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Ecology, Volume 68, Issue 5 (Oct., 1987), 1534-1547.

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COMPETITIVE INTERACTIONS AMONG ADULTS AND JUVENILES IN A CORAL REEF FISH¹

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Abstract. Considerable discussion has arisen over whether population limitation in coral reef fishes is achieved through postrecruitment processes or through factors operating prior to recruitment that lead to insufficient numbers to saturate resources. This paper presents the results of two field experiments designed to document and measure the relative effects of recruitment and subsequent intraspecific competition on populations of the planktivorous damselfish *Pomacentrus amboinensis*, a common species on the Great Barrier Reef.

I tested for effects of conspecifics on juvenile mortality, growth, and maturation by manipulating population densities on coral rubble patch reefs. Each experiment examined the potential for competition among juveniles, and between juveniles and adults. The first experiment manipulated the densities of recently settled recruits; the second manipulated 1-yr-old juveniles using a similar experimental design.

There were no consistent effects of juvenile density or of adult presence/absence on juvenile survivorship, during either the 0+ yr or the 1+ yr. However, there were substantial effects on growth and maturation. During the 1st 8 mo of experiment 1, growth was inversely related to initial juvenile density, but was not affected by the presence of adults. A marked negative effect of adults on juvenile growth developed as juveniles approached an age of 1 yr. This effect developed early in experiment 2. Both the mean and the variance in 1+ yr growth were reduced in the presence of adults. Adults primarily affected the growth of the initially largest, behaviorally dominant juveniles. A significantly greater number of 0+ yr and 1+ yr juveniles reached a mature size after 1 yr in treatments without adults present. The numbers maturing were not related to initial density, either with adults present or absent.

It is concluded that postrecruitment competitive processes play an important role in restricting adult population size in *P. amboinensis*, at least over the range of densities and on the spatial scale examined. The mechanism, however, is not one of those traditionally considered in equilibrium models. That is, competition does not appear to modify recruitment or mortality patterns directly, but influences numbers maturing through density-dependent effects on maturation time.

Key words: coral reefs; density dependence; growth; intraspecific competition; maturation; mortality; Pomacentridae; population limitation; recruitment.

INTRODUCTION

The central questions in population ecology concern the factors causing spatial and temporal patterns in adult numbers, and those factors limiting adult population size (Solomon 1970). In marine organisms with a planktonic phase during early life, processes limiting numbers may operate prior to, during, or after recruitment into the adult habitat. Recent discussion among marine ecologists has centered on the relative importance of variability in recruitment and postrecruitment processes, such as competition and predation, in determining the major patterns in space and time (Keough 1984, Underwood and Denley 1984, Connell 1985, Watanabe 1985). These problems have been a con-

tinuing source of debate among reef fish ecologists (Sale 1978, 1980, 1984, Smith 1978, Doherty 1982, 1983a, b, Jones 1984b). Doherty (1983a) listed several testable predictions from three distinct models that differ in terms of the proposed intensity and effects of competitive processes.

1) The "single-species equilibrium" model essentially argues that densities are limited by competition for critical resources, which can occur within species or between species with overlapping resource requirements (Smith and Tyler 1972, 1973, Smith 1978, Gladfelter and Gladfelter 1978, Gladfelter et al. 1980, Anderson et al. 1981, Ogden and Ebersole 1981). It is derived from the conventional view that partitioning of resources is an evolutionary response to competitive processes. It assumes that there is a surplus of larvae available, but the majority fail to settle or to survive to maturity because of competition for space, either among juveniles or between juveniles and adults. If

¹ Manuscript received 14 May 1986; revised 12 November 1986; accepted 17 November 1986.

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correct, recruitment and/or postrecruitment survival of each species should be inversely related to the densities of conspecifics and of superior competitors of other species (Doherty 1983a).

2) The "multispecies equilibrium" model is essentially a restatement of the much discussed "lottery hypothesis" (Sale 1974, 1977, 1978). Sale proposed that the diversity of species in coral reef fish communities would be maintained despite competitive interactions over living space, provided that new space was partitioned strictly by priority of settlement. The species recruiting to vacant space may then simply be determined by chance. One would predict from this hypothesis that the total density of several competitively equal species would be limited by the availability of suitable living space. Hence, the density of any one species could vary, depending on the total amount of space available and that proportion occupied by the competitors.

The assumption of space limitation forms the basis of both the single and multispecies models. It was generally believed that aggressive interactions, within and among species, would keep a population below the carrying capacity determined by the supply of other resources such as food and shelter. The arguments being used to support this assumption have been criticized (Sale 1980, Williams 1980), and at least one study purporting to test a space-limitation hypothesis has rejected it (Robertson et al. 1981). Recent studies have detected both competition for food (Thresher 1983a, b, Robertson 1984, Jones 1986) and shelter (Shulman 1984, 1985a), but the effects of these processes on adult population size are unknown.

3) The "nonequilibrium" model encompasses a group of external disturbances that are said to keep populations below a level at which resources become limiting. The common prediction is that the recruitment and postrecruitment survival of each species will be independent of all other species (Doherty 1983a). The favored mechanism is inadequate recruitment, which has been referred to as the "recruitment-limitation" hypothesis (Williams 1979, 1980, Doherty 1982, 1983a, b, Victor 1983, 1986). The hypothesis derives from empirical observations showing that spatial and temporal patterns in adult density are correlated with recruitment levels, and experimental studies that have failed to find evidence that competitive interactions influence recruitment or early postrecruitment survivorship patterns. Other workers have stressed the importance of predation as a process that keeps populations below their carrying capacities (Talbot et al. 1978, Shulman 1985b) and physical factors have also been considered (Bohnsack and Talbot 1980, Walsh 1983).

As Doherty (1983a) pointed out, the three major hypotheses can be falsified by simple direct tests for density dependence. His series of experiments on *Pomacentrus wardi* are excellent examples of the sorts of

methods that can be used to make these tests (Doherty 1982, 1983a). However, a potential problem is that the dichotomy between density dependence and density independence may not exist, since they are not mutually exclusive alternatives over the lifetime of individuals in a population. A situation in which both density-independent fluctuations in recruitment levels and subsequent density-dependent effects both contribute to explaining adult density patterns is easily visualized. Different factors can operate at different places, or at different times, or even at the same place and time. The relative importance of different factors and the degree to which they interact can only be revealed by a multifactorial experimental approach to population studies.

The factors that determine adult population size may differ, depending on the spatial scale at which the population is defined. It is clear that to examine the importance of competition, populations must be studied on a relatively small spatial scale, a scale at which biological interactions can potentially occur. It is also apparent that on such a scale, coral reef fish populations are not likely to be self-recruiting units. That is, recruitment into the local population (=numbers settling out of the plankton in a given area) is likely to be quantitatively and qualitatively different from the numbers of offspring produced by the population. Competitive interactions that reduce fecundity are less likely to limit these small populations than populations of animals that do not have dispersive larval stages. However, as far as the local population is concerned, competition may play a role in modifying recruitment patterns, or postrecruitment demographic processes that may limit adult numbers. Population and community studies should be focussed on detecting and assessing the magnitude of these effects.

The primary purpose of this study was to assess experimentally the relative importance of recruitment and postrecruitment demographic processes in explaining adult density patterns in the coral reef fish *Pomacentrus amboinensis* (Pomacentridae). I attempted to distinguish between the "recruitment-limitation" hypothesis and the equilibrium models, which stress the importance of postrecruitment competitive interactions. Attention was focussed on detecting interactions among conspecifics. This was done by using two factorially designed experiments in which the densities of juvenile and adult *P. amboinensis* on coral rubble patch reefs were manipulated and the demographic consequences measured. The importance of interspecific interactions will be examined in a later paper.

An important variable contributing to the size of the adult population is the number of individuals reaching maturity. This figure will be a function of recruitment, juvenile mortality rates, maturation time, and perhaps also juvenile movement patterns (Jones 1984b). While much effort has gone into examining recruitment patterns in coral reef fishes (e.g., Williams 1980, 1983,

Williams and Sale 1981, Shulman et al. 1983, Sweatman 1983, 1985, Sale et al. 1984, Shulman 1984, 1985c, Eckert 1985, Victor 1986), little is known of juvenile survival and growth (but see Doherty 1982, 1983a, Victor 1986). The effects of variation in maturation time on actual numbers reaching maturity has not been considered.

In a strictly recruit-limited breeding population, recruitment at settlement will be positively and linearly related to subsequent recruitment into the adult population. The two intraspecific density manipulation experiments described here were designed to measure the degree to which competitive interactions alter this relationship. In the first experiment, the effects of recruit density (natural, $2 \times$, and $3 \times$ natural) and adults (presence/absence) on the survival and growth of recently settled recruits were examined. The second experiment had a similar design, but examined the survival, growth, and maturation of 1-yr-old juveniles.

Preliminary information is presented on the age and size of maturation in *P. amboinensis* and the patterns of abundance of new recruits, immature juveniles, and adults. These data were necessary to determine the appropriate density levels to be used in the experiments.

STUDY AREA AND SPECIES

This study was carried out at One Tree Reef (23°30' S, 152°06' E), a lagoonal platform reef in the Capricorn-Bunker group, at the southern end of the Great Barrier Reef. The largest lagoon in this reef covers ≈ 5 km². The floor of the lagoon is composed of coral sand interspersed with numerous patch reefs, which are more common toward the perimeter, and a large area of reticulated emergent reef toward the center. A noteworthy hydrological feature of the lagoon is that, because it has a relatively high, unbroken reef crest, water in the lagoon is ponded for ≈ 3 h before and after low tide. At this time the lagoon does not exceed 4 m in depth. The pattern of water flow in the lagoon, as the tide rises over the crest or falls below it, is relatively predictable (Wilson 1985).

Pomacentrus amboinensis is one of the most abundant members of a guild of planktivorous pomacentrid fishes commonly found on small patch reefs within the lagoon. Williams (1979, 1980) has quantitatively described the general patterns of the distribution and abundance of these fishes within the One Tree lagoon. *P. amboinensis* reaches its highest densities on small patch reefs in deeper water along the southern perimeter. The three study sites referred to in this paper (South, Shark Alley, and North Gutter) were all located in this region, not far from the coral cay at the southeastern extremity of the lagoon (see map in Williams and Sale 1981).

As with most pomacentrids found at the Capricorn-Bunker group, breeding and recruitment are distinctly seasonal events. For *P. amboinensis*, most of the re-

productive activity occurs between November and January. Females lay demersal eggs that are defended by males. The eggs subsequently hatch into planktonic larvae, which presumably disperse out of the lagoon. Most of the recruitment of juveniles into the reef habitat (=colonization by larvae) occurs between December and April (Williams 1983). Brothers et al. (1983) estimated the mean length of larval life to be 21–23 d, and gave a mean size at settlement of 12 mm standard length (SL).

METHODS

Preliminary data

1. *Growth and reproduction.*—Size at maturity was determined from an examination of the reproductive status of a sample of 67 *P. amboinensis* collected during November, the peak month of the breeding season. The standard length of each fish was measured and the gonads were removed and preserved in Bouin's fixative. Transverse sections were cut through one lobe, stained with Eosin and Haematoxylin, and made into slides. Gonads were classified according to three sexual types: female, transitional (undergoing process of sexual transition), and male; and three stages of gametogenesis: resting, ripening, and ripe (cf. Jones 1980).

Age at maturity was estimated from the size-frequency distribution of *P. amboinensis* during the breeding season. It was confirmed by monitoring directly the growth of new recruits and 1-yr-old fish (which had a discrete size distribution) over a 1-yr period.

2. *Natural densities.*—The natural density of *P. amboinensis* was estimated to determine the baseline density to be used in the experiments in which densities were to be manipulated. A preliminary survey was carried out to assess their relative abundance on small submerged patch reefs and large emergent reefs. At two locations supporting high densities, Shark Alley and South, 2×100 m lengths of emergent reef were searched, counting all *P. amboinensis* associated with the main reef and all associated patch reefs. The average diameter of each patch reef was measured.

Forty small patch reefs in the range of 1–2 m² were surveyed immediately after two recruitment seasons (April 1984, March 1985). Half of these were located at Shark Alley and the other half at South. The survey provided density estimates for three age categories: 0+ yr fish (recruits), 1+ yr juveniles, and adults (aged 2+ or older). One-year-old fish could be aged because their size distribution remains discrete from the combined mature age classes for 12–16 mo after settlement.

Experiments

Two factorial experiments were conducted to examine whether growth, survival, and maturation of juveniles were dependent on either of two factors: (1) the density of juveniles, or (2) the presence of conspecific adults. Experiment 1 was based on manipulation

of the densities of recently settled juveniles (0+ yr), and in experiment 2, the densities of 1-yr-old juveniles were manipulated. Since most individuals mature toward the end of their 2nd yr, examination of potential density effects in both year classes provided a complete description of the demographic processes operating between recruitment to the benthic population and recruitment into the breeding population.

The experiments were carried out using uniform patch reefs, constructed out of natural coral materials, but to standard specifications (hemispherical, 1.5 m diameter, 0.3–0.5 m height). Natural patch reefs were found to be highly variable in terms of size, coral type, degree of isolation, and apparent quality of shelter. The choice was made to use artificially constructed reefs to minimize any potential effects of this variation on population processes, and hence to maximize the chances of detecting any influence of the factors in question. The reefs were built at North Gutter, a sandy area near the southeastern apex of the lagoon. They were placed 15 m from any natural reef and were separated from each other by a similar distance. The base of each reef was constructed from coral rubble collected from the reef crest. On top of this were placed similar-sized pieces of live *Porites* sp. and dead coral taken from distant natural reef areas. Any fish occupying these corals were removed, prior to constructing the reefs.

The factorial design of experiment 1 is shown in Table 1. The three levels of juvenile density were natural, twice natural, and three times natural density, based on a survey of natural reefs of this size. The adults-present treatments consisted of a pair of adults (natural density), one male and one female per reef, the sexes being distinguishable on the basis of size. The 24 reefs were constructed during January 1984. The required 192 recently settled recruits were collected from natural reef areas during the same month. Reefs were randomly assigned to treatments, and recruits were measured and randomly assigned to reefs (standard length [SL]: $\bar{X} = 17.9 \pm 0.3$ mm [SE]). Twelve adult pairs were collected from small patch reefs, measured, and placed on the adults-present reefs. It was found by trial and error that naturally paired individuals readily took up residence on the experimental reefs, whereas, when males and females were collected from different areas, one or both often emigrated. In such

instances, any remaining fish were replaced by two new ones. The great majority of juvenile transplants were successful. Fish were often seen exploring the new shelter sites and feeding in the water column within an hour of transplantation. For the few exceptions, replacement juveniles close to the average size were added to the reef as soon as their departure was noticed.

Experiment 2 was initiated in February 1984. The design was essentially the same as for experiment 1, except that 1-yr-old fish were used instead of new recruits, and there were five replicates for each orthogonal treatment combination (Table 1). The mean length of the 180 1+ yr fish collected for the experiment was 38.6 ± 0.3 mm. All fish in this experiment, including adults, were heat-branded with an individual pattern of dots and lines, to provide information on individual growth rates and the identities of maturing fish. These marks lasted a full year in adults, but only 4 mo or so in the 1-yr-olds. During this 4-mo period, 3 h of behavioral observations were made at all reefs with natural recruit densities. Records of all aggressive interactions between individuals and their outcomes permitted an assessment of the social hierarchy established on these reefs.

All surviving fish in both experiments were collected, measured, and returned to the reefs in May, September, and November 1984, and February 1985. At this time, all fish from experiment 2 were collected to examine reproductive status. An a priori decision was made to analyze the effects of the treatments on survival and mean size after 6 mo, and then again after 1 yr had elapsed.

Losses from reefs after the initial adjustment period must have been due to either mortality or emigration. In most cases, the latter would have been equivalent to mortality, as it is unlikely that many emigrants managed to establish residence successfully and survive on natural reefs in the area. These were routinely searched shortly after the experiment began, but no marked fish were found. Previous attempts at transplanting larger juveniles or adults onto reefs with conspecifics already present always failed, the transplants being chased from the reefs. However, it is probable that some displaced fish chanced upon reef areas where they did establish residence.

RESULTS

Preliminary data

1. *Growth and reproduction.*—The size-frequency distribution of *Pomacentrus amboinensis* collected during the breeding season exhibited three discrete peaks, corresponding to the 0+ yr class (sexually immature), mature females, and mature males (Fig. 1). All immature individuals were female, except for a small number of transitional-sexed individuals near the upper end of the size distribution (45–55 mm). This suggests that *P. amboinensis* is a protogynous her-

TABLE 1. Design of experiments 1 and 2. Reefs are constructed, 1–2 m² replicate, coral-rubble patch reefs.

	Juvenile density (no./reef)	Adults absent	Adults present
Experiment 1 (0+ yr juveniles)	4 (natural)	4 reefs	4 reefs
	8 (2×)	4 reefs	4 reefs
	12 (3×)	4 reefs	4 reefs
Experiment 2 (1+ yr juveniles)	3 (natural)	5 reefs	5 reefs
	6 (2×)	5 reefs	5 reefs
	9 (3×)	5 reefs	5 reefs

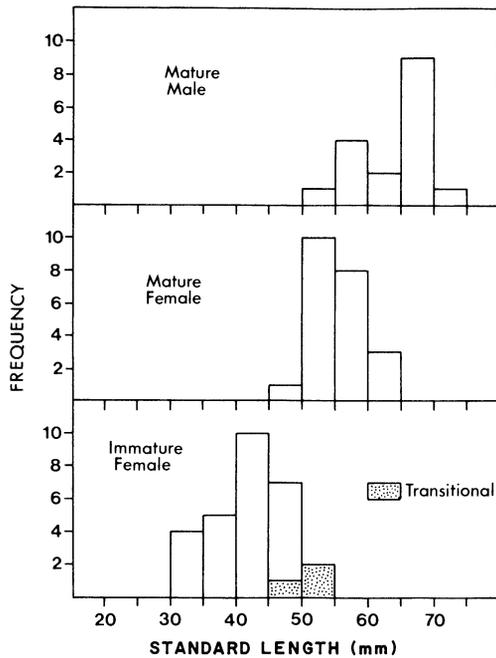


FIG. 1. Size-frequency distribution of three sexual categories of *Pomacentrus amboinensis* collected during the breeding season ($n = 67$). The immature females include three fish with gonads in transition to becoming male.

maphrodite, changing sex from female to male. The size at which females matured was ≈ 50 mm. Mature females (mean, 55.2 ± 0.8 mm) were significantly smaller than mature males (mean, 63.5 ± 1.3 mm; $t_{37} = 5.5$, $P < .05$).

The presence of a discrete size class of 0+ yr individuals during the breeding season suggested that the majority of females did not mature until the breeding season of their 1+ yr. This was confirmed by regular measurements of new recruits and 1-yr-old juveniles on the isolated experimental reefs, over a 1-yr period (Fig. 2). None of the 0+ yr cohort reached the critical size for maturity (50 mm) by the time of the breeding season. A large proportion of the 1+ yr cohort did reach 50 mm by the breeding season, ≈ 20 –22 mo after recruitment.

2. *Natural densities.*—*P. amboinensis* were common on low patch reefs over sandy areas or around the bases of large emergent reefs. Along the contiguous reef, including all associated patch reefs, 65.0% of the fish were found on patch reefs, and 84.5% of these were on patch reefs < 3 m in diameter. There were 3.1 ± 0.3 (SE, $n = 4$) individuals/m at the perimeter of patch reefs, compared with 1.8 ± 0.2 individuals/m at the bases of long emergent reefs. Thus, small patch reefs represent an important habitat for examining the dynamics of *P. amboinensis* populations.

The mean numbers of recent recruits on small patch reefs (1 – 2 m²) at the end of the settlement season ranged from 1.4 to 1.6 individuals per reef, for two sites in

1984 (Table 2A). Densities were higher in 1985, ranging from 2.9 to 3.9 individuals. Juveniles were very unevenly distributed across reefs within sites (coefficient of variation [cv] = 2.1, $G_5 = 21.8$, $P < .05$, significant departure from a Poisson distribution). Thus, the mean density estimate calculated from random samples of reefs was a poor indicator of the density being experienced by the average individual at the site. This was because the majority of the population occurred on high-density patch reefs. The reefs with no juveniles present are irrelevant when one is interested in the average densities at which juveniles are interacting. The appropriate density estimate can be determined by randomly sampling individuals at each site (rather than reefs), and for each, recording the density of fish on the patch reef. A mean value can then be calculated. These means were calculated indirectly for the *P. amboinensis* data, by plotting a frequency distribution of the densities recorded for all individuals censused at each site (Table 2B). Juvenile-density estimates were considerably larger than those calculated from the random sample of reefs (range 2.4–5.6 juveniles per site). It should be noted that the two types of density estimates will only be identical if individuals are uniformly distributed across reefs. When they are not, the latter procedure is appropriate for estimating the average density conditions under which individuals are potentially interacting. (An added advantage for analysis is that there are no zero values and the data more closely approximate a normal distribution.)

Mean densities of 1+ yr *P. amboinensis* were similar between sites and years, and ranged from 1.2 to 2.1 individuals per site (Table 2A). However, this age class

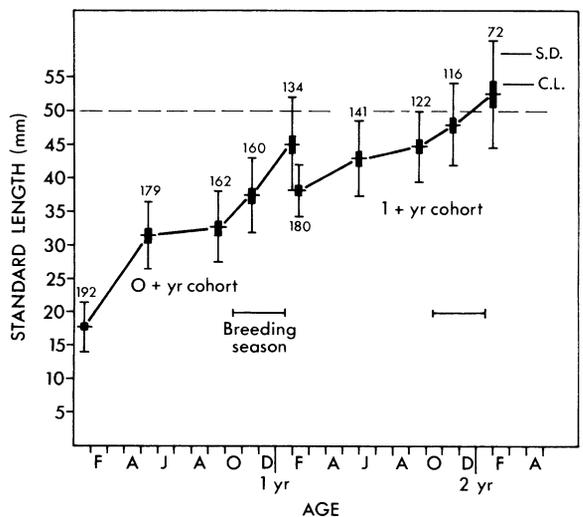


FIG. 2. Mean standard length vs. age for two cohorts of *Pomacentrus amboinensis* (0+ yr and 1+ yr) monitored over a 1-yr period. Confidence limits (C.L.), standard deviations (SD), and sample sizes are indicated. The dashed horizontal line indicates the mean size at which reproductive maturity is reached.

TABLE 2. Densities ($\bar{X} \pm SE$) of *Pomacentrus amboinensis* in three age categories on 1–2 m² patch reefs at two sites at two different times, April 1984 and March 1985.

Estimate*	Site	Age class	Density (no./reef)	
			1984	1985
A)	Shark Alley	Recruits (0+ yr)	1.45 ± 0.24	2.90 ± 0.53
		1+ yr juveniles	2.05 ± 0.35	1.85 ± 0.40
		Adults	1.35 ± 0.21	1.35 ± 0.24
	South	Recruits	1.55 ± 0.36	3.85 ± 0.68
		1+ yr	1.85 ± 0.33	1.15 ± 0.25
		Adults	1.05 ± 0.19	1.10 ± 0.21
B)	Shark Alley	Recruits	2.38 ± 0.18	4.86 ± 0.28
		1+ yr	3.24 ± 0.17	3.48 ± 0.24
		Adults	2.19 ± 0.18	2.63 ± 0.35
	South	Recruits	3.26 ± 0.32	5.57 ± 0.28
		1+ yr	3.06 ± 0.21	2.22 ± 0.21
		Adults	1.76 ± 0.15	1.91 ± 0.13

* Two types of density estimate are given: (A) mean density estimates from 20 reefs chosen at random from each site, (B) mean density calculated by randomly sampling individuals from the 20 reefs, and recording the number of fish on the patch reef.

was also unevenly distributed across reefs. The average 1+ yr juvenile densities at these sites ranged from 2.2 to 3.5 individuals per site (Table 2B). Similarly, the average density of adults ranged from 1.8 to 2.6. Invariably when two adults were present, both sexes were represented.

Experiments

1. 0+ yr survivorship, growth, and maturation.— Juvenile survivorship was not significantly influenced

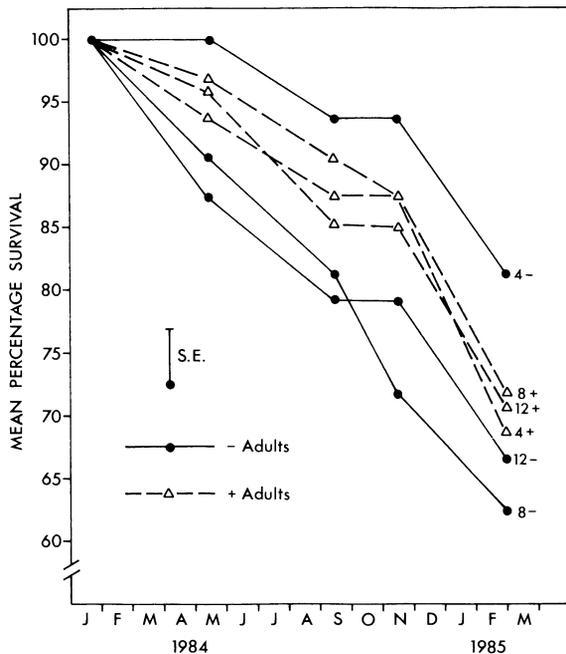


FIG. 3. Experiment 1: Mean percentage survival of 0+ yr *Pomacentrus amboinensis* at three levels of juvenile density (4, 8, and 12 per 1–2 m² patch reef), in the presence (+) and absence (-) of adults.

by either initial juvenile density or by the presence of adults, and there was no significant interaction between these factors (Fig. 3, Table 3A, B). Mean survival for the year ranged from 62.5 to 81.0% for the six treatments. The mortality rate appeared to be seasonally higher over the summer months, between November and February (Fig. 3). Linear regression analysis indicated that there were significant relationships between initial numbers of juveniles and numbers remaining at the end of the experiment in both the presence ($F_{1,10} = 101.1, P < .05, r^2 = 0.9$) and absence of adults ($F_{1,10} = 46.1, P < .05, r^2 = 0.82$). Only four (16.6%) of the adults were lost over the year period.

The mean size reached by September was negatively related to initial juvenile density, but was not affected by the presence or absence of adults during 1984 (Fig. 4, Table 3C). The density-dependent effect was not large, the highest density treatment reaching a mean size that was 86% of the mean size reached in the lowest density treatment. Rate of growth during the winter months, between May and August, was considerably slower (less than one-half) than that for the rest of the year.

The pattern in relation to mean size differed at the end of the experiment. An effect of adults appeared to develop over the last 5 mo (Fig. 4). During February 1985, juveniles were significantly smaller on the reefs with adults present, but there was no longer a significant effect of initial density (Table 3D).

An examination of the size-frequency distribution of juveniles during February showed that adults had a large effect on both the variances and mean sizes attained (Fig. 5A). That is, the variance was much greater for the adults-absent (-) treatments. This result suggests that adults affected the growth of some individuals more than that of others.

At the beginning of the breeding season, the critical size at maturity, 50 mm SL, had been reached by only

TABLE 3. Analysis of variance tables for results of experiment 1, manipulation of the densities of 0+ yr *Pomacentrus amboinensis*. In each case, data were untransformed and variances were homogeneous.

A) 0+ yr survivorship: % survival to September 1984. (Cochran's $C = 0.27$, $df = 6.3$. Residual $ms = 130.9$, $df = 18$; total $df = 23$.)				
Source	MS	df	F	
Adults (presence/absence)	58.3	1,18	0.45	NS
Density	139.8	2,18	1.07	NS
A \times D interaction	136.6	2,18	1.04	NS
B) 0+ yr survivorship: % survival to February 1985. (Cochran's $C = 0.38$, $df = 6.3$. Residual $ms = 137.0$, $df = 18$; total $df = 23$.)				
Source	MS	df	F	
Adults (presence/absence)	0.9	1,18	0.01	NS
Density	135.9	2,18	0.99	NS
A \times D interaction	262.0	2,18	1.91	NS
C) 0+ yr growth: Mean length in September 1984. (Random samples of 12 surviving juveniles from each treatment. Cochran's $C = 0.24$, $df = 6,11$. Residual $ms = 23.4$, $df = 66$; total $df = 71$.)				
Source	MS	df	F	
Adults (presence/absence)	3.1	1,66	0.13	NS
Density	165.0	2,66	7.10	$P < .05$
A \times D interaction	48.8	2,66	2.09	NS
D) 0+ yr growth: Mean length in February 1985. (Random sample of 10 surviving juveniles from each treatment. Cochran's $C = 0.41$, $df = 6,9$. Residual $ms = 56.9$, $df = 54$; total $df = 59$.)				
Source	MS	df	F	
Adults (presence/absence)	690.5	1,54	12.13	$P < .05$
Density	171.1	2,54	3.00	NS
A \times D interaction	31.1	2,54	0.54	NS

a small number of individuals all from the treatments with adults present (Table 4). By the end of the breeding season (February) approximately two juveniles had reached a mature size in all treatments without adults, regardless of starting densities. Four juveniles also grew to >50 mm in the (+) adult treatments, but in each case this was only after the loss of one of the original adults.

2. *1+ yr survivorship, growth, and maturation.*—The survivorship of 1+ yr *P. amboinensis* was affected by the presence of adults during the early part of the experiment (Fig. 6). Analysis of the survival figures for September indicated that significantly fewer individuals remained on reefs with adults present (Table 5A). The presence of adults reduced survival by $\approx 35\%$, but the effect was significant only in the two lowest density treatments (Student-Newman-Keuls test, $P < .05$). At starting densities of nine juveniles per reef, there were no apparent effects of adults, the survivorship curves being almost identical (Fig. 6). No effect of initial densities was detected (Table 5A).

By February, a different pattern had emerged. The effect of adults found earlier was no longer significant,

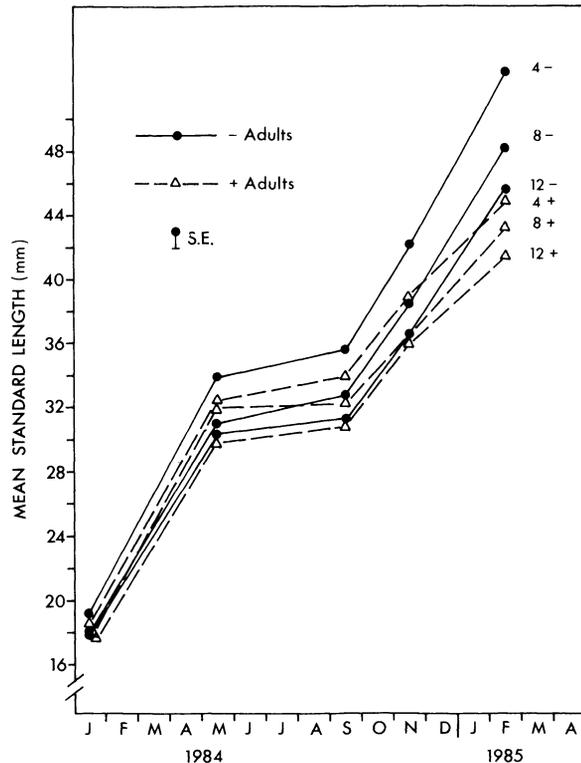


FIG. 4. Experiment 1: Mean standard length vs. time for 0+ yr *Pomacentrus amboinensis* at three levels of juvenile density (4, 8, and 12 per 1–2 m² patch reef), in the presence (+) and absence (–) of adults.

but an effect of initial densities was now apparent (Table 5B). The density effect was due to the lowest density treatment (– adults) exhibiting double the survivorship recorded for the two higher density treatments (SNK test, $P < .05$). Considerable losses (53%) of the original adults transplanted onto the reefs occurred over the September to February period, which could have a bearing on these results. The mean number of the original adults remaining in February was not influenced by the initial density of subadults (ANOVA, $F_{2,12} = 0.56$, $P > .05$).

Regression analysis indicated that final densities of the 1+ yr fish were related linearly to initial densities

TABLE 4. Mean number of 0+ yr *Pomacentrus amboinensis* having reached the critical size at maturity early in the spawning season (November 1984) and by the end of the season (February 1985).

	Density	Adults absent	Adults present
November	4	0.5 \pm 0.3	0
	8	0.3 \pm 0.2	0
	12	0.3 \pm 0.2	0
February	4	1.8 \pm 0.2	0
	8	1.8 \pm 0.4	0.8 \pm 0.4
	12	2.0 \pm 0.4	0.3 \pm 0.2

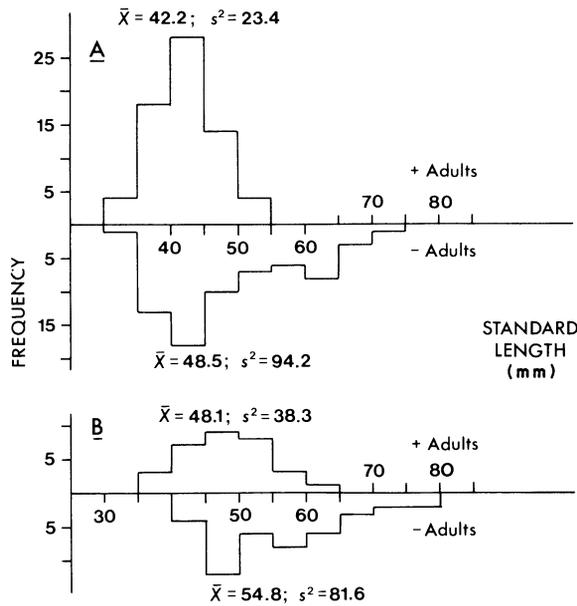


FIG. 5. Size-frequency distributions of 0+ yr and 1+ yr juveniles at the end of experiments 1 (A) and 2 (B), distinguishing between treatments with adults present (+) and adults absent (-). The mean and variance in standard length are given for each category.

in the (+) adult treatment ($F_{1,13} = 8.5, P < .05, r^2 = 0.40$), but not in the (-) adult treatment ($F_{1,13} = 2.2, NS, r^2 = 0.14$). Overall, considerably less of the variation was explained by the regressions, compared with the changes in 0+ yr numbers in experiment 1. The mortality of the 1+ yr fish appeared to be higher and more variable than that recorded for 0+ fish. However, the two experiments were conducted a short distance from each other, so these differences may have been site effects. The seasonal trends in 1+ yr mortality were similar to those for the 1st-yr cohort. Fish disappeared from the reefs at a greater rate over the summer months, between November and April.

Adults had a significant effect on the growth of 1+ yr fish (Fig. 7). The mean size for the (-) adult treatments during September 1984 and February 1985 was significantly higher than the mean for the (+) adult treatments (Table 5C, D). By February, the mean size in the presence of adults was only 89% of that reached in their absence. There was no significant effect of density or a significant interaction, indicating that the magnitude of the adult effect was not dependent on density. An obvious winter depression in growth rate was also evident.

Over twice as many 1+ yr fish reached maturity during November, in the absence of adults (Table 6; ANOVA, $F_{1,24} = 18.3, P < .05$; Cochran's test, $C = 0.29$, variances homogeneous). Nine of the 11 fish reaching 50 mm on the (+) adult treatments did so after the loss of one or both of the original adults. The other factor, initial density, did not influence the num-

TABLE 5. Analysis of variance tables for results of experiment 2, manipulation of the densities of 1+ yr *Pomacentrus amboinensis*. In each case, data were untransformed and variances were homogeneous.

Source	MS	df	F	
A) 1+ yr survivorship: % survival to September 1984. (Cochran's $C = 0.34, df = 6.4$. Residual $ms = 585.8, df = 24$; total $df = 29$.)				
Adults (presence/absence)	3224.0	1,24	5.50	$P < .05$
Density	461.5	2,24	0.79	NS
A \times D interaction	894.0	2,24	1.53	NS
B) 1+ yr survivorship: % survival to February 1985. (Cochran's $C = 0.34, df = 6.4$. Residual $ms = 383.1, df = 24$; total $df = 29$.)				
Source	MS	df	F	
Adults (presence/absence)	867.3	1,24	2.26	NS
Density	1566.2	2,24	4.09	$P < .05$
A \times D interaction	607.1	2,24	1.58	NS
C) 1+ yr growth: Mean length in September 1984. (Random samples of 10 surviving fish from each treatment. Cochran's $C = 0.37, df = 6.9$. Residual $ms = 22.4, df = 54$; total $df = 59$.)				
Source	MS	df	F	
Adults (presence/absence)	130.5	1,54	5.82	$P < .05$
Density	20.2	2,54	0.90	NS
A \times D interaction	23.5	2,54	1.05	NS
D) 1+ yr growth: Mean length in February 1985. (Random samples of six surviving fish from each treatment. Cochran's $C = 0.41, df = 6.5$. Residual $ms = 61.9, df = 30$; total $df = 35$.)				
Source	MS	df	F	
Adults (presence/absence)	330.0	1,30	5.33	$P < .05$
Density	92.8	2,30	1.50	NS
A \times D interaction	18.7	2,30	0.30	NS

bers of fish reaching maturity in November ($F_{2,24} = 1.36, NS$). That is, in the absence of adults, numbers reaching maturity were similar, regardless of the starting density. There was no significant interaction between the main factors ($F_{2,24} = 1.4, NS$). By February, the end of the spawning season, the pattern was largely unchanged (Table 6). The number of matured juveniles on reefs without adults present had not increased (cf. experiment 1). Continued losses of the original adults on the (+) adult reefs lead to a slight increase in the number of juveniles that had matured. Examination of the gonads from all surviving 1+ yr fish collected at the end of the experiment confirmed that no fish < 50 mm were mature.

At the end of the experiment there was no significant difference between the (+) and (-) adult treatments in terms of the mean numbers of adults present, including original and matured fish ($t_{28} = 0.54, NS$). At this time, 73.3% of the (-) adult reefs had two adults present on them, compared with 66.7% of the (+) adult reefs. There were no significant linear relationships between initial densities and numbers reaching 50 mm by February, whether adults were present ($F_{1,13} = 1.2, NS, r^2 = 0.08$) or absent ($F_{1,13} = 0.8, NS, r^2 = 0.05$).

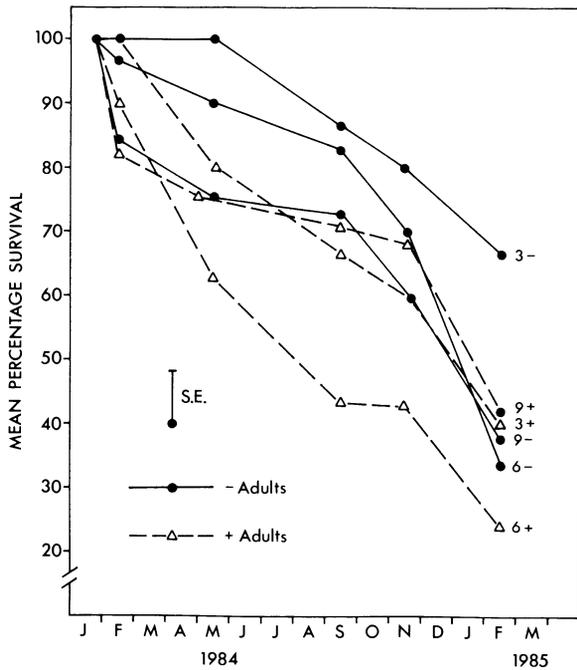


FIG. 6. Experiment 2: Mean percentage survival of 1+ yr *Pomacentrus amboinensis* at three levels of juvenile density (3, 6, and 9 per 1-2 m² patch reef), in the presence (+) and absence (-) of adults.

As in the case of experiment 1, adults had an influence on both the mean size of juveniles, and the variance (Fig. 5B). There was a much wider range of final sizes for 1+ yr fish surviving in the (-) adult treatments. It is likely that this effect on variance was of

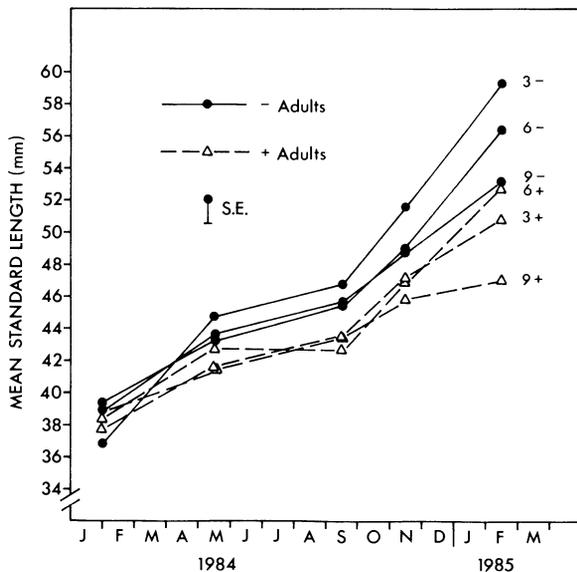


FIG. 7. Experiment 2: Mean standard length vs. time for 1+ yr *Pomacentrus amboinensis* at three levels of juvenile density (3, 6, and 9 per 1-2 m² patch reef), in the presence (+) and absence (-) of adults.

TABLE 6. Mean number of 1+ yr *Pomacentrus amboinensis* having reached the critical size at maturity early in the spawning season (November 1984) and by the end of the season (February 1985).

	Density	Adults absent	Adults present
November	3	1.2 ± 0.2	0.6 ± 0.4
	6	2.0 ± 0.0	0.4 ± 0.4
	9	2.0 ± 0.3	1.2 ± 0.3
February	3	1.8 ± 0.2	0.8 ± 0.4
	6	1.4 ± 0.0	0.8 ± 0.4
	9	2.0 ± 0.3	1.0 ± 0.3

greater significance than the effect on the mean, in terms of understanding the basis of this interaction between adults and juveniles. One explanation was that differential mortality of large juveniles was occurring where adults were present. The other was that adults were only depressing the growth of certain individuals. In the natural recruit-density treatments (i.e., reefs with three 1+ yr fish) the growth and loss of identified individuals were recorded. Analysis of the growth rates of particular behavioral categories of individuals showed that adults were affecting the growth of only the largest, socially dominant juveniles (Fig. 8). Subordinate juveniles grew at similar rates, whether adults were present or not. In terms of mortality, there were no obvious differences in the rates of loss of the largest and smallest juveniles.

DISCUSSION

Competition and its effects

Intraspecific competition played an important role in limiting adult numbers in *Pomacentrus amboinensis* under experimental conditions. The number of juveniles reaching maturity on the patch reefs was restricted, primarily through density-dependent effects of adults on the growth and maturation of juveniles. At present, a cautious interpretation is advised. The experiments were carried out at only one site at One Tree Reef, using artificial reefs, transplanted fish, and a density range from natural to three times natural density. They identified processes that may be generally important on natural reefs, but this remains to be tested. The results add to a growing number of studies on reef-associated fishes that have established the existence of competitive interactions (Hixon 1980, Thresher 1983b, Robertson 1984, Thompson and Jones 1984, Jones 1986).

It is noteworthy that a survey of recruitment levels of reef fishes at seven different reefs in the Capricorn-Bunker group showed that recruitment of *P. amboinensis* at One Tree Reef ranked sixth (Sale et al. 1984). The location with the highest recruitment, Heron Reef, recorded a 29 times higher density of new recruits than One Tree Reef. This suggests that in this general region, most of the juveniles may be experiencing local densities higher than the range used in this study. De-

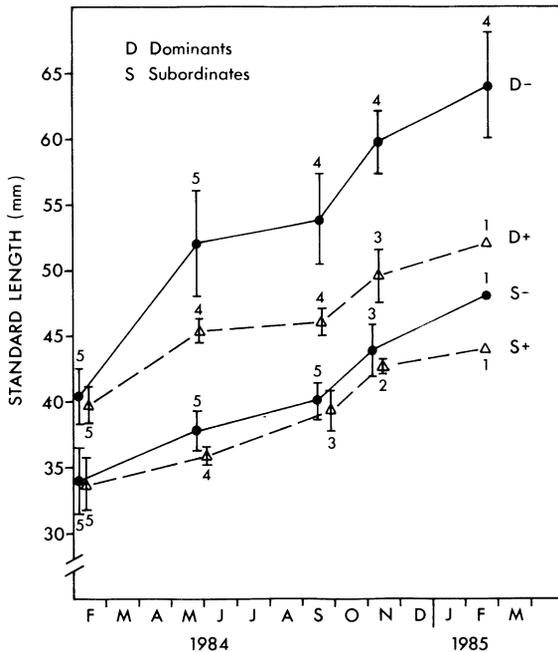


FIG. 8. Changes in mean size over time for dominant and subordinate 0+ yr *Pomacentrus amboinensis* on 1-2 m² patch reefs with densities of three individuals per reef, with (+) and without (-) adults present.

pending on the distribution of resources, competition may actually be more intense than these experiments signify.

The experiments indicated that there were ontogenetic changes in the intensity and effects of the competitive interactions. There was evidence of weak competition among 1st-yr juveniles, which was manifested as density-dependent growth but not mortality. Over the 1st 8 mo, there was no suggestion of any interactions between these small juveniles and adults. However, adults appeared to begin inhibiting juvenile growth as the latter neared an age of 1 yr.

The results were quite different for the manipulations of the densities of 2nd-yr juveniles. Adults had an immediate effect on their growth, and the mean size of juveniles was smaller in the presence of adults throughout the year. There were no significant intracohort density effects on growth. A negative effect of adults on juvenile survival was evident after 6 mo, but by the end of the year this effect was no longer apparent. As an added complication, there was a significant effect of juvenile density on survival only toward the end of the 12-mo period.

These experiments emphasize the pitfalls of extrapolating the results of short-term experiments. In neither case was the pattern that was exhibited after 6 mo still evident at the end of the year. The nature of competitive interactions among juveniles and between adults and juveniles changed as juveniles grew in size. Furthermore, the major effects of the competitive inter-

actions were expressed in terms of growth, not mortality. These interactions appeared to be most intense between large juveniles and adults, and the most important consequence, in terms of adult population size, was a reduction in the number of juveniles reaching maturity.

Another facet of the results of these experiments was that competition was asymmetric (*sensu* Begon 1984). Adults did not have a uniform effect on the growth of all juveniles within an age class, but primarily influenced the larger individuals. This is indicated by the greater variance and the negatively skewed distributions of the mean sizes of juveniles in the absence of adults. Removal of adults would not only result in an increase in mean growth rate (growth compensation), but also an increase in the variance (growth depensation). There was almost a one-to-one correspondence between loss of an adult and subsequent growth of a juvenile to reach sexual maturity.

Population limitation: equilibrial or nonequilibrial?

These experiments falsified the original hypothesis developed from the single-species equilibrial model. That is, juvenile mortality was largely independent of juvenile and adult density, which at first sight would lead one to favor the nonequilibrial "recruitment-limitation" model. However, it is clear that density-dependent effects of adults on maturation time can potentially alter patterns established at the time of recruitment to a substantial degree. This equilibrial process has not been considered previously for coral reef fishes (but see Jones 1984b for a temperate example). The hypothesis that adult numbers in *P. amboinensis* was primarily limited by the availability of recruits was also rejected.

The equilibrial-nonequilibrial dichotomy does not appear to be very useful. I favor a more comprehensive model that acknowledges that density dependence and density independence are not mutually exclusive alternatives. This model would predict that adult density patterns will result from a combination of density-independent fluctuations in recruitment and subsequent density-dependent effects on numbers reaching maturity. What we need to measure is how much of the variance in adult numbers is explained by these contributing processes.

I am cautious about making these measurements from the results of the present study. Clearly, recruit densities in *P. amboinensis* accounted for very little of the variance in numbers reaching maturity after 1 yr. The same was true for 1-yr-old juveniles. It is possible that juveniles unable to reach a mature size in the year of the study would have done so during the next breeding season, a full year later. However, one would have to consider the intervening juvenile mortality and adult mortality. In a real population, input into the adult population would come from several co-existing ju-

venile cohorts. In a better experiment, recruits would be added each year, and input into the adult population from each cohort would be measured over a number of years. The relative importance of fluctuations in recruitment and subsequent density-dependent maturation could then be assessed more fully.

The manipulations of the densities of *P. amboinensis* have produced results similar to those that have been obtained for other coral reef fishes. For both *Pomacentrus wardi* (Doherty 1982, 1983a) and *Thalassoma bifasciatum* (Victor 1986), juvenile mortality appears to be independent of density, whereas growth declines with increasing density. Doherty's experiments, in particular, showed obvious negative effects of adults and juvenile density on mean size and the variance in mean size attained. However, both Doherty and Victor have interpreted their data as supporting the nonequilibrium "recruitment-limitation" hypothesis. How can these differences in interpretation be reconciled?

It is clear that any conclusions about the factors limiting populations will depend on whether one focusses on the size of the total population (as in the case of Doherty) or the size of the breeding population size (as in the present case). Density-dependent maturation only reduces the effects of variability in recruitment on the size of the breeding population. If numerical fluctuations in the total population are the primary pattern of interest, then density-independent fluctuations in recruitment or mortality may be of primary importance. The experimental results presented here do not refute a nonequilibrium model for the entire population, although the possibility that competition has an effect on age structure may only be revealed in longer term experiments.

The traditional lack of interest in the body size and reproductive status of individuals within populations stems from the primarily community-oriented perspective of reef fish ecologists (see Sale 1980). There are, however, several important reasons for considering influences on the size structure of populations and adult population size, the upper tail of the size distribution (see Werner and Gilliam 1984). On a large spatial scale, it is the adult population, or more precisely the number and fecundity of mature females, that will determine the potential for population increase. Although this is probably irrelevant when describing patterns of density within reef systems, there are other important reasons for considering adults at a smaller scale. Focussing on patterns in the adults will reveal much about the process of habitat selection and patterns of movement within reef systems.

Criteria to establish recruitment limitation

It seems likely that variability in recruitment is important in explaining spatial patterns in adult numbers over a wide range of spatial scales (Williams 1979, 1980, Williams and Sale, 1981, Jones 1984b, Sale et al. 1984, Victor 1986). However, it has not yet been

established that adult populations of any reef fish species are primarily recruitment limited. To do so, three criteria would have to be met.

1) First, it must be shown that recruitment into the local population (numbers settling) is not influenced by the densities of conspecifics or other species at the spatial scale at which the population is defined. This appears to be the case for most fish species examined (Williams 1980, Doherty 1983a, Shulman et al. 1983, Jones 1984a), but both positive interactions (Sweatman 1983, 1985) and negative interactions (Shulman et al. 1983, Sweatman 1985) have been recorded.

2) The second criterion is that recruitment into the adult population (numbers maturing) must be linearly related to prior recruitment into the local population. This relationship would hold only under conditions of constant age-specific mortality schedules and constant maturation time. If juvenile mortality between settlement and maturity were markedly density dependent, due to interactions with conspecifics or other competitors, the relationship would not be linear. Such effects on mortality do not appear to be important in *Pomacentrus wardi* (Doherty 1982, 1983a) or *P. amboinensis*. However, nonlinearity would result also from density-dependent growth, and hence density-dependent maturation time, because fewer fish would survive to a mature size. Recruitment limitation can be rejected for *P. amboinensis* on these grounds, at least under experimental conditions. The factors influencing the timing of maturation in *P. wardi* are unknown.

A point often overlooked (e.g., Victor 1986) is that an adult population cannot be considered recruitment-limited if juvenile mortality (or maturation time) is highly variable between sites or generations, even though not related to density. Such variability would break down the relationship between numbers settling and numbers subsequently reaching maturity. For example, Doherty (1980) found that *P. wardi* recruited fairly evenly to deep and shallow reefs, but juveniles consistently survived much better on shallow reefs. This resulted in higher adult population densities in the shallow habitat. It seems that site-related mortality patterns had a greater effect than recruitment on patterns in adult density.

3) The last criterion that must be met to establish recruitment limitation is that spatial and temporal changes in adult numbers must be determined primarily by variation in numbers reaching maturity. Such changes may occur despite a fairly constant rate of input due to variation in adult mortality rates. Intuitively, one would expect this to be dependent on the age structure of the adult population. In short-lived species, in which the adult population is made up of one or two cohorts, there is a much greater likelihood that adult population size will vary in proportion to year-class strength. A prime candidate for recruitment limitation, *Thalassoma bifasciatum*, is indeed a short-lived species, the adult population being dominated by

fish that recruited the previous year (Victor 1983). This pattern would seem to be much less likely in long-lived species. However, there are very few data on the age structure of adult populations or adult mortality rates for any coral reef fish species.

Williams (1979) arbitrarily defined an adult *P. amboinensis* as any fish aged 1 yr or older, and provided good evidence that spatial patterns in "adult" numbers were correlated with recruitment. He also showed that with a 1-yr phase delay, the "adult" population did fluctuate in response to temporal variation in recruitment. The results of the density experiments reported here are consistent with his observations. I found a close linear relationship between starting densities and final densities, following new recruits over a 1-yr period. However, there was no significant relationship between numbers reaching maturity and initial density. I would predict that numbers of breeding individuals would be much less sensitive to fluctuations in recruitment than Williams's results imply.

Clearly, the three criteria for recruitment limitation have not been met for any one species. Further data are required on variation in maturation time, and juvenile and adult mortality rates, within and between generations. Models that explore the effects of variation in these demographic parameters on adult population size and age structure may prove to be useful (e.g., Frogner 1980, Roughgarden et al. 1985). So far there have been only simplistic approaches to modelling reef fish populations. Victor (1986) considered recruitment and various age-specific mortality schedules, but his assumption of age-specific maturation may not be generally applicable. Jones (1984b) considered recruitment, and the effects of density-dependent growth and mortality, showing how the combined effects can lead to a maximum attainable adult population size. Since life history events such as maturation are usually more closely related to size than to age in fishes (Alm 1959, Sohn and Crews 1977, Jones 1980) and competition appears to affect primarily the size distribution of individuals within populations, size-specific models may be the most appropriate (Kirkpatrick 1984). However, when dealing with temporal changes in numbers, the effects of age-specific mortality and age structure must continue to be considered. Populations that are structured in a similar way with respect to size, but differ in terms of their age distributions, may exhibit very different responses to fluctuations in recruitment.

Comments on spatial scale

The conclusions drawn about competition must be restricted to the spatial scale at which the experiments were conducted (i.e., small patch reefs 1.5 m in diameter). Patch reefs of this size are an important habitat for *P. amboinensis*. It is not known whether the observed interactions occur, or have the same effects, on large patch reefs or contiguous reefs. However, if competition does effect the size structure of these larger

populations, it still must be operating at the spatial scale over which individual adults move and interact with juveniles. It will be important to consider small-scale patchiness within these larger reef systems. In my preliminary survey, juveniles were found to be very unevenly distributed across small reefs. This patchiness is likely to increase the importance of competition, because most of the regional population is experiencing locally high-density conditions. The average density across such reefs is not a very useful measure when trying to gauge the effective density at which the majority of the population is interacting. It is possible that densities are too low on, say, 90% of the reefs for competitive interactions to be important. However, if 90% of the regional population is found on the other 10% of the reefs, competition may be extremely important on a per capita basis. The same conclusion may apply to large reef systems.

What are the limiting factor(s)?

Experiments in which densities are manipulated can provide a test for competition, but they do not indicate which resources are being competed for. Density-dependent growth may be due to a limited supply of food or density effects on behavioral interactions, even when resources are available in excess of requirements (Jones 1983, 1984b). Doherty (1983) suggested that in the herbivorous damselfish *Pomacentrus wardi*, growth of juveniles was controlled through social interactions with residents, independently of resource states. In the planktivore *P. amboinensis* there are indications that both limited food and behavioral interactions are implicated. Small juveniles underwent substantial increases in growth rates when provided with food in excess of the natural supply of zooplankton (Jones 1986). If food is limited, increases in density will reduce the average growth rate, and behavioral interactions among individuals may lead to an unequal distribution of the food among residents and the differential growth of dominant individuals. This growth depensation occurred in the experiments on *P. amboinensis* and appears to be a common feature of fishes in competitive situations (Magnuson 1962, Rubenstein 1981).

Dominance hierarchies are certainly evident among groups of *P. amboinensis* on patch reefs, larger individuals being dominant over smaller ones, and normally foraging further up-current from the reef. Coates (1980) described a similar situation in *Dascyllus aruanus* and established a mechanism by which dominant individuals could be reducing the food intake of subordinates. He showed that dominants were selectively feeding on larger prey items, reducing their availability to smaller fish. When dominants were removed, subordinates exhibited a marked increase in the mean size of the prey they were consuming.

CONCLUSIONS

Although intraspecific competitive interactions appear to be occurring among individuals of *P. amboi-*

nensis on small reefs, the relative importance of competition, recruitment and other untested factors (e.g., interspecific competition, predation) as determinants of spatial and temporal changes in adult density under natural conditions has yet to be determined. In future, observations of changes in natural populations and manipulative experiments will need to be conducted over longer time scales, to determine the relative contributions of recruitment and subsequent demographic processes. More complex models incorporating both density-dependent and density-independent processes need to be developed and tested.

The often repeated statement that food is less likely to be limiting than is living space (Smith and Tyler 1972, Sale 1977, 1980, 1984) must also be subjected to closer scrutiny. Information suggesting that some reef fish populations experience shortages of food is accumulating (Thresher 1983a, b, Robertson 1984, Jones 1986). Food limitation needs to be tested by manipulating the availability of food to both juveniles and adults. The possibility that social hierarchies within social groups may restrict adult population size, regardless of food levels, also needs to be investigated.

ACKNOWLEDGMENTS

This research was carried out while I held a Queen's Fellowship in Marine Science in the School of Biological Sciences, University of Sydney. A research support grant was provided by the Queen's Fellowships and Marine Research Allocations Advisory Committee. I thank those who discussed this work with me and commented on the manuscript, including Neil Andrew, Howard Choat, Peter Doherty, Gillian Eckert, Doug Ferrell, Mark Hixon, Tim Jones, Bruce Mapstone, Peter Sale, Dave Schiel, Hugh Sweatman, Dave Williams, and Tony Underwood. I also thank Sue Thompson, Anne Leorke, Penny Butcher, and Pip Smith for assistance in the field. This paper is a contribution from The University of Sydney's One Tree Island Field Station.

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