Proceedings of the 6th International Coral Reef Symposium, Australia, 1988, Vol. 1

THE POPULATION DYNAMICS OF REEF FISHES

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ABSTRACT

Recent models of populations with dispersive larvae have important lessons for the empirical ecologist studying reef fish populations. First, the models show that when recruitment is limiting, local populations will fluctuate around an equilibrium level even in the absence of any density-dependent effects. Second, when recruitment limitation occurs, variations in recruitment will cause fluctuations in population size, although it will be very difficult to detect this pattern if the population consists of long-lived organisms. Such populations will be large relative to recruitment levels, and will have stored the effects of many past recruitment events. Third, even minor variation in the mortality rates of the settled population will severely reduce the correlation between recruitment and population size. Fourth, extreme fluctuations in numbers can result from strong density dependence in mortality and recruitment.

Thus most of the criteria used in past studies to characterize populations as recruitment-limited or density-dependent are suspect and should be employed with a great deal of caution. We advocate instead that experimental approaches be used to estimate the relative magnitudes of the effects of recruitment, density-dependence, and density-independence on population size and structure.

INTRODUCTION

General demographic models appropriate for marine organisms have developed very rapidly over the past few years, and it is now clear that the dynamics of fishes on coral reefs can be included within this larger framework. Our aim here is to review these models with specific reference to reef fishes. It is not our intention to summarize the mathematical detail of any model, but rather to point out what the models predict about the structure and dynamics of populations. Empirical studies of fish dynamics measure certain demographic characteristics in an attempt to estimate the relative roles of factors such as recruitment and density-dependent mortality in regulating populations, and we will attempt to clarify several misconceptions and misinterpretations that have arisen in these studies. Following an examination of local populations, we will outline some recent efforts to describe the dynamics of the species as a whole (metapopulation theory), and discuss possible directions for future research.

LOCAL POPULATIONS

Some definitions and clarifications are necessary at the outset. Classical population theory was designed to model *closed* systems, in which offspring and their parents contribute directly to growth of the same population. However, many reef-based populations may be *open*, where the local production of dispersive young has little to do with recruitment to that same site. In a closed system, population size may be regulated by density-dependent changes in fecundity. In contrast, local fecundity in an open system has no direct impact on local dynamics, because larvae are dispersed elsewhere.

The principal dynamics of any open system are described by local recruitment rates rather than local fecundity, and by the death rates of the settled population. These rates may be constant or vary, and they may depend on current population size (density dependence) or not (density independence). In many cases, it is likely that both density-independent and density-dependent effects are acting. Several models of open populations include both effects (Vance 1980; Roughgarden et al. 1985; Roughgarden and Iwasa 1986).

We will outline the results of several models relevant to the dynamics of coral-reef fishes, starting from the simplest case. The results are drawn mostly from the simulation models of Frogner (1980) and Hughes (1984) and the analytical models of Vance (1980), Kirkpatrick (1984) and Roughgarden et al. (1985). As usual, more complex models provide more realism, but are considerably more difficult to interpret. However, even the simplest models have important lessons for the empirical ecologist.

Many of the models considered here were developed with open systems other than reef fishes in mind (e.g., sessile marine invertebrates (Vance 1980; Hughes 1984, in review; Roughgarden et al. 1985); broadly dispersed plants (Levin et al. 1984); or stream-associated insects (Frogner 1980)). We have ignored the peculiarities associated with some of these systems in order to focus more closely on fishes, but many of the conclusions are applicable to coral reef organisms in general.

A starting point for describing the population dynamics of an open population is the simple modification of the Leslie matrix provided by Hughes (1984). Once settled, individuals go through a series of ages or sizes with some set of transition probabilities. A size-based model is more realistic for fishes, because growth rates may vary widely between individuals within a single cohort, and fecundity and mortality are more probably functions of size than age (e.g. Warner 1984a). Over each time period, individuals in each size class may enter any of a number of larger size classes (depending on their growth rate), they may remain in the same size class, or they may die. In this model, recruitment is density independent, i.e. recruits are added to the smallest size class at a rate independent of the total number of individuals already present.

In order to provide some realistic examples of population characteristics under various conditions of recruitment and mortality, we have used demographic and recruitment data from the Caribbean bluehead wrasse *Thalassoma bifasciatum* (Table 1) as the basis for some matrix simulations. As will be seen below, the model describes the dynamics of *T. bifasciatum* quite well using values derived from nature. We have also altered rates of recruitment and mortality in the model to extend our examples to other situations. The point is not to model the bluehead wrasse per se, but to gauge the effects of various demographic factors on population behavior and to examine our ability to test alternative hypotheses in the field.

Case 1: Constant recruitment and mortality, no density dependence

In an open system, population size can be stable because of recruitment limitation, even in the absence of density-dependent interactions (Hughes 1984; Mapstone and Fowler 1988). In this case, where recruitment and mortality are constant and independent of density, the population grows initially, but then the growth rate slows and the population asymptotically approaches an equilibrium level (figure 1). The equilibrium represents the point where the number of recruits arriving equals the number of settled individuals dying. Note that there need be no density-dependent effects on the mortality or fecundity of the settled individuals. The slowing of population growth occurs simply because recruitment is independent of population size and thus the *per-capita* number of recruits arriving declines with increasing population size. While mortality rates do not vary stochastically in this simplest case, they may differ between age and size classes. The age structure of the population will be stable and depends on the relative magnitudes of mortality rates among the various sizes and ages present in the settled population (Hughes 1984).

At equilibrium, the population size may be well below the carrying capacity of the environment. For example, when Hughes used realistic parameters to model the long-term population dynamics of the Caribbean coral *Agaricia agaricites*, he found that it occupied a maximum of only 31% of the available substrate. The population size at equilibrium depends on the recruitment rate and the death rate of the settled individuals. Thus if 20 recruits arrive each year to a reef, and settled individuals have a 10% chance of dying each year, the equilibrium population size is 20/.1 = 200. For the bluehead wrasse, the model predicts an equilibrium density of adults of 0.33 individuals/m^2, quite close to the actual average value of 0.35 (Warner and Hoffman 1980).

Table 1. Growth transition probabilities and size-specific survival for *Thalassoma bifasciatum*. For each size class shown along the top line, the values in the corresponding column show the probabilities of surviving individuals remaining in the same size class or growing into larger size classes in one month. Monthly survival rates are shown at the bottom of each column. Together with recruitment rates, these values were used in the matrix model. Data are from Warner (1984), Victor (1986), and Schultz and Warner (in review).

		STARTING SIZE CLASSES (MM S.L.)							
		10-15	16-20	21-30	31-40	41-50	51-60	61-65	>65
ENDING SIZE CLASSES	10-15	.5							
	16-20	.4	.5						
	21-30	.1	.4	.5					
	31-40		.1	.4	.6				
	41-50			.1	.35	.7			
	51-60				.05	.25	.7		
	61-65					.05	.25	.25	
	>65						.05	.75	1.0
SURVIVORSHIP PER MONTH		.23	.70	.85	.91	.91	.91	.91	.91

Case 2: Variable recruitment, constant mortality, no density dependence

In nature, of course, constant population numbers might well be prevented by fluctuations in recruitment or mortality. Recruitment fluctuations are well documented for many organisms with a pelagic dispersal phase (reviewed in Sale 1980, 1984; Underwood and Denley 1984; Connell 1985; Doherty and Williams in press). All models agree that when there is no density dependence in post-recruitment growth and mortality, the population size and structure will be closely correlated to recent recruitment, and this prediction forms the central focus of many empirical investigations of recruitment limitation (e.g. Victor 1983; Doherty 1983; Jones 1987). The mean population size should fluctuate around a level determined by the mean recruitment rate, just as in the simpler example above. When natural variation in recruitment (see Victor 1986) is included in our model of the bluehead wrasse, the settled population size tracks recruitment closely (figure 2A), similar to what is seen in nature (Victor 1983).

It is important to stress that while the correlation between recruitment and population size will always hold as long as mortality is constant and density-independent, it may be impossible to detect by field observations alone if mortality rates are low (Underwood and Denley 1984; Shulman 1985; Jones 1987; Mapstone and Fowler 1988). This is because populations of long-lived organisms accumulate the effects of many past recruitment events (the "storage effect", see Warner and Chesson 1985), and a single recruitment fluctuation will cause only a slight change in population size. High-mortality populations are more "stochastically sensitive" (Gaines and Roughgarden 1985), and their larger variations should be easier to detect.

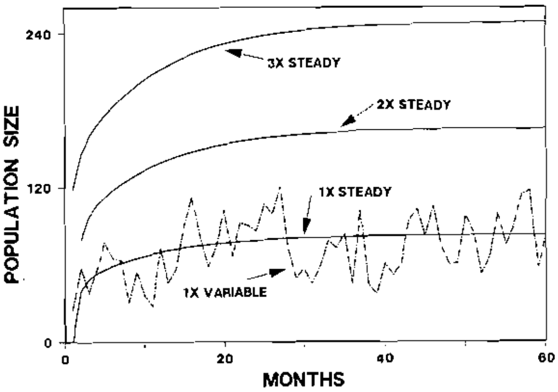
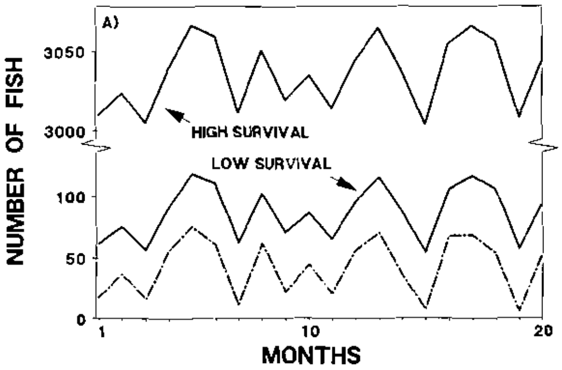


Figure 1. A graphical representation of recruitment limitation in the Caribbean bluehead wrasse *Thalassoma bifasciatum*. Using density-independent rates of individual growth and survival measured in the field (Table 1), population size is determined by the amount of recruitment. Recruits were added to the population at one, two or three times the observed mean rate (39.4/month). Note that when recruitment was allowed to vary around the mean (nsing a random number generator, SD = 24.6), the settled population fluctuated at the same equilibrium (dotted line).

We can demonstrate the effect of adult longevity on the relative variation in recruitment and population size by using a slight modification of our previous model for the bluehead wrasse. To increase longevity, the entire matrix (table 1) was multiplied by 1.1, thereby increasing monthly survivorship by 10%. With increasing overall survival, the average population size increases as more recruits grow to relatively longer-lived size-classes, and the relative variation in population size imposed by the same fluctuations in recruitment declines. With initial values taken from nature, the coefficients of variation of population size and of recruitment in the bluehead model are both large and about the same magnitude, and thus would be reasonably easy to measure and compare. If the monthly survival of the settled population is increased by only 10%



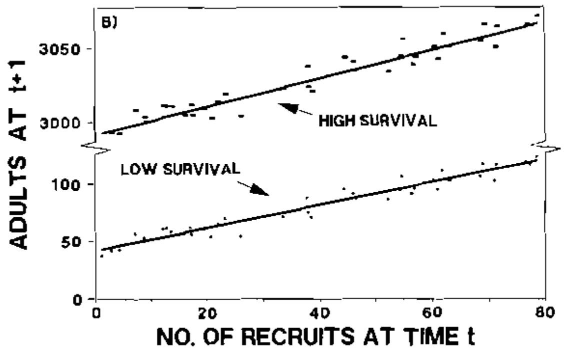


Figure 2a. The response of settled population size to random fluctuations in recruitment. As before, the average rate of recruitment was 39.4/month, and mortality and growth are constant (i.e., density-independent). Settled fish were allowed to survive either at the observed rate (lower solid line) or much higher (to simulate greater storage of recruits; upper solid line). In both cases, populations of adults closely track pulses of recruitment (dotted line). However, when storage is large, the fluctuations of adults are so small relative to total population size that they would be almost impossible to measure.

Figure 2b. Correlation between recruitment and settled populations using the same parameter values as figure 2a. Lines are fitted by linear regression (n = 40 iterations, $r^2>0.9$, $P<0.001$).

across all size classes, however, the population size increases by 3600% with the same number of recruits, and its coefficient of variation drops to 1% that of recruitment. While the correlation between population size and recruitment remains very high ($r^2 > 0.9$; figure 2B), it would be extremely difficult to detect by measuring such small changes in a real population.

Many coral reef fishes live longer than the two to three years typical of a bluehead wrasse, and therefore would show stronger effects of multigenerational storage. Thus the criterion that recruitment-limited populations should reflect fluctuations in recruitment rates (e.g. Sale et al. 1984) should be employed with caution. The modelling described above suggests that for longer-lived fishes, the correlation between recruitment and population size will be extremely difficult to detect. Thus the probability of rejecting the recruitment limitation hypothesis due to sampling problems (Type II error) becomes very high. We emphasize that such populations can be just as recruitment-limited as short-lived populations, and may exist well below the carrying capacity of the environment. Population levels may be relatively stable in number and not correlate to recent recruitment events and yet still be under recruitment limitation.

We suggest that a more rigorous approach will be necessary to quantify recruitment limitation among populations with high levels of storage (sensu Warner and Chesson 1985). Many of the problems of detection could be alleviated by investigating population age structure rather than simple population abundance. If recruitment is truly regulating a population, the abundance of younger fishes should correlate closely with recent recruitment, and the overall age structure should reflect longer-term temporal recruitment patterns.

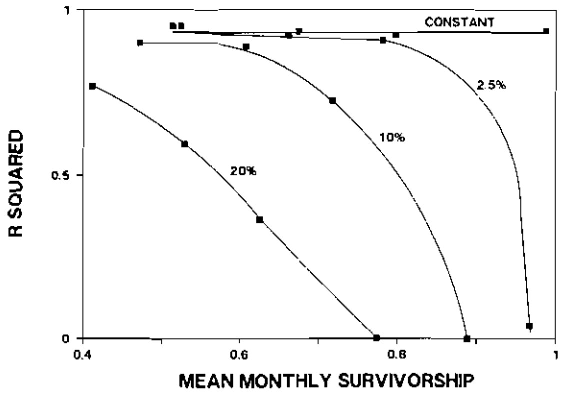


Figure 3. The effect of random mortality on the recruitment-adult correlation (e.g., fig. 2b). When mortality is constant, r^2 is always high (top line). The lower curves show that small fluctuations in mortality of settled fish destroy the relationship, especially when mean survivorship is high (i.e. when storage effects are strong). Variations around mean rates of mortality were simulated by subtracting a randomly generated percentage of the population each year that varied from zero to twice the mean values of 2.5, 10, or 20%.

Case 3 - Variable recruitment and mortality, no density dependence

It is, of course, more realistic to consider cases where the mortality of any size or age class might vary over time due to transient effects such as mobile predators or severe weather. Analytic theory for this case is still under development (see Levin 1986).

The presence of variable mortality in the settled population considerably magnifies the difficulty of detecting a correlation between recruitment and population size. As mentioned in the previous section, when population sizes are large due to low mortality, the correlation between recruitment fluctuations and population size persists but is difficult to detect. In contrast, when the settled population's mortality is variable, the correlation itself becomes less strong.

We can demonstrate this with the same model as before, by allowing mortality rates among the settled individuals to vary. At low levels of variability in mortality, the correlation between recruitment and population size remains relatively high in a population with a high mean mortality rate such as the bluehead wrasse, but the strength of the correlation declines quickly as the mean survival rate of the population is increased. Keeping mean mortality rate constant, the effect of increasing variability in mortality can be seen clearly in figure 3; with even moderate variability in mortality, the correlation between recruitment and population size is destroyed.

We stress that an obscured relationship between recruitment and population size does not indicate that recruitment limitation is absent, as has sometimes been implied (e.g., Jones 1987). It simply means that the criterion that population size and age structure should reflect recruitment fluctuations (e.g., Doherty 1983; Sale et al. 1984; Roughgarden et al. 1985; Victor 1986) may only apply to short-lived populations with relatively invariant mortality rates.

Case 4 - Density-dependent recruitment, density-dependent mortality

This case is more complex and more realistic. By adjusting the level at which rate limitations begin to act, models describing this case can accomodate the various combinations of density-independence and density-dependence in recruitment and mortality. The population can at some times be internally regulated, and at other times be recruitment limited. Density-dependent populations with nonrandom recruitment have been modeled by Frogner (1980) using simulations and by Roughgarden et al. (1985) using both simulation and analytical methods. In Roughgarden's model, which was designed for space-limited invertebrates, the recruitment rates can be affected by local population density. Frogner assumes that density most strongly affects juvenile growth, which coincidentally appears to be the case in many reef fishes (Doherty and Williams in press). Variable recruitment was not explicitly modeled in either case, but was discussed as an extension. The striking result of both models is that if the average recruitment rate is high, in many circumstances the populations can exhibit strong oscillations. These oscillations arise because strong recruitment classes eventually grow to fill the environment and restrict further recruitment for a time (Roughgarden et al. 1985; Bence and Nisbet, in review).

While the assumptions of these models may not match the actual mechanisms operating in reef fish populations, it is important to keep in mind that the predominance of single age-classes and extreme fluctuations seen in some fish populations (see Doherty and Williams in press) are not prima facie evidence for control by recruitment. Age-class dominance and population fluctuations can also occur under density-dependent limitation (Roughgarden et al. 1985). Unfortunately, these models also indicate that our interpretations of the factors affecting population size in any particular species may be dependent on the time at which the observations were made. Populations studied near the peak of an oscillation would appear density-regulated, and those near the trough would appear undersaturated and recruitment limited. Both interpretations would be correct, and only longer-term studies would reveal the true nature of the population dynamics.

The most realistic single-population models would incorporate variable recruitment, variable density-independent mortality, and density-dependence in growth and survival under crowded conditions. Such models have yet to be developed. With two or more stochastic inputs, the modeled populations would be likely to have extreme fluctuations in age structure and density. More long-term empirical observations are needed to provide reasonable values for variations in mortality and recruitment.

MULTIPLE POPULATIONS

In open systems, single population theory treats recruitment as a black box, since variability in larval availability is decoupled from the reproductive characteristics of the local population. Metapopulation models attempt to describe the dynamics of the population as a whole by making certain assumptions about the factors which affect the supply of recruits to local populations.

Because of physical barriers, predation and other factors, some areas simply receive fewer planktonic recruits than others (e.g., Roughgarden and Iwasa 1986; Gaines and Roughgarden 1987). In other cases, it is apparent that previous settlement out of the pool can cause reduced settlement at successively downcurrent sites (e.g., Gaines et al. 1985; Victor 1986). For tractability, these factors were not considered explicitly in earlier metapopulation models (e.g., Vance 1980; Chesson 1981). Instead, it was assumed that all larvae are completely mixed in the plankton.

Vance (1980) allowed both density dependence and random variability in adult mortality; all variation in recruitment was caused by changes in the numbers of adults supplying the larvae. He makes the valuable point that under certain circumstances the pooled recruitment from other areas can act to reduce population fluctuations due to mortality in a local population. Since recruitment is not closely tied to local production, the population does not suffer long-term reductions from losses of adults.

The most recent and most applicable model for coral reef fishes is that of Roughgarden and Iwasa (1986). They make the same assumption of complete mixing of available larvae, but with the important addition that local populations are allowed to be differentially accessible to the pool. Local dynamics are controlled by recruitment and density-dependent competition for space, as described earlier in Roughgarden et al. (1985). To model some populations of reef fishes, it may be appropriate to assume that local populations produce more larvae per unit of available resource than they receive (in Roughgarden and Iwasa's terminology, all populations are sources), and that larval mortality is so great that density-dependent limitations virtually never occur in the settled population. Under these circumstances, the model predicts a series of populations at equilibria similar to those described for the single populations. The population sizes and age structures are determined by reef accessibility, adult fecundities, and the mortality rates of the larval and settled populations.

This model is an important step forward, but we are still some distance away from a usable and realistic metapopulation model for marine systems. As mentioned by Roughgarden and Iwasa (1986), the next steps will be to include factors allowing the incomplete mixing of larvae, and stochasticity both in larval spatial distribution (e.g., current shifts) and in larval mortality (e.g., nutrient or predator fluctuations).

DISCUSSION

Undersaturation and recruitment limitation

In the previous sections we showed how population dynamics theory can point out some procedural difficulties in identifying when recruitment limitation may be occurring. There may be a conceptual difficulty as well. Generally, recruitment limitation is characterized as maintaining the population below a level at which resources become limiting (e.g., Sale et al. 1984; Warner 1984; Jones 1987; Mapstone and Fowler 1988). Others (e.g., Wellington and Victor in press; Doherty and Williams in press) make the implicit assumption that undersaturation means that no density-dependent *mortality* effects are present, even where there are obvious effects of density on individual fecundity or growth. Density-dependent mortality may occur as often as fecundity and growth effects, but it is more difficult to detect. Fecundity and growth are individual attributes that allow large sample sizes to be amassed relatively quickly and easily; mortality must be measured in cohorts over long periods, and thus density effects on mortality are more difficult to identify. It is important to remember that both recruitment and benthic mortality act to determine eventual population size, and one cannot be ignored in favor of the other.

Perhaps the best procedure at this point is to drop entirely the artificial dichotomy between recruitment-limited and density-dependent (or non-equilibrium and equilibrium) population regulation (e.g., Mapstone and Fowler 1988). The results of case 4 models clearly demonstrate that density-dependent adult-larval interactions can lead to large population fluctuations. Thus, it is incorrect to assume that competition among reef fishes will necessarily result in stable equilibrial populations. Similarly, an empirical demonstration of stable population size is no proof of density-dependent interactions since the same result could occur through recruitment limitation (case 1 models). In open systems, the usual equivalance of density-dependence and equilibrium (and density-independence and non-equilibrium) does not hold. Moreover, recruitment, density-independent mortality, and density-dependence may all act to control population dynamics, and we should be concerned with the relative magnitude of their effects rather than eliminating one or the other entirely from consideration (see Victor 1986, Jones 1987, and Shulman and Ogden 1987 for examples of this approach).

Future Directions

We have tried to demonstrate that the concept of recruitment limitation is only a part of a larger theory for open populations. The very strong effect of storage when organisms are long-lived makes it imperative that we actually attempt to measure the mean and variance of mortality in reef fish populations. This must be done in order to produce reasonable predictions and tests that minimize and evaluate Type-II statistical error. Sensitivity analyses of the relative effects of recruitment vs. mortality on population size (e.g., Shulman and Ogden 1987) are useful only if we know what the actual variation is in both parameters. Longer term studies are also needed to distinguish between population oscillations driven by density-dependent limitations and fluctuations due to recruitment variance.

Sources of mortality can be insidiously difficult to detect through correlational studies, and in these cases there is a great need for controlled experiments to sort out the relative roles of density independent and density dependent factors in limiting population size (Jones 1987). The direct effects of predation and abiotic factors have not received enough attention in studies of reef fishes (exceptions include Shulman et al. 1983; Shulman 1984; Hixon and Beets in press). These effects could be as or more important than recruitment in population dynamics (Doherty and Williams in press).

In terms of the species population as a whole, the larger scale models cannot be properly evaluated without sufficient knowledge of the spatial and temporal variability in recruitment. There has been great progress in this area recently (reviewed in Doherty and Williams in press), but many more studies are needed. At this point, we are at the stage of simply describing these patterns. Hopefully, future collaborations with physical and biological oceanographers will illuminate their causes.

ACKNOWLEDGMENTS

We are grateful to J. Bence, D. Breitberg, M. Carr, M. Hixon, S. Holbrook, S. Pennings, P. Sale, M. Shulman and E. Schultz for having read the manuscript. Eric Schultz kindly provided the growth transition data. Financial aid was provided by National Science Foundation grants BSR 84-06745 and BSR 87-08829 to RRW and OCE 86-08829 to TPH and J.H. Connell.

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