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DEMOGRAPHIC MODELS FOR *LEPTOGORGIA VIRGULATA*, A SHALLOW-WATER GORGONIAN[1]

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Abstract. I used time-invariant and time-varying matrix models to analyze the demography of *Leptogorgia virgulata,* a shallow-water gorgonian. For a local population in the northeastern Gulf of Mexico, I estimated monthly rates of recruitment, colony growth, and mortality in a mapped 24-m^2 plot for 2 yr. In a time-invariant model, average mortality and recruitment rates were nearly balanced, so the population growth rate, ln(λ), was close to 0.0. An elasticity analysis showed recruitment contributed <5% to the measured rate of population growth. The most important component of population growth rate was survivorship, particularly of the large size classes. Results were similar for a patch model that incorporated spatial variation in recruitment and colony growth rates. Several published transition matrices of forest trees, which have a similar life history, were also characterized by low elasticities for recruitment.

Fluctuations in population size of *L. virgulata* were analyzed with a time-varying matrix model. I randomized certain elements in the 23 monthly projection matrices and simulated the population track. For models with random temporal variation in survivorship, standard deviations (and coefficients of variation) of population size were consistently larger than observed. This result suggests that temporal variation in mortality rates tended to damp population fluctuations. The damping occurred at low population sizes: models with random variation in survivorship generated significantly smaller minimum population sizes than observed. In contrast, population tracks with random temporal variation in recruitment were not consistently different from observed. Although recruitment is widely regarded as an important factor structuring marine communities, its contribution to the temporal (but not spatial) dynamics of *L. virgulata* was minimal. This finding may be typical of long-lived organisms with delayed reproduction and indeterminate growth, such as forest trees and many sessile marine invertebrates.

Key words: Cnidaria; colony growth; demography; elasticity; gorgonian; life history theory; Octocorallia; recruitment; survivorship; temporal fluctuations; transition matrix.

INTRODUCTION

Projection matrices (Leslie 1945, 1948, Lefkovitch 1965) are an important tool for demographic studies of organisms with complex life cycles (van Groenendael et al. 1988, Caswell 1989). Examples include herbaceous perennial plants (Sarukhan and Gadgil 1974, Werner and Caswell 1977, Bierzychudek 1982), colonial marine invertebrates (Highsmith 1982, Hughes 1984, Hughes and Jackson 1985), and long-lived forest trees (Usher 1966, Hartshorn 1975, Enright and Ogden 1979). Projection matrices can also incorporate heterogeneity in life history pathways, including demographic variation among sexes (Meagher 1982), microhabitats (Hubbell and Werner 1979), and disturbance regimes (van Groenendael and Slim 1988).

Although a variety of matrix models can be constructed, there is an important dichotomy between time-invariant and time-varying models. In a time-invariant model, the vital rates of the population are constant. The time-invariant model describes exponential growth in an age- or size-structured population. Most projection matrices will yield a stable age/size distribution, regardless of the initial population structure (see Caswell [1989:57] for the mathematical conditions that guarantee convergence). The time-invariant model also generates the population growth rate (Hubbell and Werner 1979), the reproductive value distribution (Caswell 1982*a, b*), and a matrix of elasticity coefficients. These coefficients measure the relative contribution of each element in the transition matrix to the population growth rate (Caswell 1982*a, b*, 1986, de Kroon et al. 1986).

In a time-varying model, the vital rates of the population differ from one time period to the next. Consequently, populations may not converge to a stable age/size distribution (Caswell 1989:212). Oscillations in number and age/size structure are possible (Tuljapurkar 1985), as well as population crashes to extinction (Boyce 1977, Tuljapurkar and Orzack 1980). However, even if the temporal fluctuations in vital rates are autocorrelated, the expected population growth rate and its variance can be estimated (Heyde and Cohen 1985, Cohen 1986). Stochastic models also generate estimates of the probability of extinction, and the

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expected time to extinction (Lande and Orzack 1988; see also Richter-Dyn and Goel 1972, Leigh 1981).

Other descriptors of population size may not have analytic solutions, but can be studied with numerical simulations. These include the standard deviation of population size, which is a simple measure of variability through time (see Reddingius and den Boer 1989 for other measures), and the minimum population size, which is likely to be correlated with the probability of extinction.

The theoretical basis for matrix models of population growth is well established (Caswell 1989, Tuljapurkar 1989). However, empirical data are difficult to obtain, especially for time-varying models (Bierzychudek 1982). In this study, I use both kinds of models to understand the demography of a shallow-water gorgonian population. The analyses are based on field measurements for 24 consecutive months of population parameters in a mapped plot. I use these data to address two questions: (1) In a time-invariant model, how do average monthly rates of recruitment, colony growth, and survivorship contribute to the population growth rate? (2) In a time-varying model, how does variation in monthly rates of recruitment, colony growth, and survivorship contribute to numerical fluctuations of population size?

MATERIALS AND METHODS

Life cycle

Leptogorgia virgulata is a dioecious, shallow-water gorgonian that colonizes hard substrata on the western Atlantic coast and the northern Gulf of Mexico. Unlike many gorgonian species, *L. virgulata* does not reproduce asexually through cloning or fragmentation. Fertilization is external, and larvae spend 3–20 d in the plankton before settlement and metamorphosis. All recruits are derived from the successful settlement and survival of planktonic larvae. Colony growth appears to be indeterminate, and colonies reach reproductive maturity in 2 yr ($\approx$14 cm height), which is rapid for octocorals (Adams 1980). Spicule color is a highly polymorphic trait, and colonies collected from the same population exhibit intense hues of magenta, yellow, orange, or white.

Field measurements

The study was conducted in the shallow subtidal of the northeastern Gulf of Mexico. The study site was a limestone outcropping of $\approx$1 ha in area in water 2 m deep at Wilson Beach, Franklin County, Florida. The substratum at this site was heterogeneous and included areas of exposed rock, colonial invertebrates (mostly the boring sponge *Cliona cellata* and the compound ascidian *Aplidium stellatum* [Gotelli 1987]), and patches of shallow and deep sand. The spatial scale of substrate variation was small, and adjacent ¼ m^2 patches often differed significantly in substratum cover (Gotelli 1988).

In July of 1983, I established a permanent 12-m transect line, marked at 1-m intervals. The transect ran parallel to shore, and was chosen to sample an area of maximum gorgonian density. Monthly, from August 1983 through July 1985, I mapped the spatial coordinates of all colonies within 1 m of the transect line. I recorded the color of each colony (magenta, orange, or yellow) and maximum colony height in centimetres. Monthly surveys were conducted over a period of 2–3 consecutive days by a single diver; each survey required 6–16 h. I searched carefully for new recruits, some of which were detected at a size of 0.5 cm in height. It was too cold to complete the censuses in January of 1983 and 1984, but I did record colony numbers and noted the appearance of new recruits at that time. Colony heights for January data were estimated by interpolating between December and February field measurements. Mortality discovered in the February censuses was assigned randomly to the month of December or January.

Colony size and colony age were correlated, although there was considerable variation in the size of older individuals (Fig. 1). It is possible to construct population models based on either size or age (Hughes 1984, Kirkpatrick 1984, Hughes and Connell 1987) or both (Law 1983, van Groenendael and Slim 1988). I chose to analyze a model based on size because size is associated with some sources of early mortality (Fig. 4 in Gotelli 1988) and because it was not possible to directly age colonies that were present in the plot when the study began.

I classified colonies into 1 of 5 non-overlapping size classes: (1) 0.5–4.0 cm height; (2) 4.5–8.0 cm; (3) 8.5–12.0 cm; (4) 12.5–16 cm; and (5) $>$16 cm. This classification insured that there were at least 10 colonies in every size class each month for estimating survivorship rates (see Vandemeer 1978 and Moloney 1986 for other classification criteria). Ninety-three percent of the new recruits appeared in the first size class.

Most mortality occurred through whole colony disappearance, although the standing skeletons of small colonies could occasionally be found in the field. I estimated the monthly mortality rate as the proportion of colonies in each size class that disappeared from one month to the next.

Similarly, growth rate was estimated as the proportion of colonies in size class i that grew to size class $i + 1$ in the next month. Because of measurement error in colony size, it was possible to record the growth of a colony between the same two size classes more than once. There was little evidence of shrinkage in this population. During winter months, the spicules and polyps at the tips of some colonies shrunk $<$2 cm, but the central skeleton remained intact, and the tissue usually regenerated rapidly in the spring. Predation effects were also minimal (Gotelli 1985). Therefore, I assumed there was no appreciable shrinkage and adjusted the raw size data so that each colony could "grow"

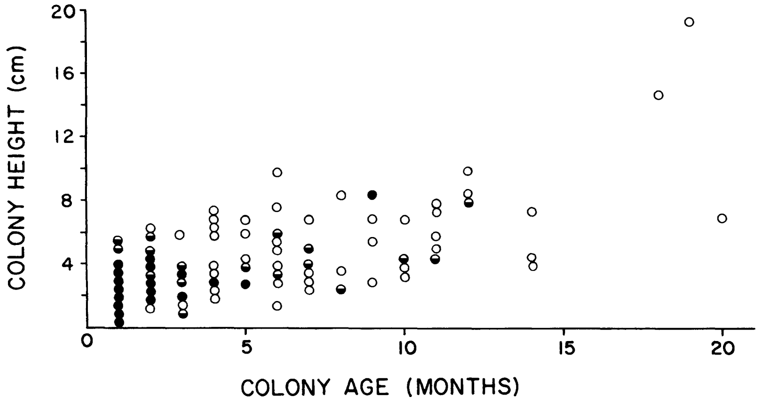

FIG. 1. Relationship between maximum colony height and age of *Leptogorgia virgulata*. Height is given for the final month before death ($n = 203$, $r = 0.703$, $P < .0001$). ○ = one point; ◑ = 2 points; ● = 3 or more points.

no more than once between two consecutive size classes. These adjustments accounted for <15% of the observed transitions.

The matrix models require an estimate of fecundity, which was not available from my field data. Therefore, I assumed (a) that recruitment was proportional to adult abundance in the three largest size classes, and (b) that reproduction was equivalent among colonies in these size classes. The first assumption is based on Adams' (1980) observation that colonies of *L. virgulata* at this site did not begin reproduction until a height of ≈14 cm. Estimates of population growth rate and elasticity were not sensitive to this assumption. I analyzed matrices in which only the largest, or largest two size classes reproduced, and the results were similar to what I present here.

The second assumption is probably unrealistic, but also did not affect the results. Even a 10-fold difference in fecundity of the largest (>16 cm) and smallest (8–12 cm) reproductive colonies did not produce a major change in the population growth rate or elasticity estimates.

Although the three color morphs varied consistently in their recruitment rates (Gotelli 1988), I have not included colony color as a factor in the demographic models. Preliminary simulations of the total population track that resulted from summing data on the three color morphs were in good agreement with simulations that did not incorporate colony color as a factor.

Population models

The population models presented here are straightforward applications of the population projection matrix. For the time-invariant model,

$$\mathbf{n}(t + 1) = \mathcal{A}\mathbf{n}(t), \qquad (1)$$

where $\mathbf{n}$ denotes a column vector whose elements n_i are the numbers of individuals in the different size classes. $\mathcal{A}$ is the population projection matrix, whose elements a_{ij} denote the transition from state n_j to state n_i during time period t (Hubbell and Werner 1979, Caswell 1982*b*). In the time-varying model, the corresponding equation is

$$\mathbf{n}(t + 1) = \mathcal{A}(t)\mathbf{n}(t). \qquad (2)$$

$\mathcal{A}(t)$ is the projection matrix describing population growth during the time interval t to $t + 1$.

For an organism with no asexual reproduction or shrinkage, indeterminate growth, and delayed, iteroparous reproduction, the structure of matrix $\mathcal{A}$ is relatively simple: the diagonal elements represent the probability that a colony remains in the same size class from one time period to the next, and the subdiagonal elements represent the probability of growth between consecutive size classes. The mortality rate for a given size class can be found by subtracting these column elements from 1.0. The fecundity function is described by nonzero elements in the first row of the matrix, that is, transitions from established colonies to recruits in the first size class. All other elements in the matrix are zero, because there is no opportunity for colony fusion into larger size classes, or fragmentation or shrinkage into smaller size classes (e.g., Highsmith 1982, Hughes 1984; see Hubbell and Werner [1979] for more complex life history representations).

I used the methods developed by Caswell (1982*b*) to calculate the stable age distribution and reproductive value. I estimated the rate of population increase by direct iteration of Eq. 1, assuming a starting population of 10 000 recruits. The resulting stable age and reproductive value distributions agreed exactly with those generated by Caswell's analytical solution. The stable age and reproductive value distributions were used to calculate the elasticity of each element in the transition matrix (de Kroon et al. 1986). Elasticity values represent the proportional contribution of each element of the projection matrix to the rate of population increase.

Comparisons with other studies

To compare the elasticity analyses with other studies, I collected stage projection matrices from the lit-

TABLE 1. Transition matrix for *Leptogorgia virgulata*. Transitions are calculated from the average of 23 consecutive monthly values. Standard deviations are given in parentheses.

Size class in month	Size class in month t				
$t + 1$	1	2	3	4	5
1	.61519 (.27668)	···	.19686 (.27668)	.19686 (.27668)	.19686 (.27668)
2	.16498 (.14709)	.78038 (.14035)	···	···	···
3	···	.09971 (.09257)	.83930 (.15460)	···	···
4	···	···	.12428 (.13724)	.86036 (.14259)	···
5	···	···	···	.11354 (.14137)	.97647 (.03659)

erature for long-lived forest trees with a life cycle similar to that of *Leptogorgia virgulata*. Life tables for some species were excluded because populations were age classified (Van Valen 1975, Grigg 1977) or because the life cycles incorporated asexual reproduction (Bullock 1980) or sexual reproduction in small size classes (Burns and Ogden 1985, Ebert 1985). Some of the forest tree matrices included estimates of seed set (fecundity) and survivorship to the seedling stage, so the effects of settlement and early survivorship on recruitment could be distinguished.

I analyzed these data according to the method outlined above and tabulated elasticity terms for fecundity (if measured), recruitment (defined as appearance in the first size class), growth (subdiagonal elements), and survivorship (diagonal elements). Throughout this analysis I refer to the subdiagonal elements as "growth" (the probability of successfully entering a larger size class), and the diagonal elements as "survivorship" (the probability of remaining in the same size class). However, both the diagonal and subdiagonal elements involve some elements of both individual growth and survivorship. Two of the studies (Enright and Ogden 1979, Pinero et al. 1984) included transition matrices from more than one population site. For these studies, I present analyses for the populations with the largest, smallest, and intermediate estimates of population growth rate.

RESULTS

Estimates of population growth rate

Several estimates of population growth rate, ln(λ), are possible, depending on assumptions about the underlying transition matrix. If there is no temporal variation in population vital rates, the population growth rate can be estimated by averaging the 23 monthly transition matrices (Table 1). This method ignores temporal variation so no variance estimate is possible.

Alternatively, one can assume that month-to-month variation is small, so the bias can be estimated by jackknifing the sample. I sequentially deleted each of the 23 monthly transition matrices, then averaged the remaining 22 matrices to determine population growth rate. This technique generates a bias-corrected estimate of the population growth rate, as well as a confidence interval (Caswell 1989). However, because this jackknife does not incorporate variation among individuals within a month, it underestimates the true confidence interval.

Both the average transition matrix and the jackknifed estimate are derived from a time-invariant model, which assumes that transition probabilities do not vary with time. Caswell (1989) describes a contingency table analysis to test whether there are significant differences among transition probabilities (although not necessarily fecundity) at different times. The data are organized as a three-way contingency table: stage (S) × fate (F) × month (M). The appropriate test is a comparison of a fully saturated model with one that excludes the $S \times F \times M$ and $F \times M$ interaction terms (see Caswell 1989:179). For the data in Table 1, the test for time effects was significant ($G^2_{550} = 617$, $P = .023$): transition probabilities were not constant from month to month. This result suggests that a stationary Markov model is not appropriate for these data.

Heyde and Cohen (1985) give formulae to estimate the population growth rate and its variance in a time-varying model. These estimates are based on the population track that results from a stochastic series of transition matrices. Following Caswell (1989), I randomly permuted the monthly transition matrices and iterated population growth according to Eq. 2. I removed transient effects with 1000 initial iterations, then constructed the population track for 5000 iterations. This technique provides a measure of the precision of the estimate of ln(λ).

The averaged transition matrix, the jackknifed matrix, and the nonstationary population growth all generated similar results (Table 2). The estimated population growth rate ln(λ), was slightly >0.0. Confidence intervals were modest and did not encompass 0.0, so the population was increasing slowly, but significantly. However, since the jackknife confidence intervals exclude individual variation, this is a very weak test and

TABLE 2. Estimates of population growth rate for *Leptogorgia virgulata*. Results are expressed as the instananeous rate of increase ln(λ). The Heyde-Cohen (1985) procedure gives the precision of the estimate of ln(λ) in a time-varying environment.

Estimate	ln(λ)	95% CI
Averaged transition matrix (Table 1)	.00917	···
Jackknifed transition matrices	.00860	±.00488
Heyde and Cohen (1985)	.00743	±.00363

TABLE 3. Stable size and reproductive value distributions for *Leptogorgia virgulata*. Estimates are based on a jackknife of the monthly transition matrices (Table 1). Standard deviations are given in parentheses.

Size class	Stable size distribution	Reproductive value distribution
1	.27468 (.00804)	.04882 (.00171)
2	.19854 (.00697)	.11588 (.00232)
3	.11414 (.00632)	.26438 (.00224)
4	.09708 (.00383)	.28383 (.00236)
5	.31552 (.02115)	.28712 (.00382)

the difference from zero should not be given much weight.

For the stationary model, colonies in the largest and smallest size classes were most common. Reproductive values increased for large colonies, probably because of both declining mortality rates and increasing fecundity of the large size classes (Table 3).

The elasticity analysis suggests that recruitment processes contributed relatively little to the rate of population increase (Table 4). Recruitment contributed approximately the same to population increase as did growth between any two size classes. The most important component of population increase was survivorship, particularly in the largest size class.

Time-varying model

Whereas a time-invariant model can be used to estimate the rate of population increase, a time-varying model can be used to understand the components of population fluctuation through time (Fig. 2), and the ways these fluctuations are affected by temporal variation in recruitment, growth, and survivorship. The temporal dynamics are highly dependent on size structure of the population, as individuals recruit and then grow into larger size classes (Fig. 3).

To analyze temporal fluctuations, I used Eq. 2 to recreate the population track by iterating the 23 sequential projection matrices, one for each month of the study. To measure the effects of variation in recruitment, growth, and survivorship on population fluctuations, I randomized the temporal sequence of certain elements in the projection matrices. For example, to evaluate the effect of variation in colony growth, I randomized the subdiagonal elements in each monthly projection matrix, sampling with replacement from the 23 growth transitions measured for each size class. The other elements in the matrix, which represent recruitment and survivorship, were not varied. I thus created 23 sequential projection matrices, with certain elements left unchanged, and others allowed to vary. Using the observed initial size distribution, I iterated Eq. 2 with the new projection matrices. This simulated population track shows the effects of variation in some components of the projection matrix (cf. Bierzychudek 1982).

I calculated the mean, standard deviation, coefficient of variation, and the minimum and maximum size of each simulated population track. I constructed 1000 simulated population tracks and compared the simulated population statistics to the observed statistics (Table 5). If a particular factor in the life history did not have a strong or consistent effect on population fluctuations, statistics derived from the simulated population track should be similar to those of the observed population track. These simulations do not consider the temporal sequence of transition matrices. Each month was chosen randomly, so seasonal effects have been ignored. Seasonality certainly contributed to population dynamics, although it is difficult to recognize discrete "boundaries" between seasons with different transition probabilities.

Most simulated population tracks could not be distinguished from the observed population track (Table 5). The exceptions were models that allowed for random variation in survivorship, or random variation in survivorship and growth concurrently. In these scenarios, the observed standard deviation of population size (and the coefficient of variation) was always much less than the simulated. In other words, the temporal sequence of mortality tended to "damp" population fluctuations. The damping occurred at small population sizes: the simulated minimum population size ($\bar{X} = 63$) was significantly smaller than the observed minimum (min = 89; $P = .031$). In contrast, none of the population statistics varied significantly from those of the observed population track when recruitment varied randomly. However, there was an interaction between survivorship and recruitment, because the significant effects of survivorship disappeared when both survivorship and recruitment varied concurrently.

TABLE 4. Elasticity matrix for *Leptogorgia virgulata*. Elements of this matrix give the relative contribution of each transition (Table 1) to the population growth rate. Estimates are based on a jackknife of the monthly transition matrices. Standard deviations are given in parentheses.

Size class in month	Size class in month *t*				
t + 1	1	2	3	4	5
1	.04323 (.00265)	...	.00510 (.00073)	.00448 (.00054)	.01744 (.00090)
2	.02701 (.00208)	.09474 (.00508)	...	...	...
3	...	.02701 (.00208)	.13428 (.00875)	...	...
4	...	...	.02190 (.00139)	.12656 (.00571)	...
5	...	...	...	.01744 (.00090)	.48027 (.02703)

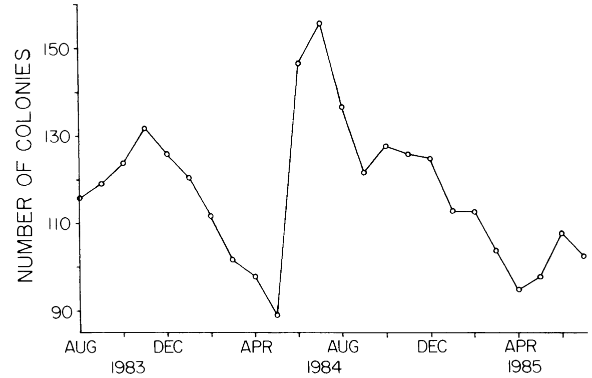

FIG. 2. Population size of *Leptogorgia virgulata* recorded during monthly censuses in a marked 24-m^2 plot.

Spatial model

The results of both the time-invariant and time-varying analyses suggest that recruitment played a relatively small role in temporal dynamics. In contrast, recruitment was very important in determining spatial pattern in this population (Gotelli 1988). It may be unrealistic to treat spatial and temporal processes independently, and a model that simultaneously incorporates both factors may reveal more important effects of recruitment (e.g., Platt et al. 1988). Data on spatial variation in patch quality can be used to construct an expanded matrix that includes transition probabilities for different patches as well as different size classes. Previous experimental work (Gotelli 1988) suggests the following simplifying assumptions. (1) The environment can be divided into patches of two discrete types: exposed rock and sand patches. Exposed rock patches are 25% of the surface and sand patches are 75% of the surface. (2) Recruitment is twice as high on exposed rock as on sand. (3) Survivorship after recruitment is identical in both patches. (4) Growth of colonies from size class 1 to size class 2 is 36% higher on sand patches. (5) All other growth probabilities after the first size class are the same for the two patches.

These assumptions lead to a 10 × 10 projection matrix, for the five size classes on the two patch types (see Meagher 1982 for a similar matrix model of two sexes). The result of the elasticity analysis was similar to the stationary model that ignored spatial variation: population growth was very close to 0.0, and survivorship contributed the most to population growth rate (Table 6). In contrast to the simplified model, the patch model suggests that the population was declining slowly, probably due to reduced recruitment on sand patches. This model encompasses the major features of small-scale habitat variation at the study site. Although recruitment was important in determining spatial pattern, its effects can be safely ignored when thinking about temporal fluctuations.

DISCUSSION

The demographic models presented here make a variety of assumptions about temporal constancy, fecundity, and patch dynamics. Yet, they all point to a similar result: population growth rate was close to 0.0, and was most sensitive to variation in adult survivorship. The consistency of the different estimates of population growth (Table 2) is noteworthy. Because the asymptotic distribution of population sizes in a stochastic environment is log normal (Caswell 1989), the average transition matrix (Table 1) will overestimate the population growth rate (Lewontin and Cohen 1969, Boyce 1977, Tuljapurkar and Orzack 1980). Stochastic vari-

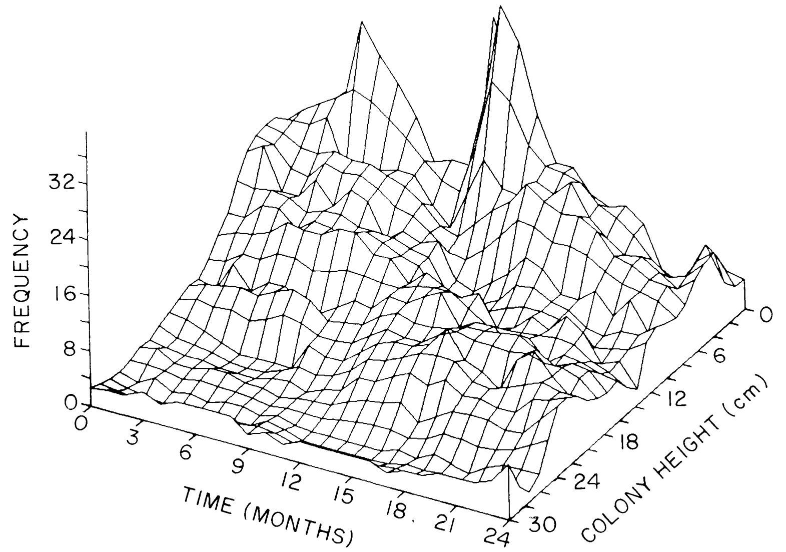

FIG. 3. Distribution of colony sizes of *Leptogorgia virgulata* during monthly censuses. Time is measured in months since the first census.

TABLE 5. Observed and expected population statistics. Elements in the first column were allowed to vary randomly in each monthly transition matrix. Probability values were estimated as the proportion out of 1000 simulated population tracks, for which the observed statistic exceeded the simulated. Expected values are averages based on 1000 simulated tracks. * $P < .05$; ** $P < .01$.

	Mean population size	Standard deviation of population size	Minimum population size	Maximum population size	Coefficient of variation (SD/$\bar{X}$)
Observed	117.2	16.98	89	156	.145
Simulated, with random variation in:					
Recruitment (R)	121.0	16.56	96	157	.135
Growth (G)	136.5	28.32	97	209	.203
Survivorship (S)	108.6	32.34**	63*	169	.302**
R, G	124.4	28.97	81	183	.227*
R, S	109.6	22.31	76	157	.207
G, S	128.8	34.28**	83	201	.264*
R, G, S	124.6	24.31	88	176	.191

ation in transition matrix elements can seriously destabilize population growth (Boyce 1977, Tuljapurkar and Orzack 1980).

However, any negative covariation between pairs of vital rates will increase the population growth rate and decrease its variance, thereby reducing the impact of temporal fluctuations (Tuljapurkar 1982). Table 7 gives the correlation matrix for the transition probabilities, measured across time. The vital rates of this population were highly intercorrelated, although this is to be expected for survivorship and growth, which must sum to (1.0 − mortality) each month. However, the recruitment rate was also negatively correlated with survivorship in all size classes, which will effectively damp fluctuations. The strong correlations between vital rates buffer the population track and may account for the close correspondence of the stationary and nonstationary estimates of population growth rate.

In spite of the consistency of the results, it is difficult to know how general these findings are. Of course, the results are limited by population events occurring during the brief 2-yr period, and it wouldn't be surprising to find different patterns if the study were conducted at other scales of time (e.g., Bierzychudek 1982, Pimm and Redfearn 1988), or space (e.g., Werner and Caswell 1977). Results might also differ for a metapopulation model that considers dispersal of larvae between population sites (Hanski 1989).

One way to assess the "generality" of this study is to compare the demographic analysis with others for organisms with similar life histories. For *L. virgulata,* that means comparisons with the demography of forest trees, which are long lived, have indeterminate growth, and reproduce in the larger size classes.

These comparisons (Table 6) show that the population parameters for *L. virgulata* are quite similar to those for other organisms with a similar life history: population growth rates were close to 0.0, and fecundity and recruitment did not contribute much to population growth. Measured rates of population growth were close to replacement, with populations neither increasing nor decreasing rapidly in size. Even in cases where fecundity and recruitment were measured separately, these two processes did not contribute >5% to the rate of population increase. Instead, survivorship, particularly in larger size classes, was the most important component of population growth. However, note that generation times and sampling intervals vary among studies, which complicates the comparisons.

The results of these surveys stand in contrast to demographic analyses of annual plants and herbaceous perennials. Population growth rates of annual plants often differ greatly from 0.0; populations appear to be either rapidly increasing or decreasing in size (Law et al. 1977, Leverich and Levin 1979). For herbaceous perennials, fecundity (de Kroon et al. 1986) and individual growth (Bierzychudek 1982) can often contribute substantially to the rate of population growth. These patterns are not seen in long-lived forest trees, or other organisms with a long life-span (e.g., Crouse et al. 1987). Caswell (1986) presents some of these same elasticity analyses graphically and arrives at a similar conclusion.

Importance of recruitment

Variation in recruitment had only a minor effect on the rate of population growth (time-invariant models) and on the pattern of population fluctuations (time-varying models). Obviously, recruitment "contributed" to both, because the population would decline to zero if there were no new input of juveniles. However, the response of population growth rate (and population fluctuations) to changes in recruitment would be much smaller than the response to comparable changes in survivorship.

Recruitment has long been recognized as an important component of the population dynamics of sessile marine invertebrates (Thorson 1950, Underwood and Denley 1984, Warner and Chesson 1985). The high fecundity of many marine invertebrates, combined with spatial and temporal patchiness in larval supply, occasionally leads to spectacular recruitment pulses in local populations (Fig. 2; Coe 1956, Loosanoff 1964, 1966, Caffey 1985). Some authors have suggested that

TABLE 6. Elasticity analyses of published transition matrices. Fecundity measures the elasticity contribution from adults to seeds (if measured), and recruitment measures the elasticity contribution from seeds to seedlings. Survivorship is the sum of the elasticity elements along the matrix diagonal, and growth is the sum of the elasticity elements along the subdiagonal.

			Population dynamics data			Elasticity analysis	
Species	Length of study (yr)	Sampling interval	Number of stages in life cycle	Stage at first reproduction	Population growth rate [ln (λ)]	Fecundity	Recruitment
Leptogorgia virgulata	2	1 mo	5	3	.0086	···	.0270
*Leptogorgia virgulata**	2	1 mo	5	3	−.0006	···	.0163
Pentaclethra macroloba	1	1 yr	15	11	.0017	.0090	.0090
Araucaria cunninghami	2	1 yr	11	7	.0203	.0097	.0097
Nothofagus fusca†	2	1 yr	4	3	−.0004	···	.0047
Nothofagus fusca‡	2	1 yr	4	3	.0095	···	.0095
Nothofagus fusca§	2	1 yr	4	3	.0276	···	.0173
Astrocaryum mexicanum‖	7	1 yr	14	5	−.0020	.0098	.0098
Astrocaryum mexicanum¶	7	1 yr	14	6	.0113	.0085	.0085
Astrocaryum mexicanum#	7	1 yr	14	7	.0391	.0112	.0112

* Patch model.
† Lower stand, assuming a 20-yr seedling life.
‡ Middle stand, assuming a 20-yr seedling life.
§ Middle stand, assuming a 5-yr seedling life.
‖ Plot BB.
¶ Plot AA.
# Plot C.

recruitment dynamics may even override the effect of adult interactions, such as competition and predation, on local population and community structure (Underwood and Denley 1984, Caffey 1985, Dayton et al. 1989).

However, the "importance" of recruitment can only be understood relative to other demographic processes, such as survivorship and growth. For long-lived species, variation in recruitment may be overridden by mortality occurring after settlement (Paine 1984). This is especially true in populations with generally high settlement rates (Roughgarden et al. 1985). The present study suggests that even if recruitment is sparse, mortality in later stages of the life cycle may have the most important consequences for population growth rate and fluctuations in population size.

Nevertheless, I do believe that recruitment is important in this population, although for a subtler reason than most other authors have emphasized: recruitment stabilizes the population growth of *L. virgulata.* Estimates of population growth in a stochastic model are meaningful only if the effects of the initial age distribution disappear (Tuljapurkar and Orzack 1980). The weak ergodic theorem (Lopez 1961) establishes the conditions for which differences in initial population structure decay to zero when populations experience the same sequence of transition matrices (Caswell 1989). One condition that will guarantee weak ergodicity is that each individual transition matrix is irreducible and primitive, with nonzero elements in the same locations. It is easy to demonstrate that a population projection matrix of the form in Table 1 meets these conditions. Therefore, if each of the monthly transition matrices also exhibits this form, any random sequence of these matrices will be weakly ergodic. Specifically, weak ergodicity requires that "some population classes which are reproductive in one environment always have some fecundity, however small, in all environments, and that there is always a non-zero probability of surviving to the same final stage in all environments" (Tuljapurkar and Orzack 1980). Although the number of recruits of *L. virgulata* varied tremendously from one month to the next (see Fig. 2 in Gotelli 1988), there was only one month during the study (January 1986) in which I found no new recruits. Similarly, although survivorship of small juveniles was low and varied temporally, mortality was never so great as to completely eliminate an age class in any month. Therefore most random sequences of matrices are weakly ergodic. Continual recruitment thus contributed to the long-term stability of population growth at this site.

Continual recruitment also reduces the probability of extinction in a stochastic environment. Lande and Orzack (1988) use a diffusion model to estimate the probability of extinction, given an initial population size, and the population growth rate and its variance. Assuming an initial population size of 116 colonies (recorded August 1984 at the start of the census), the probability of extinction for this population of *L. virgulata* is vanishingly small ($P = 2.7 \times 10^{-31}$). Although the number of recruits varied strongly from one month to the next, the presence of recruits in 22 of 23 censuses stabilized population growth and reduced the probability of random extinction.

Constraints on elasticity

The consistency of the results in Table 6 is striking, considering the differences in life-span of the organisms, sampling frequency, and measurement techniques of the different studies. These similar findings suggest that selection may have constrained population parameters for this life history. Alternatively, the results may be an algebraic consequence of the structure of this particular transition matrix.

TABLE 6. Continued.

Elasticity analysis		
Growth	Survivorship	Citation
.0917	.8813	current study
.0589	.9248	current study
.0954	.8866	Hartshorn (1975)
.0556	.9250	Enright and Ogden (1979)
.0129	.9824	Enright and Ogden (1979)
.0245	.9660	Enright and Ogden (1979)
.0414	.9413	Enright and Ogden (1979)
.0820	.8927	Pinero et al. (1984)
.0817	.9011	Pinero et al. (1984)
.1035	.8574	Pinero et al. (1984)

To test the latter hypothesis, I created transition matrices with the same dimensions and structure as the *L. virgulata* matrix. The zero elements were left unchanged, but the nonzero elements were filled randomly from a uniform distribution with a range of zero to one. For 1000 such randomly constructed matrices, I calculated the population growth rate and performed an elasticity analysis. This analysis confirms that the elasticity contributions were always of the form: survivorship > growth > recruitment, and that the population growth rate ranged from -0.2231 to 0.1823. However, the recruitment contribution for *L. virgulata* was still unusually small ($P = .048$ for a value this extreme), and the population growth rate was unusually close to 0.0 ($P = .037$ for a deviation this small). So, although the elasticity and growth rates in Table 6 are in part a consequence of the structure of the transition matrix, the values observed for *L. virgulata* are more extreme than expected by chance. Selection due to fluctuating juvenile mortality (Murphy 1968, Stearns 1976) is one such explanation for the minor contribution of recruitment to population growth rate.

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TABLE 7. Correlations among population vital rates. Each entry is the correlation coefficient between pairs of vital rates measured for 23 consecutive months. Bold-faced values are significant at $P = .01$ (two-tailed test). R = recruitment; S = survivorship; G = growth. Subscripts of S and G refer to size classes (1–5).

	R	S_1	S_2	S_3	S_4	S_5	G_{12}	G_{23}	G_{34}
R									
S_1	**−.58**								
S_2	**−.59**	**.82**							
S_3	**−.54**	**.61**	**.55**						
S_4	**−.55**	**.60**	**.64**	**.77**					
S_5	−.48	.34	.43	.40	.38				
G_{12}	**.70**	**−.76**	**−.84**	−.41	**−.55**	.49			
G_{23}	**.66**	**−.65**	**−.80**	−.36	**−.57**	−.35	**.81**		
G_{34}	**.53**	**−.58**	−.51	**−.96**	**−.77**	−.31	.34	.35	
G_{45}	.43	−.46	**−.52**	**−.68**	**−.95**	−.25	.39	.50	**.69**

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