A COMPARATIVE DEMOGRAPHIC ANALYSIS OF CLONAL REPRODUCTION IN A TEMPERATE SOFT CORAL[1]

Catherine S. McFadden[2]
Department of Zoology NJ-15, University of Washington, Seattle, Washington 98195 USA, and
Friday Harbor Laboratories, 620 University Road, Friday Harbor, Washington 98250 USA

Abstract. In order to evaluate the relative importance of asexual and sexual reproduction to the fitness of a clonal organism, matrix projection models were used to quantify the contributions of each of these reproductive modes to population growth of the soft coral, *Alcyonium* sp., a species that undergoes frequent colony fission. The demographic and fitness consequences of eliminating either asexual or sexual reproduction from the life cycle of this species were examined by sensitivity analysis and by altering selected entries in the transition matrices to simulate changes in reproductive allocation.

Four populations of *Alcyonium* sp. were monitored photographically for two years to record colony growth, mortality, fission, sexual reproduction, and larval recruitment. Despite high turnover, population densities remained reasonably constant. The 24–52% mortality was matched approximately by recruitment of daughter colonies produced by fission. Sexual reproduction was infrequent, and no larval recruitment was observed. The frequency of both fission and sexual reproduction increased with increasing colony size, while mortality decreased with increasing size.

Size-class transition matrices constructed from the demographic data were analyzed by the methods of Caswell (1986, 1989). In both years of the study the size distributions of colonies observed in the field did not differ from the stable size distributions predicted from the projection models. Eliminating sexual reproduction from the life cycle did not alter the predicted stable size distributions; eliminating fission shifted the size distributions of all four populations towards the larger size classes. Reproductive value increased with increasing colony size. Damping ratio, ρ, a measure of the rate of convergence to the stable size distribution, increased with increases in both fission and sexual reproduction, suggesting that rapidly growing populations are more stable than slowly growing populations.

Projected growth rates (=relative fitness, λ) of the four populations ranged from 0.66 to 1.15. Sensitivity analyses indicated that sexual reproduction contributes <1% of the value of λ, while >40% of λ is accounted for by transitions between the upper size classes in the population, either by fission or growth. Eliminating sexual reproduction from the life cycle had a negligible effect on fitness (λ); eliminating fission greatly reduced λ and suggested rapid extinction for all populations. This result held even when sexual reproductive output was increased by an order of magnitude. The results of these simulations suggest that selection for increased λ will increase fission at the expense of sexual reproduction in this species.

Key words: Alcyonium; clonal reproduction; demography; fission; life history evolution; population projection model; recruitment; sexual vs. asexual reproduction; size-class transition matrix; size-dependent reproduction; soft coral; stable size distribution.

Introduction

Clonal life histories are widespread throughout both the plant (Harper 1977, Abrahamson 1979, Cook 1983, 1985) and animal kingdoms (Bell 1982, Hughes and Cancino 1985, Jackson 1985), and their evolutionary significance has fuelled considerable discussion among both plant ecologists and marine invertebrate zoologists (Williams 1975, Jackson 1977, Janzen 1977, Abrahamson 1979, Cook 1979, 1983, Jackson et al. 1985, Harper et al. 1986).

[2] Present address: Department of Biology, Harvey Mudd College, Claremont, California 91711 USA.

Two fundamental evolutionary questions underlie all discussions of the adaptive significance of clonality (Cook 1985). First, how does the inclusion of asexual reproduction in an otherwise sexual life cycle affect the fitness of the individual organism? Second, what factors determine when and whether an individual allocates energetic resources to sexual vs. asexual reproduction, and what are the fitness consequences of different patterns of reproductive allocation? Comparative demographic analyses of clonal species afford a direct approach to answering these important questions (Sarukhan and Harper 1973, Caswell 1985, Cook 1985). To date, however, most discussions of the adaptive significance of clonal reproduction have relied on broad ecological comparisons drawn between clonal

and aclonal species (Sarukhan and Harper 1973, Bell 1982, Highsmith 1982, Jackson 1985, Jackson and Coates 1986). Few studies have actually quantified the relative contributions of asexual and sexual reproduction to the fitness of organisms that incorporate both forms of reproduction into one life cycle (Sarukhan and Gadgil 1974, Bierzychudek 1982).

In clonal organisms each genetic individual (genet) is itself a population, composed of genetically identical physiological individuals (ramets), and possessing a unique set of demographic properties. The rate of growth of a population of ramets is a measure of the rate of spread of the genet to which they belong, and, therefore, is an estimate of the fitness of that genotype relative to others. Size-classified transition matrix models have been used to quantify the rate of increase, stable size distribution, and transient behavior of populations of various aclonal organisms (Hartshorn 1975, Werner and Caswell 1977, Caswell and Werner 1978, Enright and Ogden 1979, Crouse et al. 1987), as well as to explore the sensitivity of populations to changes in environmental conditions or life history parameters (Enright and Ogden 1979, Hughes 1984, Crouse et al. 1987, Done 1987) or to changes in reproductive strategy (Caswell and Werner 1978, Bierzychudek 1982). With some modification (Hughes 1984, Caswell 1985, 1989), these models can be applied to demographic data for clonal organisms, and can be used to evaluate the relative contributions of sexual and asexual reproduction to the fitness of different clonal life histories.

Because detailed descriptions of matrix projection models can be found elsewhere (Hartshorn 1975, Werner and Caswell 1977, Caswell and Werner 1978, Enright and Ogden 1979, Bierzychudek 1982, Hughes 1984, Caswell 1986, 1989), I will not elaborate on their general form and assumptions here. Bierzychudek (1982) gives a particularly clear explanation of these types of models and their application to questions of life history evolution, while Caswell (1985, 1989) outlines their use with respect to clonal reproduction.

In this paper I use matrix projection models to quantify the contributions of sexual and asexual reproduction to the relative fitness of populations of an undescribed alcyonacean soft coral. Based on demographic data collected from four separate populations over a period of two years, I have constructed size-class transition matrices that incorporate both types of reproduction. I analyze these matrices using the methods of Caswell (1986, 1989) to determine the relative fitness (λ) of each population, and to estimate the sensitivity of λ to changes in sexual and asexual reproductive parameters. In addition, I alter specific entries in the transition matrices to simulate shifts in allocation between sexual and asexual reproduction, and to estimate the fitness consequences of these particular changes in life history. Specifically, I compare the relative fitness of the observed reproductive parameters to life histories in which I: (a) eliminated sexual reproduction

from the life cycle, (b) eliminated asexual reproduction from the life cycle, (c) replaced sexual reproduction by an equivalent increase in the frequency of asexual reproduction, (d) replaced asexual reproduction by an equivalent increase in the frequency of sexual reproduction, and (e) eliminated asexual reproduction, but increased fecundity by more than an order of magnitude over observed values. Based on the results of these simulations and sensitivity analyses, I discuss the relative ecological and evolutionary advantages of sexual and asexual reproduction, and the direction of life history evolution in this species.

Natural history

The undescribed alcyonacean soft coral *Alcyonium* (?) sp. (F. M. Bayer, *personal communication*) is common on exposed rocky shores from northern California to British Columbia, where it is typically found in wave-swept crevices and beneath overhangs in the lower intertidal zone. At those sites at which I have studied it, its lower distributional limit occurs abruptly at mean lower low water. Its subtidal distribution, if any, is unknown.

Colonies of *Alcyonium* sp. are thinly encrusting, circular or oval in shape, and rarely exceed 1.5 cm in the longest dimension. Each colony consists of numerous feeding polyps that are ≈ 5–6 mm in length when fully extended and are connected to one another by a shared gastrovascular network. The feeding polyps are surrounded by a $CaCO_3$ spicule-reinforced coenenchyme matrix into which they can retract fully. Colony growth involves both radial expansion of this coenenchyme tissue and the addition of new feeding polyps within the matrix. Like some other alcyonaceans (Benayahu and Loya 1981, LaBarre and Coll 1982, Dai 1990), *Alcyonium* sp. colonies are capable of active locomotion across hard surfaces, creeping at rates of up to 1–2 cm/mo (Fig. 1).

Alcyonium sp. reproduces asexually by binary fission (Fig. 1), typically producing two (occasionally three) daughter colonies of approximately equal size. As a colony prepares to undergo fission it elongates, and its polyps become segregated into two discrete groups within the coenenchyme matrix, separated from one another by a region of thinner tissue that lacks polyps. This tissue connection eventually is resorbed or degenerates, and the newly separated daughter colonies move apart from one another. The entire process of fission takes several weeks to complete. Fission occurs throughout the year, but reaches its highest frequency in most populations between February and May, coincident with peak colony growth rates (McFadden 1988).

As a result of continual fission, colonies of *Alcyonium* sp. are always found in groups such as the one shown in Fig. 1. These groups often are composed of thousands of colonies and may cover several square metres of rock surface. The spatial arrangement of col-
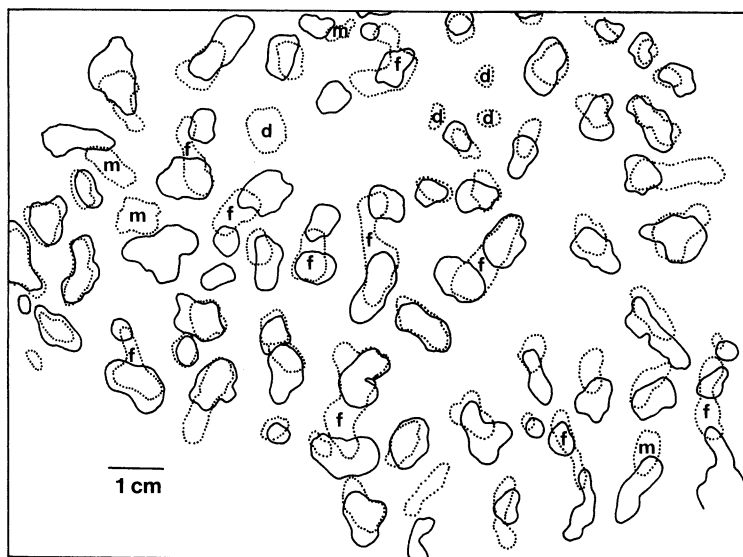
FIG. 1. Overlaid tracings of photographs of a group of *Alcyonium* sp. colonies taken two months apart at Tatoosh Island, Washington. Dotted lines show the positions of colonies present in March 1986; solid lines indicate the positions of the same colonies in May 1986. Examples of fission (f), movement (m) and death (d) can be seen.

onies within these groups is strikingly regular (Mc-Fadden 1988), due to colonies maintaining a distance of several millimetres between one another by colony movement. Aggression or other means of direct interference between neighboring colonies has not been observed; colonies (clonemates or non-clonemates) placed in contact with one another respond simply by moving apart (McFadden 1986). Fusion between colonies that come into contact with one another is rare (C. S. McFadden, *personal observation*).

Sexual reproduction in *Alcyonium* sp. occurs on a yearly cycle. Fertilization is internal, and presumably takes place in late spring, although the timing has not been verified. The embryos develop within the maternal colony over a period of several months, and from mid-August to mid-September planula larvae, 1–2 mm in length, emerge through the mouths of the feeding polyps (C. S. McFadden, *unpublished data*). Following a short free-living period during which dispersal may occur, planulae attach to rock surfaces and metamorphose into primary polyps, the initial stage in colony formation.

Observations of larval behavior in both the field and laboratory indicate that the planulae are demersal and crawl only very slowly over hard surfaces. Most dispersal, therefore, probably occurs over very short distances (centimetres) across the rock surface adjacent to the maternal colony. If deprived of a surface suitable for settlement, planulae kept in the laboratory are able to delay metamorphosis for 3–4 wk. This suggests that a larva dislodged from its natal site by water movement might be dispersed passively over a considerable distance, provided it remained suspended in the water column. Estimates of gene flow between populations based on electrophoretic data, however, suggest that such long distance dispersal is probably rare (C. S. McFadden, *unpublished data*).

STUDY SITES AND METHODS

Study sites

I studied *Alcyonium* sp. populations at two localities in the Pacific Northwest: Botanical Beach, Port Renfrew, British Columbia (48°33′ N, 124°25′ W) and Tatoosh Island, Washington (48°24′ N, 124°44′ W). Tatoosh Island and Botanical Beach lie on opposite sides of the Straits of Juan de Fuca, ≈23 km apart. Although they are topographically quite different, both are outer coastal sites exposed to heavy wave action and frequent winter storms. Both sites are typical examples of the habitat in which one finds *Alcyonium* sp. along the Pacific coast of northwestern North America (C. S. McFadden, *personal observation*).

At Botanical Beach I studied populations of *Alcyonium* sp. at two intertidal sites, separated from one another by ≈100 m. Site B1 was the vertical wall of a deep tide pool that drains partially at low tide; soft coral colonies occupied an ≈1 m vertical section of wall between the lower low-water mark and the lip of the pool. The only spatial competitors present at this site were small colonies of two sponge species, *Mycale richardsonii* and *Ophlitaspongia pennata*. In addition, this rock surface and the soft coral colonies living on it were overgrown temporarily each summer by an ephemeral mat of diatoms and filamentous algae. Site B2 was the roof of a low overhanging shelf, ≈1 m wide and 10 m long. *Alcyonium* sp. colonies occupied nearly the entire expanse. Few spatial competitors were pres-

TABLE 1. Summary of the population dynamics of *Alcyonium* sp. at four sites. Populations at sites T1 and T2 (Tatoosh Island, Washington) were monitored for 20 mo from September 1985 to May 1987; populations at sites B1 and B2 (Botanical Beach, Port Renfrew, British Columbia) for 15 mo from June 1985 to September 1986. Q = number of photographic quadrats (6.5 × 8 cm) at each site.

Site (Q)	No. colonies			Initial colonies dying		No. daughter colonies produced	Daughter colonies dying		No. colonies sexually reproducing	No. larval recruits
	Initial	Final	% Δ	No.	%		No.	%		
T1 (8)	177	160	−9.6	63	35.6	57	11	19.3	13	0
T2 (12)	307	284	−7.5	120	39.1	115	18	15.7	4	0
B1 (10)	164	204	+24.3	39	23.8	86	7	8.1	0	0
B2 (6)	129	111	−14.0	67	51.9	63	14	22.2	0	0
Total	777	759	−2.3	289	37.2	321	50	17.3	17	0

ent, and, in contrast to B1, there was no overgrowth by ephemeral algae.

At Tatoosh Island I studied *Alcyonium* sp. populations at two sites, T1 and T2, both of which were vertical walls of deep intertidal crevices, separated from one another by ≈30 m. Numerous encrusting sponges, compound ascidians and bryozoans, most of which are capable of overgrowing *Alcyonium* sp. (C. S. McFadden, *personal observation*), were present on the lowermost region of the wall at site T2, and colonies of the sponge *O. pennata* were present within the soft coral aggregations at site T1. At both sites the rock surface was partially covered by a short canopy of foliose red algae during the summer months.

Methods

Permanent quadrats were established at each site (T1, T2, B1, and B2), and photographed at intervals of ≈2 mo. Because I could not reach both Botanical Beach and Tatoosh Island during the same low tide series, and because access to the study sites was occasionally restricted by storms and poor tides, the sampling dates and total length of time over which quadrats were monitored differed at the two locations. Quadrats at sites B1 and B2 (Botanical Beach) were monitored for 15 mo from June 1985 to September 1986; those at sites T1 and T2 (Tatoosh Island) were monitored for 20 mo, from September 1985 to May 1987. The number of quadrats and total number of colonies monitored at each site are shown in Table 1.

All colonies present at the start of the study were identified and followed through the photographic time series to record their fates (e.g., mortality or fission). Because colonies may remain in a retracted, non-feeding state of quiescence for periods of several months (e.g., Hartnoll 1975), only the complete disappearance of a colony from the population was scored as mortality. Fission and movement both occur slowly; consequently it was not difficult to track individuals as they moved over the rock surface, or to assign the correct "parentage" to daughter colonies produced by fission during a 2-mo sampling interval (see Fig. 1).

The size (surface area) of each colony on each sampling date was determined by digitizing photographs with an image analysis system (Motion Analysis, Santa Rosa, California). Colonies were divided into four size classes (<0.14 cm², 0.14–0.24 cm², 0.25–0.36 cm², and >0.36 cm²), chosen using Vandermeer's (1978) a posteriori method for determining the boundaries of size classes that minimize the estimation errors incurred in calculating transition probabilities.

In August of each year I determined the frequency and identities of sexually reproductive colonies in each population. Reproductive colonies could be distinguished visually by their dark pink color (the color of the planulae within), and by the extrusion of planulae when gentle pressure was applied to the colony surface. The relationship between colony size and fecundity was established by dissecting and counting the number of planulae found within sexually reproductive colonies collected in 1986 and 1988 from populations adjacent to study sites T1 and T2. I estimated larval recruitment both by monitoring the appearance of new colonies within established quadrats, and by searching the rock surfaces within and adjacent to each study site for the presence of newly settled primary polyps in the months during and immediately following release of planulae.

RESULTS

Due to marked seasonal variation in the rates of colony growth and fission (McFadden 1988) and the periodic nature of sexual reproduction, I divided each year into two distinct periods, September–May and May–August, which I will treat separately throughout this analysis. During the ≈8-mo period from September to early May, rates of colony growth and fission were high (McFadden 1988), but no sexual reproduction occurred. During the 4-mo period from May through August, on the other hand, sexual reproduction took place, but growth and fission rates were low (McFadden 1988).

For each of the four study sites, data were available for three sequential periods, although these periods differed between sites. Data were collected at all four sites during September 1985–May 1986 and May–Au-
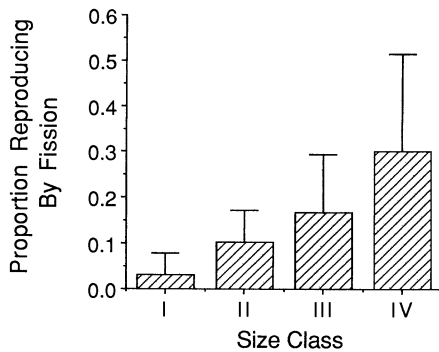
FIG. 2. Proportion (means and 1 SD) of colonies that underwent fission in each of four size classes (<0.14 cm^2, 0.14–0.24 cm^2, 0.25–0.36 cm^2, and >0.36 cm^2) of *Alcyonium* sp. Each time period (see *Results*) at each site was treated as an independent observation ($n = 12$).

gust 1986. Data were available only for sites B1 and B2 during the period May–August 1985, and only for sites T1 and T2 during September 1986–May 1987.

Population dynamics

Over the course of this study there was a high turnover of colonies within each of the four populations (Table 1). Mortality of colonies present at the start of the study ranged from 24% (site B1) to 52% (site B2), while mortality among the daughter colonies produced by fission during the study was lower, ranging from 8 to 22%. Despite the high mortality rates the number of new colonies produced by fission approximately equalled or exceeded the number lost from the population by mortality (Table 1), and overall population densities remained reasonably constant throughout the study. The major agent of colony mortality was not identified.

Sexual reproduction occurred at a very low frequency within these four *Alcyonium* sp. populations (Table 1). I found planulae in only 4 of 307 colonies (1.3%) at site T2 in 1985, and in 13 of 164 colonies (7.9%) at site T1 in 1986. Sexually reproductive colonies were not seen in either year at sites B1 and B2.

During the study I saw no recruitment that I could reliably attribute to settlement of planulae. New colonies that appeared at the study sites each year in the several months following sexual reproduction could all be traced to fission events. I observed 10 newly settled primary polyps near site B1 in September 1986, but all had disappeared by November 1986. Although larval recruitment must occur occasionally, it takes place at a rate I was unable to detect within the temporal and spatial scales of this study.

Size-dependent reproduction and mortality

Colony fission was a function of colony size (Fig. 2). Differences between size classes were tested separately for each period, using a log-linear analysis of variance

model (CATMOD procedure, SAS Institute, 1985). In each of the four periods encompassed by the study (May–August 1985, September 1985–May 1986, May–August 1986, September 1986–May 1987), the fission × size-class interaction term was highly significant ($x^2 > 12.67$, df $= 3$, $P < .005$).

Sexual reproduction also was a function of colony size (Fig. 3), although site T1 was the only site at which the frequency of sexually reproductive colonies was high enough to test for differences between size classes. At this site in 1986, the proportion of sexually reproductive colonies differed significantly between size classes ($G = 38.62$, df $= 3$, $P < .001$).

The proportion of colonies that reproduced by fission and the proportion that reproduced sexually both increased monotonically with increasing size class; small colonies rarely reproduced by either mechanism. Colonies of size-class IV, for instance, were approximately twice as likely to divide or to produce planulae as were colonies of size-class III. As seen above (Table 1), fission was the more frequent mode of reproduction. A mean of 30% of size-class IV colonies underwent fission during each period (e.g., September–May or May–August) of the study (Fig. 2), whereas $<15\%$ of colonies in that same size class reproduced sexually each year (Fig. 3).

Fecundity increased with colony size (Fig. 4), as expected for an organism in which brood space is limited by internal volume. Colony size alone, however, was a poor predictor of fecundity ($R^2 = 0.24$), because many large colonies produced only a few planulae (Fig. 4). The median fecundities of colonies in size-classes III and IV were 9 ($n = 7$) and 22 ($n = 32$), respectively. Only two reproductive colonies of size-class II were found, with brood sizes of 1 and 25. The largest brood recorded for any colony was 238.

Colony mortality also was size dependent (Fig. 5). Differences between size classes were tested separately for each period (May–August 1985, September 1985–May 1986, May–August 1986, and September 1986–May 1987), using a log-linear analysis of variance mod-
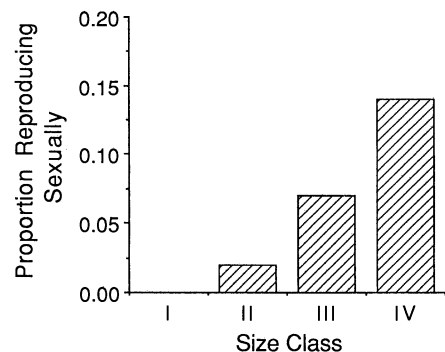

FIG. 3. Proportion of colonies that were brooding planula larvae within each of four size classes of *Alcyonium* sp. at site T1 during the summer of 1986. Size classes as in Fig. 2.
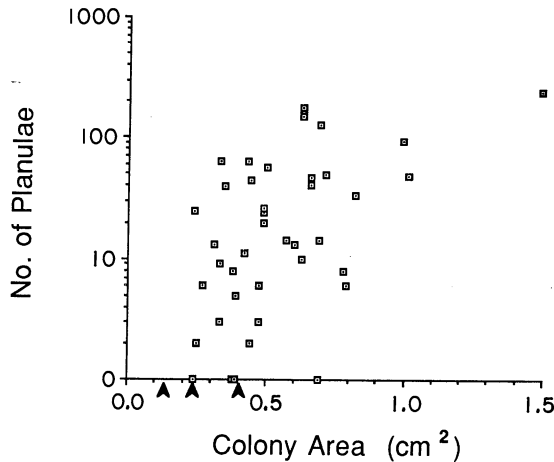
FIG. 4. Relationship between fecundity (number of planula larvae brooded) and colony size in *Alcyonium* sp. colonies collected from Tatoosh Island, Washington, in August 1988 ($n = 41$). Arrows indicate the boundaries of the size classes used in the transition matrix models.

el (CATMOD procedure, SAS Institute 1985). In all four periods the proportion of mortality in size-class I was significantly greater than in the three upper size classes (mortality × size-class interaction, $\chi^2 > 6.56$, df = 3, $P < .01$). There were no differences in mortality among the three upper size classes (mortality × size-class interaction, $\chi^2 < 3.37$, df = 2, $P > .18$) except in September 1986–May 1987, when the mortality × size-class interaction term was highly significant ($\chi^2 = 78.55$, df = 2, $P < .001$).

Size-class transition probabilities

During each period of the study, a soft coral colony could undergo one of five different types of size-specific transitions: it could (a) grow into a larger size class, (b) shrink to a smaller size class, (c) remain in the same size class, (d) undergo fission, or (e) die. The proportion of colonies in each size class that underwent each of these transitions during September 1985–May 1986 and May–August 1986 are shown in Fig. 6 for each of the four study populations.

Seasonal differences in the transition probabilities at each site are evident from Fig. 6. During May–August most colonies either remained in their original size class or shrank into a lower size class. In contrast, during September–May a greater proportion of colonies grew than shrank, and those that grew often increased in size by >1 size class. With the exception of site B2, the proportion of colonies that underwent fission was also higher in September–May than in May–August, and the daughter colonies produced by colonies of a given size class were larger in September–May. Mortality was higher during September–May, particularly among colonies in the three upper size classes.

POPULATION PROJECTION MODELS

Size-class transition matrices

From the transition probabilities illustrated in Fig. 6, I constructed separate size-class transition matrices for each of the May–August and September–May periods for which I had complete transition probability data for each of the four populations (Table 2).

Because of the possibility of fission, each transition probability, a_{ij}, entered in the matrix is the sum of two separate terms, g_{ij} and f_{ij}. g_{ij} is the proportion of colonies of size-class i that move to size-class j as a result of growth ($i < j$) or shrinkage ($i > j$). It is, therefore, the familiar transition probability of conventional size-class transition matrices (e.g., Caswell 1986, 1989), and, in the absence of fission, $a_{ij} = g_{ij}$. f_{ij}, on the other hand, is the expected number of colonies of size-class j produced per colony of size-class i by fission. Because each fission event yields two or more daughter colonies, the sum of f_{ij} for a population equals at least twice the proportion of colonies that underwent fission, and, consequently, the sum of a_{ij} for a given column of the transition matrix may exceed 1.0. In Fig. 6 the solid bars represent g_{ij}, while the hatched bars represent f_{ij} for each *Alcyonium* sp. population.

Each entry in the top row of the transition matrix (Table 2) denotes the number of planula larvae (P) produced per colony of size-class i, and is the product of two independently estimated terms: (1) the proportion of colonies of size-class i that reproduced sexually, and (2) the median number of planulae produced per reproductive colony of size-class i. For sites T1 and T2 I calculated the proportion of reproductive colonies in each size class directly from the number of colonies that produced planulae at those sites in August 1985 and 1986. At sites B1 and B2, however, I found no sexually reproductive colonies during this study. I made the assumption that sexual reproduction does occasionally occur at these sites (reproductive colonies were found at nearby sites in both years), but at such a low
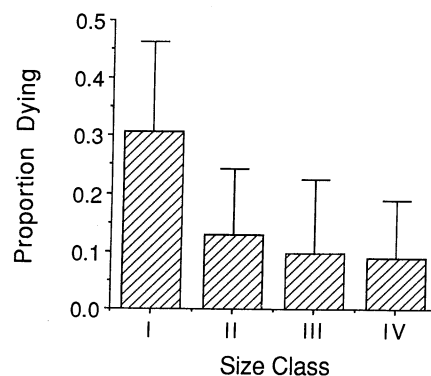

FIG. 5. Proportion (means and 1 SD) of colonies in each size class of *Alcyonium* sp. that died during the study. (Size classes as in Fig. 2.) Each time period (see *Results*) at each site was treated as an independent observation ($n = 12$).

TABLE 2. Size-class transition matrices for *Alcyonium* sp. populations at sites T1 and T2 on Tatoosh Island (Washington) and sites B1 and B2 at Botanical Beach (British Columbia). P = planula larva.

Size class at time $t+1$	P	I	II	III	IV	P	I	II	III	IV	P	I	II	III	IV
									Tatoosh Island						
		September 1985–May 1986					May–August 1986					September 1986–May 1987			
								Site T1							
P	.00	.00	.00	.00	.00	.00	.00	.22	.45	4.09	.00	.00	.00	.00	.00
I	.007	.13	.12	.04	.10	.00	.58	.18	.13	.05	.007	.30	.14	.16	.00
II	.00	.26	.37	.20	.10	.00	.17	.76	.34	.21	.00	.13	.21	.28	.06
III	.00	.17	.35	.47	.24	.00	.00	.00	.47	.36	.00	.17	.31	.23	.17
IV	.00	.17	.09	.29	.76	.00	.00	.00	.03	.43	.00	.09	.18	.52	.87
								Site T2							
P	.00	.00	.00	.00	.00	.00	.06	.16	.17	2.99	.00	.00	.00	.00	.00
I	.007	.37	.25	.16	.00	.00	.70	.28	.14	.19	.007	.14	.13	.12	.08
II	.00	.30	.47	.27	.20	.00	.03	.70	.44	.36	.00	.40	.40	.44	.23
III	.00	.02	.18	.36	.53	.00	.00	.05	.40	.27	.00	.14	.31	.20	.38
IV	.00	.00	.05	.16	.40	.00	.00	.00	.09	.46	.00	.08	.32	.56	.85
								Botanical Beach							
		May–August 1985					September 1985–May 1986					May–August 1986			
								Site B1							
P	.00	.00	.06	.13	.77	.00	.00	.00	.00	.00	.00	.00	.06	.13	.77
I	.00	.36	.14	.02	.05	.007	.27	.16	.02	.13	.00	.56	.18	.12	.08
II	.00	.14	.46	.35	.08	.00	.40	.38	.23	.28	.00	.19	.55	.33	.16
III	.00	.00	.24	.50	.36	.00	.20	.27	.43	.22	.00	.00	.21	.61	.37
IV	.00	.00	.08	.17	.56	.00	.07	.27	.38	.83	.00	.00	.00	.06	.56
								Site B2							
P	.00	.04	.19	.24	3.30	.00	.00	.00	.00	.00	.00	.04	.19	.24	3.30
I	.00	.54	.30	.05	.04	.007	.08	.25	.03	.07	.00	.90	.09	.28	.10
II	.00	.13	.61	.48	.24	.00	.15	.21	.25	.21	.00	.20	.62	.17	1.10
III	.00	.00	.12	.48	.40	.00	.08	.14	.25	.21	.00	.00	.41	.70	.20
IV	.00	.00	.00	.08	.48	.00	.04	.06	.09	.21	.00	.00	.08	.27	.30

frequency that I would have been unlikely to have found a sexually reproductive colony given the number of colonies I sampled. Using a binomial distribution, I calculated the highest frequency at which reproductive colonies could have been present in each population and still produce 0 reproductive colonies in a randomly drawn sample of 182 (site B1) or 138 (site B2) colonies with probability $P > .05$. I used these values as maximum estimates of the proportion of colonies reproducing sexually at sites B1 and B2, and distributed sexual reproduction among the four size classes at these two sites according to the size-class distributions of reproductive colonies observed at sites T1 and T2.

I included sexual reproduction in the May–August transition matrices only, since planulae are released only at this time of the year. Fission is the only means by which new colonies enter the population during the rest of the year; consequently, all of the entries for sexual reproduction in the September–May transition matrices have 0 values.

Estimates of larval recruitment rates present the same difficulty as those for frequency of sexual reproduction. Larval recruitment obviously occurs occasionally, but at a rate I was unable to detect given the spatial and temporal scales of this study. The highest frequency of sexual reproduction I recorded occurred at site T1 in 1986. From the number of reproductive colonies I observed, their size-class distribution, and the median fecundity value for each size class, I estimated that ≈415 planulae would have been produced that year at site T1. I have made the conservative assumption that no planulae emigrated from or immigrated to this site (or, alternatively, that emigration equaled immigration), and that these 415 planulae therefore represented the entire larval pool available for recruitment at this site. Using a binomial distribution, I calculated the highest rate at which recruitment could have occurred and still produced an observation of 0 recruits from a randomly drawn sample of 415 larvae with probability $P > .05$. The resulting estimate of a maximum recruitment rate of 0.007 was used for the transition probability between size classes P and I for all four study sites.

Tests of homogeneity

To determine if transition probabilities were constant (1) between populations and (2) between different periods and years, the completed transition matrices
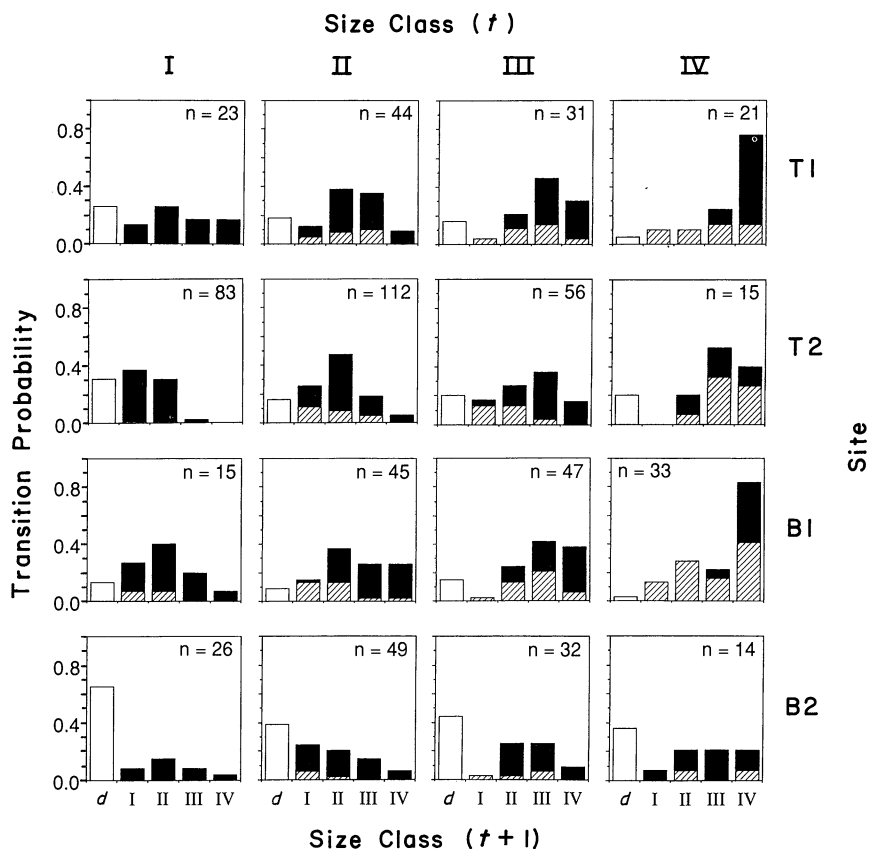
FIG. 6. Size-class transition probabilities between time periods t and $t + 1$ for *Alcyonium* sp. colonies at sites T1, T2, B1, and B2 during September 1985–May 1986 and May–August 1986 (for site information, see *Study sites and methods: Study sites,* above). Solid portions of bars represent transitions caused by growth or shrinkage, hatched portions represent fission, and open bars denote mortality (d). Because each fission event yields two or more daughter colonies, the sum of the transition probabilities within each size class may exceed 1.0.

were compared using Anderson and Goodman's test for homogeneity of Markov processes (Anderson and Goodman 1957, Usher 1979, Bierzychudek 1982). Pairwise comparisons were made between years for each site (e.g., between September 1985–May 1986 and September 1986–May 1987 at sites T1 and T2, and between May–August 1985 and May–August 1986 at sites B1 and B2), and between periods within years (e.g., matrices for May–August compared to those for September–May). Within each period the transition matrices for each site were tested against one another (sites B1 and B2 compared in May–August 1985, sites T1 and T2 compared in September 1986–May 1987, all four sites compared in September 1985–May 1986 and May–August 1986). In all cases, the departure from homogeneity was highly significant (pairwise comparisons of periods, years, and sites; $\chi^2 > 152$, df = 12, $P < .001$; comparisons of all four sites: $\chi^2 > 405$, df = 36, $P < .001$), justifying individual treatment of each population and each period.

Population projections

Population growth can be described by the equation $n(t + 1) = A(t)n(t)$, where A is the matrix of transition probabilities, a_{ij}, and $n(t)$ is the vector describing the size-class distribution of individuals in the population at time t. The time interval I have used to model the growth of *Alcyonium* sp. populations is a year, since sexual reproduction occurs on a yearly cycle. I incorporated the three different transition matrices for each population into a single matrix representing the yearly transition probabilities of colonies in that population. I first averaged those transition probabilities that were measured for the same period in different years at a site to determine a mean transition matrix for that period (e.g., for May–August at sites B1 and B2 and September–May at sites T1 and T2). I then computed the product of the transition matrices for the two different periods at each site. For this calculation, 4- and 8-mo periods were treated as equal (e.g., 6-mo) lengths
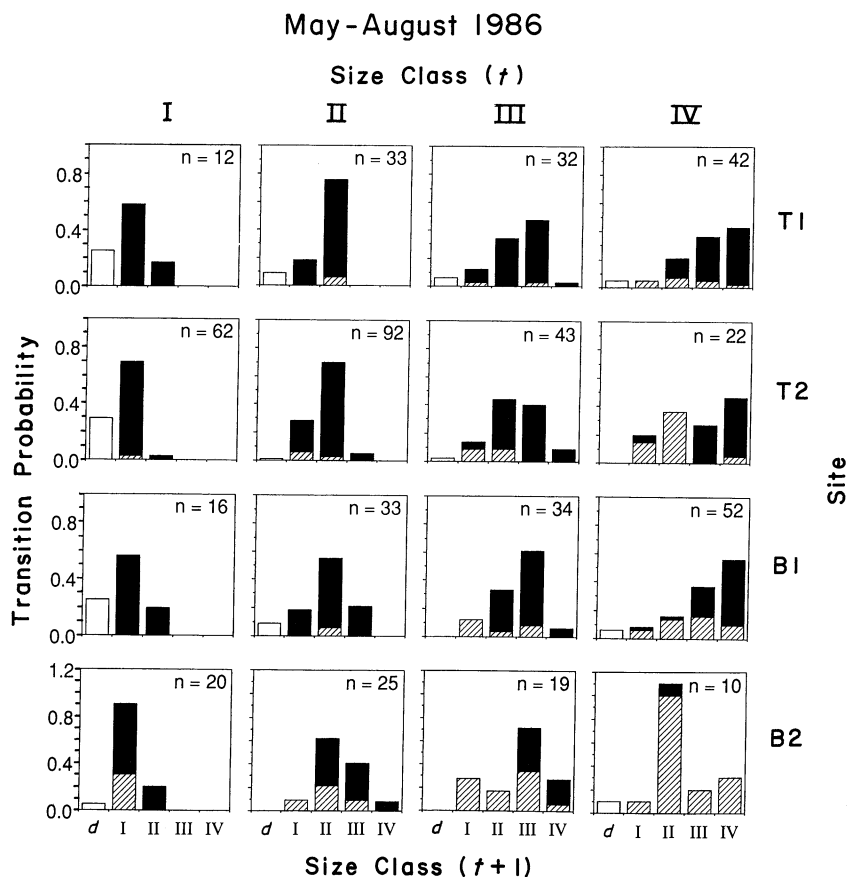
May – August 1986

Size Class (*t*)

FIG. 6. Continued.

of time. The result is a single transition matrix for each site, which is the analytical equivalent of a simulation model in which two different types of years (e.g., "good" years and "bad" years) occur with equal probability, but in a stochastically determined sequence (e.g., Bierzychudek 1982). In combining matrices for different periods and years, I have made the assumptions that successive matrices are independent of one another and occur with equal probability (Cohen 1979, Bierzychudek 1982).

Simulation of alternative reproductive life histories

To assess the demographic and evolutionary consequences of changes in the life history of *Alcyonium* sp., I altered certain entries in the transition matrices to simulate shifts in reproductive allocation. I compared the observed life history of *Alcyonium* sp. (unaltered transition matrices; LH 1) to life histories in which:

(LH 2) I eliminated sexual reproduction from the life cycle, simply by replacing the size-class-specific fecundity estimates with 0s; or

(LH 3) I eliminated fission from the life cycle. To simulate the elimination of fission, I estimated the size each colony that underwent fission would have been in each time interval had it not divided, as the sum of the areas of its component daughter colonies. For instance, a 0.30-cm² colony (size-class III) that divided into daughter colonies of 0.15 cm² and 0.25 cm² was treated as if it had simply grown to 0.40 cm² (size-class IV). The size-class transition probabilities estimated in this manner for fission colonies, g'_{ij}, were added to the original g_{ij} (size-class transitions of non-fission colonies) for each population to construct a new size-class transition matrix, $A' = g_{ij} + g'_{ij}$.

If either sexual reproduction or fission were eliminated from the life cycle of *Alcyonium* sp., but the total amount of energy invested in reproduction was held constant, we would expect allocation to the remaining reproductive mode to be increased by an energetically equivalent amount (e.g., Abrahamson 1979). Unfortunately, the relative energy costs of fission and sexual reproduction are unknown for *Alcyonium* sp., and would be difficult (perhaps impossible) to determine. For the purpose of these simulations, I have made the arbitrary assumption that dividing once per year is energetically

TABLE 3. Summary of the six alternative life histories analyzed by population projection (see *Population projection models: Simulation of alternative reproductive life histories*).

Simulation code	Life history
LH 1	Observed life history (sexual reproduction and fission)
LH 2	Sexual reproduction eliminated from life cycle
LH 3	Fission eliminated from life cycle
LH 4	Sexual reproduction eliminated, but replaced by equivalent increase in fission
LH 5	Fission eliminated, but replaced by equivalent increase in sexual reproduction
LH 6	Fission eliminated, but sexual reproduction increased so that all colonies in size-classes II, III, and IV reproduce sexually each year

equivalent to producing one sexual brood of median size. I included three additional life histories in the simulations in which:

(LH 4) I eliminated sexual reproduction, and simultaneously increased the frequency of fission by an amount equivalent to the original frequency of sexually reproductive colonies; or

(LH 5) I eliminated fission, and simultaneously increased the frequency of sexually reproductive colonies by an amount equivalent to the original fission frequency; or

(LH 6) I eliminated fission, and simultaneously increased the total allocation to reproduction. I recalculated the number of planulae produced per colony of size-class i to simulate all colonies in size-classes II, III, and IV producing planulae every year. The number of planulae produced per colony of size-class i (for $i > 1$) was then simply the median fecundity estimate for that size class.

These six alternative life histories are summarized in Table 3.

ANALYSIS OF PROJECTION MATRICES

All transition matrices were analyzed using the methods of Caswell (1986, 1989) to determine for each population:

(a) the projected rate of population growth, λ, given by the dominant eigenvalue of the matrix;

(b) the stable size-class distribution, w, given by the right eigenvector corresponding to the dominant eigenvalue, λ_1;

(c) the damping ratio, ρ, a measure of the rate of convergence to the stable size distribution, defined as $\lambda_1/|\lambda_2|$, the ratio of the dominant eigenvalue of the matrix to the second largest absolute eigenvalue;

(d) reproductive value, v, a measure of the relative contribution of a particular size class to the future growth rate of the population, given by the left eigenvector corresponding to the dominant eigenvalue, λ_1;

(e) elasticity, e_{ij}, a measure of the sensitivity of λ to proportional changes in a_{ij}, as defined by Caswell (1986, 1989). e_{ij} estimates the relative contribution of each a_{ij} to the overall value of λ.

Projected population growth rates (λ)

The four *Alcyonium* sp. populations vary greatly in their projected rates of population growth, λ (Table 4). The populations at sites T2 and B1 are both increasing ($\lambda > 1.0$), while those at sites T1 and B2 are declining ($\lambda < 1.0$), and, provided the transition probabilities measured over the course of this study remain constant, rapidly heading for extinction.

Eliminating sexual reproduction from the life cycle of *Alcyonium* sp. (LH 2) had a negligible effect on population growth rate (Table 4), decreasing λ by <1% in all populations. Moreover, when sexual reproduction was replaced by a corresponding increase in the frequency of fission (LH 4), eliminating sexual reproduction from the life cycle actually increased λ for three of four populations. Eliminating fission, however, so that new colonies only enter a population by larval

TABLE 4. Projected rates of population growth, λ, for four populations of *Alcyonium* sp. for simulations of six different life histories (see Table 3 for explanations of numbered life histories). Numbers in parentheses indicate the percentage difference in λ between observed (LH 1) and modified (LH 2–6) life histories.

Life history	Site*			
	T1	T2	B1	B2
LH 1 (observed)	0.920	1.047	1.152	0.660
LH 2	0.914	1.045	1.151	0.659
	(−0.7%)	(−0.2%)	(−0.1%)	(−0.2%)
LH 3	0.808	0.840	0.866	0.579
	(−12.2%)	(−19.8%)	(−24.8%)	(−12.3%)
LH 4	0.958	1.047	1.166	0.672
	(+4.1%)	(0.0%)	(+1.2%)	(+1.8%)
LH 5	0.843	0.863	0.902	0.593
	(−8.4%)	(−17.6%)	(−21.7%)	(−10.2%)
LH 6	0.863	0.878	0.927	0.626
	(−6.2%)	(−16.1%)	(−19.5%)	(−5.2%)

* See Table 1 and *Study sites* (above) for site information.

TABLE 5. Results of statistical tests comparing the stable size distributions predicted from the projection matrix models to the observed size distributions of *Alcyonium* sp. colonies in each of the four study populations in September 1985 and September 1986 and to the size distributions of the daughter colonies produced by fission during the study.*

Study populations	Observed size distribution in 1985			Observed size distribution in 1986			Distribution of daughter colonies		
	Δ	G	P	Δ	G	P	Δ	G	P
Site T1	3.4	0.59	NS	2.4	0.36	NS	8.3	3.09	NS
Site T2	6.7	5.86	NS	7.5	4.52	NS	4.3	1.20	NS
Site B1	3.2	0.90	NS	9.9	7.43	NS	13.2	8.92	<.05
Site B2	4.2	1.05	NS	5.6	1.86	NS	9.4	4.37	NS

* Keyfitz's Δ (Keyfitz 1977) is a measure of the percentage of the population that falls in the "wrong" size-class. Statistical significance was determined using a G test for goodness of fit, 3 degrees of freedom. NS = not significant, $P > .05$.

recruitment following sexual reproduction (LH 3), decreased λ in all four populations by 12–25%, to values considerably <1.0 (Table 4). In the absence of fission, therefore, all four *Alcyonium* sp. populations would rapidly go extinct. When fission was replaced by a corresponding increase in the frequency of sexual reproduction (LH 5), λ increased only slightly, and extinction was still rapid. Even the highest levels of sexual reproduction simulated here, representing increases in reproductive output of as much as 1.5 orders of magnitude (LH 6), failed to prevent all four populations from rapidly going extinct when fission was eliminated from the life cycle (Table 4).

λ can be equated with the relative fitness of a population (or of a genotype, if we make the assumption that all of the ramets in a population belong to the same genet). The four *Alcyonium* sp. populations can be ranked in terms of fitness, therefore, as: B1 > T2 > T1 ≫ B2. Throughout all of the simulated changes in life history, the relative fitness rankings of the four populations remained unchanged.

Stable size distribution and transient behavior

In both September 1985 and September 1986 the size distributions of colonies observed in the field for these four populations did not differ from the stable size distributions predicted from the population projection model (Table 5). There were, however, differences between the size distributions of the four populations (Fig. 7). The populations at sites T2 and B2 had distributions skewed towards smaller colonies (size-classes I and II), while both the observed and predicted stable size distributions at sites T1 and B1 had higher proportions of the upper size classes represented. At sites T1, T2, and B2, colonies in size-class II dominated the population; at site B1 the proportion of colonies in size-class III was slightly higher than that in size-class II (Fig. 7). For three of four populations the size distribution of daughter colonies produced by fission during the study also did not differ significantly from the predicted stable distribution (Table 5).

Eliminating sexual reproduction from the life cycle (LH 2) had no effect on the stable size distribution of colonies in any population (Fig. 8). At sites T2 and B2,

replacing sexual reproduction by an equivalent increase in fission (LH 4) had virtually no effect on the stable size distribution. At site T1, increased fission shifted the size distribution slightly towards smaller colonies (size-classes I and II). At site B1, an increase in fission had the opposite effect, resulting in an increase in the proportion of colonies in size-class IV (Fig. 8).

Eliminating fission from the life cycle (LH 3) shifted the stable size distribution towards larger colonies in all four populations (Fig. 8). At sites T1 and T2 the proportions of colonies in size-classes II, III, and IV were approximately equal in the absence of fission. As sexual reproduction was increased (LHs 5 and 6), the size distribution shifted slightly towards the smaller size classes, further evening out the size distribution among size classes. At both sites B1 and B2, eliminating fission (LH 3) produced a size distribution that was skewed greatly towards colonies of size-class IV (Fig. 8). Colonies of size-class I made up only 3.8% of the population at site B1, while 56.4% of the population were colonies of size-class IV; at site B2, 11.4% of colonies were in size-class I, while 41.9% were in size-class IV. At these two sites also, an increase in sexual reproduction in the absence of fission (LHs 5 and 6) shifted the size distribution back slightly towards smaller colonies (Fig. 8).

The damping ratios, ρ, for the four populations ranged from 3.61 to 11.57 (Fig. 9). Because damping ratios have rarely been reported in the literature, the magnitudes of these values are difficult to interpret, but they appear to be high: damping ratios reported by Caswell (1986) for seven populations of teasel ranged from ≈1.1 to 1.3. High damping ratios indicate rapid convergence to the stable size distribution following perturbation of the population size structure.

Eliminating sexual reproduction from the life cycle (LH 2) had little effect on the damping ratio of any of the four populations (Fig. 9). Eliminating fission from the life cycle (LH 3), on the other hand, decreased the damping ratios of all populations to similar values of ≈3.1. In all four populations, ρ was lowest when fission was absent and the frequency of sexual reproduction was low (LH 3), and increased with an increase in sexual reproduction (LHs 5 and 6). Increasing the fre-
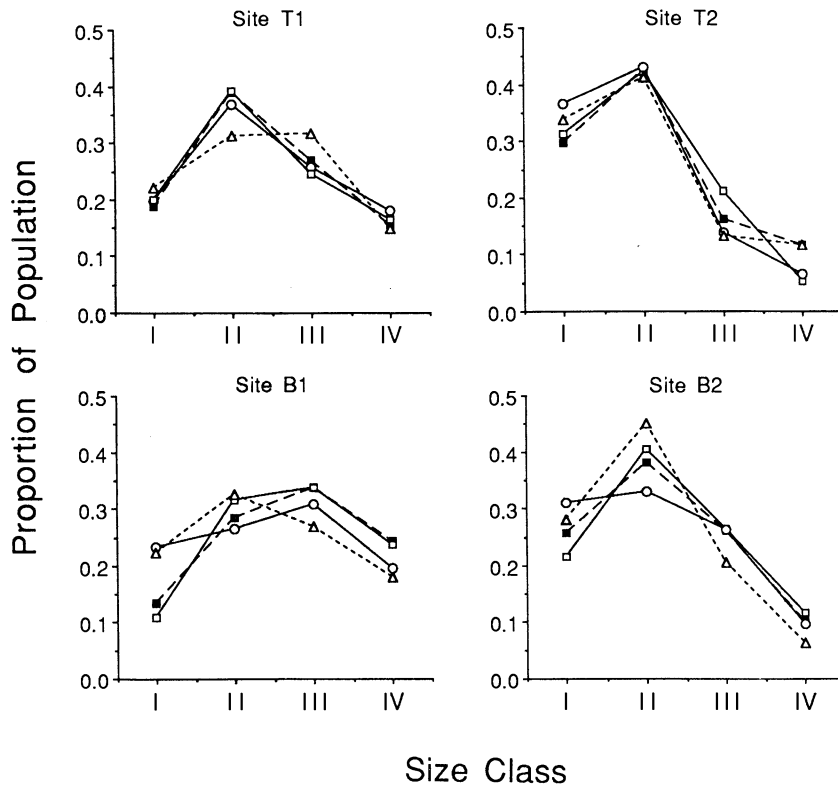
FIG. 7. Observed and predicted stable size distributions for the populations of *Alcyonium* sp. at the four sites. ■– – –■ stable size distribution predicted from population projection model; □———□ observed size distribution in September 1985; O———O observed size distribution in September 1986; △– – –△ observed size distribution of daughter colonies produced by fission. For site information see *Study sites*.

quency of fission in the absence of sexual reproduction (LH 4) increased ρ in population T1, but had little effect on the damping ratios of the other three populations.

In contrast to the suggestion of Caswell (1986), there does not appear to be a negative relationship between λ and ρ (Fig. 10). Population B2, which had a λ much smaller than the other populations, did have a much higher damping ratio than the more rapidly growing populations. The results of the six life history simulations, however, show no clear relationship between λ and ρ (Fig. 10). ρ increased with increasing λ for populations T1 and B2; for the other two populations ρ initially increased with increasing λ, but then decreased at the highest λ values. If only the sexual life histories (LHs 3, 5, and 6) are plotted, a positive relationship between λ and ρ emerges, suggesting—in contrast to Caswell's observations—that more rapidly growing populations are more stable than slowly growing populations.

Reproductive value

In all four *Alcyonium* sp. populations, reproductive value increased monotonically with colony size (Fig. 11), and a colony of size-class IV made a proportionally greater contribution to future generations than a colony

in any lower size class. This increase in reproductive value with increasing size is not surprising, given that fission and sexual reproduction both increase in frequency with colony size. Reproductive values were not affected by the elimination of sexual reproduction from the life cycle (LHs 2 and 4). Eliminating fission (LHs 3, 5, and 6) increased the reproductive values of the lower size classes relative to size-class IV, but did not alter their rankings.

Sensitivity analysis: elasticity

All four *Alcyonium* sp. populations are very insensitive to changes in sexual reproductive parameters (fecundity or recruitment) (Table 6). e_{ij} for a_{ij} representing sexual reproduction (first row and column of each matrix) are 1–3 orders of magnitude lower than e_{ij} for size-class transitions that occur by growth, shrinkage, or fission. Altogether, the matrix cells representing sexual reproduction contribute <1% of the value of λ. The relative insensitivity of λ to order-of-magnitude changes in sexual reproduction already shown by simulation (Table 4) is evident from these elasticity values.

All four populations are most sensitive to transitions among the three upper size classes of colonies, partic-
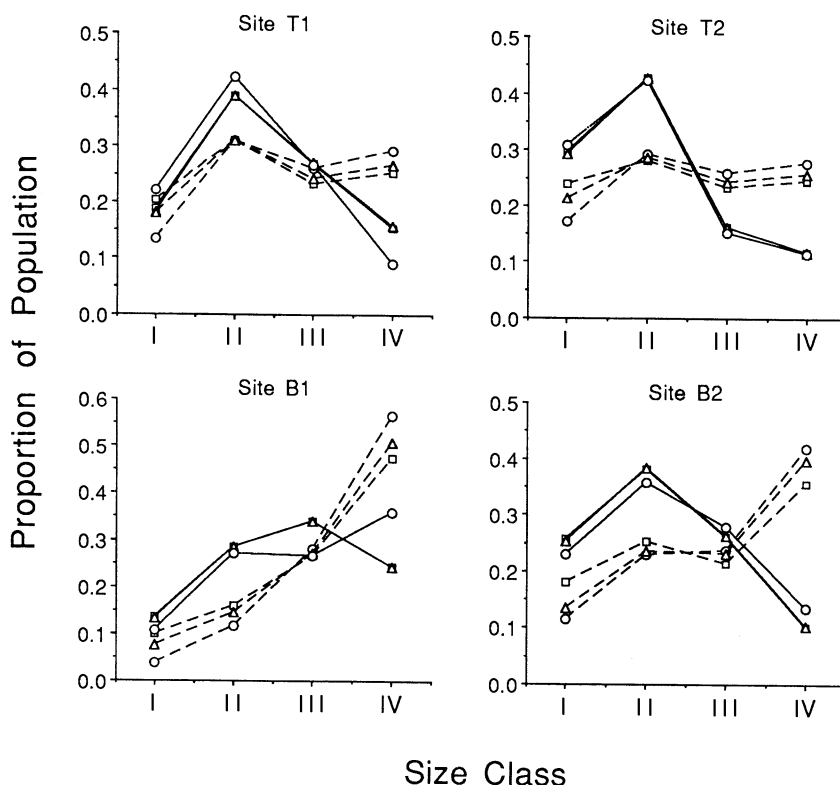
FIG. 8. Predicted stable size distributions, *w*, for the populations of *Alcyonium* sp. at the four study sites for simulations of six different life histories. Solid lines represent life histories that include fission (LHs 1, 2, and 4), dashed lines represent purely sexual life histories (LHs 3, 5, and 6). See Table 3 for explanation of numbered life histories. Life history 1: □——□; (LH 2) △——△; (LH 3) ○-- -○; (LH 4) ○——○; (LH 5) △---△; (LH 6) □---□. For site information see *Study sites*.

ularly size-classes II and III (Table 6). In populations T1, T2, and B2, >40% of λ is accounted for by transitions between size-classes II and III alone (growth from II to III, shrinkage or fission from III to II, and colonies that survive and remain in II or III). For all three of these populations, the single transition to which λ is most sensitive is colonies of size-class II remaining in size-class II. In population B1, the population in which the stable size-class distribution is skewed most strongly towards large colonies (Fig. 7), transitions between size-classes III and IV contribute 48% of the value of λ, while transitions between size-classes II and III account for an additional 23.5%. λ is most sensitive to colonies of size-class IV remaining in size-class IV.

Unfortunately, in the elasticity matrices the contributions of fission alone to λ cannot be separated from the simultaneous contributions of growth, shrinkage, and survival. For instance, the relatively high elasticity value associated with the transition from size-class III to size-class II in all four populations can be accounted for either by fission of size-class III colonies to produce daughter colonies of size-class II, or by shrinkage of size-class III colonies into size-class II. Likewise, colonies of size-class II that remain in size-class II can do so simply by surviving and not growing, or by under-

going fission to produce daughter colonies that are also in size-class II.

DISCUSSION

Demographically, *Alcyonium* sp. is a typical clonal organism, conforming well to generalities that have emerged from studies of other clonal species. Like most clonal plants (Cook 1985) and many clonal marine invertebrates (Jackson 1985, McFadden 1988, Lasker 1990), the population dynamics of this soft coral are dominated by the births and deaths of asexual ramets, while new genets, the products of sexual reproduction, rarely enter the population. During this study the mortality rate of *Alcyonium* sp. ramets was approximately matched by the fission rate, so that despite a high turnover of individuals, population density remained relatively constant. Populations of clonal plants are similarly characterized by constant population sizes despite high turnover rates (Cook 1985). Low recruitment rates of sexual propagules, limited dispersal, and size-dependent rates of reproduction and mortality are additional life history traits that *Alcyonium* sp. has in. common with many other clonal species, both plants and marine invertebrates (Cook 1985, Jackson 1985). Many of the conclusions reached from the study of this
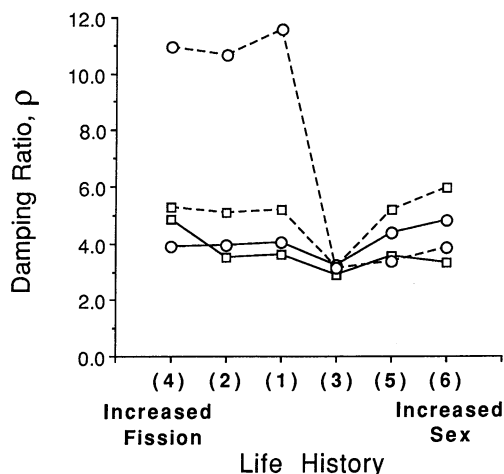
FIG. 9. Damping ratio, ρ, plotted as a function of life history for the *Alcyonium* sp. populations at the four study sites. The six simulated life histories (LH) are arranged on the x axis according to relative allocation to sexual reproduction vs. fission. Allocation to fission increases from right to left, allocation to sexual reproduction increases from left to right. LHs 3, 5, and 6: sexual reproduction only; LHs 2 and 4: fission only; LH 1: fission and sexual reproduction, observed values. See Table 3 for further descriptions of the numbered life histories. □——□ site T1; ○——○ site T2; □–––□ site B1; ○–––○ site B2. For site information see *Study sites*.

soft coral should apply to other clonal species, both plant and animal, that share these general demographic and life history characteristics.

Consequences of a purely sexual life history

The size-specific schedules of growth and mortality that underlie the dynamics of these soft coral populations are such that sexual reproduction alone is not a viable life history for *Alcyonium* sp. The only way in which the relative fitness of a purely sexual population could equal or surpass that of a population of colonies that undergo some fission is if the total amount of energy allocated to reproduction were increased. Provided rates of energy acquisition remain unchanged, increased allocation to reproduction can be achieved only at the expense of colony growth and maintenance, thereby shifting the population size distribution towards smaller colonies with lower reproductive output and higher mortality rates. The effect of increasing the total energy expenditure of the population was illustrated by the outcome of the simulation in which all colonies in size-classes II or above reproduced sexually (LH 6). Even though the increased reproductive output was not compensated for by decreased growth rates or higher mortality rates, λs were still reduced by 5–20%, and all four populations rapidly went extinct. In a different environment in which colony growth rates were higher, mortality lower, or larval

TABLE 6. Elasticity matrices for four *Alcyonium* sp. populations. Each elasticity value, e_{ij}, represents the proportional contribution of the size-class transition probability, a_{ij}, to the projected population growth rate, λ (see *Analysis of projection matrices: Sensitivity analysis*). Size-class transitions that contributed >10% are shown in boldface. P, I, ..., IV are the size classes.

			Site T1		
	P	I	II	III	IV
P	0.0000	0.0005	0.0012	0.0020	0.0022
I	0.0044	0.0247	0.0481	0.0314	0.0121
II	0.0015	0.0468	**0.1380**	**0.1000**	0.0446
III	0.0000	0.0307	**0.1020**	**0.1070**	0.0783
IV	0.0000	0.0179	0.0414	0.0778	0.0870

			Site T2		
	P	I	II	III	IV
P	0.0000	0.0002	0.0008	0.0005	0.0006
I	0.0020	0.0473	0.0748	0.0268	0.0172
II	0.0001	0.0873	**0.2020**	0.0802	0.0659
III	0.0000	0.0210	0.0856	0.0434	0.0501
IV	0.0000	0.0122	0.0724	0.0491	0.0610

			Site B1		
	P	I	II	III	IV
P	0.0000	0.0000	0.0002	0.0003	0.0004
I	0.0006	0.0156	0.0274	0.0192	0.0238
II	0.0003	0.0328	0.0743	0.0799	0.0623
III	0.0000	0.0258	0.0811	**0.1230**	**0.1010**
IV	0.0000	0.0123	0.0666	**0.1090**	**0.1440**

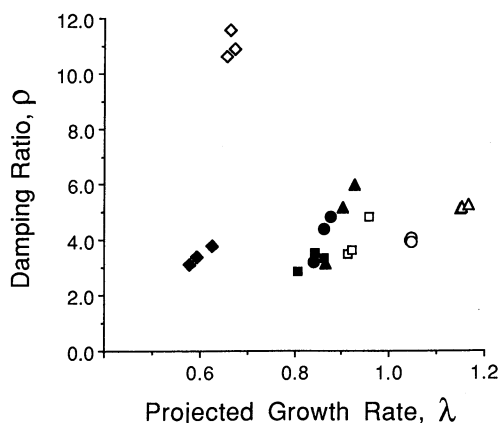|			Site B2		
	P	I	II	III	IV
P	0.0000	0.0004	0.0010	0.0010	0.0007
I	0.0023	0.0237	0.0854	0.0278	0.0128
II	0.0008	0.0626	**0.1520**	**0.1210**	0.0548
III	0.0000	0.0460	**0.1080**	**0.1140**	0.0446
IV	0.0000	0.0193	0.0449	0.0488	0.0269

FIG. 10. Damping ratio, ρ, plotted against projected rate of population growth, λ, for four populations of *Alcyonium* sp. for six simulated life histories (descriptions in Table 3). Open symbols represent life histories that include fission (LHs 1, 2, and 4), solid symbols represent purely sexual life histories (LHs 3, 5, and 6). Squares: site T1; circles: site T2; triangles: site B1; diamonds: site B2. For site information see *Study sites*.
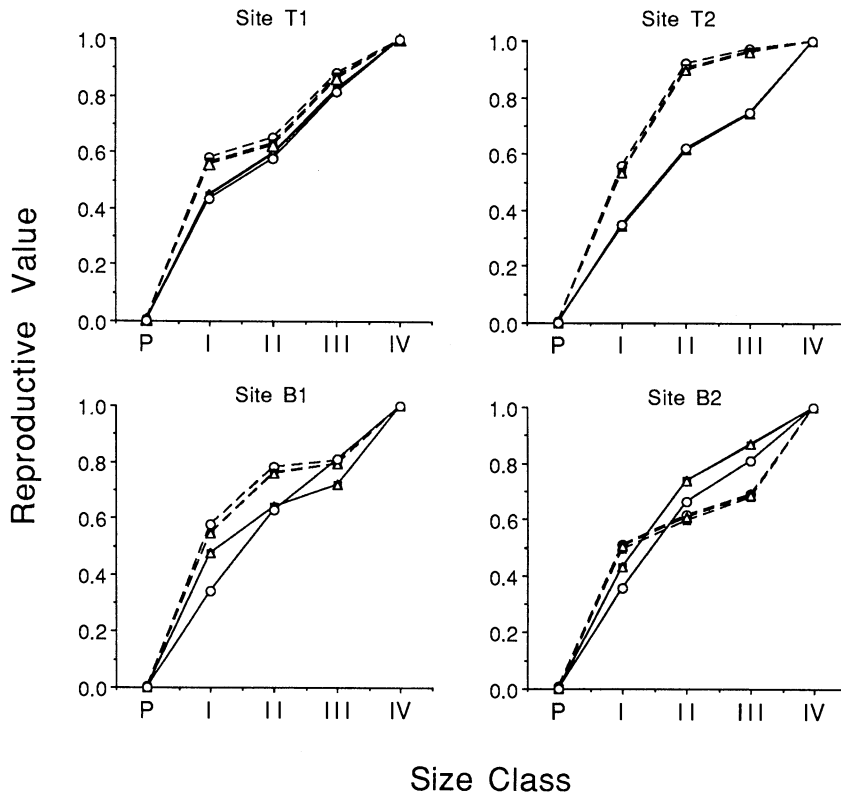
FIG. 11. Size-class reproductive values, v, for four populations of *Alcyonium* sp. following simulated changes in life history. Reproductive values are scaled proportional to the size class with the highest reproductive value (=1.0). Solid lines represent life histories (LH) that include fission (LHs 1, 2, and 4), dashed lines represent purely sexual life histories (LHs 3, 5, and 6). See Table 3 for explanation of numbered life histories. LH 1: □——□; LH 2: △——△; LH 3: ○‐‐‐○; LH 4: ○——○; LH 5: △‐‐‐△; LH 6: □‐‐‐□.

recruitment more frequent, sexual reproduction alone might be a feasible life history strategy for *Alcyonium* sp., but under the observed conditions even an increase in energy acquisition will not permit a population to persist by sexual reproduction alone.

Selection for increased λ in *Alcyonium* sp. should increase fission at the expense of sexual reproduction. As indicated by the elasticity matrices, a small increase in rates of fission, particularly among colonies of size-classes II, III, or IV, will have a much greater effect on λ than a proportionally similar increase in sexual reproductive output. Provided the energy costs of the two processes are comparable (e.g., a 10% increase in fission is energetically equivalent to—or more economical than—a 10% increase in sexual reproduction), fission is the more efficient method of reproduction. Daughter colonies produced by fission are "born" already attached to the rock surface, and, in most cases, already larger than the size class in which the risk of colony mortality is highest (Fig. 7). Planulae, on the other hand, must survive a free-living larval period, locate a suitable settlement site, undergo metamorphosis, and risk high mortality rates while small in

order to recruit into a population. Furthermore, the process of fission can be completed in a month or less, and at any time of the year, and the resulting daughter colonies may themselves be capable of dividing immediately. The complete cycle of sexual reproduction from gametogenesis to release of larvae, however, requires a full year in alcyoniids (Hartnoll 1975, Benayahu and Loya 1983, Sebens 1983), meaning that a minimum lag of at least 2 yr must pass between successive sexual generations.

Because *Alcyonium* sp. relies on fission rather than sexual reproduction for recruitment, populations can increase rapidly in response to favorable environmental conditions. Fission is associated with high colony growth rates (McFadden 1988), so any conditions that enhance growth will promote fission as well. As indicated by the high damping ratios, an *Alcyonium* sp. population that experiences a sudden change in size-class transition probabilities (due, for instance, to an increase in colony growth rates) will rapidly converge to a new stable size distribution, thereby achieving the rate of increase (λ) dictated by the altered transition probabilities. The stability of these soft coral popula-

tions is most likely due to the fact that, rather than all being born into the lowest size class, daughter colonies produced by fission are distributed among all four size classes in the population in approximately the same proportions as the stable size distribution (Table 5, Fig. 7).

Consequences of a purely asexual life history

The results of the sensitivity analyses and the simulations suggest that eliminating sexual reproduction from the life cycle would not lower, and, if replaced by fission, could increase the fitness of *Alcyonium* sp. populations. Why then has this species retained sexual reproduction? Many entirely asexual plants and animals are extremely successful ecologically, and maintain large populations over wide geographic ranges (Bell 1982, Cook 1985). While it has been suggested that asexual groups speciate less often than do sexual species, and ultimately, therefore, represent evolutionary dead ends, natural selection operating over ecological time scales often appears to favor eliminating sexual reproduction from the life cycle (Cook 1985).

Irrespective of arguments citing the advantages of genetic diversity as reason enough for the maintenance of sexual reproduction (Williams 1975, Maynard Smith 1978, Bell 1982), in *Alcyonium* sp. the sexually produced planula larva is also the primary means of dispersal and colonization. Adult colonies may be capable of creeping considerable distances, given enough time and available surface area, but once detached from a rock surface they are unlikely to reattach under natural conditions (see McFadden 1986). It seems unlikely that much dispersal takes place by adult colonies "rafting" on other organisms or floating objects (e.g., Jokiel 1984, Highsmith 1985, Jackson 1986), since the species is rarely found growing on anything other than very stable rock surfaces. If the free-living larval stage was eliminated from the life cycle, therefore, dispersal would, in most cases, be limited by any physical or biotic barriers that could not be surmounted by a creeping colony, and every genet would be confined to a single, contiguous rock surface. In the event of a site becoming unsuitable for habitation, or of all colonies at a site dying as a result of physical disturbance or predation, the genes carried by any non-dispersing (asexual) genets at that site would be eliminated from the population. Genets that had dispersed (sexual) propagules to sites unaffected by the disturbance, however, would leave descendants within the population. Sexual reproduction could be retained in the life cycle of *Alcyonium* sp. simply as a result of selection for dispersal ability. This, and other long-term benefits of sexual reproduction, might become apparent if the population dynamics of genets could be examined over longer time scales and wider spatial scales than those encompassed by this study.

Higher order demographic models

Consideration of the role of sexual propagules in this species' life history highlights the need to develop demographic models that incorporate the dynamics of both genets and ramets. In the models presented here I have treated colonies (=ramets) as the evolutionarily relevant demographic units, ignoring their genetic identity, and have equated the genet with the population of colonies. The conclusion that emerges is that genets (=populations) that reproduce by fission alone have higher fitness than genets that produce some sexual propagules at the expense of fission. New genets, however, only arise as a result of either sexual reproduction or mutation. In a demographic model of genets, therefore, the only possible outcome of eliminating sexual reproduction from the life cycle would be extinction, unless new genets are produced by mutation at a rate equal to or greater than the rate at which genets are lost from the population. Obviously, we would be in error if we assumed that conclusions reached from demographic models of ramets applied equally to populations of genets.

Although the genet is clearly the appropriate demographic unit with which to address long-term evolutionary questions (Caswell 1985, Cook 1985), quantifying the dynamics of genets presents numerous difficulties, for *Alcyonium* sp. as well as most other clonal organisms (Cook 1985, Jackson 1985). The most obvious difficulty is the estimation of birth and death rates of genets. Recruitment of sexual propagules is often negligible within the time scale of most demographic studies (Cook 1985, Jackson 1985, Lasker 1990), making it difficult to accurately estimate the rate at which new genets enter a population. Likewise, genets of clonal organisms are often extremely long lived (Cook 1985, Potts et al. 1985, Jackson 1985), and genet mortality may be undetectable within the lifespan of the human investigator. Furthermore, it is usually difficult or impossible to assign genetic identities to ramets in the field or to accurately account for all of the ramets comprising a genet, making it difficult to recognize when or if a genet is really dead.

It is tempting to use models of ramet dynamics to estimate genet mortality rates by assuming that the probability of mortality of the genet is simply the product of the independent probabilities of mortality of each of its component ramets (Cook 1979). For large, old clones, however, death probably occurs less often by independent deaths of ramets than by catastrophic physical disturbance or habitat destruction that results in the simultaneous and non-independent deaths of all ramets. Catastrophic mortality of this sort is unlikely to be a function of the size or age of the genet, however, and would have to be incorporated into a demographic model of genet dynamics as a stochastic element that occurred with some probability in each generation. Again, if such catastrophic events happen infrequently,

estimating their true probability of occurrence or periodicity becomes impossible.

Faced with the intractability of demographic studies of genets, we can nonetheless learn much from evolutionary analyses of ramet dynamics. Many of the conclusions reached in this study would not differ if the analysis had been based on the dynamics of genets rather than ramets. The outcomes of the simulations in which fission was eliminated from the life cycle (LHs 3, 5, and 6) would remain unchanged, since in the absence of asexual reproduction each ramet is also a unique genet. In a genet-level analysis, we would still conclude, therefore, that a purely asexual life history yields higher fitness than a purely sexual life history. For reasons discussed above, however, we would not necessarily conclude from a genet-level analysis that a purely asexual life history yields higher fitness than a life history that incorporates both fission and sexual reproduction. In a model based on genet population dynamics, the genet with the highest relative fitness will, by the definition of λ, be the one that gives rise to the greatest number of new genets. The balance between fission and sexual reproduction that yields the highest relative fitness cannot be determined without accurate estimates of rates of genet establishment and extinction.

LITERATURE CITED

Abrahamson, W. G. 1979. Demography and vegetative reproduction. Pages 89–106 *in* O. T. Solbrig, editor. Demography and evolution of plant populations. Botanical Monograph 15. Blackwell, Oxford, England.

Anderson, T. W., and L. A. Goodman. 1957. Statistical inference about Markov chains. Annals of Mathematics and Statistics **28**:89–110.

Bell, G. 1982. The masterpiece of nature: the evolution and genetics of sexuality. Croom Helm, London, England.

Benayahu, Y., and Y. Loya. 1981. Competition for space among coral-reef sessile organisms at Eilat, Red Sea. Bulletin of Marine Science **31**:514–522.

Benayahu, Y., and Y. Loya. 1983. Surface brooding in the Red Sea soft coral *Parerythropodium fulvum fulvum* (Forskal, 1775). Biological Bulletin **166**:32–43.

Bierzychudek, P. 1982. The demography of Jack-in-the-Pulpit, a forest perennial that changes sex. Ecological Monographs **52**:335–351.

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

———. 1986. Life cycle models for plants. Lectures on Mathematics in the Life Sciences **18**:171–233.

———. 1989. Matrix population models. Sinauer, Sunderland, Massachusetts, USA.

Caswell, H., and P. A. Werner. 1978. Transient behavior and life history analysis of teasel (*Dipsacus sylvestris* Huds.). Ecology **59**:53–66.

Cohen, J. E. 1979. Comparative statics and stochastic dynamics of age-structured populations. Theoretical Population Biology **16**:159–171.

Cook, R. E. 1979. Asexual reproduction: a further consideration. American Naturalist **113**:769–772.

———. 1983. Clonal plant populations. American Scientist **71**:244–253.

———. 1985. Growth and development in clonal plant populations. Pages 259–296 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology **68**:1412–1423.

Dai, C. 1990. Interspecific competition in Taiwanese corals with special reference to interactions between alcyonaceans and scleractinians. Marine Ecology Progress Series **60**:291–297.

Done, T. J. 1987. Simulation of the effects of *Acanthaster planci* on the population structure of massive corals of the genus *Porites*: evidence of population resilience? Coral Reefs **6**:75–90.

Enright, N., and J. Ogden. 1979. Application of transition matrix models in forest dynamics: *Araucaria* in Papua New Guinea and *Nothofagus* in New Zealand. Australian Journal of Ecology **4**:3–23.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York, New York, USA.

Harper, J. L., B. R. Rosen, and J. White. 1986. The growth and form of modular organisms. The Royal Society, London, England.

Hartnoll, R. G. 1975. The annual cycle of *Alcyonium digitatum*. Estuarine and Coastal Marine Science **3**:71–78.

Hartshorn, G. S. 1975. A matrix model of tree population dynamics. Pages 41–51 *in* F. B. Golley and E. Medina, editors. Tropical ecological systems. Springer-Verlag, New York, New York, USA.

Highsmith, R. C. 1982. Reproduction by fragmentation in corals. Marine Ecology Progress Series **7**:207–226.

———. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. Marine Ecology Progress Series **25**:169–179.

Hughes, R. N., and J. M. Cancino. 1985. An ecological overview of cloning in metazoa. Pages 153–186 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.

Hughes, T. P. 1984. Population dynamics based on individual size rather than age: a general model with a reef coral example. American Naturalist **123**:778–795.

Jackson, J. B. C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. American Naturalist **111**:743–767.

———. 1985. Distribution and ecology of clonal and aclonal benthic invertebrates. Pages 297–355 *in* J. B. C. Jackson, L. W. Buss, and R. E. Cook, editors. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.

———. 1986. Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. Bulletin of Marine Science **39**:588–606.

Jackson, J. B. C., L. W. Buss, and R. E. Cook, editors. 1985. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Connecticut, USA.

Jackson, J. B. C., and A. G. Coates. 1986. Life cycles and evolution of clonal (modular) animals. Philosophical Transactions of the Royal Society B **313**:7–22.

Janzen, D. H. 1977. What are dandelions and aphids? American Naturalist **111**:586–589.

Jokiel, P. L. 1984. Long distance dispersal of reef corals by rafting. Coral Reefs **3**:113–116.

Keyfitz, N. 1977. Introduction to the mathematics of populations. Addison-Wesley, Reading, Massachusetts, USA.

LaBarre, S., and J. C. Coll. 1982. Movement in soft corals: an interaction between *Nephthea brassica* (Coelenterata: Octocorallia) and *Acropora hyacinthus* (Coelenterata: Scleractinia). Marine Biology **72**:119–124.

Lasker, H. R. 1990. Clonal propagation and population dynamics of a gorgonian coral. Ecology **71**:1578–1589.

Maynard Smith, J. 1978. The evolution of sex. Cambridge University Press, New York, New York, USA.

McFadden, C. S. 1986. Colony fission increases particle capture rates of a soft coral: advantages of being a small colony. Journal of Experimental Marine Biology and Ecology **103**:1–20.

———. 1988. Growth, feeding biology, and clonal demography of a fragmenting soft coral. Dissertation. University of Washington, Seattle, Washington, USA.

Potts, D. C., T. J. Done, P. J. Isdale, and D. A. Fisk. 1985. Dominance of a coral community by the genus *Porites* (Scleractinia). Marine Ecology Progress Series **23**:79–84.

Sarukhan, J., and M. Gadgil. 1974. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. III. A mathematical model incorporating multiple modes of reproduction. Journal of Ecology **62**:921–936.

Sarukhan, J., and J. L. Harper. 1973. Studies on plant demography: *Ranunculus repens* L., *R. bulbosus* L. and *R. acris* L. I. Population flux and survivorship. Journal of Ecology **61**:675–716.

SAS Institute. 1985. SAS user's guide: statistics. Version 5 edition. SAS Institute, Cary, North Carolina, USA.

Sebens, K. P. 1983. The larval and juvenile ecology of the temperate octocoral *Alcyonium siderium* Verrill. II. Fecundity, survival and juvenile growth. Journal of Experimental Marine Biology and Ecology **72**:263–285.

Usher, M. B. 1979. Markovian approaches to ecological succession. Journal of Animal Ecology **48**:413–426.

Vandermeer, J. 1978. Choosing category size in a stage projection matrix. Oecologia (Berlin) **32**:79–84.

Werner, P. A., and H. Caswell. 1977. Population growth rates and age versus stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). Ecology **58**:1103–1111.

Williams, G. C. 1975. Sex and evolution. Princeton University Press, Princeton, New Jersey, USA.