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American Naturalist, Volume 120, Issue 2 (Aug., 1982), 139-159.

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American Naturalist
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STOCK-RECRUIT RELATIONSHIPS AND REGIONAL COEXISTENCE IN A LOTTERY COMPETITIVE SYSTEM: A SIMULATION STUDY

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Submitted March 20, 1981; Accepted January 8, 1982

The now very extensive body of theoretical studies of the coexistence of competing species has been derived almost entirely from the competition equations of Volterra and Lotka (examples are MacArthur and Levins 1964, 1967; Levin 1970; May 1973; Roughgarden 1974*b*; Armstrong and McGehee 1980; Rappoldt and Hogeweg 1980 among many others). It deals with species whose rate of population growth is strongly dependent on current population size and on the size of populations of competitors, and with cases of exploitative competition rather than interference competition. It deals principally with species competing in a closed and spatially homogeneous environment (but see Roughgarden 1974*a*). Texts by MacArthur (1972) and Roughgarden (1979) give good access.

Some recent studies have been notable exceptions in examining coexistence in spatially divided universes within which migration between cells, as well as competitive interactions within cells, are permitted. The competitive interactions within cells are modeled on Lotka-Volterra systems, or are assumed to always lead rapidly to exclusion of one species by another (Levins and Culver 1971; Horn and MacArthur 1972; Slatkin 1974; Levin 1976; Caswell 1978). Huffaker (1958) had empirically explored such a system 20 years earlier.

While models have frequently incorporated time lags or some stochasticity into the Lotka-Volterra equations, rate of population growth has been a direct, if not linear and immediate function of the sizes of a species' and its competitors' populations at each time interval (although see Murphy 1968). Systems in which the competition between species is by interference among individuals which must obtain a single unit of a resource, such as a living site, or die, have also been neglected. In fact, a system incorporating both a variable relationship between growth rate and population size and competition by interference for critical units of resource seems likely to have considerable realism for marine organisms which seek adult habitats on the substratum after a pelagic larval phase, and may also apply to terrestrial species with high juvenile mortality and precise territorial or nest-site requirements as adults.

The present paper results from simulation studies begun as a consequence of an empirical investigation of territorial reef fish. I investigate conditions for coexis-

tence in a lottery (Sale 1977) competitive system. The emphasis is on local coexistence. Simulation was chosen as a straightforward way of obtaining direct information on the behavior of lottery systems. Recently, Chesson and Warner (1981) have analytically investigated persistence in such systems. Our results are extensively compatible, although there are important differences in approach which are discussed. The present results, and those of Chesson and Warner may encourage others to a formal analysis of the behavior of lottery systems.

THE EMPIRICAL DATA

The lottery concept was derived from a study of coexistence in territorial pomacentrid fishes in which each individual defends a small permanent territory within which it obtains food, shelter, and, for males, nest sites (Sale 1974, 1975, 1976, 1978a, 1978b, 1979). The study, which included experimental manipulations and long-term monitoring of selected, undisturbed groups of fish, principally concerned three species of fish which occurred together in patches of coral rubble on the shallow southern reef face of Heron Reef, Great Barrier Reef. These species, *Eupomacentrus apicalis*, *Plectroglyphidodon lacrymatus*, and *Pomacentrus wardi*, are not restricted to this habitat, and do not always occur together (Sale 1979; Sale et al. 1980; Robertson and Lassig 1980). Nevertheless, when found together, individuals of all three species were able to persist, and to engage in reproductive activities despite the fact that several lines of evidence indicated that available space was in short supply. No evidence was found of subtle microhabitat partitioning by the three species in this rubble habitat. Individuals that colonized rubble patches settled without regard to whether neighbors were of their own or other species, and survivorship was not affected by this factor (Sale 1979).

These results led me to propose that coexistence of these species was permitted because their competition had elements of a lottery in which individuals of each species, by producing pelagic larvae, competed for new living sites. Each vacated site was colonized by the first new recruit to arrive and, once resident, this fish, regardless of its species, could defend that site from subsequent colonists. I suggested that the production of many clutches of dispersive pelagic larvae (a feature nearly universal among coral reef fishes [Sale 1977]) is precisely the strategy expected of species living in an environment in which resources such as newly vacated living sites, are made available unpredictably in space and in time. I argued that the demands on larval morphology imposed by a pelagic life, the advantages of prior residence known to accrue to fish in territorial encounters, and, especially, the lack of a strong correlation between stock size and rate of recruitment in fish favored the development of lottery competitive systems, rather than patterns of niche diversification when species of reef fish came into competition for resources (Sale 1977, 1979).

The essential features of a lottery system for living sites are as follows. Individuals of each species involved can successfully survive and reproduce only if they hold living sites. While living sites may vary they do not differ from one another in any way which differentially influences fitness of any of the species

living in them. Recruits arrive randomly from a pool of pelagic larvae, and when a site is vacated through the loss or emigration of its occupant, it is colonized by the first recruit to arrive regardless of species. This recruit defends its site successfully from later recruits.

THE LOTTERY MODEL

The model explored here deals with a closed environment containing 100 similar living sites each of which can be occupied by one fish. Any of several species can occupy any of the sites, and not all sites need be filled. The initial composition of species is determined by randomly allocating fish to sites until the required proportion of sites is filled. Chance of each species in gaining sites is proportional to its fecundity. Preliminary tests showed that the species composition of communities established in this way first reached its final state in about six time periods. At each time period (= year) each site is inspected in turn. If the resident has died, or if it was already empty, the site may be recolonized by one or other of the species. Recruitment is from a pool of larval progeny of the resident fish. Immigration from populations outside the 100-site environment is not permitted. The model keeps track of the age and species of fish in each occupied site, and runs until the adult population of any species falls to two or fewer animals (arbitrarily considered extinction), or until a specified number of years have elapsed.

The first version of the model permitted any number of ecologically identical species to enter the lottery. Subsequently it was modified to one in which three not necessarily identical species compete for sites. This use of three species resulted only from the fact that the earlier empirical studies had concerned three species. Qualitatively, results are identical with other numbers of species competing.

Each species has (1) a fixed per capita mortality rate per year (d), and a maximum permitted age of $3/d$ yr, after which individuals must die; (2) a fixed, per capita fecundity per yr (r); (3) a specified stock-recruit relationship (see below); and (4) a fixed age in years to maturity, after which all individuals are members of the adult breeding population, and breed every year. These parameters need not be identical for different species. Since, on average, less than 5% of any cohort reaches the age of $3/d$ yr, the model eliminates the possibility of eternal life, without generating strongly truncated survivorship curves.

Central to the model is the existence of nonlinear stock-recruit relationships. The competing species are presumed to spawn numerous eggs which suffer a very high mortality during larval life. Only those reaching the end of larval life are capable of colonizing sites in the 100-site environment. The model assumes that each site to be colonized is equally likely to be taken by any of the recruits available that year. Thus the relative chance of each species occupying a vacant site is explicitly calculated by using (1) the size of the adult (breeding) population the previous year, (2) its per capita fecundity, and (3) its species-specific stock-recruit relationship to determine the number of potential colonists of that species that year. This number, as a proportion of the total of all potential colonists that year, is the probability with which that species captures each new site. Each site

to be colonized is allocated randomly among the species on this basis. The probability of a site remaining vacant for a year is also specified.

To model stock-recruit relationships, I chose to use the Beverton and Holt (1957) formula:

$$R_t = \frac{1}{\alpha + \frac{\beta}{S_{t-1}}}$$

where R_t = number of recruits at time t , S_{t-1} = a measure of the production of eggs in year $t - 1$, and α and β are constants representing components of larval mortality for that species.

This formula describes a curved relationship in which number of recruits rises from zero to a maximum level as production of eggs increases. The formula has had wide application in the fisheries literature, although it is now less frequently used than the Ricker (1958) formula (or formula 2 of Beverton and Holt) which generates dome-shaped curves with lower recruitment at very high as well as at very low levels of egg production.

For the purposes of the present work, the formula was modified by using rN_{t-1} as a measure of S_{t-1} where r is per capita fecundity and N is stock size at year $t - 1$. The degree of curvilinearity in this relationship depends on the values of α and β . A series of values of each coefficient were chosen (fig. 1) which (1) assured that (for $r = 1$) the primary region of curvature of the graph fell in the region, $0 < N < 75$ and (2) provided a range of curvilinearity from very strong to nearly linear. This approach is justified in the discussion, as is use of this curve rather than the Ricker curve.

RESULTS

Conditions Allowing Persistence

The lottery hypothesis on which the model is based does not claim to generate equilibrial coexistence of the species involved. Through chance alone, over enough years, one or other of the species will become extinct, but the time involved probably will be very long. In examining the behavior of the model I have examined those factors likely to modify the length of time to extinction of one or other species. Values chosen for age at maturity and per capita mortality rate are typical of small reef fish (Sale 1980). Fecundities, and coefficients of the stock-recruit equation were chosen to generate stock-recruit relations comparable in shape with those in the fisheries literature, though on the smaller scale imposed by the 100-site environment. Conditions generating stable equilibria have not been searched for.

1. *Coexistence of ecologically identical species.*—The occurrence in nature of ecologically identical species is infinitely unlikely. However, if conditions favoring persistence of these cannot be found, there would appear to be little point in looking into the model's behavior when species differing in competitive ability are brought together. Factors considered were: (1) the number of analogous species

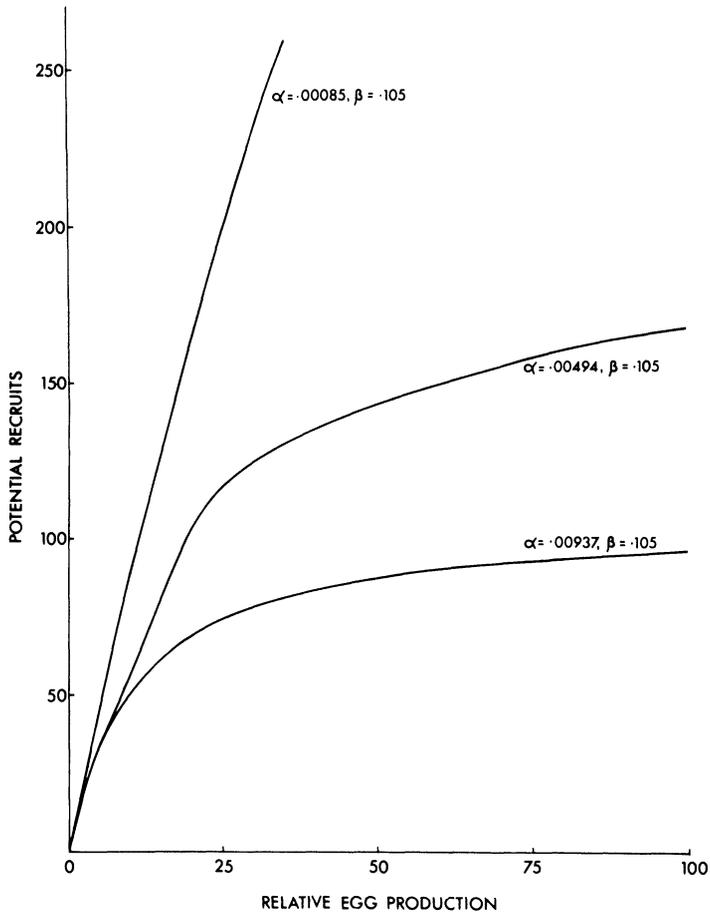


FIG. 1.—Three stock-recruit curves used in the analysis of persistence of ecologically identical species.

competing for sites; (2) their mortality rates, and hence the degree of temporal overlap of generations; (3) their fecundities; (4) their ages at maturity; (5) the shape of their stock-recruit curves; and (6) the probability that vacant sites would fail to be colonized in a given year.

Factors 1, 4, and 6 had trivially straightforward effects. An increase in the number of competing species, a prolonging of the age to maturity, or an increase in the probability of a site remaining uncolonized all reduce the average size of the adult populations of the species present, thus increasing the likelihood of one of them wandering to extinction. After some preliminary studies, I centered attention on the case of three competitors maturing either at recruitment, or 1 or 2 yr later, in an environment in which no vacant site goes undetected.

Factors 2, 3, and 5 had more interesting effects. I first examined persistence for groups of three identical species with mortality rates of 0.125, 0.25, or 0.5 per yr, per capita fecundities of one or four offspring per yr, and with one of the three

stock-recruit relationships shown in figure 1. Animals were assumed to enter the breeding population in the year of recruitment, and competition for sites was such that none remained empty. The experiment was treated as a 3 (mortality rate) \times 3 (α value) \times 2 (fecundity) factorial with 5 replicates run for each set of conditions. Each run was for 100 yr.

All but one of the 90 runs persisted the full 100 yr. The one which failed did so at 95 yr. It comprised species with the highest mortality rate (0.5), the lower fecundity (1), and the most linear stock-recruit relationship ($\alpha = 0.00085$). The effects of the three factors on the variance in numbers over the 100 yr of one species chosen randomly were examined by analysis of variance. Greater variances during a run indicate greater change through time in numbers present, and therefore, greater risk of extinction. The analysis showed significant interactions between the effects of fecundity and of α value, and between those of α value and mortality rate ($F_{2,72} = 5.2$, and $F_{4,72} = 3.9$, respectively, $P < .01$ in both cases). Variance was generally smaller at the higher fecundity, although the difference was not significant when $\alpha = 0.00937$ (averaged across mortality rates). Variance was also smaller when the stock-recruit relationship departed most from linearity (fig. 2).

The interaction of fecundity and α value is expected. At the higher fecundity value ($r = 4.0$) species present at, on average 33 animals each, will be referred to the right-hand, asymptotic portion of the curves in figure 1 when the relative chances of recruitment are determined (eggs produced = rN). With the exception of the near-linear curve ($\alpha = 0.00085$), their relative chances of recruitment will be little affected by substantial differences in the size of their populations. By contrast, with per capita fecundity of $r = 1.0$, variations in population size will cause marked changes in relative chance of recruitment because these will be calculated with reference to the left-hand portions of the stock-recruit curves. In these cases, when the numbers of a species happen to diverge from about 33, its chance of continuing to diverge will be enhanced. The tendency for variance to be less with the more nonlinear stock-recruit curves results because, for these, chance of recruitment is effectively independent of population size over a wide range of population sizes. This tendency emphasizes the importance of the shape of this relationship in determining persistence in the model.

A subsequent test ran five replicates of each of the six sets of parameters for $\alpha = 0.00085$ for 1,000 yr. All but two of these 30 replicates persisted. One with mortality rate of 0.125 failed at 823 yr; one with a mortality rate of 0.25 failed in 583 yr. Both had the lower per capita fecundity (1.0). Overall, these results confirm that for a relatively wide range of conditions, persistence of three identical species for periods on an ecological time scale is quite likely.

2. *Coexistence of ecologically different species.*—These studies pitted one species with different (usually apparently inferior) characteristics against two identical competitors. Initially species with identical values of α and β were used. Subsequently, the effect of differences in these coefficients was also explored. All vacant sites were assumed to be filled each year.

a) *Species with identical stock-recruit relationships.*—Using the moderately inflected stock-recruit curve specified by $\alpha = 0.00937$, and $\beta = 0.105$, I investigated the degree to which a test species could differ in fecundity or mortality rate,

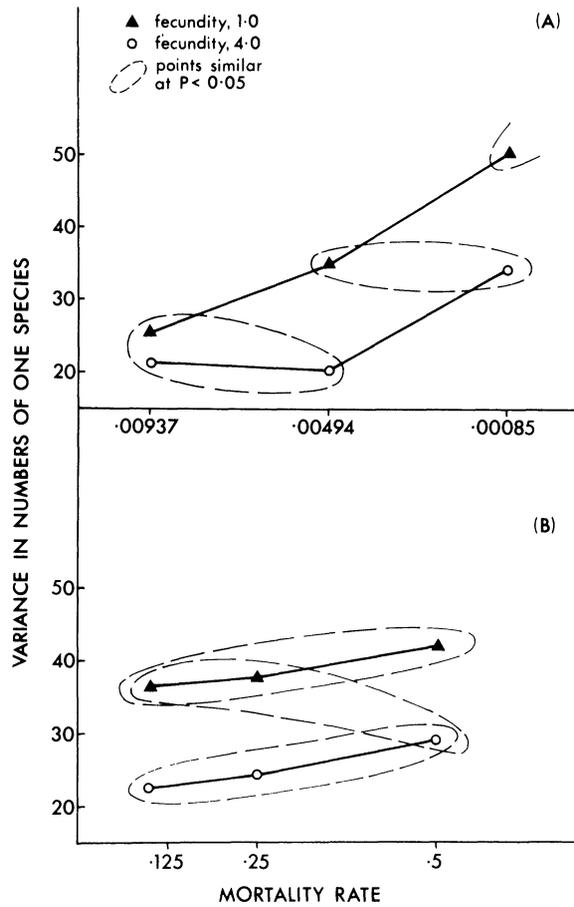


FIG. 2.—Variance in numbers of a species present when 3 identical species coexist for 100 yr. Data in *a* are averaged over mortality levels; those in *b* over levels of α . Dotted lines enclose points which do not differ significantly.

yet still persist successfully with two competitors identical to one another. Fecundities in the region of 1.0 and 4.0 were investigated. In the former, effects of differences in population size among the species will have a substantial effect on subsequent chance of recruitment. In the latter, such effects will be less pronounced. Competitor species with mortality rates of 0.125 or 0.25 per yr, and fecundities of 1.0 or 4.0 per yr were used. Individuals of all species were capable of breeding the year after recruitment. Two competitors with each combination of fecundity and mortality rate were matched with a single test species. The test species had a fecundity = 0.5, 0.75, 1.00, 1.25, 1.50, or 1.75 times that of its competitors, and a mortality rate = 0.5, 0.8, 1.00, 1.33, 1.50, or 1.75 times the mortality rate of its competitors. Five replicate runs were made with each of the 144 sets of species.

Persistence over 200 yr was reliable over a wide range of values of relative

mortality or fecundity of the test species. When competitors had fecundity = 4.0, all runs of all combinations of species persisted 200 yr. When fecundity of competitors was 1.0, 17 of 360 runs failed in fewer years. These 17 runs were all ones in which the test species was distinctly inferior in both fecundity and survivorship to its competitors. In 16, the test species' fecundity was 0.5 (0.75 in the 17th run). Five of the 17 runs occurred with competitors having mortality rates of 0.125; in these the test species' mortality rate was 1.5 (2 cases) or 1.75 (3) times that of the competitors. The remaining 12 of the 17 runs occurred when competitors had mortality rates of 0.25. In these, the test species' rate was 1.33 (1), 1.5 (5), or 1.75 (6) times that of its competitors. The effects of variation in mortality and fecundity on the mean number of the test species present were examined in separate two-factor analyses of variance for each of the four combinations of competitors' fecundities and mortality rates. In all four cases significant effects of both factors were found. Significant interactions between them existed in the two cases in which competitor mortality rates were 0.25 per yr (for competitors' fecundity = 4.0, $F_{25,144} = 2.13$, $P < .05$; for fecundity = 1.0, $F_{25,144} = 2.57$, $P < .01$). In general, numbers of the test species fall as its mortality rate relative to that of its competitors rises, and as its relative fecundity declines. These effects are non-additive at the higher overall mortality rate.

Two preliminary comparisons among the four sets of competitors were carried out using analysis of covariance. Figure 3 plots the mean number of the test species present against relative mortality rate for the four sets of conditions in which test species and competitors had identical per capita fecundities. Covariance analysis was done ignoring the slight curvilinearity evident in figure 3. This analysis, and the simultaneous testing procedure of Sokal and Rohlf (1969) showed significant differences among slopes. The effect of relative mortality rate is more pronounced for the lower set of fecundities, but within each set, is unaffected by differences in overall mortality rates of the three species.

Figure 4 examines the effect on mean number of the test species of variation in relative fecundity for the four sets of conditions in which test species and competitors had identical mortality rates. Covariance analysis and the simultaneous testing procedure indicated significant differences in slope of this effect between the low and the high sets of fecundities. The effect of relative fecundity is more pronounced for the lower set of fecundities.

The primary message of this analysis must be that for the particular stock-recruit curve considered here, substantial differences are possible between the competing species in per capita mortality or fecundity without elimination of the inferior species occurring in a reasonable span of time. To examine just how great the differences would have to be for elimination to be likely within 200 yr, I extended the analysis for species with equal fecundities to consider even more inferior test species. Test species with mortality rates 2.0 or 2.5 times greater than those of their competitors persisted successfully for 200 yr except when fecundities were set at 1.0, and test species had mortality rates 2.5 times those of their competitors. In these cases some replicates failed sooner (table 1). Further analysis is possible, and might permit a more precise statement of the limits to differences tolerated if persistence is to be likely. Yet the data presented amply

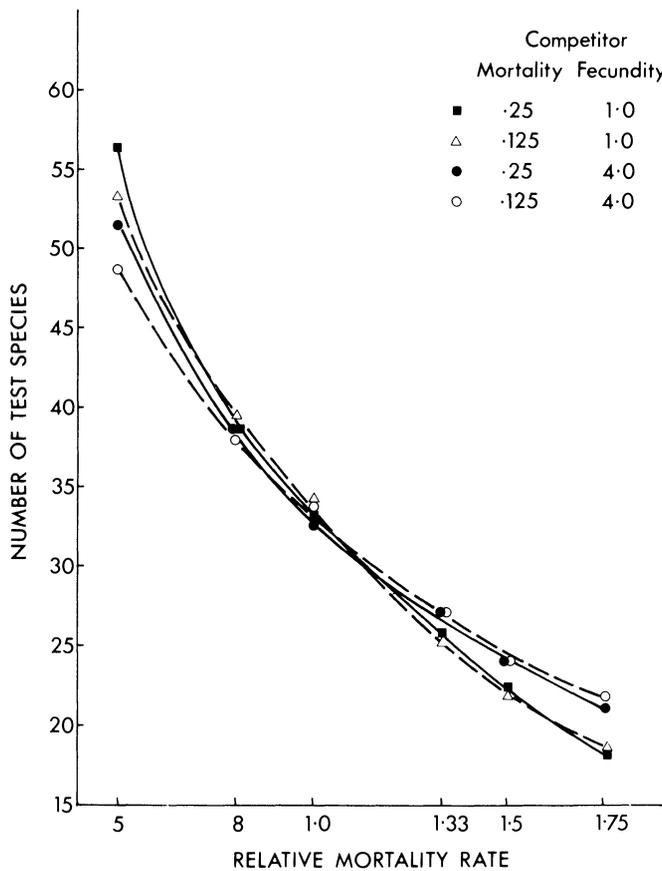


FIG. 3.—Mean number of a test species present over 200 yr when it differs in mortality rate, but not in fecundity, from 2 otherwise equivalent competitors.

confirm that twofold differences in mortality rates or fecundities, or combinations of these, can exist among competing species in this system without seriously impairing chance of persistence on an ecological time scale.

When the stock-recruit curve shared by the three species is more linear, differences tolerated among the species are smaller. Preliminary studies with the initially nearly linear curve specified by $\alpha = .00085$, and $\beta = .105$ (figure 1) showed that persistence for 200 yr or more is only likely (all of 5 replicates persist) if the inferior species' mortality rate is no more than 1.07 times that of its competitors when fecundities are equal. Conversely, if the stock-recruit curve rises rapidly to an early asymptote (e.g., $\alpha = .01112$, $\beta = .07$, fig. 5), or if fecundities are generally so high that the asymptotic part of the stock-recruit curve comes into play even at low population sizes (e.g., $\alpha = .00085$, $\beta = .105$, but fecundity, $r = 100$), even greater differences among competitors can be tolerated (table 2).

b) Species with differing stock-recruit relationships.—The ability to persist of

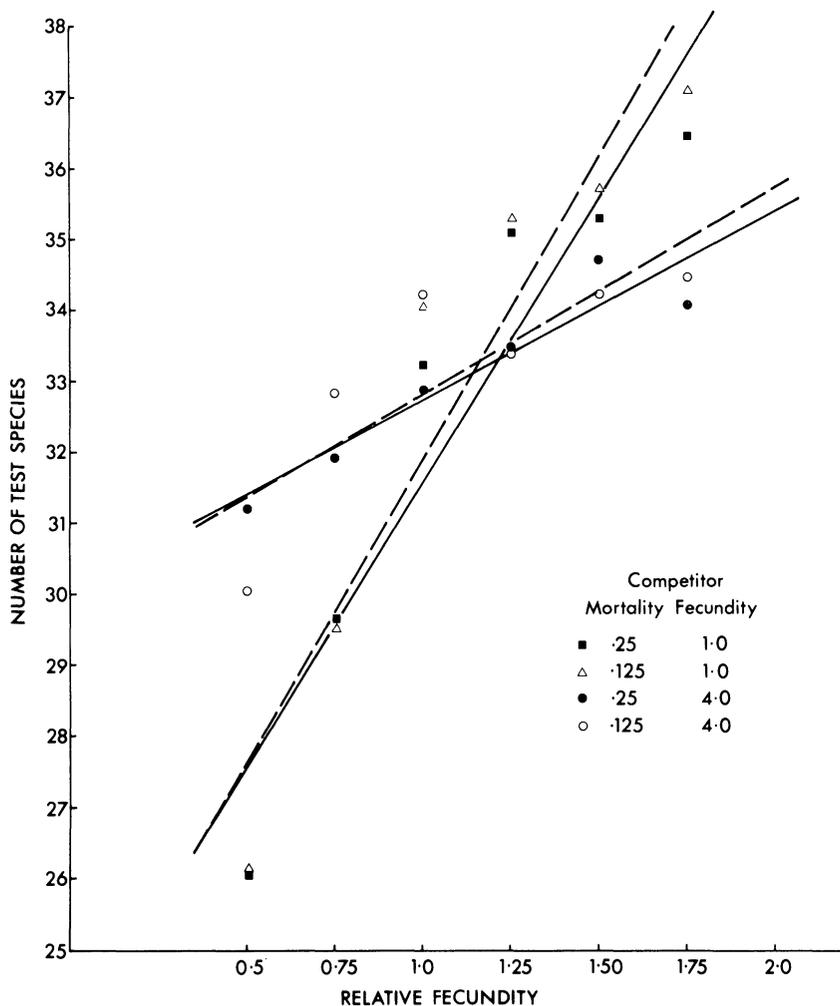


FIG. 4.—Mean number of a test species present over 200 yr when it differs in fecundity, but not in mortality rate, from 2 otherwise equivalent competitors.

species with differing stock-recruit relationships was examined in a series of experiments in which a single test species was pitted against two competitors which had $\alpha = .00937$, $\beta = .105$, fecundity of 1.0, and a mortality rate of 0.25 per year. In each experiment, the survivorship of the test species was varied in order to establish how much lower it might be than that of the competitors without persistence failing within 200 yr.

The relative ability of two species to recruit can be examined by comparing their stock-recruit curves as specified by the values of α , β , and fecundity of each. Five sets of values of these parameters were chosen for the test species in order to achieve the following relative advantages in recruitment: (1) The test species is advantaged in chance of recruitment at all possible sizes of adult stock. (2) It is

TABLE 1

PERSISTENCE AND MEAN NUMBER PRESENT FOR TEST SPECIES OF IDENTICAL FECUNDITY, BUT MARKEDLY GREATER MORTALITY RATES THAN THEIR COMPETITORS

| Fecundity | Competitors' Mortality | Test Species Mortality | Persistence* | Mean No. Present† |
|-----------|------------------------|------------------------|--------------|-------------------|
| 4.0 | .125 | .25 (2x) | 200 | 18.7 |
| | | .313(2.5x) | 200 | 16.1 |
| | .25 | .50 (2x) | 200 | 19.3 |
| | | .625(2.5x) | 200 | 15.1 |
| 1.0 | .125 | .25 (2x) | 200 | 15.2 |
| | | .313(2.5x) | 143 | 11.8 |
| | .25 | .50 (2x) | 200 | 15.8 |
| | | .625(2.5x) | 122 | 11.8 |

* Mean of 5 replicates set to run 200 yr.

† Mean of those replicates which persisted 200 yr.

TABLE 2

PERSISTENCE OF TEST SPECIES INFERIOR IN SURVIVORSHIP TO THEIR COMPETITORS WHEN ALL THREE SPECIES HAVE IDENTICAL FECUNDITY AND STOCK-RECRUIT RELATIONSHIPS

| STOCK-RECRUIT CURVE* | | | MORTALITY RATES | | PERSISTENCE† | | |
|----------------------|---------|-----------|-----------------|--------------|--------------|----------|----------|
| α | β | FECUNDITY | Competitors | Test Species | <i>N</i> | <i>n</i> | <i>m</i> |
| .00085 | .105 | 1.0 | .25 | .25 (1.00) | 5 | 5 | 200 |
| | | | .25 | .27 (1.08) | 10 | 9 | 193 |
| | | | .25 | .28 (1.11) | 5 | 2 | 176 |
| | | 1.0 | .125 | .133(1.06) | 5 | 5 | 200 |
| | | | .125 | .143(1.14) | 5 | 4 | 183 |
| | | | 100.0 | .25 | .33 (1.33) | 5 | 5 |
| .00937 | .160 | 1.0 | .25 | .438(1.75) | 10 | 10 | 200 |
| | | | .25 | .50 (2.0) | 10 | 7 | 181 |
| .01112 | .07 | 1.0 | .25 | .50 (2.0) | 10 | 10 | 200 |
| | | | .25 | .562(2.25) | 15 | 13 | 176 |
| | | | .25 | .625(2.5) | 5 | 4 | 181 |
| .00937 | .105 | 1.0 | .25 | .50 (2.0) | 10 | 10 | 200 |
| | | | .25 | .562(2.25) | 10 | 8 | 191 |
| | | | .25 | .625(2.5) | 10 | 1 | 97 |
| .00937 | .035 | 1.0 | .25 | .687(2.75) | 10 | 10 | 200 |
| | | | .25 | .75 (3.0) | 10 | 9 | 191 |
| | | | .25 | .812(3.25) | 10 | 8 | 179 |
| .01007 | .035 | 1.0 | .25 | .75 (3.0) | 10 | 10 | 200 |
| | | | .25 | .812(3.25) | 10 | 9 | 194 |
| | | | .25 | .875(3.5) | 10 | 7 | 163 |

NOTE.—Data for the six stock-recruit curves examined are presented in order of increased ability of the test species to persist.

* Curves with each pair of coefficients are shown in fig. 5.

† *N* and *n* refer to the number of replicates, and the number persisting 200 yr, respectively. *m* = mean persistence time.

TABLE 3

SETS OF VALUES OF PARAMETERS FOR A TEST SPECIES WHICH GIVE IT SPECIFIED TYPES OF ADVANTAGE OR DISADVANTAGE IN RECRUITMENT RELATIVE TO ITS COMPETITORS (Competitors are species with $\alpha = .00937$, $\beta = .105$, fecundity = 1.0, and mortality rate = 0.25.)

| TYPE OF ADVANTAGE | TEST SPECIES | | |
|--|--------------|---------|-----------|
| | α | β | Fecundity |
| A, always advantaged | .00937 | .035 | 1.0 |
| B, advantage decreases to 0 as stock approaches 100 | .01007 | .035 | 1.0 |
| C, advantaged below stock of 20, disadvantaged above | .01112 | .07 | 1.0 |
| D, disadvantage increases as stock approaches 100 | .01637 | .07 | 1.0 |
| E, always disadvantaged | .00937 | .16 | 1.0 |

advantaged at low adult stock sizes, but the degree of advantage decreases, approaching 0 as stock size approaches 100 animals. (3) It is advantaged at low adult stock sizes, but the degree of advantage decreases so that at a stock of 20 adults the species have equal probabilities of recruiting. At higher stock sizes the test species is disadvantaged. (4) It is disadvantaged at high adult stock sizes, but the degree of disadvantage diminishes at lower stock sizes so that it reaches 0 at a stock size of five adults. (5) The test species is disadvantaged at all possible stock sizes.

The parameter values providing each of these sets of conditions are set out in table 3, and the curves are shown in figure 5. The relation, for each set of conditions, between the mortality rate of the test species relative to its competitors, and persistence of the system is shown in figure 6.

The ability of the test species to persist with its competitors is enhanced when it has a stock-recruit relationship giving it a relative advantage in rate of recruitment. Cases A and B in table 3 show that this is particularly so if the test species' relative advantage occurs primarily at low stock sizes. Curve B which represents the strongest tendency to persist, derives from conditions specifying an advantage in recruitment at low stock sizes, but no advantage when stocks are very high (compare curves in fig. 5). Curve A derives from a set of conditions in which the relative advantage of the test species in recruitment is more uniform.

Case C in table 3, which shows an ability to persist that is slightly greater than when test species and competitors have equal stock-recruit relationships, indicates that a slight advantage in recruitment when at low numbers can compensate well for a substantial disadvantage at higher stock sizes. Finally, cases D and E in table 3 indicate that, even when a species is always disadvantaged relative to its competitors in chance of recruitment (see fig. 5), its persistence for in excess of 200 yr may still be possible despite a slight disadvantage in survivorship as well.

Clearly, there is no reason, a priori, to expect that stock-recruit relationships of competing species will be identical. The preliminary tests presented here indicate convincingly that differences in stock-recruit relationships can play an important role in determining whether or not a particular lottery system will persist. A

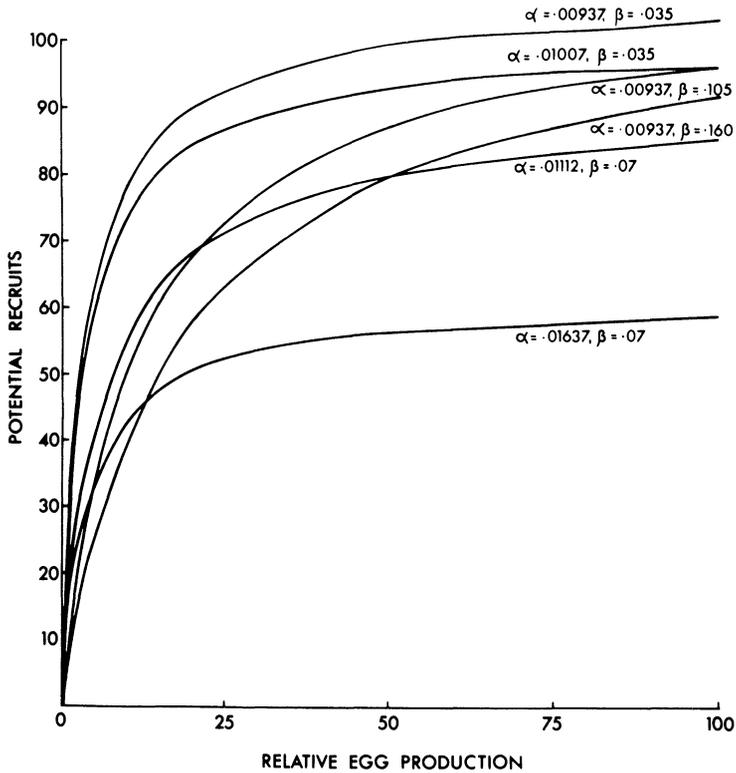


FIG. 5.—Stock-recruit curves used in the analyses of persistence of groups of 3 competitively different species.

species which is otherwise inferior to its competitors will have a greater chance of persisting with them if its stock-recruit relationship is one which enhances its ability to recruit relative to that of its competitors. This is particularly so if its ability to recruit is enhanced when at low stock sizes. An enhanced ability to recruit when at high stock sizes is less important.

Despite the above, it remains possible for a species with an inferior ability to recruit to persist for substantial periods with its competitors, even when it is also slightly inferior in survivorship.

DISCUSSION

The model examined here pits species with similar or differing attributes in a lottery competition for living sites. Each individual must obtain a site following a hypothetical larval stage if it is to survive as an adult. Individuals which do obtain sites are not further influenced by competition with neighbors of their own or other species.

The analyses demonstrated that, over a wide but realistic range of conditions, the possibility of local persistence in this system is high. In particular, under

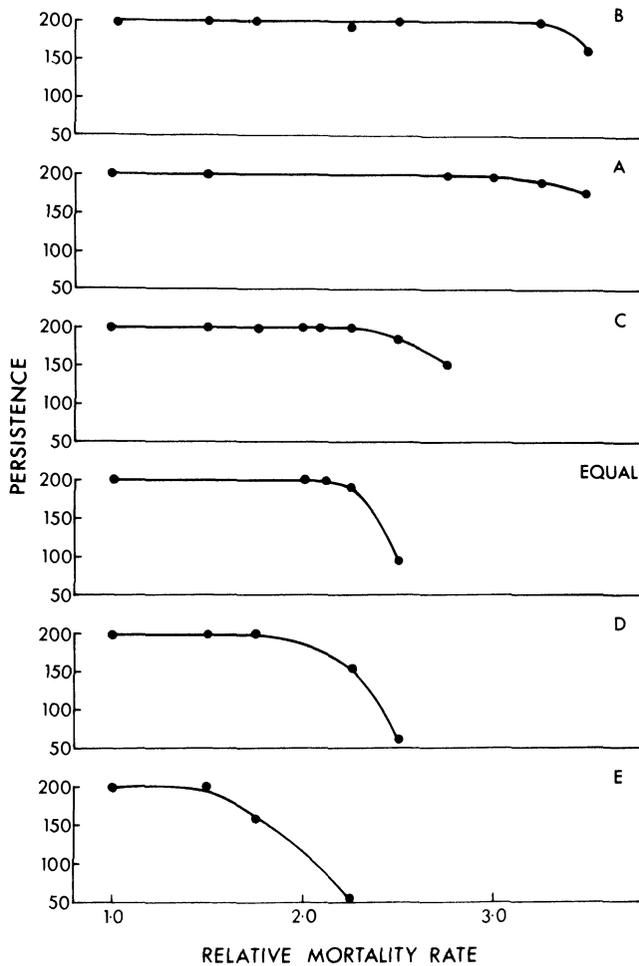


FIG. 6.—Limits of deficiency in survivorship compatible with persistence for 200 yr by a test species with a specified type and degree of advantage or disadvantage in recruitment relative to its competitors. A–E refer to parameter combinations in table 3. Each point is mean of 5 or more replicates.

specified, but not narrowly restrictive conditions, a species which is substantially inferior to its competitors in fecundity, survivorship, or both, can successfully coexist for ecologically long periods of time. The primary factor responsible for this successful persistence of competitively inferior species is the incorporation into the model of nonlinear stock-recruit curves. Persistence was found to be much less likely when a nearly linear stock-recruit curve ($\alpha = .00085$, $\beta = .105$) was used.

How realistic is this incorporation of curved stock-recruit relationships? Two additional alternative approaches exist. One is to assume a directly linear relationship between the chance of recruitment by a species and the number of adults of

that species present and breeding in the local population. Superficially, this is the more logical approach to take. If each adult present produces a certain number of offspring each year, the number of offspring produced will be directly proportional to the number of adults present. The number of potential recruits following larval life might be expected to be some specified proportion of this number of offspring, namely, the proportion likely to survive larval life.

The second alternative is to assume that, for any stock greater than 0, no relationship exists between the probability of recruitment and the stock of adults of a species present and breeding at a site. Since the model is of a small but closed environment to which recruitment from other places is not permitted, this possibility seems very unlikely. In real situations, recruitment could only be essentially independent of stock size on the local scale if it was primarily of larvae derived from breeding elsewhere, or if factors regulating larval mortality adjust to larval numbers in a density-dependent way so that no matter how many offspring are produced, a rather constant number complete their larval life.

Of these two alternatives, that of direct linear stock-recruit patterns would reduce the possibilities for persistence. That of recruitment virtually independent of local stock size would enhance them further than seen here.

Empirical fisheries data indicate that stock-recruit relationships are not linear for any fish examined, and fisheries practice routinely uses curved relationships (Cushing 1973; Gulland 1977). The theoretical argument used is the same one used to justify logistic population growth curves: that of density-dependent mortality. In fact, however, the data available for any real fish stock are insufficient to discriminate between a curved stock-recruit relationship, and total independence of the two, let alone decide the correct shape of the curve if one exists. Figure 7 is modified from Cushing (1975), and represents some of the better fisheries data on this point. Lines shown have been fitted assuming the Ricker (1958) formula relating stock and recruitment. They cannot be derived from the data. Larkin (1978) has explicitly drawn attention to this problem by stating that the use of the stock-recruit curves derived by Ricker (1958) and by Beverton and Holt (1957) has been a matter of faith, bolstered by the logical necessity that in the total absence of a stock there will be no recruitment.

In the present instance, by using curved stock-recruit relationships in calculating the relative numbers of potential recruits of each species available each year, the model has introduced a degree of direct dependence of recruitment on local stock size which is of the same form, but probably stronger, than would exist in reality.

Although the Ricker curve is currently preferred by fisheries biologists, I have used the curve of Beverton and Holt because it is simpler, yet is as appropriate for real fisheries data. Use in the model of the Ricker curve, with its reduced generation of recruits at high, as well as at low stock sizes, would permit persistence of species with even greater differences in competitive abilities than has been shown here.

The only logical alternative to use of the Beverton and Holt, Ricker, or similar curves would be to ignore the stock-recruit relationship, and assume chance of recruitment to the local site to be constant and species-specific. In the present model, this effect is easily mimicked by specifying sufficiently high fecun-

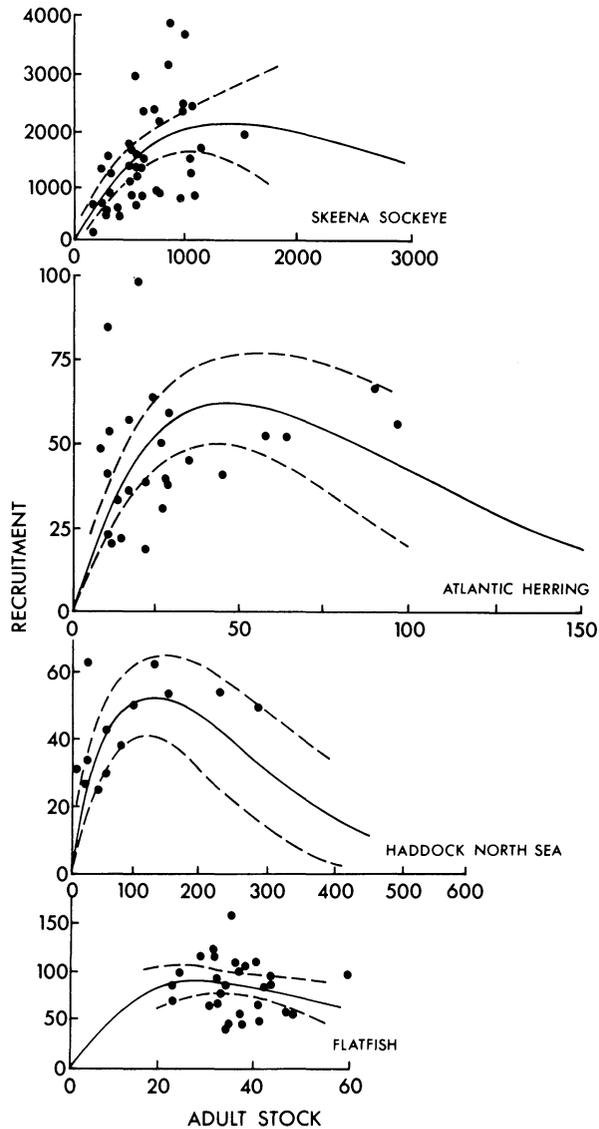


FIG. 7.—Representative stock-recruit data from the fisheries literature. Curves shown are the best-fit Ricker curves and 95% confidence limits on the curves (modified from Cushing 1977).

dities for each of the species. Even for very small stocks, the asymptotic part of the chosen stock-recruit curve will then be used in calculating probability of recruitment.

The analyses of the model that are reported here have generally avoided this perhaps more real situation. Instead, fecundities have been chosen which result in relative numbers of potential recruits often being calculated from the left-hand

pre-asymptotic part of the chosen stock-recruit curve. The curves chosen have been (with the exception of the near-linear curve, $\alpha = .00085$, $\beta = .105$) similar in shape to those derived from empirical fisheries data (e.g., fig. 7). These various choices have been made deliberately in order to test the lottery model under stringent, but still realistic conditions. I reject the argument that a linear stock-recruit relationship is realistic, because empirical data offer no support for this suggestion.

The realism of other aspects of the model needs consideration also. The model assumes that competition only occurs at the time sites are chosen by new recruits, that this competition is randomly decided among the available recruits on the basis of which arrived first, and that subsequent to obtaining its site, a successful recruit is no longer influenced, in terms of adjustment to either its fecundity or its survivorship, by the species composition of animals in adjacent sites. Limited data supporting these assumptions exist for the territorial pomacentrid fishes for which I originally formulated the lottery concept. *Pomacentrus wardi* colonizes reef slope rubble patches without regard to the species composition of its new neighbors, and its subsequent survivorship is not affected by this factor (Sale 1979). Nor is survivorship of *Eupomacentrus apicalis* or *Plectroglyphidodon lacrymatus* in these same sites influenced by the species composition of their neighbors, but data on recruitment by these two species are too limited for a satisfactory test (Sale 1979). Data do not exist for any of the three species on variability in fecundity in this habitat.

Dybdahl (1978) has recently demonstrated the considerable importance of prior residency in competitions for nesting cavities among blennies of the species *Meiacanthus lineatus* and *Petroscirtes fallax*. He also demonstrated that male fecundity was a function of the quality of the site held, rather than of the male itself. It seems likely that the assumptions of the lottery model are applicable to a number of instances in which fish with pelagic larvae compete for identifiable living or breeding sites, and to other taxa as well.

The model also assumes that the sites taken by recruits are of sufficient size to serve them throughout life. This assumption is unrealistic for pomacentrids which enlarge their sites as they grow by adjusting the borders at the expense of their neighbors (Sale 1979). It would not be unrealistic for species competing for shelter sites or nesting holes as young adults. Modification of the model to permit adjustment to all of these assumptions would be straightforward.

The model, as tested, indicates that when competition among species takes the form of a lottery for living sites gained at the end of a larval stage, persistence is possible despite substantial differences among the species in competitive abilities (see figs. 3, 4, 6). This persistence occurs because the per capita chance of further recruitment is enhanced when a species is rare. The curved stock-recruit relationship is responsible for this effect.

Chesson and Warner (1981) have used an analytical approach to reach very similar conclusions though for rather different reasons. They used an indefinitely large population of two competing species, and showed that long-term, though nonequilibrium persistence was achieved under certain circumstances because of a similar nonlinearity of chance of recruitment. Provided generations overlapped,

and there was stochastic variation in birth and death rates, species that were currently rare had substantially greater chances (per capita) of increasing their numbers when conditions for them chanced to be favorable, than did common species. Conversely, common species suffered more losses when conditions were poor than did currently rare species. They thus made more sites available to recruits of other species than did rare species when conditions for them were poor. The Chesson and Warner model requires that birth rates always be sufficient for all sites to be filled, and that birth and death rates vary so that each species is at some times competitively superior to the others, but it does not require stock-recruit relationships to be other than linear.

By contrast, the present study shows that long-term, though still unstable persistence is possible even on a local scale, with no necessity for immigration of recruits from other refuge areas (although such immigration would further enhance the possibility of local coexistence [Huffaker 1958; Caswell 1978; Sale 1979]). Further, this persistence is possible for species which are always inferior to their competitors, or in cases where reproduction is not sufficient to fill all vacant sites. Birth and death rates of the species involved are constant, a situation in which the Chesson and Warner model could not yield persistence. These results are obtained only by including the added, but realistic assumption that stock-recruit relationships are curved. The study substantially bolsters the conclusions reached by Chesson and Warner (1981).

These two different, but complementary studies must raise doubts about the efficiency with which competition leads to competitive exclusion when that competition is expressed in other than a continuous exploitative fashion. The extent to which lottery systems actually occur, and thus their importance, will require further empirical studies. I have elsewhere argued that they should be expected whenever species with a dispersive larval phase, high larval mortality, and similar adult habitat requirements occur. These life history features seem widespread among sessile or sedentary marine species, and among terrestrial species other than higher vertebrates. Where such species come into competition for living sites or similar resources, the variability in recruitment, and the independence of recruitment from local population sizes will be the driving force maintaining a lottery competitive system. This study, and that of Chesson and Warner, indicate that the coexistence of substantially unequal, yet competing species may be tolerated for ecologically meaningful lengths of time.

The characteristic variability and lack of dependence on local populations of recruitment also plays a major role in structuring nonequilibrium, disturbance-mediated communities in which competition for resources seldom occurs. Despite the emphasis that has been placed on the role of the disturbance in such systems (Dayton 1971; Connell 1978; Sousa 1979*a*, 1979*b*) in maintaining diversity, its effect depends upon the species present recruiting in a way independent of local population densities. Further attention to the role of recruitment will be profitable whether in lottery systems where competition is occurring, or in situations where the rate of disturbance, or simply a lack of recruits, keeps numbers below carrying capacity (Denley and Underwood 1979; Doherty 1980).

SUMMARY

A lottery competition occurs among species when individuals compete for access to units of resource without which they cannot join the adult (breeding) population. It is a form of interference competition in which the chance of an individual's winning or losing is largely determined by priority of arrival at a vacant unit of resource. Resources involved may be such things as living sites for sessile or sedentary species, or nest sites, or spawning or display sites. Such resources become available for reoccupancy on the death or departure of the current owner. Lottery competition may be particularly important in marine demersal forms which produce large numbers of pelagic larvae which disperse prior to settling into adult habitat.

Lottery competitive systems are inherently unstable but can be persistent under a wide range of conditions (Chesson and Warner 1981). A simulation model is developed to explore the effect on local persistence of differences among the competing species in (1) their survivorship after gaining a unit of resource, (2) their fecundity, (3) the age, after gaining the resource unit, at which individuals become sexually mature, and (4) the shape of their stock-recruitment curves (which relate number of recruits in a cohort to the size of the adult population, and thus to the number of eggs produced initially). In addition, the effect on persistence of the number of species involved in the competition, and of some resource units remaining unused was also examined.

The shape of the stock-recruitment curve was found to be very important in determining local persistence. Linear curves prevented persistence for all except ecologically very similar groups of species. However, when the relationship had moderate curvature (with number of recruits becoming asymptotic as population size increased) persistence for ecologically realistic periods of time was possible for groups of species which differed substantially in the other attributes affecting their competitive abilities. Such curved stock-recruitment relationships are usual for species such as most fish in which there is production of large numbers of larvae which suffer a heavy mortality prior to recruiting to the juvenile and adult habitat. It is suggested that a wide range of species of terrestrial as well as marine organism may possess attributes predisposing them to enter into lottery competitive systems. In such cases, the effectiveness of competitive exclusion seems likely to be much less than previously expected.

ACKNOWLEDGMENTS

I wish to thank the ecology group at Sydney University as well as R. R. Warner, J. H. Connell, S. A. Levin, J. Roughgarden, and P. H. Chesson for discussion on the subject of lotteries. Graham Pyke and Tony Underwood made comments on the manuscript which materially improved it. This work has been supported by grants from the Australian Research Grants Committee and the University of Sydney.

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