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## THE IMPORTANCE OF RECRUITMENT TO THE DYNAMICS OF A CORAL REEF FISH POPULATION<sup>1</sup>

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**Abstract.** An experiment on a coral reef fish is described that assesses the effects of recruitment success on adult abundance over a 3-yr period. The damselfish *Pomacentrus amboinensis* was examined on natural patch reefs of  $\approx 8 \text{ m}^2$  in the lagoon of One Tree Reef. Recruitment levels were adjusted to 0, 0.5, 1, and 2 recruits  $\cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  by transplanting juveniles among reefs at the end of four successive recruitment seasons (with four replicates per treatment). Natural recruitment success was monitored on 16 undisturbed reefs, and adult numbers were monitored at irregular intervals on both experimental and undisturbed reefs. The adult population density at the end of the experiment increased significantly with recruitment within the 0–1 recruit/ $\text{m}^2$  range. However, doubling recruitment from 1 to 2 recruits/ $\text{m}^2$  did not lead to any further increase in adult density. The recruitment treatments did not affect adult density until a 2-yr period had elapsed (corresponding to average maturation time). At this time, treatments receiving 1 and 2 recruits/ $\text{m}^2$  showed a dramatic increase in adult numbers, whereas in the low-recruitment treatments, adult densities declined. The experiment indicated that a recruitment success of between 0.5 and 1 recruit/ $\text{m}^2$  was necessary to maintain adult numbers at pre-experimental levels. Natural recruitment success was highly variable among years, but adult densities remained relatively constant over time at  $\approx 0.8$  adult/ $\text{m}^2$ . Differences in the final adult densities among reefs were correlated with average recruitment levels, but above 0.8–1.0 recruit/ $\text{m}^2$ , adult densities did not increase with increasing recruitment success. The results from experimental and undisturbed reefs suggest that natural variation in recruitment success affects the importance of post-recruitment processes. In good recruitment years, adult densities on a substantial number of reefs may be limited by density-dependent processes, which may affect the majority of individuals in a region. Density-dependent juvenile growth may buffer adult populations on these reefs against the effects of poor recruitment years, since input may come from a number of immature age classes. Where recruitment success is always below a certain level, the dynamics of adult populations will reflect variation in recruitment success.

**Key words:** coral reefs; density dependence; growth; maturation; mortality; Pomacentridae; population limitation; recruitment; reef fish.

### INTRODUCTION

Recent studies in many areas of marine ecology indicate a renewed interest in larval supply and recruitment (Underwood and Denley 1984, Connell 1985, Keough 1988, Roughgarden et al. 1988, Underwood and Fairweather 1989). It is the current view that variation in the structure of coral reef fish assemblages and the sizes of their component populations is primarily a consequence of patterns in recruitment (Doherty 1983a, b, Victor 1983, 1986, Sale 1984, Doherty and Williams 1988). The implicit assumption is that recruitment is independent of adult numbers and determined by processes occurring during the pelagic larval phase. Input is highly variable and too low to lead to the saturation of resources available in the reef habitat. This recruitment-limitation model challenged and modified previous beliefs that assemblages were structured under regimes of intense competition during the

post-recruitment or reef-associated phase of the life cycle (Smith and Tyler 1972, Sale 1977). However, without information on the degree to which recruitment patterns are modified by subsequent demographic events, it is impossible to evaluate the relative importance of recruitment and post-recruitment processes (Connell 1985, Jones 1987a, b, Keough 1988, Mapstone and Fowler 1988, Warner and Hughes 1988).

One generally accepted feature of coral reef fishes is the large fluctuations in recruitment they exhibit (Williams and Sale 1981, Williams 1983, Sale et al. 1984, Shulman 1985a, Doherty and Williams 1988). The dynamic nature of species composition and abundance is also widely acknowledged (Talbot et al. 1978, Sale 1980, Sale and Douglas 1984, Doherty and Williams 1988) and is plausibly explained by the recruitment phenomenon. However, few workers have attempted to test whether or not the recruitment-limitation model applies to the dynamics of coral reef fish populations (but see Jones 1987a, Shulman and Ogden 1987, Robertson 1988a, b, Hunte and Cote 1989). Correlations

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between recruitment levels and population density over a period of years may (Victor 1983, Doherty and Williams 1988) or may not (Robertson 1988a, b) exist. Simulations by Warner and Hughes (1988) suggest the examination of such relationships will not resolve the issue. This is because population density may not follow recruitment levels in recruitment-limited populations, and under some circumstances, density-dependent mortality may cause extreme fluctuations in numbers (Warner and Hughes 1988).

The experimental approach has been advocated to assess the relative magnitudes of the effects of recruitment, density dependence and density independence on adult population size (Jones 1987a, Warner and Hughes 1988). Several short-term experiments have been carried out that have failed to detect density-dependent mortality (Doherty 1982, 1983a, Jones 1987a, b, 1988). However, other mechanisms such as density-dependent growth (Jones 1987a) and density-independent mortality (Shulman and Ogden 1987) may completely alter patterns established at the time of recruitment. Coral reef fishes tend to live for many years, whereas the experiments referred to have not extended for much more than 1 yr. The real effects of recruitment on the fundamental ecological parameters of structure and dynamics will only be revealed by experiments conducted on a time scale appropriate to the longevity of the species concerned. While changes in population numbers may reflect recruitment variation in short-lived species (e.g., *Thalassoma bifasciatum*, Victor 1983), it is not at all certain whether this conclusion would apply to the majority of longer lived fish species (Jones 1987a, Warner and Hughes 1988).

The contribution of variation in recruitment to the dynamics of populations can be assessed by a combination of (1) long-term experiments in which recruitment levels are manipulated, and (2) parallel observations on undisturbed populations. This paper describes such an approach using natural populations of the coral reef fish *Pomacentrus amboinensis*. This damselfish has been the subject of a number of previous studies in which attempts were made to assess the relative importance of recruitment and post-recruitment demography (survival and growth), and the processes affecting these parameters (Jones 1986, 1987a, b, 1988). By focusing on factors affecting the abundance of reproductively mature adults (rather than by treating populations as a homogeneous unit), it was found that intraspecific interactions were both statistically significant and potentially very important (Jones 1987a). One-year experiments indicated that density-dependent growth was not only capable of damping the effects of fluctuations in recruitment, but above a certain minimum recruitment level, it limited input to the adult population (see also Jones 1984). However, individuals of this species take 2 yr to reach maturity and many live to 5–6 yr of age. This paper extends previous work by describing the results of an experiment in which

recruitment to natural patch reefs was manipulated in each of four successive recruitment seasons, and changes in the size of the adult population monitored. The magnitude of the experimental effects was examined in the context of recruitment levels and changes in adult numbers on unmanipulated reefs.

#### METHODS

This experiment was located at One Tree Reef (23°30' S, 152°06' E), along the southern channel of the main lagoon. Thirty-two patch reefs within a 2-ha area were selected and marked for future identification, the two nearest being 15 m apart. All reefs were as similar to each other as could be found, in terms of size, topography, and composition. Their size, in terms of horizontal dimensions, was  $7.8 \pm 0.6 \text{ m}^2$  ( $\bar{X} \pm \text{SE}$ ). They were all low-topography reefs, extending not more than 1 m from the sand in depths of 4–5 m of water. They were composed largely of *Porites*, but only 5–10% of the surface area was alive. The latter two characteristics appear to be a good indicator of substantial populations of *P. amboinensis* on reefs of this size.

During May 1984, all reefs were carefully searched to count recent recruits (settled between December 1984 and April 1985), subadults (juveniles of older cohorts, but <50 mm estimated standard length) and adults (>50 mm) (Jones 1987a). Since the reefs were all slightly different in size, densities throughout will be expressed as numbers per square metre. The densities ( $\bar{X} \pm \text{SE}$ ) were as follows: (1) recent recruits:  $0.20 \pm 0.06$  recruit/m<sup>2</sup> or  $\approx 2$  recruits per reef. (2)  $0.68 \pm 0.14$  subadult/m<sup>2</sup> or 5 subadults per reef. (3)  $0.81 \pm 0.10$  adult/m<sup>2</sup> or 6 adults per reef.

One hypothesis derived from the recruitment-limitation model is as follows. If recruitment is held constant over a number of years (long enough for these recruits potentially to enter and replace the existing adult population), adult population size should be directly proportional to recruit densities. Any tendency for adult numbers to be independent of recruitment levels would lead to the rejection of this model. To test this, 16 of the reefs were chosen at random to be subject to four different regimes of recruitment success. That is, they were adjusted to the same level each year, at the end of each recruitment season. These treatments were 0, 0.5, 1, and 2 recruits·m<sup>-2</sup>·yr<sup>-1</sup> (i.e., approximately 0, 4, 8, and 16 recruits per reef). This encompassed and extended the natural range observed in 1984. The remaining 16 reefs were left unmanipulated, to observe natural variation in recruitment success and adult numbers.

Recruitment success was defined as the density of recent recruits present at the end of the recruitment season. Hence, it was very much a minimum and potentially inaccurate estimate of actual numbers settling on a reef over the recruitment period. At the end of the recruitment period (either late February or early May) in 1984, 1985, 1986, and 1987, successful re-

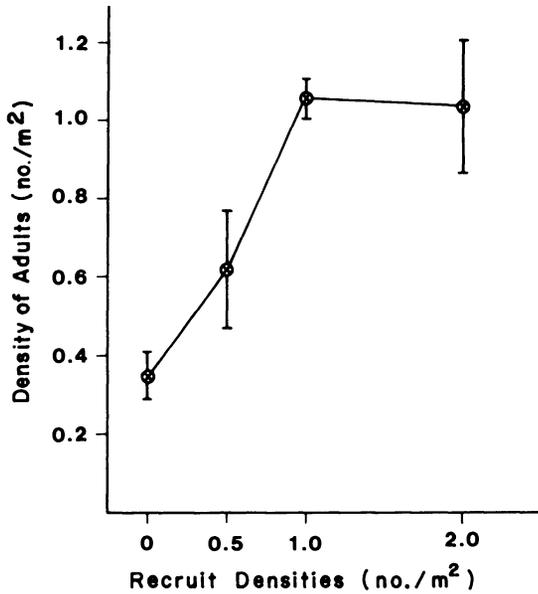


FIG. 1. Final adult densities (means  $\pm$  SE) of *Pomacentrus amboinensis* on reefs subject to three years of four different recruitment regimes.

cruits on all the experimental reefs were collected using quinaldine. Juveniles from the resulting pool were haphazardly distributed among the reefs at the predetermined treatment levels. Unmanipulated reefs were simply surveyed for recruitment success.

Adult and subadult *P. amboinensis* present at the beginning of the experiment, and all other fish species, were left undisturbed. These categories were counted on all reefs (experimental and control), both at the end of these recruitment seasons and at irregular times during the year.

In general, it was not difficult to get transplanted

recruits to remain on their host reefs. Spontaneous emigrations were observed, particularly from some reefs. However, with repeated transplants over a 1-wk period it was possible to get the required number of recruits to stay in place. Each treatment was monitored daily until the appropriate densities were maintained over a 3-d period, after which it was considered that they had become resident. Subsequent losses may have been due either to mortality or emigration. The reefs were sufficiently isolated to ensure that immigration of recruits or adults was not a major problem.

RESULTS

The four different recruitment regimes applied at the end of four annual recruitment periods had a significant effect on the final adult densities observed ( $F_{3,12} = 6.3$ ,  $P < .01$ ; Fig. 1). Adult densities increased in proportion to recruitment success between 0 and 1 juvenile/m<sup>2</sup>. However, doubling recruitment success from 1 to 2 juveniles/m<sup>2</sup> did not lead to any further increases in adult numbers. The four density treatments were too few to describe the shape of what appears to be a non-linear relationship between adult numbers and recruitment.

The magnitude and direction of change in the density of adults observed over the 3-yr period was also informative (Fig. 2). It took almost 2 yr before a difference among the different recruitment treatments arose. At this time a similar increase in adult numbers occurred on reefs receiving both 1.0 and 2.0 recruits/m<sup>2</sup>. At the end, it was only the 1.0 recruit/m<sup>2</sup> treatment that had undergone an increase in adult numbers, relative to former levels. At lower recruitment levels, adult numbers underwent a gradual decline over the 3-yr period. Adult numbers did not decline to zero, even on reefs receiving no recruitment. A recruitment suc-

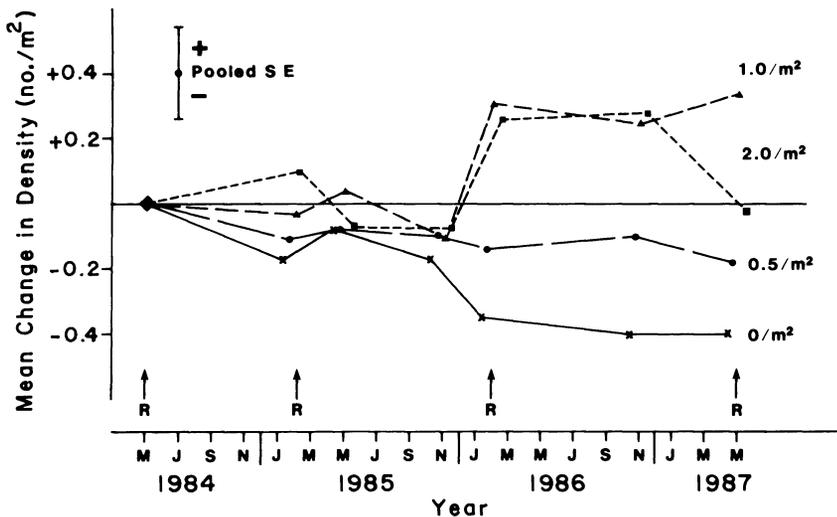


FIG. 2. Mean change in adult density (deviation  $\pm$  from initial density) vs. time for *Pomacentrus amboinensis* on reefs subject to three years of four different recruitment regimes (0, 0.5, 1, and 2 recruits  $\cdot$  m<sup>-2</sup>  $\cdot$  yr<sup>-1</sup>). The times of recruit adjustments are indicated by "R," and the pooled standard error for adult densities is indicated top left.

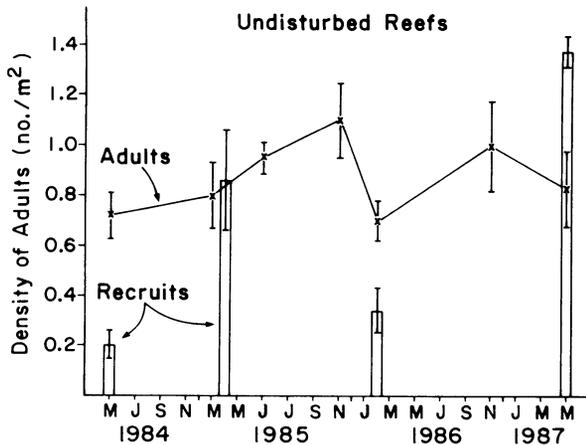


FIG. 3. Density vs. time for adults of *P. amboinensis* on natural, undisturbed patch reefs over a 3-yr period (line graph). Recruitment success each year is also indicated (histogram). Both kinds of data are shown as means  $\pm$  SE.

cess of somewhere between 0.5 and 1 juvenile/m<sup>2</sup> appeared to be necessary to maintain adult density at the level observed at the start of the experiment.

Recruitment success and changes in adult numbers on the 16 unmanipulated reefs provided a framework for interpreting the experimental results. Recruitment success differed substantially among years, ranging from an average of 0.20 recruit/m<sup>2</sup> in 1984 to 1.38 recruit/m<sup>2</sup> in 1987 (Fig. 3). Adult numbers began and finished at  $\approx$ 0.8 adult/m<sup>2</sup>, with a marginally significant difference among all sampling times ( $F_{6,21} = 3.5$ ,  $P < .05$ ; Fig. 3). The overall average recruitment, 0.70 recruit/m<sup>2</sup>, agrees with the level exhibited in the experiment that was necessary to maintain adult numbers.

There were very large differences in recruitment success among reefs each year. It was also apparent that certain reefs consistently ranked higher than others in all four summer seasons. That is, there was a tendency for positive correlations among years, in terms of the magnitude of recruitment to each reef (Table 1). Correlations between recruitment in 1984 and each subsequent year were not significant, perhaps because 1984 was such a poor recruitment year.

If adult numbers were recruit-limited, a strong correlation would be expected between final adult density and the average recruitment over all years (Fig. 4). While there was a positive correlation ( $r = 0.39$ ), there is also a strong suggestion from the graph that above a recruitment success of 0.8–1.0 recruit/m<sup>2</sup>, adult density does not increase in a linear fashion with increasing recruitment. A nonlinear regression of the form  $y = a + be^{-cx}$  (asymptotic regression) was fitted to the data with an 18% improvement in fit when compared to the linear regression (Fig. 4). The predicted asymptote for adult density is  $1.03 \pm 0.20$  adults/m<sup>2</sup>. This tends to confirm the experimental result, that above a certain level, adult numbers reach a maximum and are not explained by the magnitude of recruitment success.

TABLE 1. Correlation coefficients for relationship between recruitment of *P. amboinensis* to 16 undisturbed patch reefs in four different years. Significant correlations ( $P < .05$ ) are underlined.

	1984	1985	1986	1987
1984	...			
1985	+0.33	...		
1986	+0.18	<u>+0.46</u>	...	
1987	+0.16	<u>+0.74</u>	<u>+0.61</u>	...

The results from both the experimental and undisturbed reefs suggest that adult numbers were largely recruit-limited over the 0–1 recruit/m<sup>2</sup> range. Above this, there was strong evidence that other limiting factors were more important (see Figs. 1 and 4). It would probably require up to 10 density treatments to determine the shape of any quantitative relationship between average recruitment levels (independent variable) and consequent adult numbers (dependent variable), although this would clearly tend toward an asymptote. Arbitrarily, one could consider the proportion of reefs naturally exceeding 1 recruit/m<sup>2</sup> to make an approximate assessment of the relative importance of recruitment and post-recruitment (density-dependent) processes (i.e., below 1 recruit/m<sup>2</sup>, recruitment is important; above 1 recruit/m<sup>2</sup>, post-recruitment density dependence is important). Clearly this changes in response to fluctuations in recruitment among years. Table 2 shows that in 1984 and 1986, only 0 and 6.3% of the reefs, respectively, exceeded this arbitrary recruitment level. In 1985 and 1987, 25% and 50% of the reefs exceeded 1 recruit/m<sup>2</sup>; however, there was always a large number of reefs in which adult numbers would be likely to respond to recruitment levels. Thus, recruitment levels should always be a major consideration, but other factors should become increasingly important in high recruitment years.

The above calculations were based on the number of reefs recording certain levels of recruitment. However, from the point of view of the population biology

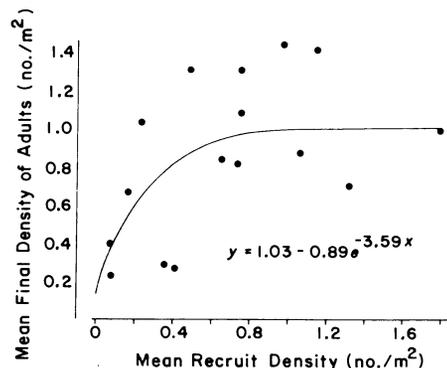


FIG. 4. Relationship between final adult densities and average recruitment success over 4 yr for 16 natural, unmanipulated patch reefs. Asymptotic regression fitted using SAS, following method outlined in Snedecor and Cochran (1967).

TABLE 2. Proportion of all patch reefs and proportion of all recruited *Pomacentrus amboinensis* experiencing local juvenile densities of  $\geq 1.0$  juvenile/m<sup>2</sup>, at the end of four separate recruitment seasons.

	1984	1985	1986	1987
% reefs	0	25	6.3	50
% individuals	0	51	22	74.6

of *P. amboinensis*, it is the number of individuals experiencing the different recruit densities which is important. How do fluctuations in recruitment affect the proportion of juveniles in a region experiencing local density conditions greater than 1 individual/m<sup>2</sup>? The recruitment-limitation model has considerably less generality when these more appropriate calculations are considered (Table 2). In the four years examined, anything from none to three-quarters of the population were experiencing recruitment densities in the range where other processes intervened to restrict adult numbers.

#### DISCUSSION

Recruitment is a relatively brief demographic event marking the beginning of a long period during which a cohort of a coral reef fish will be associated with the reef habitat. While variation in recruitment, within and among years, clearly has a major influence on the structure of populations (Doherty 1983a, b, Victor 1983, Doherty and Williams 1988), attention has recently been drawn to the variety of ways in which patterns established at the time of recruitment can be modified (Jones 1987a). Variation in mortality, both density dependent and independent (Jones 1987b, 1988, Shulman and Ogden 1987, Hunte and Cote 1989), density-dependent growth (Jones 1987a), and movement (Robertson 1988a, b) may all contribute to explaining quantitative changes in the abundance and structure of adult populations. In this paper I developed a method, with observational and experimental components, for assessing the extent to which recruitment is modified by these post-recruitment events for a sedentary reef fish species.

The development of this method is best placed in an historical context. Previous experiments conducted on small, isolated populations of *Pomacentrus amboinensis* at One Tree Reef established that input into the adult population from a single cohort was limited by density-dependent growth (Jones 1987a). This was largely due to the suppressed growth of large juveniles in the presence of adults and interactions among juveniles. On the basis of this experiment, it was argued that the recruitment-limitation model would not explain variation (or indeed constancy) in adult numbers above a certain minimum recruitment. However, the experiment was unrealistic in a number of ways and the interactions detected could only be considered potentially important.

Three elements of realism were introduced to the experimental design employed here to examine the importance of recruitment. First, manipulations of recruitment were shifted to natural patch reefs, as opposed to those constructed from relocated coral material, as in previous experiments focusing on this species (Jones 1986, 1987a, b, 1988). Hence, the importance of interactions could be assessed under normal conditions of resource availability and predator pressure.

In a real population, input to the adult population in any one year may come from a number of different cohorts, and any one cohort may contribute over a number of years. The previous experiment was limited to a manipulation of one cohort at a time, for one year only (Jones 1987a). Hence, it could not measure all potential sources of adult recruitment. The second modification was to carry out experimental manipulations of the recruitment of successive cohorts over a much longer period (3 yr).

The previous experiment was limited to manipulations of density on very small patch reefs, where resident populations were essentially small social groups containing a pair of breeding adults (Jones 1987a). Social control of growth, maturation, and other life history events is a common feature of such groups (e.g., Robertson 1972, Fricke and Fricke 1977, Moyer and Nakazono 1978, Ochi 1986). No doubt fish populations respond to their environment at a variety of spatial scales, and processes important at one of these may not be so at another (Sale et al. 1985, Jones 1987b, Doherty and Williams 1988, Mapstone and Fowler 1988, Williams, *in press*). Although *P. amboinensis* is regularly found on very small patch reefs, it is also common around the perimeter of larger bodies of reef. Proponents of both the recruitment-limitation model and competition-based alternatives have resorted to arguments to the effect that data conflicting with their views were collected at inappropriate spatial scales (e.g., Ogden and Ebersole 1981, Munro and Williams 1985). In view of this practice, and the need to consider other spatial scales, larger reefs (8 m<sup>2</sup>) were used in the present study to examine whether density-dependent processes could potentially operate within larger populations, where the movements of juveniles were not confined to the home ranges of particular adults.

This more realistic test of the recruitment-limitation model supports the previous finding that patterns of change in adult numbers in this species are not directly proportional to recruitment (Jones 1987a). Above a certain recruitment level, there is strong evidence that adult numbers are independent of changes in input of juvenile fishes to patch reefs. The sorts of competitive interactions observed in small social groups on artificial reefs, with a simplistic age structure, appear to be relevant to natural populations on larger patch reefs.

Support for this conclusion came from both experimental manipulations of recruitment, and observa-

tions on patterns of change on unmanipulated reefs. On experimental reefs, adult numbers increased as a function of recruitment between 0 and 1 recruit/m<sup>2</sup>, but a doubling of recruitment from 1 to 2 recruits/m<sup>2</sup> produced no further increase. Unfortunately, with only four recruitment treatments, it was not possible to determine the exact nature of the relationship between recruitment and adult numbers. Observations on the undisturbed reefs supported the interpretation that above an average of  $\approx 1$  recruit/m<sup>2</sup>, adult numbers appeared to reach some asymptotic level. This suggests that there may be an upper limit to the number of reproductively mature adults that reefs of  $\approx 8$  m<sup>2</sup> can support. On the undisturbed reefs, recruitment success was highly variable among years, but adult numbers remained relatively stable.

The importance of the competitive interactions described in Jones (1987a) could not be assessed, because there was no long-term information on natural variation in recruitment to determine how often recruitment attained a level where competitive interactions would come into play. Such experiments, when carried out without reference to natural demographic information, are always of limited value. The strength of this study was in being able to make some assessment of the relative importance of recruitment and post-recruitment interactions, on the basis of 4 yr of data on natural recruitment levels. In the best recruitment year, 50% of the reefs and 75% of the regional population experienced a recruitment success large enough for post-recruitment density-dependent processes to be the major determinant of adult population size. In the poorest recruitment year, no reefs reached this level. During these periods, variation in recruitment might be expected to be the major determinant of changes in adult numbers.

Historically, discussion in the coral reef fish literature has centered around what are essentially single-factor explanations of pattern, either in community structure or population dynamics. The suggestion from this study is that all these models, including recruitment limitation (Doherty 1983a, b, Victor 1983), the lottery hypothesis (Sale 1977), traditional competition arguments (Smith and Tyler 1972), and the predation-disturbance models (Talbot et al. 1978, Shulman 1985b) are too simplistic to explain the processes limiting or inducing change in adult numbers in *P. amboinensis*. Fluctuations in recruitment clearly affect the intensity of post-recruitment density-dependent processes. Competitive interactions may have a major effect on strong year classes, but no effect at all on weak year classes. The results presented here favor the comprehensive model suggested by Jones (1987a). That is, both density-independent fluctuations in recruitment and density-dependent effects on settled juveniles contribute to explaining patterns in adult numbers. At any one instant in time, one may be more important than the other, but on a time scale appropriate to the lon-

gevity of the species, no single factor will explain the majority of the variance observed. I also suspect that on this time scale, effects due to temporal variation in the intensity of predation and disturbance will also need to be incorporated into this comprehensive model. When all these factors are considered, it is unlikely that the arbitrary distinction between equilibrium and nonequilibrium models (sensu Doherty 1983a) will remain a useful dichotomy.

In realizing that population limitation is a complex problem that must start with recruitment, Victor (1986) introduced the idea of primary and secondary recruitment limitation. He distinguished situations in which there were simply too few recruits ever to saturate the habitat (primary recruitment limitation) from those in which recruitment was sufficient, but mortality so great as to keep the population below carrying capacity. Resource limitation (the third option) would only occur when recruitment was so high that even with intervening mortality, enough juveniles would survive to maturity to saturate the habitat.

Victor's (1986) categories may place undue emphasis on mortality, and not other processes controlling the rate of maturation. If one considers growth effects, for example, it is equally possible to distinguish between two categories of resource limitation. Primary resource limitation would be the situation in which recruitment is always high enough to provide sufficient input to saturate the habitat. Secondary resource limitation could occur in situations where recruitment only occasionally reaches levels necessary to provide an input to saturate the habitat. In good years, juveniles may essentially be "stored" in the population, and may enter the adult population only as vacancies occur. Such populations would essentially be buffered from the effects of poor recruitment years by social inhibition of maturation during good years. Warner and Chesson (1985) have examined similar mechanisms by which a perennial adult phase may buffer populations against poor recruitment years.

Perhaps a better course of action than classifying species on the basis of the above criteria would be to consider the demographic parameters (e.g., recruitment, growth, mortality) and limiting processes (e.g., competition, predation, disturbance) that are important in each case. This can only be achieved by concurrent studies on natural population dynamics and experimental manipulations over relevant time periods.

Density-dependent growth and maturation time were clearly implicated as the major demographic processes by which adult numbers in *P. amboinensis* were limited on small artificial patch reefs (Jones 1987a). In most of the other cases where density dependence has been examined, effects on growth or size distributions have been detected (Doherty 1982, 1983a, Jones 1984, 1987b, 1988, Victor 1986). The demographic mechanism was not considered in this experiment, although

it is almost certain that density-dependent growth plays a role, as might density-dependent emigration. The average growth of juveniles was certainly reduced, perhaps even completely halted at high densities, by the presence of adults (G. P. Jones, *personal observation*).

Direct effects of behavioral interactions on mortality, indirect effects on mortality due to the increased susceptibility of stunted individuals to predators, and density-dependent emigration may also explain the limits on adult density in *P. amboinensis*. In future experimental designs, emphasis must go into marking individuals from each cohort, to determine the relative contributions of each cohort to the adult population each year (input) and to assess changes in mortality and emigration rates, within and between cohorts (output). Despite the advances made in this experiment by extending the observation period to 3 yr, it is clear that even this is not long enough. Experimental effects due to manipulating recruitment took 2 yr to appear, which corresponds with the average maturation time observed in a previous study (Jones 1987a). To allow an opportunity for 3–4 cohorts all to reach adult age, the experiment should run at least 5–6 yr. Even this is probably well within the potential life expectancy of juveniles of this species.

In conclusion, while recruitment will be a major parameter in a general model that accounts for the limitation of adult numbers in reef fishes, it cannot always be the sole or even the major factor. It is but one of a host of potentially significant demographic phenomena, whose importance varies in response to recruitment levels, and no doubt in response to many other factors (e.g., food and shelter resources, predation pressure, physical and biological disturbances). In view of this complexity, models based on single factors, such as recruitment or competition, are likely to become a thing of the past.

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