

POPULATION DYNAMICS BASED ON INDIVIDUAL SIZE
RATHER THAN AGE: A GENERAL MODEL
WITH A REEF CORAL EXAMPLE

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Changes in the number of individuals in a population, and in their relative ability to replace themselves, form the quantitative basis for many ecological and evolutionary studies. The familiar demographic life-table traces these changes using two fundamental parameters, the age-related schedules of birth and mortality. Predictions of population dynamics based on age work best for cohorts of animals or plants which develop synchronously through consecutive life stages such as seed or larva, juvenile, and adult. For many organisms the growth rates of members of a single cohort can vary enormously from one individual to the next because of genetic or environmental differences, chance, or a combination of all three (Schaffer and Leigh 1976; Horn 1979, Hubbell and Werner 1979). Such developmental variance can result in a very poor correlation between age and the probabilities of mortality and natality. Often the fate of an individual can be predicted more accurately from its size (Connell 1973; Werner 1975; Harper 1977; Hughes and Jackson 1980; Highsmith 1982). Large individuals are typically more fecund, while small individuals usually have higher rates of mortality, regardless of age (Lefkovitch 1965; Hartshorn 1975; Jackson 1977; Werner and Caswell 1977; Enright and Ogden 1979; Highsmith et al. 1980). I present here a general model of population dynamics using size-related parameters appropriate to organisms with highly variable development. The model is based on a modified Leslie matrix and is designed to incorporate such diverse demographic processes as fragmentation, regression (shrinkage), and partial mortality, as well as the more familiar processes of growth, sexual reproduction, and death.

Clonal Organisms

A population model based on size rather than age is particularly useful in describing the dynamics of clonal invertebrates and plants. The body of a clonal organism is made up of repeated building blocks or modules, e.g., the polyps of a

coral or hydroid, the zooids of a bryozoan, or the shoots of a clonal plant. After larval or seed settlement and metamorphosis, most of the growth of a colony is achieved by increasing the number of genetically identical modules (Harper 1977; Jackson 1977, 1979). Individual colony growth is potentially indeterminate in many species, but may be inhibited to varying degrees by physical stress, local availability of resources, or by mortality of modules. Therefore, there is often enormous variation in size between colonies within an age cohort (Harper 1977; Solbrig et al. 1980; Vaughan 1911). In addition, many colonies regress periodically from large adult size to small resting stages, especially in seasonal habitats, e.g., sponge gemmules, bryozoan hibernacula, or plant bulbs. Frequently, it is impossible to distinguish morphologically between a rejuvenating individual and a newly settled one (Mertz and Boyce 1956; Hughes and Jackson 1980).

In some species, single modules or larger clumps of modules may break off and lead a separate existence. Thus, clones of individuals or separated "daughter" colonies of identical genotype may be common (Rosen and Taylor 1969; Sarukhan and Harper 1973; Francis 1976; Janzen 1977; Highsmith 1982). Counts of distinct physiological individuals may therefore far exceed the genetic population size. After fragmentation, individual clone members may reproduce or die more or less independently. Even where modules remain firmly connected, some may be killed while others remain healthy. Because colonial organisms by definition have replicated feeding structures, gonads, etc., they can frequently survive extensive partial mortality (i.e., shrinkage) on a scale far beyond the regenerative capacity of most solitary animals or plants.

Many of these characteristics have been described in population studies of reef corals. Vaughan (1911) followed a newly settled cohort of the coral *Porites astreoides* for 12 mo, and found that a few of the survivors grew very quickly, while most showed only a small increase in size. Although the corals were all of the same age, there was a sixfold difference in maximum colony diameter within a single year (a tiny fraction of the potential life span). Connell (1973) and Loya (1976) showed further that smaller colonies usually have faster growth rates, but are more likely to be killed than larger corals. Hughes and Jackson (1980) measured rates of shrinkage, fragmentation, and colony fusion, and showed that these processes combine to decouple size-age correlations.

Conventional age-related population analysis is totally unsuited to the demographic characteristics of colonies. Small or medium-sized individuals are frequently older than large ones, especially if they are crowded, and may become even smaller if they regress or are injured. Furthermore, it is usually impossible or impractical to calculate ages without actually following a colony throughout its entire life, perhaps for many decades. Not surprisingly, data collection on the population biology of colonial organisms has been hampered by the lack of an appropriate theoretical framework. Here I present a simple size-related demographic model for animals and plants for which age-related models are unsuitable. Using a reef coral example, I show the effects of shrinkage, fragmentation, and differential growth on the population dynamics of clonal organisms. In addition, I use the model to make testable predictions on the effects of rare storms and the role of clonal population dynamics in community development.

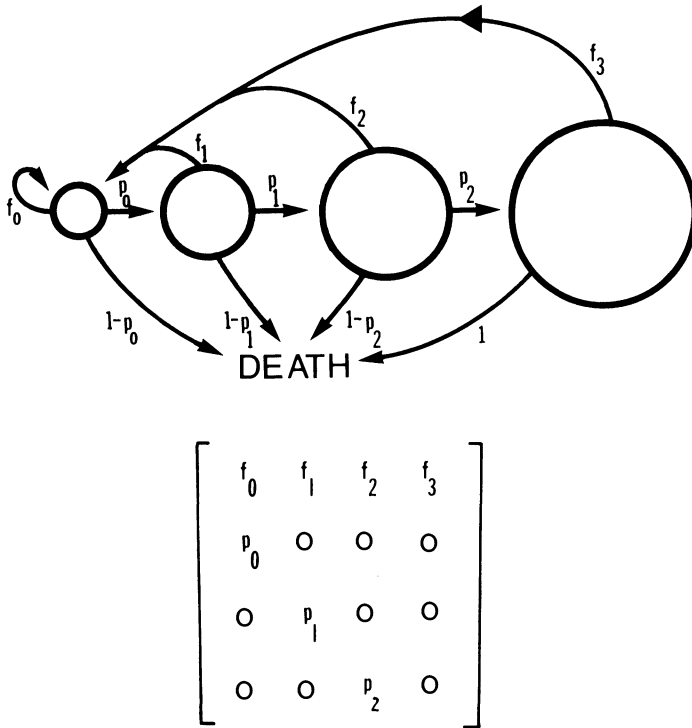


FIG. 1.—A graphic representation of the Leslie matrix model. Larger circles depict increasing age. During each time interval individuals may either die or survive, progressing into the next age class. Each age group (the columns of the matrix) may contribute sexual recruits to the youngest age class (the top row of the matrix). $0 \leq p \leq 1$, $0 \leq f$.

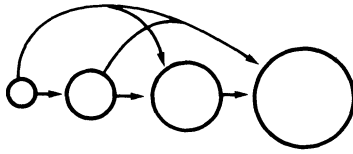
The Model

Leslie's (1945) deterministic model predicts the age structure of a population, given the age structure at some past time and the age-specific rates of fecundity and survival. The model is shown graphically in figure 1. The form of the model is:

$$\bar{x}_{t+1} = \bar{A} \cdot \bar{x}_t$$

where \bar{x}_t is a column vector describing the population age structure at time t , and \bar{A} is a matrix which determines the dynamics of the population. \bar{A} has two types of elements: the elements f_i ($f \geq 0$) along the top row of the matrix represent the average number of sexual recruits born between time t and $t + 1$, to each individual of age i to $i + 1$ at time t . The elements p_i ($0 \leq p \leq 1$) along the subdiagonal of the matrix represent the probability that an individual, aged i to $i + 1$ at time t , will be alive at time $t + 1$, in the next oldest age class. It follows that $1 - p_i$ is the age-specific mortality rate. All other elements of the matrix are zero, reflecting the biological absurdity of, say, a 2-yr-old individual becoming a 1-yr-old again, or becoming a 4-yr-old without first being a 3-yr-old. An important property of this model is that whatever the population structure initially, the

GROWTH



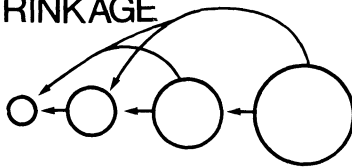
$$\begin{bmatrix} 0 & 0 & 0 & 0 \\ g & 0 & 0 & 0 \\ g & g & 0 & 0 \\ g & g & g & 0 \end{bmatrix} \quad (A)$$

LOOP



$$\begin{bmatrix} L & 0 & 0 & 0 \\ 0 & L & 0 & 0 \\ 0 & 0 & L & 0 \\ 0 & 0 & 0 & L \end{bmatrix} \quad (B)$$

SHRINKAGE



$$\begin{bmatrix} 0 & s & s & s \\ 0 & 0 & s & s \\ 0 & 0 & 0 & s \\ 0 & 0 & 0 & 0 \end{bmatrix} \quad (C)$$

GENERAL MODEL

$$\begin{bmatrix} f+L & f+s & f+s & f+s \\ g & L & s & s \\ g & g & L & s \\ g & g & g & L \end{bmatrix} \quad (D)$$

FIG. 2.—A graphic representation of a size-dependent matrix model of population dynamics. Larger circles depict increasing individual size. During each time interval surviving individuals may (A) grow, (B) stay the same size, or (C) contribute to smaller size classes by shrinking or fragmentation. Sexual recruits are contributed by each size class to the smallest size class as in fig. 1. Transitional probabilities are as follows: (growth) $0 \leq g \leq 1$, (loop) $0 \leq L \leq 1$, (shrinkage) $0 \leq s \leq 1$, (asexual reproduction) $0 \leq s$, (sexual reproduction) $0 \leq f$.

population will grow (or shrink) ultimately at a constant rate, λ , and a stable age distribution will be maintained. Exponential growth of the population is indicated by λ greater than one, stability by λ equal to one, and a decline to extinction by values between one and zero.

This model can be adapted for populations whose structure is described by size rather than age classes (see review in Usher 1972; Werner and Caswell 1977). In a size-stage matrix, probabilities below the diagonal represent net growth into a larger size class (fig. 2A). The diagonal describes the likelihood of an individual

remaining in the same size class, either through a slowing down in growth rate, or a balance between growth and shrinkage (fig. 2*B*). Finally, probabilities above the diagonal represent contributions to a smaller size class, i.e., through shrinkage, fragmentation or sexual reproduction (figs. 2*C*, 2*D*). Thus, the elements of the original Leslie matrix which are usually zero, may here take on nonzero values. In the modified model, the size-specific mortality rate is one minus the sum of probabilities in each column of the matrix, provided individuals do not fragment or fuse.

The most general form of the size-staged matrix is given in figure 2*D*. All previously published population matrices are special cases of this general model (e.g., Enright and Ogden 1979; Hartshorn 1975; Lefkovitch 1965; Meagher 1982; Sarukhan and Gadgil 1974; Werner and Caswell 1977). I describe below the construction of a matrix for a population of the reef coral *Agaricia agaricites*. This massive or foliaceous stony coral is abundant over a wide depth range throughout the Caribbean. Individuals commonly live for 50 yr or more, but they cannot be accurately aged without disturbing or killing the colony (Hughes and Jackson 1980). I use the matrix firstly to predict changes in the number and sizes of colonies within a single cohort, over time scales that are impractical to measure directly. Secondly, sexual recruitment is added to the model to examine the dynamics of populations of mixed ages. Finally, I examine some of the assumptions of the model and their biological meaning.

A CASE STUDY

The fate of 246 *Agaricia agaricites* colonies was followed from analysis of several hundred in situ photographs taken of 12 1-m quadrats placed on a vertical wall between -10 m and -20 m at Rio Bueno, Jamaica. Colonies were assigned to one of four size classes based on their area in the first year of each set of observations. The size classes were 0-10 cm², 10-50 cm², 50-200 cm², and >200 cm². These particular categories were chosen to encompass the range of colony area observed in the population, while maintaining at least 25 corals in each size class. Dividing up the population into more than four size classes would have increased the resolution of the projected size structure (see below), but at the expense of increased sampling error around measured matrix probabilities. The transitional probabilities calculated from the field population (table 1) depend in part on the size-frequency distribution within each size class. I have attempted to minimize this source of error by defining size classes as narrowly as possible in the range most sensitive to size-related changes, i.e., size classes I and II.

At the beginning of the study, *Agaricia agaricites* occupied 15.2% of the space within the quadrats, and the measured population structure was dominated by small corals (see size class sample sizes in fig. 3). Total living cover, mainly by corals, sponges, and algae, was 61.7%. From one annual census (taken in August) to the next, surviving *Agaricia* colonies shrank, stayed in the same size class, or grew larger (fig. 3). In the first year (1977/1978), whole colony mortality was highest among small corals, and absent in the largest individuals. The largest colonies suffered extensive partial mortality, however, and shrank more often

TABLE 1

MATRICES OF TRANSITIONAL PROBABILITIES FOR FOUR SIZE CLASSES OF *A. agaricites*
IN A CALM AND STORMY YEAR

CALM (1977/78)					STORMY (1978/79)				
	I	II	III	IV		I	II	III	IV
I	.6020	.1167	.0217	.0741	I	.5135	.0794	.0727	.0714
II	.1681	.6167	.1087	.0370	II	.2072	.6349	.2364	.2500
III	.0000	.2000	.8043	.1481	III	.0000	.1746	.6545	.0714
IV	.0000	.0171	.0217	.9259	IV	.0000	.0000	.0000	.7500
Σ	.7701	.9504	.9564	1.1851	Σ	.7207	.8889	.9636	1.1428
d_x	.2301	.0667	.0652	.0000	d_x	.2793	.1587	.2182	.1786
$\lambda = .9824$					$\lambda = .8869$				

NOTE.—Sample sizes as in fig. 3. The sum of transitional probabilities in each column exceeds one when the number of colonies alive increases from one time interval to the next, i.e., if gains from asexual reproduction exceed losses from mortality. d_x is the size-specific probability of mortality. Sexual reproduction is not included in either matrix. Lambda is the equilibrium growth constant. (Lambda less than one describes population decline.)

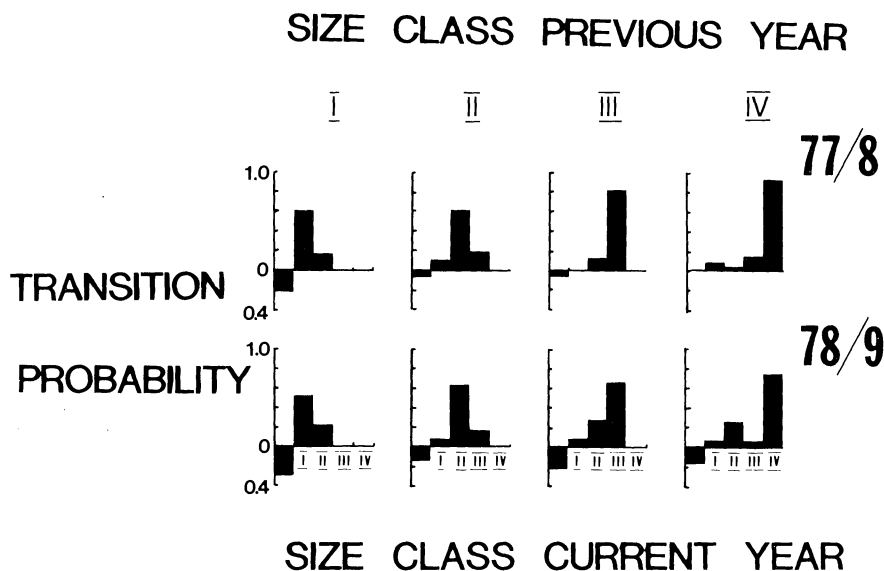


FIG. 3.—Size class transition probabilities of *A. agaricites* colonies in 1977/1978 and 1978/1979. Bars below zero represent colonies that died. Colony size was grouped as follows: I, 0–10 cm²; II, 10–50 cm²; III, 50–200 cm²; IV, >200 cm². Sample sizes are 113, 60, 46, and 27 colonies in 1977, and 111, 63, 50, and 28 colonies in 1978.

compared to small ones (Hughes and Jackson 1980). The zero whole-colony mortality rate for size class IV does not mean that colonies greater than 200 cm² are never killed; rather, it implies that mortality is preceded by shrinkage into a smaller size class. Most colonies remained in the same size class from one year to the next, reflecting the slow net growth rate of this species (<2 cm lateral extension rate per annum, Hughes and Jackson, unpubl. data). Colony fragmentation was initiated among large colonies when partial mortality severed tissue connections between polyps. Because one colony can produce several by fission, the sum of transitional probabilities in a column of the population projection matrix may overestimate survivorship, and mortality rates cannot be calculated directly from the matrix (see table 1 for the mortality rates and the matrix form of fig. 3).

The following year, in March 1979, a severe storm with waves up to 4 m high, caused extensive damage to many coral populations on the North coast of Jamaica (Tunncliffe 1980). In *Agaricia agaricites*, whole and partial mortality increased, especially in larger size classes, while there was a concomitant decrease in net rates of growth (fig. 3, table 1). In the year of the storm, there was a total absence of growth into the largest size class. Clearly, the 1978/1979 "storm" matrix cannot be too regular a demographic occurrence, or the observed population structure on Jamaican reefs would not be realized. Tunncliffe (1980) estimated that a storm of this severity only occurs about every 20 yr. The most recent severe hurricane before this storm was in 1917, and the next one was Hurricane Allen, 17 mo later in August 1980 (Woodley et al. 1981).

The deterministic Leslie matrix model defined earlier assumes transitional probabilities are constant from one time interval to the next. Frequently, however, changes in demographic parameters can result from a variety of factors, such as crowding or thinning, seasonal changes, or disasters. Sarukhan and Gadgil (1974) incorporated temporal changes in their models of buttercup populations by alternating different matrices for different seasons. A similar technique can be used here to simulate the effects of storms.

The differences between the calm and storm matrices become clearer when they are used to predict demographic behavior over a considerable time. Consider the dynamics of a single cohort, starting from an initial settlement of, say, 1,000 individuals, i.e., at t_1 , \bar{x} equals [1000, 0, 0, 0]'. The population structure changes through time as surviving colonies grow into larger size classes. Using the calm matrix only (zero storm frequency) to project the dynamics of the cohort, peak numbers of colonies in the II, III, and IV size classes occur at 3, 9, and 21 years, respectively, after the initial settlement (fig. 4A). In contrast, for the storm matrix only (100% storm frequency), size classes II and III contain a maximum number of colonies after only 3 and 6 yr, while size class IV always remains empty (fig. 4B). The decreasing rate of elimination of smaller size classes from the cohort through time is caused by the formation of new, small corals from shrinking and fragmenting larger colonies. After a time, the rate of decline is constant for all size classes, reflecting an equilibrium size-frequency distribution analogous to the stable age distribution of the Leslie matrix model. The storm matrix dictates a

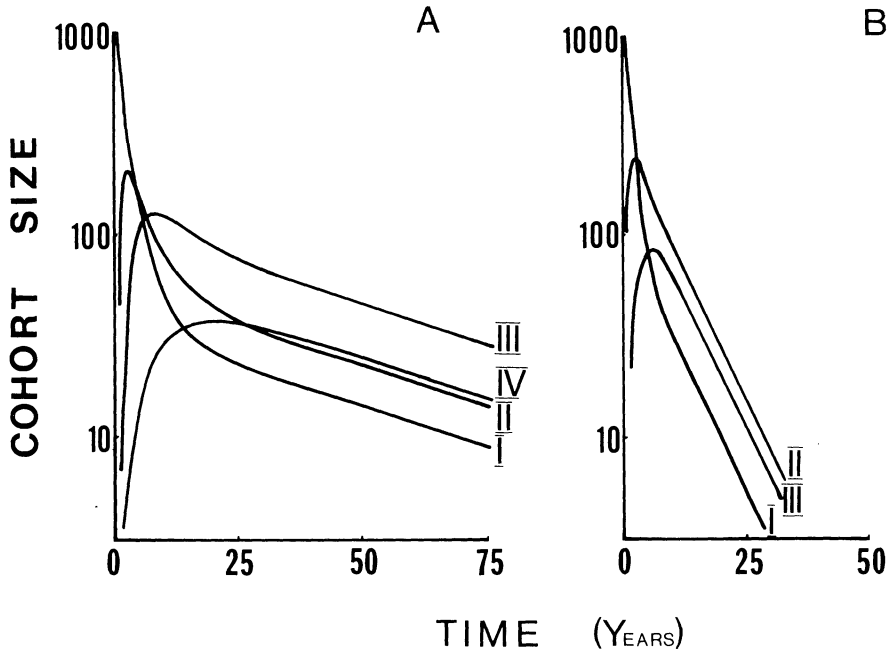


FIG. 4.—Changes in the number and sizes of coral colonies in a single cohort as a function of cohort age. Cohort behavior is projected by the rules of the calm (A) or storm (B) matrix (see table 1), from an initial settlement of one thousand colonies. Coral size classes as in fig. 3. Note that as size class I declines because of mortality and growth of colonies into larger size classes, each consecutive size group peaks and then declines to eventual extinction.

faster rate of turnover, so equilibrium size-frequency is reached much sooner, after 12 yr versus 35 for the calm matrix.

This analysis shows how differential growth causes huge variations in colony size within a single cohort (fig. 4A, 4B). Even if the size-frequency distribution within each size class is such as to minimize population variance, the ratio of variance to mean colony size of 20-yr-old colonies is over 45 for the calm population, and over five for the storm population. The exact value of this ratio is unimportant; the calculation is included to indicate how colony size can become extremely variable in a relatively short period of time because of individual differences in rates of growth and shrinkage. In addition, the coral population biomass (and presumably reproductive output) will be dominated in time by larger colonies. Colony longevity will also differ greatly between corals of equal age, because some remain small while others grow larger, and hence less likely to be killed.

In reality, of course, storms usually occur after some period of relative calm. An occasional storm would therefore have considerable impact on larger colonies which develop during more normal years. The effect of storm frequency other than 0% and 100% is modeled here by alternating the calm and storm matrices.

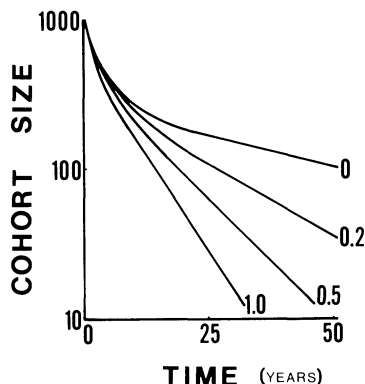


FIG. 5.—Cohort size through time as a function of storm frequency. The effect of storms was simulated by alternating the storm and calm matrices (table 1) in repeated multiplications of the population structure vector, e.g., a storm frequency of 0.2 is modeled by changing the matrix from the calm to the storm rules every fifth iteration of the simulation.

Starting again with an initial settlement of 1,000 individuals, the cohort declines to extinction at varying rates, proportionate to storm frequency (fig. 5). The rate of decline is not a linear function of number of storms, however, e.g., a doubling of storm frequency from every tenth to every fifth year would have less effect on extinction rate (λ) compared to a doubling from a 20- to a 10-yr cycle. Thus, the model predicts that the effect of a storm on the survival of a cohort is proportionately greater when it is a rare event. This prediction is independent of any conjectured acclimation by individual corals to frequent storms, and results from differences in population structure (see below).

As well as numbers of colonies, the coral population structure can be estimated as a function of storm frequency. As storms become more common, there is a steady decline at equilibrium in the relative numbers of large colonies (size classes III and IV) in the cohort, with a corresponding rise in the proportion of small individuals (size classes I and II; fig. 6). Note, however, that in absolute terms the numbers in all size classes decline as storms become more common.

Strictly speaking, only the 0% and 100% storm populations ever reach an equilibrium size structure. At intermediate storm levels, the population is perpetually recovering from the latest upset in size class distribution. This is shown by the range bars in figure 6. These indicate the variation caused by storms in population structure between t_{40} and t_{50} , well after fluctuations due to development of a size class structure from the original settlement have been eliminated.

The model predicts that population structure will change considerably along a disturbance gradient, e.g., between reefs close to, versus away from, storm tracks. The well-known phenomenon of deep-water gigantism in many species of corals (Goreau 1966; Glynn 1973) in part may result from decreased mortality and injury rates along depth gradients during severe storms (Woodley et al. 1981). Large *Agaricia* are more common in deeper water despite slower growth rates (T. P. Hughes and J. B. C. Jackson, in prep.).

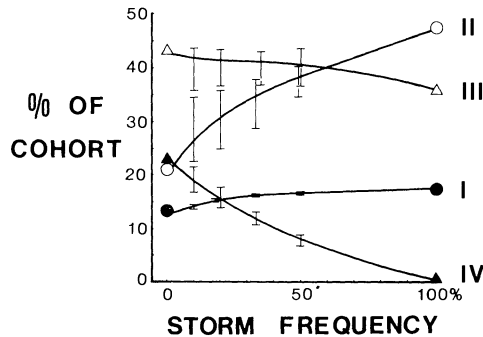


FIG. 6.—Cohort size structure between 40 and 50 yr after settlement as a function of storm frequency. The bars indicate the range in values as the cohort slowly tends to equilibrium between storms. Colony size classes as in fig. 3.

Sexual Reproduction

The analysis above shows the development of a size structure within a cohort because of differential rates of colony growth and shrinkage. In this section, I use the model to demonstrate how the rate of larval settlement will also influence population growth and structure. The probability of an individual producing sexual offspring is unknown for this and all other coral species (Connell 1973). Even if colony fecundities were known, they probably would be of very little use in predicting local population growth, because larvae are dispersed. Because of dispersal, there is a very poor correlation between a species' local population density and the rate of observed settlement (Rylaarsdam 1983). Annual larval settlement, from 1977 to 1981, into the smallest size class of the study population varied from 18 to 25 colonies per 12 m². The matrix model can be used to project population growth from annual larval input of, say, 20 colonies by adding that number to the first element of the population vector \bar{x} , each year. This approach makes no assumptions about size- or age-specific fecundities, but is probably a reasonable imitation of a planktonic input from a larval pool. It is of course true that the rate of recruitment in real life varied from year to year. However, a simulation run with fluctuating numbers of recruits around a mean of 20 larvae per year gave essentially the same results as those described below. The initial population structure and size will not affect equilibrium values, so for convenience I assume a local population of zero at t_1 . Using the calm matrix, the number of corals increased rapidly at first, then extremely slowly to an asymptotic level after about 250 yr (fig. 7, C_{20}).

Population growth declines to zero when the constant number of annual recruits balances the proportion of colonies dying. As the population increases in size, the number of larvae added per individual colony decreases. Therefore a constant input of recruits effectively becomes a fecundity term which is inversely related to population size. This in no way implies that mean individual reproductive output is density dependent. The number of sexual offspring produced by the coral population, whether increasing or not, is assumed to have no role in local larval

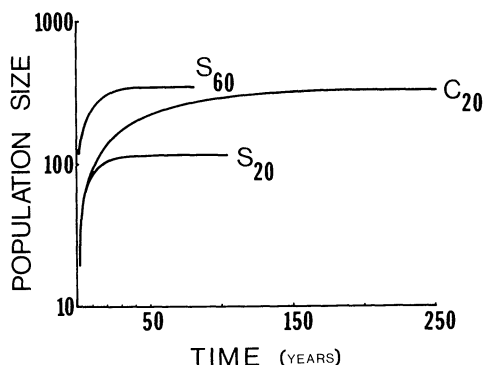


FIG. 7.—Population growth predicted respectively by the storm and calm matrices at various levels of larval recruitment. C_{20} represents a population behaving by the rules of the calm matrix, with an annual larval input of 20 colonies. S_{20} and S_{60} represent storm populations with annual inputs of 20 and 60 recruits, respectively.

input. More complex simulations could incorporate the likely decline in the rate of successful recruitment as the established population grows, e.g., by making the number of larvae added at time t_i some negative function of the area already covered at time t_{i-1} . There are no density-dependent mortality or growth terms in the simulation presented in figure 7, i.e., transitional probabilities are constant regardless of population size or structure. Yet population growth declines to zero just as it would if mortality increased as a function of population density. The length of time needed to reach equilibrium indicates how long it would take a totally obliterated population to recover if it relied solely on new sexual recruitment, probably far longer than the interval between catastrophes.

In comparison, for the same larval input of 20 colonies per yr, a population growing by the rules of the storm matrix will reach equilibrium size five times faster, after about 50 yr, but the maximum number of colonies is only one-third that of the calm population. To attain an equal number of corals at equilibrium, the storm matrix would need about 40 additional recruits every year (fig. 7).

The population structure at equilibrium for both the calm and storm matrices differs from that shown for a single cohort changing through time (fig. 4), because larval input increases the relative numbers of small corals. For the calm matrix, the relative numbers in size classes I and II increased by 17% and 31%. For the same larval input of 20 colonies, the distortion of the storm matrix population was even larger: the relative numbers of size class I increased by more than 150%, while II and III decreased by about 25% and 50%, respectively. Surprisingly, this population structure does not continue to change at higher recruitment rates. Even with 60 colonies added each year, the equilibrium size structure is exactly the same. Thus, the influence of sexual recruitment on size-frequency distribution decreases above a certain level, and may be predicted using the matrix model.

Finally, population development can be expressed in terms of area covered by using population structure and a rough estimate of mean colony size in each size

class. With the same level of larval input of 20 colonies per year, the calm population grows to a maximum of 31% cover, while the storm population reaches only 3%. Three times the sexual input increases the storm population area to only about one-third the calm population (10% cover), even though the number of colonies is almost equal.

Biologically, this is a remarkable result. The model predicts that the measured demographic characteristics of this coral species will restrict population development, even where there is ample space remaining for settlement and growth.

DISCUSSION

The model clearly predicts that for organisms with developmental plasticity, individuals of the same age may be of very different size (fig. 4). Because of size-related variations in mortality and fecundity, individuals of the same age will have widely different capabilities of obtaining representation in subsequent generations. A corollary of variable size within a cohort is that individuals of similar size may vary greatly in age. This has been shown for colonies of *A. agaricites* by examining growth patterns in the coral skeleton (Hughes and Jackson 1980). In a similar study Mertz and Boyce (1956) showed that nearly three quarters of oak "seedlings" developing after a forest cutting were in fact sprouts attached to root systems varying in age up to 40 yr old. The age of stems inferred from size, number of terminal bud scars, and number of annual growth rings could not be used to establish the time of seed germination.

Ideally, the accuracy of predictions made by a size-staged model should be compared with a similar age-staged matrix, using long-term field observations. This has only been done once, in a 5-yr study of a nonclonal biennial plant *Dipsacus sylvestris* (Werner 1975; Werner and Caswell 1977). It was elegantly shown that various plant fates could be predicted more accurately from size than age. The size-staged matrix describing the dynamics of *Dipsacus* was relatively simple (Werner and Caswell 1977); there were no elements describing shrinkage or fragmentation, so that the decoupling of size and age resulted entirely from differential growth rates between individual plants. Presumably, the more complex development of *A. agaricites* or oak trees, and their much greater longevity, would make predictions based on age even less appropriate for them.

Historical Effects

Can size alone adequately predict the fate of an individual? The answer is often no, for a variety of reasons. One of the assumptions of the model is that there is no discrimination between individuals in a size class in the demographic options open to them. Thus, for example, all small individuals are supposed to behave identically regardless of whether they are newly settled recruits, asexually formed fragments, or a small remnant of a previously large individual that has shrunk. These distinctive demographic types will probably have rather different schedules of survivorship and fecundity. Daughter colonies of *Agaricia agaricites* usually share a common skeletal framework built before overlying tissue connections

TABLE 2
A TEST FOR HISTORICAL EFFECTS

		A. FATE OF COLONY IN 1978/1979			
		Injured	Escaped	Killed	Total
Fate in 1977/1978	Injured	50 (60.2)	15 (18.1)	18 (21.7)	83 (100)
	Escaped	37 (29.6)	61 (48.8)	27 (21.6)	125 (100)
		Chi sq. = 24.1, $P < .0001$			
		B. FATE OF COLONY IN 1979/1980			
		Injured	Escaped	Killed	Total
Fate in 1978/1979	Injured	47 (54.0)	31 (35.6)	9 (10.3)	87 (100)
	Escaped	22 (28.9)	45 (59.2)	9 (11.8)	76 (100)
		Chi sq. = 10.9, $P = .004$			
		C. FATE OF COLONY IN 1979/1980			
		Injured	Escaped	Killed	Total
Fate in 1977/1978	Injured	37 (56.9)	26 (40.0)	2 (3.1)	65 (100)
	Escaped	35 (35.7)	48 (49.0)	15 (15.3)	98 (100)
		Chi sq. = 10.3, $P = .006$			

NOTE.—A, Number (and percent) of colonies which were killed, injured, or escaped injury-free in 1978/1979 as a function of whether they were injured or not in 1977/1978. B, Number (and percent) of colonies killed, injured, or escaped injury-free in 1979/1980 as a function of past events in 1978/1979. C, Number (and percent) of colonies killed, injured, or escaped injury-free in 1979/1980 as a function of events 2 yr previously, in 1977/1978.

were severed. Because of their somewhat elevated position on top of old skeleton, small daughter colonies may avoid some sources of mortality prevalent in juvenile colonies of the same size, e.g., shading, or smothering by sedimentation. On the other hand, a small shrunken colony is often the result of partial overgrowth. If, for example, a long-lived sponge grows over and kills part of a coral, the chances are it will eventually smother the rest of the colony. These differences in fate as a function of past events may be termed historical effects. Note that historical effects are not necessarily caused by variations in age, since they also occur between individuals born at the same time. For example, Slobodkin (1954) showed that the level of food available early in the life of a cohort of *Daphnia* can produce differences in later growth rate and population structure.

A test for historical effects is shown in table 2A. All colonies surviving from 1977 to 1978 were classified as to whether they were injured or not (escaped injury-free) during that year. The injury and escape rates were then recorded for the next year, 1978/1979, as a function of this past history. The resulting contin-

gency table shows clearly that injured corals were almost twice as likely to be injured again (chi square = 24.1, $P < .0001$, table 2A). This pattern occurs regardless of whether injury rates to the population as a whole increased or decreased. Consequently, historical effects were also highly significant the year after the storm, from 1978/1979 to 1979/1980 (chi square = 10.9, $P = .004$, table 2B). Furthermore, the fate of colonies in 1979/1980 depended on their past experiences 2 yr earlier, in 1977/1978 (chi square = 10.3, $P = .006$, table 2C). The observed decrease in the significance level of the chi-square values from 1–2-yr historical effects (table 2A, 2C) is to be expected, as injured corals recover and the demographic differences between them and uninjured colonies diminish.

Historical effects such as these probably vary considerably from year to year in both their intensity and persistence. In terms of the matrix, table 2 indicates that transitional probabilities for injured colonies into smaller size classes will tend to be higher, while growth and loop probabilities will tend to be lower relative to mean values. This trend may be somewhat offset by the common observation that rates of regeneration of damaged tissue are faster than new growth (Liming and Johnston 1944; Marshall and Sagar 1965; Loya 1976).

The model also assumes that there are no historical effects on fecundity. Again this is highly unlikely. Consider a hypothetical clonal organism which grows for a time before sexual reproduction can begin. After this prereproductive period, sexual modules develop, but are confined to the middle of the colony surrounded by nonreproductive tissue (e.g., Braverman 1963; Francis 1976). Such a reproductive colony, if it shrinks to a small size again, might still be reproductive, depending on what parts of it died, and on its physiological response to partial mortality and regression. Jackson and Palumbi (1979), Karlson (1981), and Wahle (1983) have suggested that energy depletion during regeneration results in reduced future reproductive output for a variety of clonal species.

The matrix model can take into account historical effects like these by calculating transitional probabilities for different demographic types within each stage. Human demographers often do this for simultaneous population analysis of males and females (Usher 1972). While no one has had to deal with more than two sexes, there is no mathematical limitation on the number of within-stage categories, e.g., individuals injured recently, injured a long time ago, or never injured. Unfortunately, these data do not exist yet for any nonhuman population, and their importance remains untested. Conceivably, the implied inability to distinguish between presently comparable individuals (i.e., same size or age) which will differ in the future because of unknown past experiences, could have important consequences for the outcome and variability of some experimental manipulations. Perhaps many of the differences within as well as between manipulated and control individuals are caused long before the experiment begins.

In addition to historical effects, there may be genetic or environmentally induced variation between colonies. The storm in 1979 killed 22% of the population. It is interesting to note that Hurricane Allen, which struck Jamaica in 1980, had very little effect on these corals (Hughes, table 1, in Woodley et al. 1981), probably because vulnerable colonies had already been dislodged or killed.

Community Structure

If a particular species is unable to increase its local population density, space may be available for others to coexist with it, even if they are competitively inferior. Thus, diversity is maintained by any mechanism which limits in space and time the dominance of better competitors (see review by Connell [1979]). Current models of community development and succession have focused almost exclusively on species interactions, especially competition and predation, to explain the coexistence of species between disturbances. While such interactions obviously exist and are important, the matrix model predicts that intrinsic demographic factors, e.g., the availability of recruits, could also strongly influence community structure and dynamics (fig. 7). This prediction is not new (e.g., Connell and Slatyer 1977, p. 1123; Sale 1978), but it has been somewhat neglected.

More direct inclusion in the *Agaricia* matrices of inputs resulting from sexual reproduction would require a detailed study of the relationship between coral size and fecundity, as well as information on dispersal and habitat selection. Our present knowledge of these factors, for any coral species, is disappointingly low (Connell 1973; Bak and Engel 1979; Rinkevich and Loya 1979; Rylaarsdam 1983). The model predicts that the larval input observed at Rio Bueno would be more than enough to maintain the population size and percent cover at 1977 levels, provided deviations from the demographic behavior projected by the calm matrix are small and/or infrequent.

Life Histories

The effect of changes in matrix probabilities on the population growth constant provides a powerful tool in life history analysis. For example, the effects of increased fecundity, faster growth rate, or enhanced survivorship of individuals can be examined by their effects on λ . Caswell (1978) has shown that the sensitivity of λ to perturbations in life history parameters can be calculated from the stage-specific reproductive values and the equilibrium population structure. However, the evolutionary interpretation of a size- rather than age-related reproductive value is unclear when more complex life cycles are considered. Asexually formed colonies are particularly bothersome. To be useful in evolutionary arguments, reproductive value must refer to the ability of a genotype to contribute its genes to future generations, regardless of how many bits and pieces make up its fragmented phenotype (Harper 1977; Janzen 1977). This distinction between physiologically and genetically distinctive individuals was recognized by Cook (1979) when he proposed that natural selection will favor asexual reproduction versus continued connected growth if the probability of genotype death is reduced by the formation of two or more physically separate individuals. This argument, however, neglects the fundamental role of sexual reproduction in defining fitness; i.e., if the combined reproductive output of clone mates is low, genotype fitness may be reduced even though survivorship is higher. The trade-offs involved could be examined using the matrix model presented here.

SUMMARY

Models of population dynamics based on age-related parameters do not provide accurate predictions if within-age-class variance in those parameters is high. Often the demographic fate of an individual or population may be predicted more accurately using size rather than age classifications. I describe here a general model of size-related population dynamics, based on a modified Leslie matrix. The model is designed to include demographic processes, such as fragmentation and shrinkage, which are excluded from conventional age-related demographic analysis. The parameters of the model were measured during a calm and a stormy year in a field study of a colonial, sessile coral. These data were used in computer simulations to predict the fate of a cohort over long periods of time. Measured differences in individual rates of growth and shrinkage resulted in huge long-term variations in calculated colony size, fecundity, and mortality rates, between corals of equal age. Therefore, individuals of the same age will have widely differing probabilities of obtaining representation in subsequent generations.

Population growth was simulated by adding a constant number of juvenile corals every year to the smallest size class. Although the model has no density-dependent parameters, population growth stops. The population size attained depends on the number of settling juveniles. Local populations of sessile organisms may be regulated by larval input, as well as by recurring disturbances or density-dependent interactions.

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