X}$	SD	
4	9	189.44	7.42	A
9	9	194.55	6.58	A
25	9	203.22	7.55	B
64	9	213.44	8.00	C

\* Means with different letters are significantly different at  $P < .05$  (Student-Newman-Keuls multiple comparison test for differences among means).

two sessile, colonial marine invertebrates, the bryozoan *Membranipora membranacea* and the indeterminate growing iteroparous morph of the colonial ascidian *Botryllus schlosseri*, sexual maturation is proximally triggered by extrinsic cues associated with reduced potential for further growth and survival.

Eventually, both *Membranipora* and *Botryllus* will begin to reproduce sexually, even in the absence of crowding or predation. For example, the majority of *Membranipora* colonies >90 mm in diameter are sexually mature, but such large colonies constitute a small fraction of the entire population (C. D. Harvell, *personal observation*); large (>800 zooids) iteroparous *Botryllus* in the field and laboratory also initiate sexual reproduction before reaching the bounds of large substrata. The presence of an upper limit to colony size above which reproduction begins indicates that other factors, either extrinsic (e.g., food availability, day length, temperature, lunar cycle, etc.) or intrinsic (e.g., age), can interact with crowding or predation to initiate sexual maturity. Our laboratory results for *Botryllus* also suggest that there are minimum sizes and ages below which sexual reproduction does not occur, although these minima are different for semelparous (6 asexual cycles;  $\approx 175$  zooids) and iteroparous (8–9 asexual cycles;  $\approx 50$  zooids) colonies. However, in field populations of both *B. schlosseri* and *M. membranacea*, we have occasionally observed very small (<10 zooids), sexually mature colonies of unknown age.

Aside from the data presented here, there are few studies on sessile, clonal organisms that experimentally examine the induction of sexuality, and document patterns of intrapopulation variation for age and size at maturity. The few available data on other ephemeral, indeterminate growing clonal invertebrates suggest that (1) very small (i.e., <5–10 zooids) hydroid (Berrill 1949, Muller 1969, Braverman 1974, Stebbing 1980), bryozoan (Hayward and Ryland 1975, Jackson and Wertheimer 1985), and ascidian (Yamaguchi 1975) colonies can mature sexually and (2) crowding, or other extrinsic limitations to growth, are correlated with the onset of sexual maturity in hydrozoans (Loomis and Lenhoff 1956, Braverman 1974, Stebbing 1980) and ascidians (Yamaguchi 1975).

In contrast to reproductive data on short-lived, clonal species, several observational studies on long-lived cnidarians (Connell 1973, Rinkevich and Loya 1979, Kojis and Quinn 1981, 1985, Wahle 1983, Szmant-Froelich 1985, Karlson 1986) and bryozoans (Jackson and Wertheimer 1985) suggest that there are relatively large minimum sizes below which gametogenesis generally does not occur. The few data on individual variation in sizes at sexual maturity within populations of scleractinian corals show that relatively few individuals actually initiate reproduction at these minima (Rinkevich and Loya 1979, Babcock 1984, Kojis and Quinn 1985). Thus, the timing of onset of sexual maturity appears to be a labile character, even in perennial clon-

al invertebrates. For example, in the scleractinian coral *Montastrea annularis*, the size at which colonies become sexually mature (indicated by the simultaneous presence of spermaries and ovaries) varies eightfold within sampling sites (Szmant-Froelich 1985). Similarly, in long-lived tropical bryozoans, there is substantial intraspecific variation for size at first reproduction (Winston and Jackson 1984). Whether this variation in size at first reproduction is underlain by spatial or temporal variation in the intensity of competition or predation, or other factors such as age (Connell 1973, Kojis and Quinn 1985, Hughes and Connell 1987), physiological condition (Wahle 1983, Rinkevich and Loya 1985, Karlson 1986, Chornesky and Peters 1987), or genetic variation, remains largely unstudied.

The correlation between the initiation of sexual reproduction and extrinsic limits to clonal expansion includes short-lived, motile invertebrates (reviewed in Bell 1982), as well as sessile invertebrates. For instance, high population densities induce the conversion of wingless, asexually reproducing aphids into winged, sexually reproducing morphs (Lces 1966, reviewed in Harrison 1980). Likewise, laboratory studies show that intraspecific crowding often stimulates the production of sexually reproducing individuals in both cladocerans (summarized by Bell 1982) and rotifers (Gilbert 1977).

Most botanical studies analyze processes affecting changes in reproductive effort, rather than the initiation of sexual maturity (e.g., Armstrong 1982, 1984). Several studies of clonal plants indicate a shift from somatic growth to sexual seed production at high population densities (Abrahamson 1975, Thomas and Dale 1975, Holler and Abrahamson 1979, reviewed in Abrahamson 1980). Furthermore, in the annual jewelweed, *Impatiens capensis*, flowering phenology varies with population density: crowding accelerates the production of cleistogamous (selfing) flowers and delays the production of chasmogamous (outcrossing) flowers (Schmitt et al. 1987). Presumably, differences in growth rate, mediated by spatially varying density, modulate this phenological variation, much as individual variation in growth rate affects the onset of sexual maturity in other plants (e.g., Lacey 1986) and metamorphosis in amphibians (Wilbur and Collins 1973). Many perennial plants, like long-lived clonal animals, postpone sexual reproduction at high population densities of conspecifics (Law et al. 1979, Abrahamson 1980, Willson 1983) or herbivores (Collins and Aitken 1970, reviewed in Crawley 1983), perhaps because perennation allows such organisms to outlast unfavorable conditions. Indeed, the few available data on perennial, clonal plants indicate that the onset of sexual maturity among genets is variable, and weakly correlated with either size or age (e.g., Harberd 1961, Harper and Bell 1979).

Taken together, the data on clonal organisms with potentially indeterminate growth indicate that the tim-



ing of sexual maturity is often phenotypically plastic. This pattern is most striking for annual organisms in which age at first reproduction is often linked to the onset of conditions unfavorable for continued asexual growth. Nevertheless, size and age at first reproduction vary widely in numerous perennial, clonal organisms. Consequently, neither size nor age is necessarily an accurate predictor of when sexual reproduction will begin during the life cycles of clonal organisms. Rather, some complex interaction between intrinsic factors such as size, age, and physiological condition, as well as extrinsic factors such as density, food availability, physical disturbance, and predation regulate the timing of sexual maturity. Thus, even size-dependent demographic models that assume fixed life tables (e.g., Hughes 1984, Kirkpatrick 1984, reviewed in Caswell 1985) may poorly reflect patterns of life history evolution in clonal organisms (Lacey et al. 1983, Hughes and Connell 1987). A more complete portrait of clonal life history evolution will require the development of demographic models that incorporate both environmentally mediated phenotypic plasticity (e.g., Mirmirani and Oster 1978, Caswell 1983, 1985, Via and Lande 1985, Stearns and Koella 1986) and size and age classification.

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