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RECRUITMENT, LOTTERIES, AND COEXISTENCE IN
CORAL REEF FISH

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The coexistence of relatively large numbers of similar species of coral reef fish has interested many ecologists. Sale (1977) proposed that coexistence was facilitated because the mechanism of competition between species was essentially a lottery for living spaces. Unfortunately, Sale's (1977) paper did not contain a precise mathematical description of what constituted a lottery. Subsequent work by Chesson and Warner (1981) and Sale (1982) has provided two alternative models of lottery competition, each with a different mechanism allowing coexistence. Sale suggested that both his 1982 study and that of Chesson and Warner (1981) argue that competitive exclusion may be less likely in lottery competition systems than in systems with other mechanisms of competition. Here, I am mainly concerned with evaluating this assertion. An analytical model based on Sale's simulation model is developed and used to determine which aspects of the model are responsible for coexistence. I argue that an implicit (and unjustified) assumption of only intraspecific competition in the larval stages is responsible for coexistence of competitors in Sale's model. The lottery aspects of the interaction do not facilitate coexistence. I discuss Chesson and Warner's 1981 model briefly; here again, the lottery does not appear to be required to obtain coexistence. Lottery models are not the only hypotheses for reef fish coexistence. Coexistence via more traditional mechanisms of resource partitioning are favored by Robertson and Lassig (1980), Dale (1980), Anderson et al. (1981), and others. I conclude with an evaluation of the various hypotheses which have been advanced to explain coexistence in reef fish.

I. AN ANALYTICAL MODEL BASED ON SALE'S (1982) SIMULATION MODEL

Sale (1982, p. 140) states that, "Simulation was chosen as a straightforward way of obtaining information on the behavior of lottery systems." If, however, one is interested in determining which aspects of a model are essential to account for some property (e.g., coexistence), analytical models are more useful, and at least as straightforward as simulations.

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In Sale's model, the per capita death rate of each species is constant. The number of species i adults dying in one time interval is equal to $d_i N_i$, where d_i is a constant, and N_i is the adult population size of species i .

The number of spaces which become available for new adults in one time interval is the sum of the deaths of all of the species (i.e., $\sum_j d_j N_j$).

The number of eggs produced by a given species in a unit of time is a linear function of adult population size; i.e., $E_i = r_i N_i$, where r_i is the per capita egg production rate of species i .

The number of mature larvae of species i is a function of the number of eggs produced, and is given by $M_i = E_i / (\alpha_i E_i + \beta_i) = r_i N_i / (\alpha_i r_i N_i + \beta_i)$. Here, α_i and β_i are parameters which determine the amount of density dependence in larval mortality. Note that the survivorship of the larvae of a given species is assumed to be independent of the population density of other species' larvae. Sale (1982) refers to the number of eggs times their survivorship to the end of the larval period as recruitment. For territorial reef fish, however, individuals must not only survive, but also settle successfully in order to recruit. Therefore, the function relating M_i and E_i will be referred to as a larval survivorship function, rather than a stock-recruitment relationship.

The expected number of recruits of species i during a given time interval is given by the fraction of all mature larvae that are of species i times the number of empty spaces which become available in that time interval. This is given by

$$\frac{M_i}{\sum_j M_j} \left(\sum_j d_j N_j \right).$$

In Sale's model, recruitment is determined by randomly drawing a number (equal to $\sum_i d_i N_i$) of mature larvae from the pool of all mature larvae. Thus, the number of new recruits of a specific species is given by a hypergeometric random variable. In the model considered here, recruitment is set equal to the expectation of recruitment in Sale's model; it is therefore applicable to the case in which the number of empty spaces is very large, and the total number of larvae is much greater than the number of empty spaces. It is thus a deterministic analogue of Sale's stochastic model.

The change in the population density of adults of species i during one time interval is simply recruitment minus death, and is therefore given by

$$\Delta N_i = \left[\frac{r_i N_i / (\alpha_i r_i N_i + \beta_i)}{\sum_j \left(\frac{r_j N_j}{\alpha_j r_j N_j + \beta_j} \right)} \right] \left(\sum_j d_j N_j \right) - d_i N_i. \quad (1)$$

It should be noted that this model is essentially equivalent to Chesson and Warner's (1981) deterministic overlapping generations model (their eq. [11]). The only difference is that their model assumes that the number of mature larvae is directly proportional to adult population density, rather than the density-dependent larval survivorship assumed here.

In addition to its deterministic nature, this system differs from Sale's (1982) model in several minor respects. (1) In the present model, unlike Sale's, adult fish have no maximum lifespan. In Sale's simulations, very few individuals (a fraction $\exp(-3)$ of recruits) reach the maximum age. This therefore has very little effect on the behavior of the model. (2) Here, there is no time lag between settlement and reproduction. Strictly speaking, this is unrealistic, but it allows one to ignore adult age, simplifying the model considerably. Sale found that changing the age of first reproduction in his simulations did not seem to affect his results except insofar as it changed average adult fecundity. (3) The present model assumes that there are enough larvae to fill all sites. The model therefore cannot be used to describe population growth in an unsaturated environment. In all of Sale's reported simulation results, all sites became filled, and saturation was generally achieved in 6 time units, while simulations were run for at least 100 units. Thus, Sale's model is also a description of population processes in a saturated environment. When there are abundant empty spaces, there is no competition in this model, so this situation is of less interest.

It is possible to determine directly whether this model is a reasonable approximation to Sale's by comparing its properties with those reported for the simulation. This is done in the following section.

II. PROPERTIES OF THE MODEL

Two of the properties examined by Sale were: (1) the mean numbers of one competitor as a function of its relative mortality or relative fecundity, and (2) whether all of the competitors persisted for the duration of the simulation run.

A. *Relative Abundances of Unequal Competitors*

As shown by Chesson and Warner (1981, p. 928), two species in a lottery will not change in relative abundance if the following relationship is satisfied:

$$\frac{\text{Per capita production of mature larvae of species } i}{\text{Per capital production of mature larvae of species } j} = \frac{\text{Per capita death rate of species } i}{\text{Per capita death rate of species } j}$$

This relationship can be used to derive expressions for the equilibrium abundances of competitors. For the case examined by Sale (1982), there are two identical species, and a third which differs either in mortality or fecundity from the first two. The expression for the equilibrium density of the odd species derived using the above relationship is

$$N_1 = \frac{2r_1d_0\beta_0 - 2r_0d_1\beta_1 + r_1d_0\alpha_0r_0K}{r_1r_0(2\alpha_1d_1 + \alpha_0d_0)} \quad (2)$$

where zero subscripts denote parameters for the two equivalent species, and a subscript 1 is used for the odd species. K is the number of adult sites. Substituting the parameter values used by Sale in his figures 3 and 4 into expression (2) results

in values very close to those found in the simulations. A lack of error bars in figures 3 and 4 precludes statistical comparison. It is worth noting that, if mortality rates of all species are equal, expression (2) is not affected by the absolute mortality level. This seems to be true for Sale's figure 4.

B. Conditions for Coexistence

A necessary condition for the persistence of a given species is that it be able to increase when it is very rare and the other species are at equilibrium densities. As Armstrong and McGehee (1980) have pointed out, this condition is not always sufficient to guarantee coexistence, but numerical results suggest that it is a sufficient condition in all of the special cases examined here. Thus, from equation (1), species i will persist if

$$d_i < \frac{(r_i/\beta_i)\left(\sum_j d_j N_j\right)}{\left[\sum_j \frac{r_j N_j}{\alpha_j r_j N_j + \beta_j}\right]}. \quad (3)$$

This condition is more easily interpreted by examining some special cases.

1. *Equivalent competitors*.—In this case, all species have the same population growth parameters. If the total number of sites is denoted by K and the number of resident species by n , condition (3) becomes

$$1 < \frac{\beta n + \alpha r K}{\beta n}. \quad (4)$$

This inequality is always satisfied; the model predicts coexistence of any number of species. Sale observed coexistence in the majority of all simulation runs for every set of parameters when the competitors did not differ in population growth parameters.

2. *Two unequal competitors*.—An application of inequality (3) shows that if species 1 is the inferior competitor, both species can coexist if

$$d_1 < d_2 \frac{r_1 (\alpha_2 r_2 K + \beta_2)}{r_2 \beta_1}. \quad (5)$$

This shows that a species which is inferior in all respects (smaller β , larger α , larger d , and smaller r) can coexist with a superior competitor.

3. *One inferior and n equivalent superior competitors*.—Again applying condition (3), and denoting the inferior competitor as species 1, coexistence is possible if

$$\frac{d_1}{d_2} < \frac{n\beta + \alpha r K}{n\beta}. \quad (6)$$

This shows that if per capita death rates are sufficiently similar, coexistence is always possible. It also shows, however, that it becomes increasingly difficult for an inferior species to exist as the number of species of superior competitors

increases. The larger the number of species, the closer the invader's death rate must be to those of the superior residents. This occurs because increasing the number of species increases the probability of a larva surviving, as a result of decreased intraspecific competition among larvae. It should be noted from (6) that large values of αrK relative to $n\beta$ are favorable to coexistence. Most of Sale's simulations involved three species. He states (p. 141) that, "Qualitatively, results are identical with other numbers of species competing." Expression (6) argues against this assertion.

In the above examples, conditions on the death rates of coexisting competitors were explored. Similar results may be obtained if fecundity is the parameter of interest.

If one substitutes the parameter values reported by Sale in the above expressions, coexistence is predicted in every case simulated. The extinctions which Sale observed may be attributed to the demographic stochasticity arising because of his small population sizes, because this is the only substantive difference between the two models. Sale (1977) argued that unpredictability facilitated coexistence, but this particular type of uncertainty seems to make coexistence less probable. Setting α equal to zero in any of the above inequalities confirms Sale's (1982) claim that coexistence cannot occur if larval survivorship is density independent. Sale's simulations all used a single functional form for determining larval survivorship. The present model can be used to show that the coexistence of equivalent competitors is possible for any larval survivorship function which decreases as larval density increases. Chesson and Warner (1981) did not observe coexistence in their deterministic model because it assumed density-independent larval survival; if density-dependent larval survival were incorporated, their model (for a constant environment) would be the same as the one analyzed here.

III. SUFFICIENCY OF DENSITY-DEPENDENT LARVAL MORTALITY AND THE NECESSITY OF A LOTTERY FOR ACHIEVING COEXISTENCE

A. *Sufficiency of Density-Dependent Mortality*

Sale's larval survivorship curve assumes that larval competition is totally intraspecific (competition is being used in a broad sense, to include all sorts of density-dependent mortality). No justification for the assumption is made. In fact, the similar size of different species' larvae and the lack of discrete reproductive seasons suggest that larvae of different species should compete if there is intraspecific competition as well. I know of no evidence suggesting extensive food or habitat differentiation for the larvae of closely related reef fish species. If all larvae are competitively equivalent, the larval survival probability should be modified to $1/[\alpha_i(\sum_j r_j N_j) + \beta_i]$. In this case, it is easy to show that two equivalent competitors cannot coexist in the lottery model. This complete larval competition model is discussed in more detail in the following section. I will show that at most two species can coexist at equilibrium in this case. Thus, the possibility of multispecies coexistence depends on an assumption which may be implausible for

coral reef fish. Density dependence per se is not sufficient to account for coexistence.

B. Necessity of a Lottery

While the assumption of no interspecific larval competition may be unlikely for coral reef fish, there may be other lottery systems for which this is reasonable. It is therefore of interest to ask, if larval competition is solely intraspecific, is a lottery required for coexistence? This question is somewhat difficult to answer because of the many different descriptions of what constitutes "lottery competition" in Sale's (1977, 1979, 1982) articles. The following elements seem to be assumed: (1) Occupants of newly available spaces are determined by a random process; (2) no species' larvae have an advantage in obtaining empty sites; and (3) once it has settled, an individual cannot be displaced. These are examined in turn.

1. The analytical model presented here does not have the element of stochasticity in determining which larvae succeed in settling in empty places. A comparison of the analytical conditions for coexistence with simulation results showed that the demographic stochasticity in Sale's model actually renders coexistence less likely.

2. The model presented here predicts that coexistence of two competitors is possible even when the larvae of one species are better at finding or keeping empty spaces. Unequal larval space-obtaining abilities are modeled in the same manner as a fecundity advantage; the species with the superior site-acquisition abilities would be assigned a larger r value, and it was shown above that species with different r values could coexist. Chesson and Warner (1981) also noted the equivalence of higher fecundity and greater space acquisition ability; both quantities were incorporated into a single parameter (β^*) in their model.

3. Equation (1) is consistent with a first come-first served mechanism of distributing territories. It is also consistent with any amount of exchange of territories after settlement. All that is required is that each species eventually end up with a number of territories proportional to its abundance in the pool of mature larvae.

While these three conditions may describe reef fish larvae, none of them seems to be an essential part of a lottery system. What is essential is that the expected fraction of available adult living spaces obtained by the larvae of one species be proportional to its larval abundance divided by the total larval abundance of all species (where abundances may be weighted by competitive abilities). This is the central feature incorporated into Chesson and Warner's (1981) model. Sale suggests that coexistence is easier to obtain in lottery competition than when adults engage in exploitative competition. This could only be justified by comparing similar models which differ in the presence or absence of a lottery. In fact, Sale's larval survival functions guarantee coexistence of equivalent competitors for any type of adult competition. The larval competition assures that overall, intraspecific competition will be greater than interspecific, a condition which

results in the coexistence of otherwise equivalent competitors (e.g., Maynard Smith 1974).

The above general argument does not show that lotteries cannot in some sense make coexistence more likely than in systems with adult competition but no lottery. The following simple model shows that a lottery is not always advantageous for obtaining coexistence. Consider two species that are equivalent in all respects except for mortality. The "ease of coexistence" will be measured by the maximum ratio of mortality rates which will allow coexistence. If my version of Sale's lottery model applies, then the maximum ratio of mortalities is (from eq. [3]), $d_1/d_2 < (\beta + \alpha rK)/\beta$, where $d_1 > d_2$. Consider an alternative model in which larval survival curves are identical, but (1) there is no lottery because all surviving larvae recruit, and (2) per capita egg production by adults is a linearly decreasing function of total adult population density (i.e., per capita egg production is $r[1 - c(N_1 + N_2)]$). This could describe a situation in which adults compete for food with total overlap in food utilization. The general equation for the change in population density of adults of species i is

$$\Delta N_i = -d_i N_i + \frac{r(1 - c \sum_j N_j) N_i}{\alpha r(1 - c \sum_j N_j) N_i + \beta}. \quad (7)$$

In this case, the condition for invasion by the inferior competitor when the superior competitor is at equilibrium is simply $d_1 < (r - rc\hat{N})/\beta$, where \hat{N} is the equilibrium density of the superior competitor. \hat{N} may be found by solving a quadratic equation. All that need be noted here, however, is that if c is sufficiently small, the inferior competitor can always invade. (d_1 must be less than r/β to permit existence of the inferior competitor alone.) Also, note that by choosing β much larger than αrK , conditions for coexistence in the lottery model become very restrictive; the death rate of the inferior competitor must be very close to that of the superior to allow coexistence (see inequality [5]). Results similar to the above can be obtained using other alternative competition models. The conclusion is that the lottery need not result in a lower probability of competitive exclusion than a similar system with a different form of adult competition.

IV. A LOTTERY MODEL WITH NO LARVAL RESOURCE PARTITIONING

In the previous section I suggested that the lottery model might be more plausible for reef fish if it incorporated interspecific larval competition. I also presented a larval survivorship function which did this. Here I show that, if there is no larval resource partitioning, this model allows coexistence of two competitors, but no more.

A. Coexistence of Two Competitors

The model in this case is identical to that summarized by equation (1), except that larval survivorship is given by $1/(\alpha_i(\sum_j r_j N_j) + \beta_i)$.

The criteria for each of two species to be able to increase when the other is at equilibrium are as follows:

$$\frac{d_1}{d_2} < \frac{r_1}{r_2} \left[\frac{\alpha_2 r_2 K + \beta_2}{\alpha_1 r_2 K + \beta_1} \right] \quad \frac{d_1}{d_2} > \frac{r_1}{r_2} \left[\frac{\alpha_2 r_1 K + \beta_2}{\alpha_1 r_1 K + \beta_1} \right]. \quad (8)$$

No pair of death rates can satisfy both inequalities unless the following condition is satisfied

$$(\alpha_2 r_2 K + \beta_2)(\alpha_1 r_1 K + \beta_1) > (\alpha_2 r_1 K + \beta_2)(\alpha_1 r_2 K + \beta_1). \quad (9)$$

It follows that a necessary criterion for coexistence is that the species with the higher fecundity (r) must have a larval survivorship which decreases more rapidly with population density (a larger α/β). The high fecundity species can invade a system with the high larval survivorship species because larval densities are relatively low when the latter is at equilibrium. The high larval survivorship species can invade when the high fecundity species is at equilibrium, because the high larval densities give it the advantage. It is worth noting that it is possible to have coexistence even if $d_1 = d_2 = 1$, so that overlapping generations are not required.

The above result might seem to contradict the competitive exclusion principle (Armstrong and McGehee 1980), but it actually does not, because there are two resources in the system; the resource which determines larval survival, and the adult living spaces, apportioned by the lottery. Coexistence requires that there be both larval and adult competition.

The effects of parameters upon the ease of coexistence differ considerably from the case of no larval interspecific competition examined previously. The range of d_1/d_2 values yielding coexistence may be found directly from the invasion criteria given above. Differentiating this range with respect to K shows that increasing K favors coexistence (i.e., it increases the range of d_1/d_2 values which yield coexistence) for all values of K less than $\beta_1/\alpha_1 \sqrt{r_1 r_2}$; for greater values of K , increasing the number of adult sites decreases the range of mortality ratios permitting coexistence. Multiplicative increases in the α_i/β_i or the r_i have the same effect as increasing K ; coexistence is favored until $K = \beta_1/\alpha_i \sqrt{r_1 r_2}$. Above the value of αr or below the value of β specified by this equation, further changes will make coexistence less likely.

B. Three or More Competitors

As one would expect from the competitive exclusion principle, it is impossible to have three species coexist at fixed densities with no larval or adult resource partitioning. This statement can be justified nonrigorously as follows. Any species may be characterized by a curve relating relative fitness to total larval population density. At equilibrium, relative fitnesses must be equal. It is extremely unlikely (and not evolutionarily stable) for the three curves for three different species to intersect at a single point. Thus, coexistence would be prohibited. The same argument may be made for any larger number of species. Appendix A shows that it is impossible to find three species such that all of the following conditions are

satisfied: (1) Species 1 can invade the subcommunity consisting of species 2 and 3; (2) species 2 can invade the subcommunity of 1 and 3; and (3) species 3 can invade the subcommunity with 1 and 2.

C. *Partial Resource Partitioning*

The two models discussed above clearly represent extreme cases in that they assume either no larval resource partitioning or complete partitioning. Both assume complete overlap of adults in habitat utilization, an assumption which is contradicted by most data on reef fish. A wide variety of partial overlap models are possible, and most real lottery systems are likely to be best described by such models. In general, sufficient resource partitioning in either stage of the life cycle will allow coexistence of competitors in a constant environment.

V. A NOTE ON CHESSON AND WARNER'S (1981) MODEL

Unlike Sale's simulation, Chesson and Warner's model assumes that there is environmentally caused variation in birth rates. This variation is required to obtain coexistence of competitors with no adult resource partitioning. As noted before, they also assume density-independent larval survivorship. As in the case of Sale's model, however, the lottery mechanism itself is not required for coexistence. Chesson (1983) and Abrams (1984) have both extended Chesson and Warner's (1981) analysis to nonlottery models. Abrams (1984) shows that environmental variation in per capita resource consumption rates can allow the coexistence of two or more species on a single resource under quite general conditions.

VI. THEORY AND EVIDENCE FOR VARIOUS HYPOTHESES EXPLAINING REEF FISH COEXISTENCE

Here I assess what the preceding analysis implies regarding hypotheses advanced to explain the coexistence of coral reef fish.

A. Coexistence resulting from a lottery with environmentally caused variation in birth and death rates.—This is the mechanism proposed by Chesson and Warner (1981). It should be noted that they do not claim that this mechanism is the main one promoting coexistence in reef fish. Unfortunately, there is insufficient data on the variability and cross-correlations of birth and death rates in reef fish to adequately assess the importance of this effect. The fact that some variability in recruitment is observed for most fish species (Larkin 1978) does suggest that this may contribute to coexistence.

B. Coexistence resulting from larval resource partitioning.—This is essentially the hypothesis of Sale (1982), although he did not recognize it as such. There is, to my knowledge, no empirical support for two aspects of the model.

(1) Density-dependent mortality of larvae. It is common to assume density-dependent mortality in fisheries models (Cushing 1973; Larkin 1978), but the evidence for such density dependence is relatively weak (Larkin 1978). In addition, fisheries models are generally based on observations on temperate species

which are nonterritorial, and whose population processes may differ greatly from those of coral reef species. Sale (1982) argues that linear stock-recruitment relationships have never been observed, so larval survivorship could not be density independent. If one were to determine a stock-recruitment relationship for a coral reef fish species, however, recruits would be censused after settlement (recruits are settled juveniles; not old larvae). Because of the limited number of available spaces, the stock-recruitment relationship would be nonlinear and would have an upper asymptote even if larval survivorship were independent of density. The evidence for the density-dependent survivorship required by the model is lacking. Stock-recruitment relationships are probably very difficult to measure for reef fish. Given larval periods of at least 10 days (Sale 1979), the stock population producing potential recruits for a given locale is likely to be too large to be effectively censused.

(2) Larval resource partitioning. Sale's model requires not only density-dependent larval survivorship, but it requires complete larval resource partitioning. Evidence for any sort of larval resource partitioning seems to be lacking.

C. Coexistence resulting from adult habitat or food partitioning.—There is no theoretical problem in accounting for the coexistence of a number of species in one area if there are other areas in which each species occurs alone or has some advantage over other species, and larvae from the exclusive or semiexclusive areas can reach the areas in which species are sympatric. Theoretical support for these statements can be derived from essentially any model of the competitive process. There is strong empirical support for habitat partitioning in reef fish (Dale 1980; Robertson and Lassig 1980; Anderson et al. 1981). Partitioning of food resources may also occur in some guilds (Anderson et al. 1981). The fact that there are some habitats within which there is relatively little partitioning (Sale 1979) cannot be used to argue that none occurs on a larger scale. Resource partitioning can contribute to coexistence in nonequilibrium as well as equilibrium models (May 1973). Therefore, evidence of changing densities or species compositions cannot be used to argue against the resource partitioning hypothesis (as does Sale [1979]).

Given the lack of knowledge of larval biology, it would be premature to conclude that the mechanisms represented by the first two hypotheses do not contribute to reef fish diversity. However, there is as yet no evidence that such mechanisms are required to account for that diversity.

SUMMARY

The main goal of this analysis has been to evaluate Sale's (1982) suggestion that competitive exclusion was less likely in lottery competitive systems than in those having other mechanisms of competition. An analytical lottery model based on Sale's (1982) simulation was developed and used to show that the presence of totally intraspecific competition in the larval stages was responsible for the coexistence of the species in the model. This assumption could allow coexistence for any possible mechanism of adult competition. A model incorporating the more likely assumption of equal inter- and intraspecific larval competition allows at

most two species to coexist in a constant-environment lottery model. Although some types of environmental variability promote coexistence in the lottery model (Chesson and Warner 1981), analogous types of variability promote coexistence in nonlottery models (Chesson 1983; Abrams 1984). Available evidence for territorial coral reef fish most strongly supports an explanation of coexistence based on resource partitioning over other possible explanations.

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APPENDIX A

STABILITY OF BOUNDARY EQUILIBRIA IN A THREE-SPECIES SYSTEM WITH INTERSPECIFIC LARVAL COMPETITION

For a three-species community to have a globally stable equilibrium point or limit cycle, it is necessary that each species be able to increase when the other two are present at equilibrium (i.e., the boundary equilibria must be unstable). Determining the invasibility of two-species communities requires that one determine equilibrium population densities. For the model described in section IV, A, the expression for the equilibrium density of species 1 when 1 and 2 are present together may be found using Chesson and Warner's (1981) equilibrium relationship given in Section II, A. This results in

$$N_1 = \frac{r_1 d_2 \beta - r_2 d_1 \beta + r_1 r_2 d_2 \alpha_2 K - r_2^2 d_1 \alpha_1 K}{r_1 r_2 \alpha_1 d_1 - r_2^2 \alpha_1 d_1 - r_1^2 d_2 \alpha_2 + r_1 r_2 \alpha_2 d_2} \quad \text{assuming } \beta_1 = \beta_2 = \beta_3.$$

N_2 is simply $K - N_1$. Analogous expressions may be found for the other two-species subcommunities. The condition for species 3 to increase when it is rare and the other two are at equilibrium is

$$\frac{d_3}{d_1} < \frac{r_3}{r_1} \frac{\alpha_1(r_1 N_1 + r_2 N_2) + \beta}{\alpha_3(r_1 N_1 + r_2 N_2) + \beta}.$$

Substituting for N_1 and N_2 and simplifying gives

$$d_3 < \frac{d_1 d_2 r_3 (\alpha_1 - \alpha_2)}{r_1 d_2 (\alpha_3 - \alpha_2) + r_2 d_1 (\alpha_1 - \alpha_3)}. \quad (\text{A1})$$

Similarly, the condition for species 1 to invade a 2,3 subcommunity is

$$d_1 < \frac{r_1 d_2 d_3 (\alpha_2 - \alpha_3)}{r_2 d_3 (\alpha_1 - \alpha_3) + r_3 d_2 (\alpha_2 - \alpha_1)}. \quad (\text{A2})$$

For 2 to invade a 1,3 community, it is necessary that

$$d_2 < \frac{r_2 d_1 d_3 (\alpha_1 - \alpha_3)}{r_1 d_3 (\alpha_2 - \alpha_3) + d_1 r_3 (\alpha_1 - \alpha_2)}. \quad (\text{A3})$$

Expression (A3) may be rearranged to obtain conditions on d_1 or d_3 . It will be seen that these are simply expressions (A1) and (A2) with the inequality reversed. This contradiction shows that at least one boundary equilibrium must be stable; three species cannot coexist. (It should be noted that the last step assumes that $r_1 > r_2 > r_3$ and that $\alpha_1 > \alpha_2 > \alpha_3$. The

relative magnitudes of the r_i can be chosen arbitrarily. However, the α_i must have the same ordering if the two species subcommunities are to exist [see inequalities (8) in the text].)

LITERATURE CITED

- Abrams, P. A. 1984. Variability in resource consumption rates and the coexistence of competing species. *Theor. Popul. Biol.* (in press).
- Anderson, G. R. V., A. H. Ehrlich, P. R. Ehrlich, J. D. Roughgarden, B. C. Russell, and F. H. Talbot. 1981. The community structure of coral reef fishes. *Am. Nat.* 117:476-495.
- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *Am. Nat.* 115:151-170.
- Chesson, P. L. 1983. Coexistence of competitors in a stochastic environment: the storage effect. *Proc. 1st Int. Conf. Theor. Popul. Biol.*, Edmonton, Alberta (in press).
- Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.* 117:923-943.
- Cushing, D. H. 1973. Recruitment and parent stock in fishes. Washington Sea Grant Program, University of Washington Press, Seattle.
- Dale, G. 1980. Money in the bank: a model for coral reef fish coexistence. *Environ. Biol. Fishes* 3:103-108.
- Larkin, P. A. 1978. Fisheries management—an essay for ecologists. *Annu. Rev. Ecol. Syst.* 9:57-74.
- May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, N.J.
- Maynard Smith, J. 1974. *Models in ecology*. Cambridge University Press, Cambridge.
- Robertson, D. R., and B. Lassig. 1980. Spatial distribution patterns and coexistence of a group of territorial damselfishes from the Great Barrier Reef. *Bull. Mar. Sci.* 30:187-203.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *Am. Nat.* 111:337-359.
- . 1979. Recruitment, loss, and coexistence in a guild of territorial coral reef fishes. *Oecologia* 42:159-177.
- . 1982. Stock-recruitment relationships and regional coexistence in a lottery competitive system: a simulation study. *Am. Nat.* 120:139-159.